Calculating Biological Quantities

CSCI 2897

Prof. Daniel Larremore
2021, Lecture 21

daniel.larremore@colorado.edu
@danlarremore

- HW #5 due @ 11:59 P.M.

Last time on CSCI 2897

diagonal matrix

$$\begin{pmatrix} M_{11} & 0 & 0 & 0 \\ 0 & M_{22} & 0 & 0 \\ 0 & 0 & \ddots & 0 \\ 0 & 0 & 0 & M_{nn} \end{pmatrix}$$

$D = D^T$ if D diagonal

upper triangular matrix

$$\begin{pmatrix} M_{11} & M_{12} & M_{13} & \cdots \\ 0 & M_{22} & & \vdots \\ 0 & 0 & \ddots & \\ \vdots & & 0 & \\ 0 & \cdots & 0 & M_{nn} \end{pmatrix}$$

lower triangular matrix

$$\begin{pmatrix} M_{11} & 0 & 0 & \cdots & 0 \\ M_{21} & M_{22} & 0 & & 0 \\ M_{31} & & \ddots & 0 & \vdots \\ \vdots & & & 0 & 0 \\ & \cdots & & & M_{nn} \end{pmatrix}$$

symmetric matrix

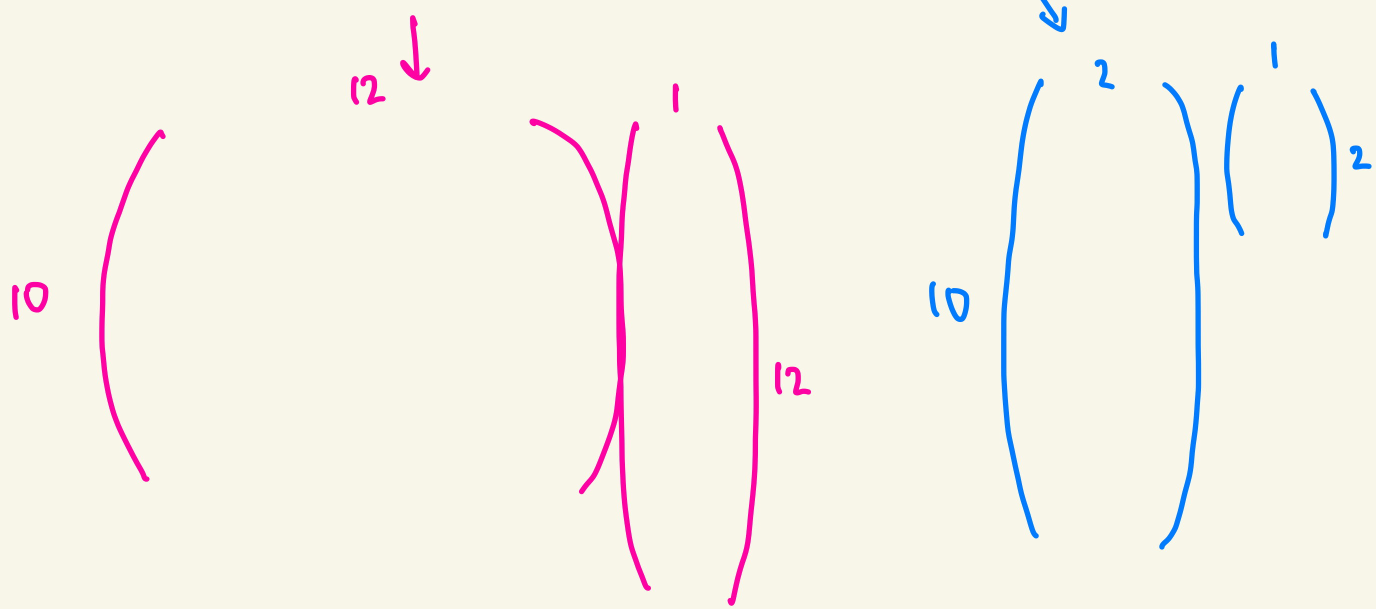
$S = S^T$

Multiplication (side note)

- consider work by hand
- consider computer memory as well!

$$P^{10\times 2} \quad Q^{2\times 12} \quad V^{12\times 1}$$

$$PQV = (PQ)^{10\times 12}\, V^{12\times 1} = P^{10\times 2}(QV)^{2\times 1}$$



Hard Way

Easy Way

Complex Eigenvalues

Unreal! Sometimes we can have eigenvalues which are *complex numbers*.

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \qquad \rightarrow \qquad \lambda_1, \lambda_2 = \frac{\text{tr}(A) \pm \sqrt{\text{tr}^2(A) - 4\text{det}(A)}}{2}$$

If $\text{tr}^2(A) - 4\text{det}(A) < 0$, then λ_1, λ_2 will be **complex numbers**.

A **complex number** is a number $c = a + bi$, where a and b are real and $i = \sqrt{-1}$ is "imaginary."

In our formula above, what's the **real part**? And the **imaginary part**?

$$\text{Re} = \frac{\text{tr}(A)}{2} \qquad \text{Im} = i\,\frac{\sqrt{4\,\text{det}(A) - \text{tr}^2(A)}}{2}$$

Complex Eigenvalues

Unreal! Sometimes we can have eigenvalues which are *complex numbers*.

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \quad \to \quad \lambda_1, \lambda_2 = \frac{\text{tr}(A) \pm \sqrt{\text{tr}^2(A) - 4\text{det}(A)}}{2}$$

If $\text{tr}^2(A) - 4\text{det}(A) < 0$, then λ_1, λ_2 will be **complex numbers**.

A complex number is a number $c = a + bi$, where a and b are real and $i = \sqrt{-1}$ is "imaginary."

$$a = \frac{\text{tr}(A)}{2}, \quad \text{and} \quad b = \frac{\sqrt{-\text{tr}^2(A) + 4\text{det}(A)}}{2}$$

and therefore $\lambda_1 = a + bi, \quad \lambda_2 = a - bi$

Notice: either both eigenvalues are complex, or both are real.

Euler's Equation

$$e^{i\theta} = \cos\theta + i\sin\theta$$

$$e^{i\pi} = -1 + 0$$

$$\boxed{e^{i\pi} + 1 = 0}$$

identity

$$e^{x} = 1 + x + \frac{x^2}{2!} + \frac{x^3}{3!} + \frac{x^4}{4!} + \dots$$

Taylor Series

$$e^{ix} = 1 + ix + \frac{i^2x^2}{2!} + \frac{i^3x^3}{3!} + \frac{i^4x^4}{4!} + \dots$$

$i^3 = i^2 \cdot i = -1 \cdot i = -i$

$$= 1 + ix - \frac{x^2}{2!} - i\frac{x^3}{3!} + \frac{x^4}{4!} + i\frac{x^5}{5!} - \frac{x^6}{6!} - i\frac{x^7}{7!} + \frac{x^8}{8!} + \dots$$

every other term is imaginary!

(the odd terms)

$$= 1 - \frac{x^2}{2!} + \frac{x^4}{4!} - \frac{x^6}{6!} + \dots \longrightarrow \cos x$$

$$+$$

$$+\, i\left(x - \frac{x^3}{3!} + \frac{x^5}{5!} - \frac{x^7}{7!}\right) + \dots \longrightarrow i\sin x$$

Solutions to linear systems

$$e^{i\theta} = \cos\theta + i\sin\theta$$

$$e^{ibt} = \cos bt + i\sin bt$$

$$e^{-ibt} = \cos(-bt) + i\sin(-bt)$$

$$= \cos bt - i\sin(bt)$$

$$\frac{d\vec{n}}{dt} = A\vec{n} \qquad \text{Solution: } \vec{n}(t) = k_1\vec{x_1}e^{\lambda_1 t} + k_2\vec{x_2}e^{\lambda_2 t}$$

So what's going to happen when λ_1 and λ_2 are complex?

$\lambda_1 = a + bi$

$\lambda_2 = a - bi$

$$n(t) = k_1 x_1 e^{(a+bi)t} + k_2 x_2 e^{(a-bi)t}$$

$$= k_1 x_1 e^{at} e^{bit} + k_2 x_2 e^{at} e^{-bit}$$

$$= e^{at}\left(k_1 x_1 e^{bit} + k_2 x_2 e^{-bit}\right)$$

$$= e^{at}\left(k_1 x_1 (\cos bt + i\sin bt) + k_2 x_2 (\cos bt - i\sin bt)\right)$$

Solutions to linear systems

$$e^{i\theta} = \cos\theta + i\sin\theta$$

$$\frac{d\vec{n}}{dt} = A\vec{n} \qquad \text{Solution: } \vec{n}(t) = k_1\vec{x}_1 e^{\lambda_1 t} + k_2\vec{x}_2 e^{\lambda_2 t}$$

What are $\vec{x}_1$ and $\vec{x}_2$?

$$(A - \lambda_1 I)\vec{x}_1 = \vec{0}$$

$$\begin{pmatrix} a-\lambda_1 & b \\ c & d-\lambda_1 \end{pmatrix}\begin{pmatrix} x_1^{(1)} \\ x_1^{(2)} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$(a-\lambda_1)x_1^{(1)} + b\,x_1^{(2)} = 0$$

$$x_1^{(2)} = \frac{(\lambda_1 - a)}{b}x_1^{(1)} \qquad \vec{x}_1 = \begin{pmatrix} 1 \\ \frac{\lambda_1 - a}{b} \end{pmatrix}$$

$$\frac{\lambda_1 - a}{b} = \frac{Re(\lambda) + i\,Im(\lambda) - a}{b}$$

$$= \frac{Re(\lambda) - a}{b} + i\frac{Im(\lambda)}{b}$$

$$\vec{x}_1 = \begin{pmatrix} 1 \\ \frac{Re(\lambda)-a}{b} \end{pmatrix} + i\begin{pmatrix} 0 \\ \frac{Im(\lambda)}{b} \end{pmatrix}$$

$$\vec{x}_2 = \begin{pmatrix} 1 \\ \frac{Re(\lambda)-a}{b} \end{pmatrix} - i\begin{pmatrix} 0 \\ \frac{Im(\lambda)}{b} \end{pmatrix}$$

$$\boxed{\begin{aligned} \vec{x}_1 &= \vec{y} + i\vec{z} \\ \vec{x}_2 &= \vec{y} - i\vec{z} \end{aligned}}$$

$\vec{x}_1$ and $\vec{x}_2$ are complex conjugates of each other!

Solutions to linear systems

$$e^{i\theta} = \cos\theta + i\sin\theta$$

$x_1 = y + iz$

$x_2 = y - iz$

$$\frac{d\overrightarrow{n}}{dt} = A\overrightarrow{n} \qquad \text{Solution: } \overrightarrow{n}(t) = k_1\overrightarrow{x_1}e^{\lambda_1 t} + k_2\overrightarrow{x_2}e^{\lambda_2 t}$$

$$= e^{at}\left(k_1 x_1 (\cos bt + i\sin bt) + k_2 x_2 (\cos bt - i\sin bt)\right)$$

$$= e^{at}\left(k_1 (y + iz)(\cos bt + i\sin bt) + k_2 (y - iz)(\cos bt - i\sin bt)\right)$$

$$= e^{at}\left(k_1 \begin{bmatrix} y\cos bt + iy\sin bt \ldots \\ - z\sin bt + iz\cos bt \end{bmatrix} + k_2 \begin{bmatrix} y\cos bt - iy\sin bt \\ - z\sin bt - iz\cos bt \end{bmatrix}\right)$$

$$= e^{at}\left((k_1 + k_2)\vec{y}\cos bt + (k_1 - k_2)i\vec{y}\sin bt - (k_1 + k_2)\vec{z}\sin bt + (k_1 - k_2)i\vec{z}\cos bt\right)$$

Solutions to linear systems

$$e^{i\theta} = \cos\theta + i\sin\theta$$

$$k_1 + k_2 \equiv C_1$$

$$(k_1 - k_2)i \equiv C_2$$

$$\frac{d\vec{n}}{dt} = A\vec{n} \qquad \text{Solution: } \vec{n}(t) = k_1\vec{x_1}e^{\lambda_1 t} + k_2\vec{x_2}e^{\lambda_2 t}$$

$$= e^{at}\left(\underbrace{(k_1+k_2)}_{C_1}\vec{y}\cos bt + \underbrace{(k_1-k_2)i}_{C_2}\vec{y}\sin bt - \underbrace{(k_1+k_2)}_{-C_1}\vec{z}\sin bt + \underbrace{(k_1-k_2)}_{C_2}i\vec{z}\cos bt\right)$$

$$\vec{n}(t) = \underbrace{e^{at}}_{\text{growth (decay)}}\underbrace{\left[C_1\left(\vec{y}\cos bt - \vec{z}\sin bt\right) + C_2\left(\vec{z}\cos bt + \vec{y}\sin bt\right)\right]}_{\text{rotation/oscillation}}$$

Solutions to linear systems

$$e^{i\theta} = \cos\theta + i\sin\theta$$

$$\frac{d\overrightarrow{n}}{dt} = A\overrightarrow{n}$$

Solution: $\overrightarrow{n}(t) = k_1\overrightarrow{x_1}e^{\lambda_1 t} + k_2\overrightarrow{x_2}e^{\lambda_2 t}$

What do solutions look like if eigenvalues are complex?

$\lambda_{1,2} = a \pm ib$

growth/decay

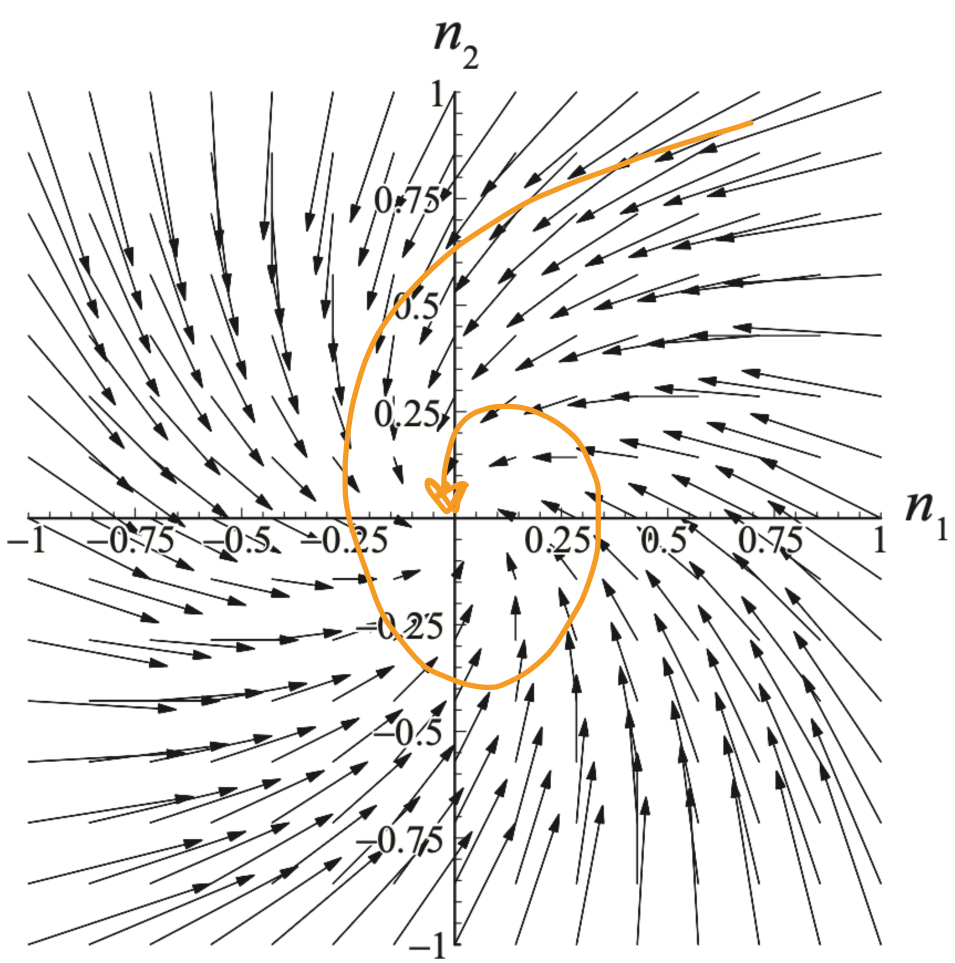
speed of rotation

Solutions to linear systems

$$e^{i\theta} = \cos\theta + i\sin\theta$$

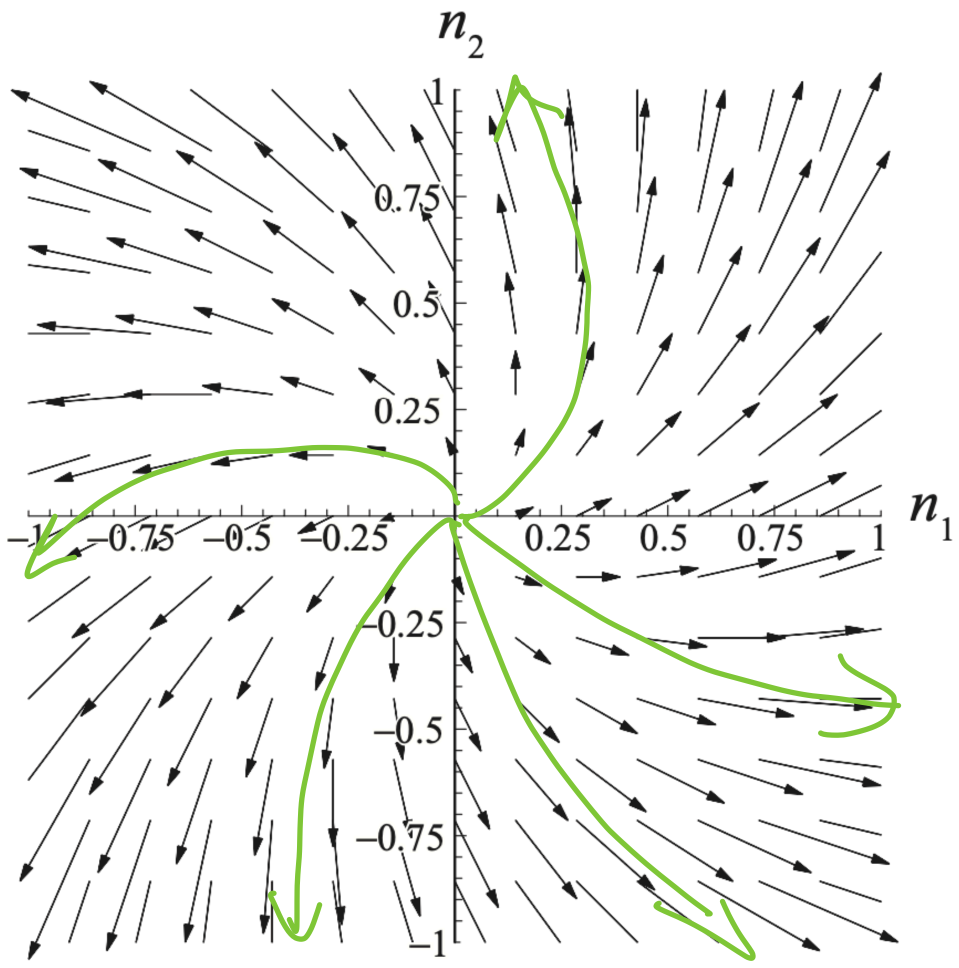
$$\frac{d\vec{n}}{dt} = A\vec{n}$$

Solution: $\vec{n}(t) = k_1\vec{x_1}e^{\lambda_1 t} + k_2\vec{x_2}e^{\lambda_2 t}$



$\lambda = -2 \pm i$

inward spiral.



$\lambda = 2 \pm i$

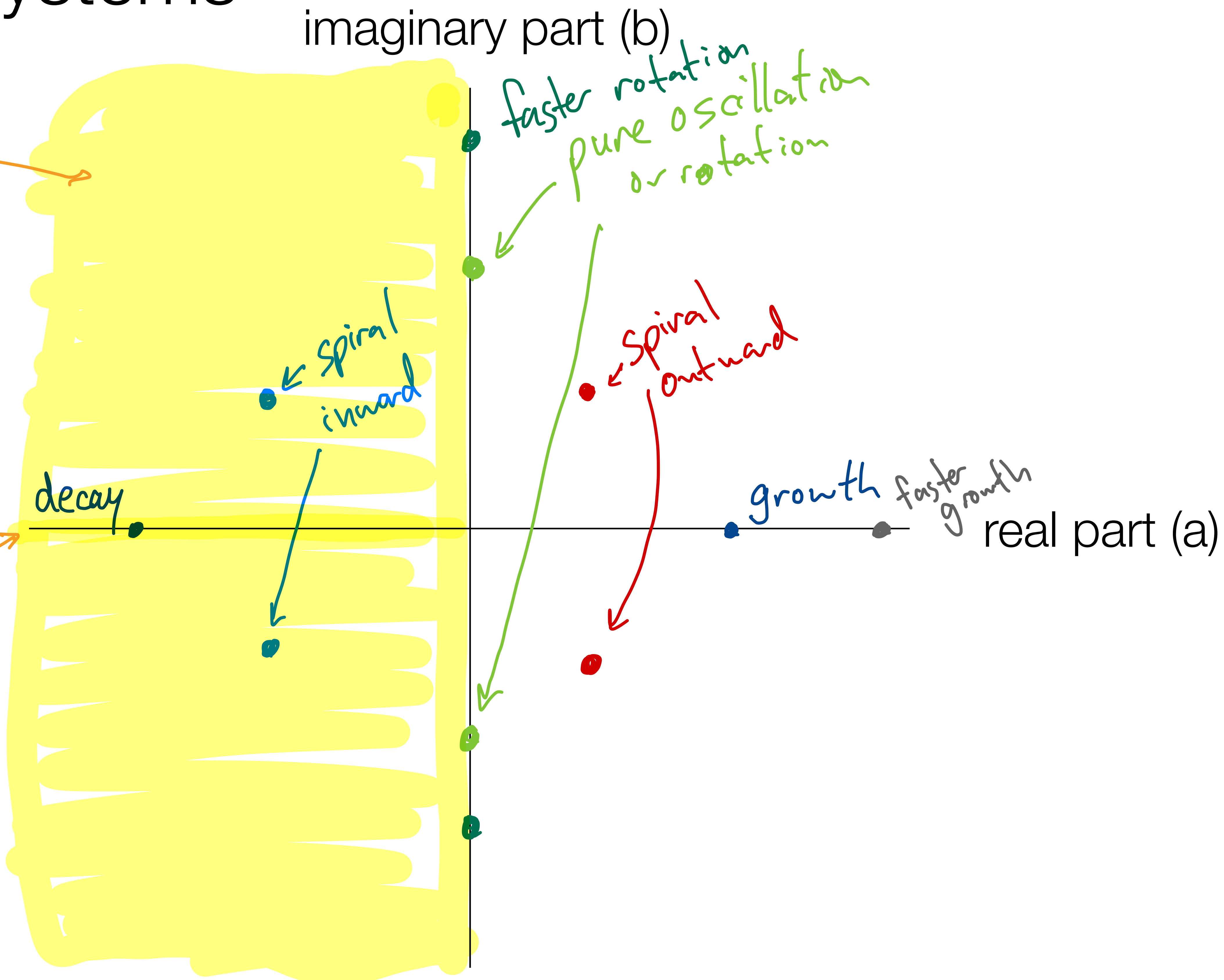
outward spiral

Solutions to linear systems

$\lambda = a \pm bi$

Complex:

Real parts of eigenvalues must be negative to have stability.



Real: both eigs must be neg. to have stability.

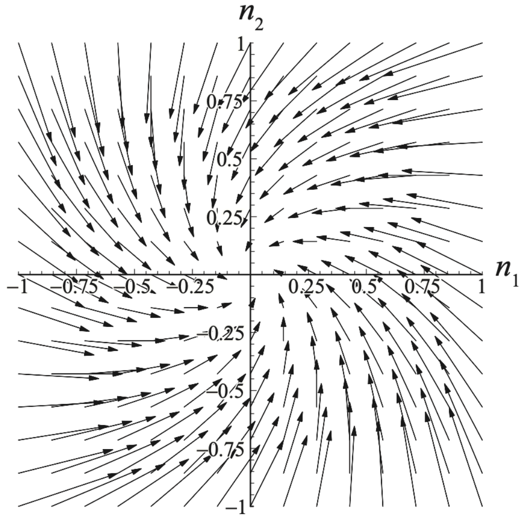
Last time on CSCI 2897

The eigenvalues of a **diagonal** or **triangular (upper or lower)** matrix are easy to get: they are just the values on the diagonal of the matrix!

Stability of equilibria (real eigenvalues):

- If all eigenvalues are negative, the system is stable.
- If one or more eigenvalues are positive, the system is unstable.

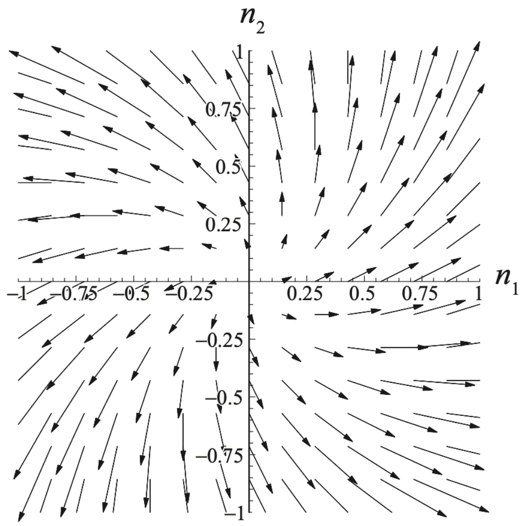
Re < 0



Stability of equilibria (complex eigenvalues):

- If the real part of all eigenvalues is negative, the system is stable.
- The complex part of the eigenvalues tells us about rotation.

Re > 0



The **complex conjugate** of a complex number $a + bi$ is $a - bi$.
If all the entries of a matrix are real, then the eigenvalues are real or come in conjugate pairs — no lon~~g~~e complex eigenvalues.

Class structured populations

The study of population *age* structure or *size* structure is known as **demography**.

There are ~~four~~ three kinds of questions we can ask which commonly come up:

1. What is the **long-term growth rate** of a population? conservation.

2. What is the **long-term class structure** of a population?
   (age, life stage, body size)

3. Which **classes contribute most** to the long-term growth rate of a population.

conservation

Class structured populations: Juveniles & Adults

J A

Say we have a population with two classes: **juveniles & adults**.

Model:

$$J(t+1) = bA(t) + \underbrace{0 \cdot J(t)}$$

$$A(t+1) = p_j J(t) + p_a A(t)$$

First, what is this model *doing*?
What clues has the modeler left for us?

$A, J \geq 0$

$b > 0, \quad 0 \leq p_j, p_a \leq 1$

- discrete time
- b = per-capita birth rate (per adult!)
- p_j = probability that each juvenile becomes an adult. → survival probability for juveniles
- p_a = prob. that each adult survives, stay as adult. → survival prob. for adults.
- $\Delta t = 1$ is amount of time for a juvenile to mature into an adult.

Class structured populations: Juveniles & Adults

Recipe: equations → matrix/vector

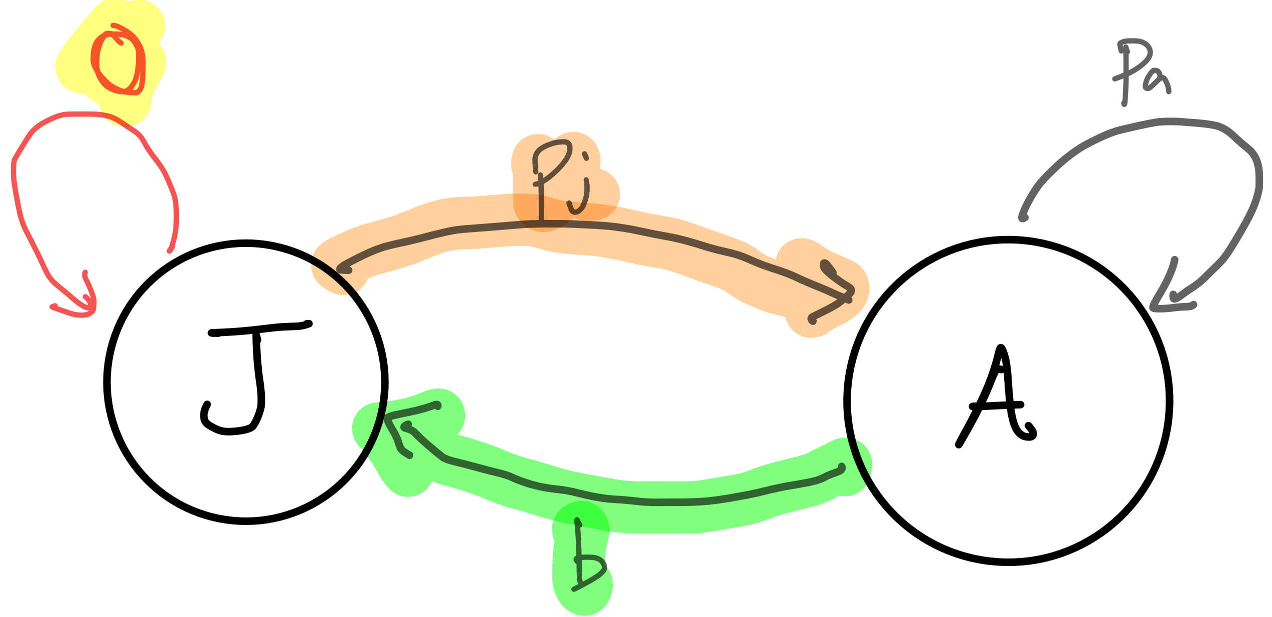
equations → flow diagram

Rewrite this model in matrix form.

$$J(t+1) = bA(t) + 0 \cdot J(t)$$

$$A(t+1) = p_j J(t) + p_a A(t)$$

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$



- Relationships between a variable and itself (at next timestep) are on diagonal of matrix. (between-variable interactions are on the off diagonal)

note: different interpretation of flow diagram in discrete time.

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

Ex: $J(0) = 0.1$
$A(0) = 0.9$

$b = 10$ • each adult produces 10 J per time step.

$p_j = 0.1$ • 10% of Juv. survive to adulthood.

$p_a = 0.2$ • 20% of adults survive from one time step to the next.

In demography, the matrix of coefficients is referred to as the **transition matrix** or sometimes as the **projection matrix**.

Age-specific mortality rates and birth rates are known as **vital statistics**.

1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?
3. Which **classes contribute most** to the long-term growth rate of a population.

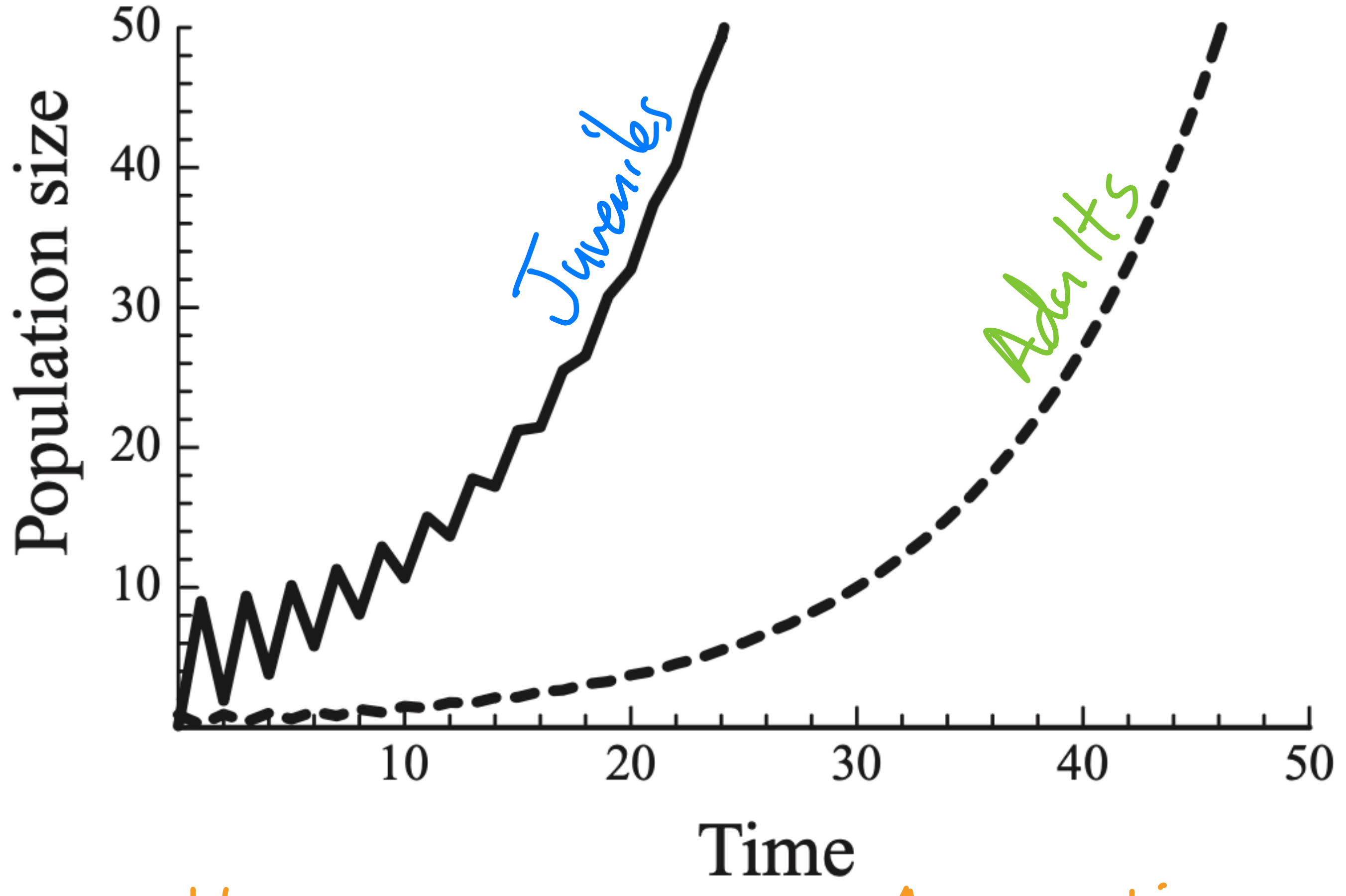
Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

$b = 10 \quad p_j = 0.1 \quad p_a = 0.2$

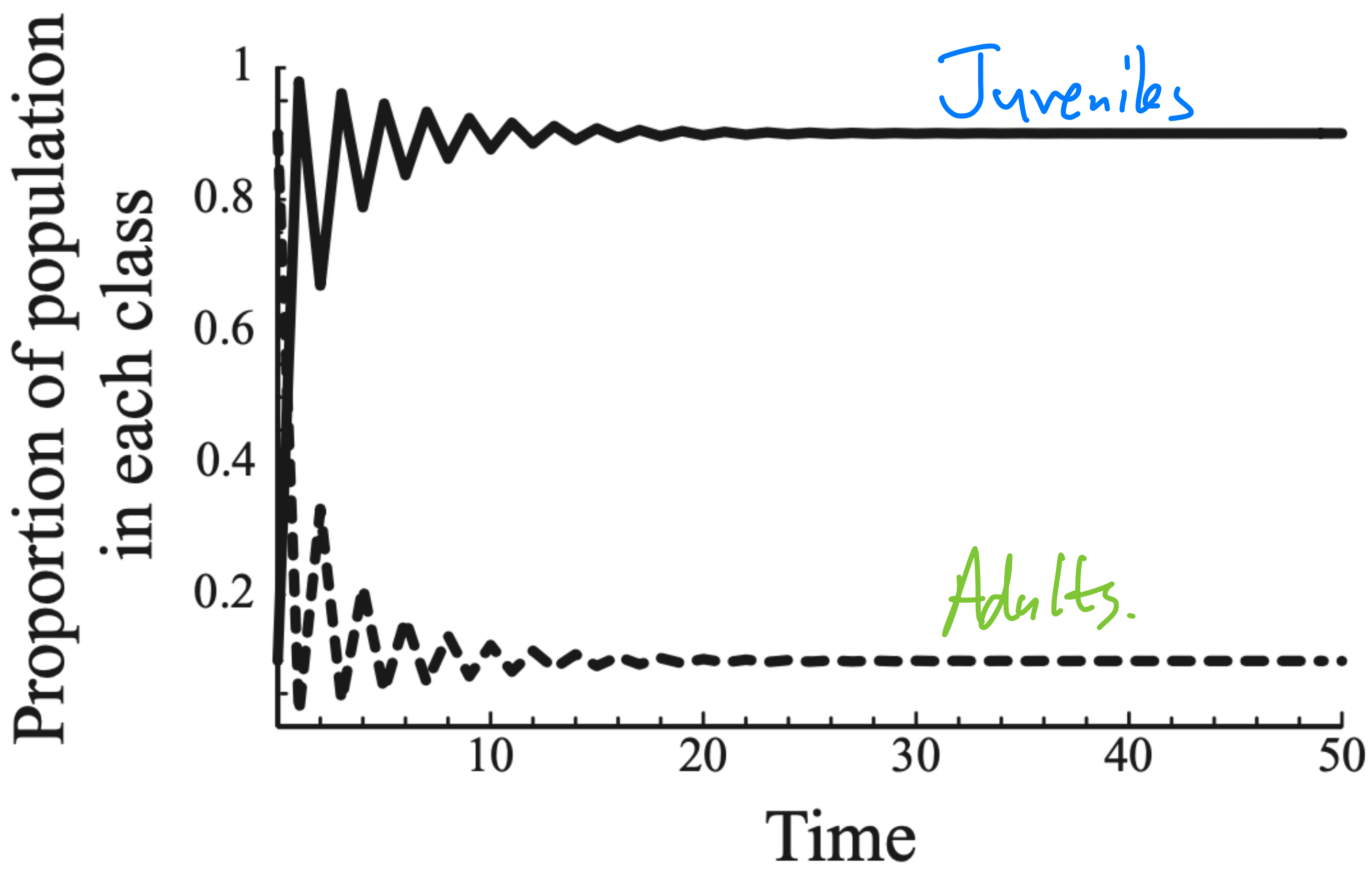
$J(0) = 0.1 \quad A(0) = 0.9$

(a)



• growth regime – pop size ↑ over time

(b)



• pop proportions stabilized!

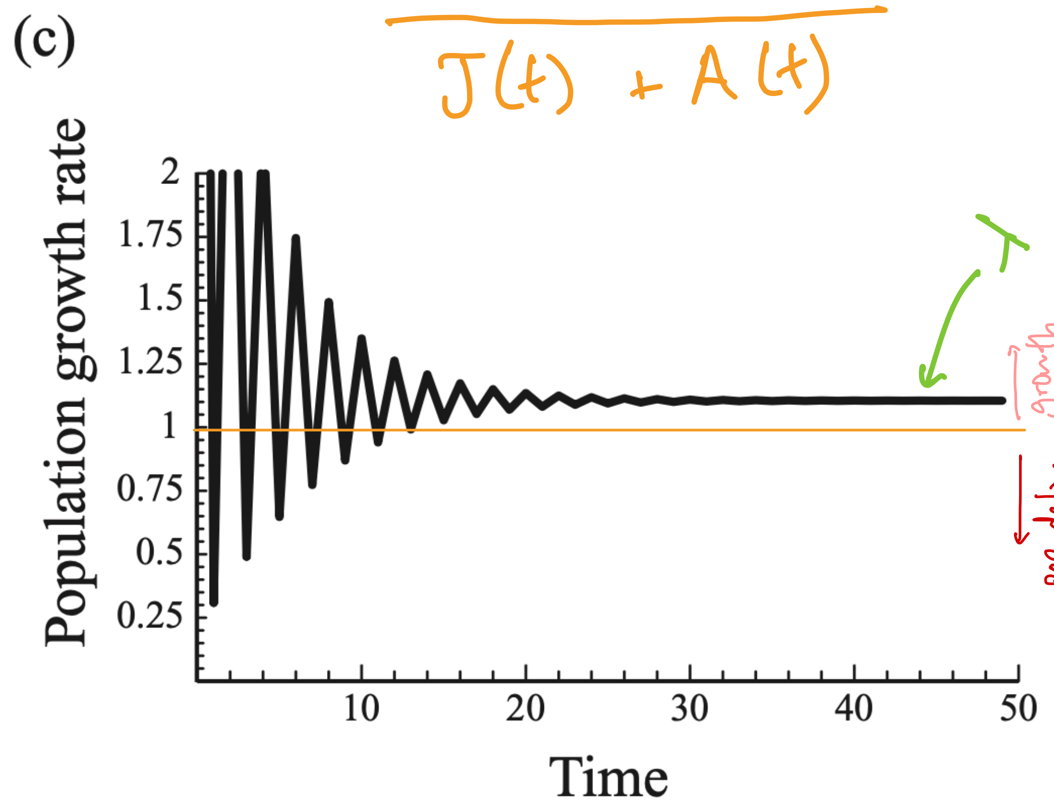
Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \overbrace{\begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix}}^{M} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

$b = 10 \quad p_j = 0.1 \quad p_a = 0.2$

$J(0) = 0.1 \quad A(0) = 0.9$

$$\frac{J(t+1) + A(t+1)}{J(t) + A(t)}$$

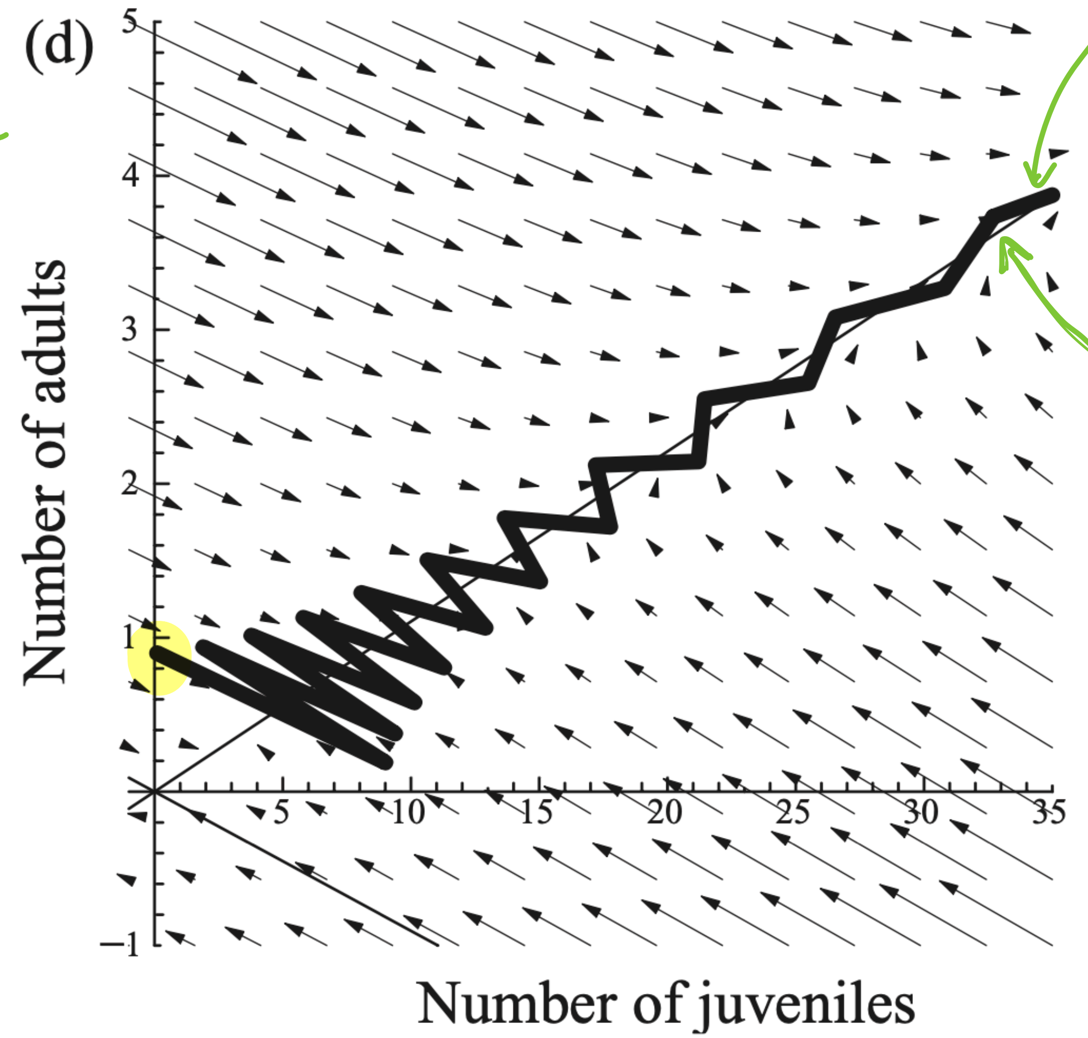


λ eigenvalue

growth ratio > 1

pop. decline ratio < 1

eigenvector of M

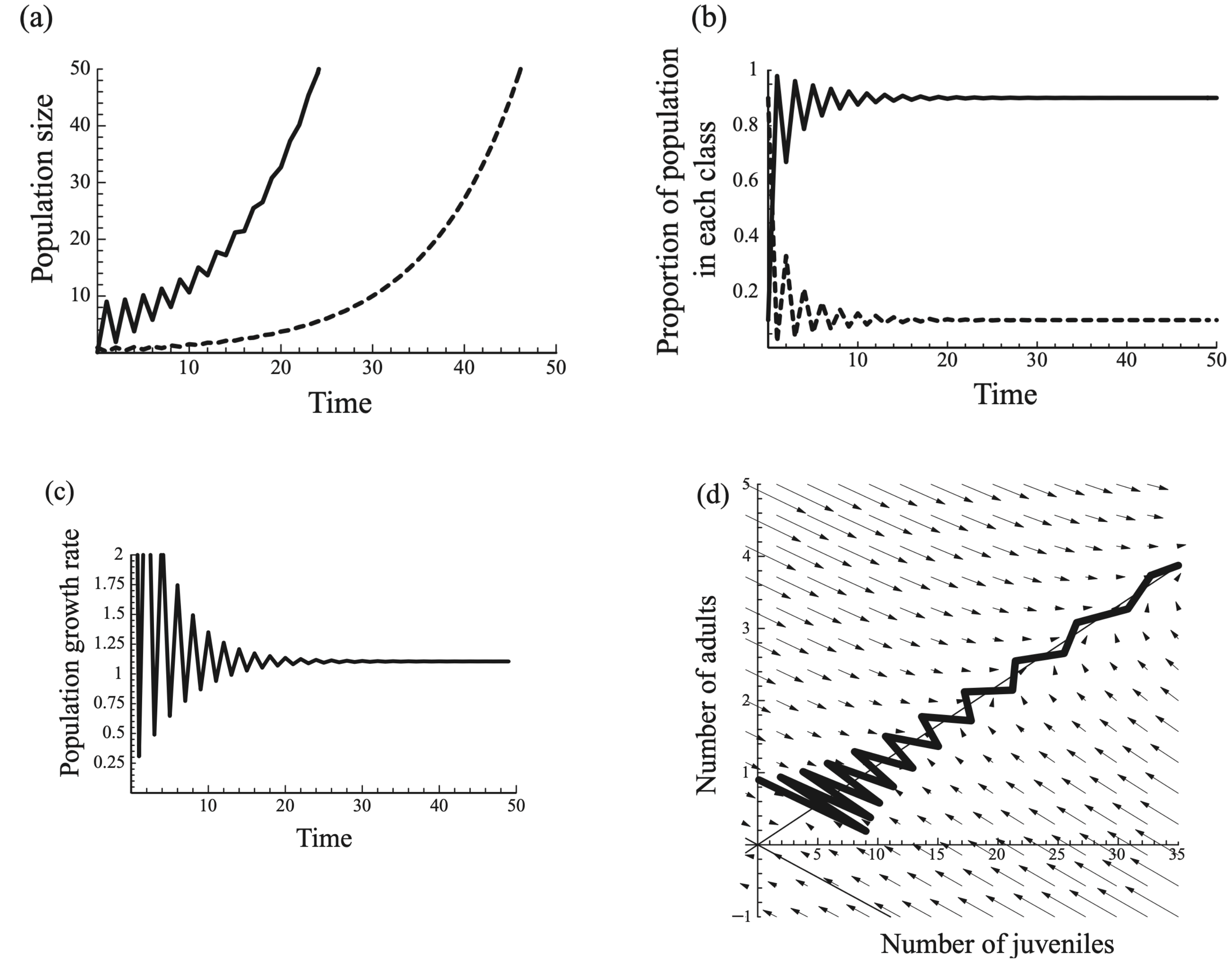


slope of this line is the long-term ratio of adults to juveniles

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

$$b = 10 \quad p_j = 0.1 \quad p_a = 0.2$$
$$J(0) = 0.1 \quad A(0) = 0.9$$



1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?
3. Which **classes contribute most** to the long-term growth rate of a population.
4. Which **parameters have the greatest impact** on the long-term growth rate?

We have our answers!

But what if we had different parameters?
Or started from different conditions?

Class structured populations: Juveniles & Adults

$$\underbrace{\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix}}_{n(t+1)} = \underbrace{\begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix}}_{M} \underbrace{\begin{pmatrix} J(t) \\ A(t) \end{pmatrix}}_{n(t)}$$

transition matrix
projection matrix.

$$\underbrace{\vec{n}(t+1) = M\vec{n}(t)}_{\text{generic problem}}$$

The general solution for this kind of **linear discrete time** problem is given by:

$\vec{n}(t) = AD^tA^{-1}\ \vec{n}(0)$. Let's dissect this equation.

$$\underbrace{n(t)}_{\text{answer solution}} = A\ D^t\ A^{-1}\ \overbrace{n(0)}^{\text{initial conditions}}$$

diagonal matrix
entries are the eigenvalues of M

Matrix A has columns which are the eigenvectors of M.

$$A = \left([\vec{x}_1] [\vec{x}_2] [\vec{x}_3] \dots \right)$$

$$D = \begin{pmatrix} \lambda_1 & & 0 \\ & \lambda_2 & \\ 0 & & \lambda_3 \dots \end{pmatrix}$$

$$M\vec{x}_1 = \lambda_1 \vec{x}_1$$

$$D^t = ?$$

Ex:

$$D = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}$$

$$D^2 = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} = \begin{pmatrix} \lambda_1^2 & 0\cdot\lambda_1 + \lambda_2 \cdot 0 \\ 0\cdot\lambda_1 + \lambda_2 \cdot 0 & \lambda_2^2 \end{pmatrix} = \begin{pmatrix} \lambda_1^2 & 0 \\ 0 & \lambda_2^2 \end{pmatrix}$$

$$D^t = \begin{pmatrix} \lambda_1 & & & \\ & \lambda_2 & & \\ & & \ddots & \\ & & & \lambda_n \end{pmatrix}^t = \begin{pmatrix} \lambda_1^t & & & \\ & \lambda_2^t & & \\ & & \ddots & \\ & & & \lambda_n^t \end{pmatrix}$$

Class structured populations: Juveniles & Adults

$\frac{a^t}{b^t} = \left(\frac{a}{b}\right)^t$

$\vec{n}(t) = A \; D^t \; A^{-1} \; \vec{n}(0)$

$$\begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} = \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right) \begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix} \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right)^{-1} \begin{pmatrix} n_1(0) \\ n_2(0) \end{pmatrix}$$

generic solution.

What happens here when t gets big?

Pull out λ_1^t from D^t

$$D^t = \begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix} = \lambda_1^t \begin{pmatrix} 1 & 0 \\ 0 & \frac{\lambda_2^t}{\lambda_1^t} \end{pmatrix} = \underbrace{\lambda_1^t}_{\text{gets big}} \begin{pmatrix} \overset{\text{same. stay 1.}}{1} & 0 \\ 0 & \underbrace{\left(\frac{\lambda_2}{\lambda_1}\right)^t}_{\text{this goes to zero as } t \to \infty} \end{pmatrix} \underset{t \text{ large}}{=} \lambda_1^t \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}$$

Suppose $\lambda_1 > \lambda_2$.

Suppose t gets large

- Long term growth rate is given by λ_1, largest eigenval.
- Long term growth direction is given by $\vec{x}_1$.

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} = \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right) \begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix} \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right)^{-1} \begin{pmatrix} n_1(0) \\ n_2(0) \end{pmatrix}$$

What happens here when t gets big?

$$\begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} = \lambda_1^t \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right) \begin{pmatrix} 1 & 0 \\ 0 & \left[\frac{\lambda_2}{\lambda_1} \right]^t \end{pmatrix} \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right)^{-1} \begin{pmatrix} n_1(0) \\ n_2(0) \end{pmatrix}$$

1. What is the **long-term growth rate** of a population? ✅ λ_1
2. What is the **long-term class structure** of a population? ✅ $\vec{x}_1$

you can always $\vec{x}_1 \frac{1}{\text{sum } \vec{x}_1}$ to get proportions.

Class structured populations: right whales

Class structured populations: right whales

- Up to 60 feet (18m) long — 300k lbs (135k kg).

- Distinguished by rough patches on head, which are parasitized by whale lice, making them white.

- Migratory seasonally, for feeding and calving.

- Gentle, docile, surface feeding, with lots of blubber — thus, killed by whalers for their oil. The blubber makes them float upon death.

- Now threatened by entanglements and fishing.

- ~400 alive in the N. Pacific. ~1150 W. Pacific.

Population growth rates are **absolutely critical for conservation**.

Class structured populations: right whales

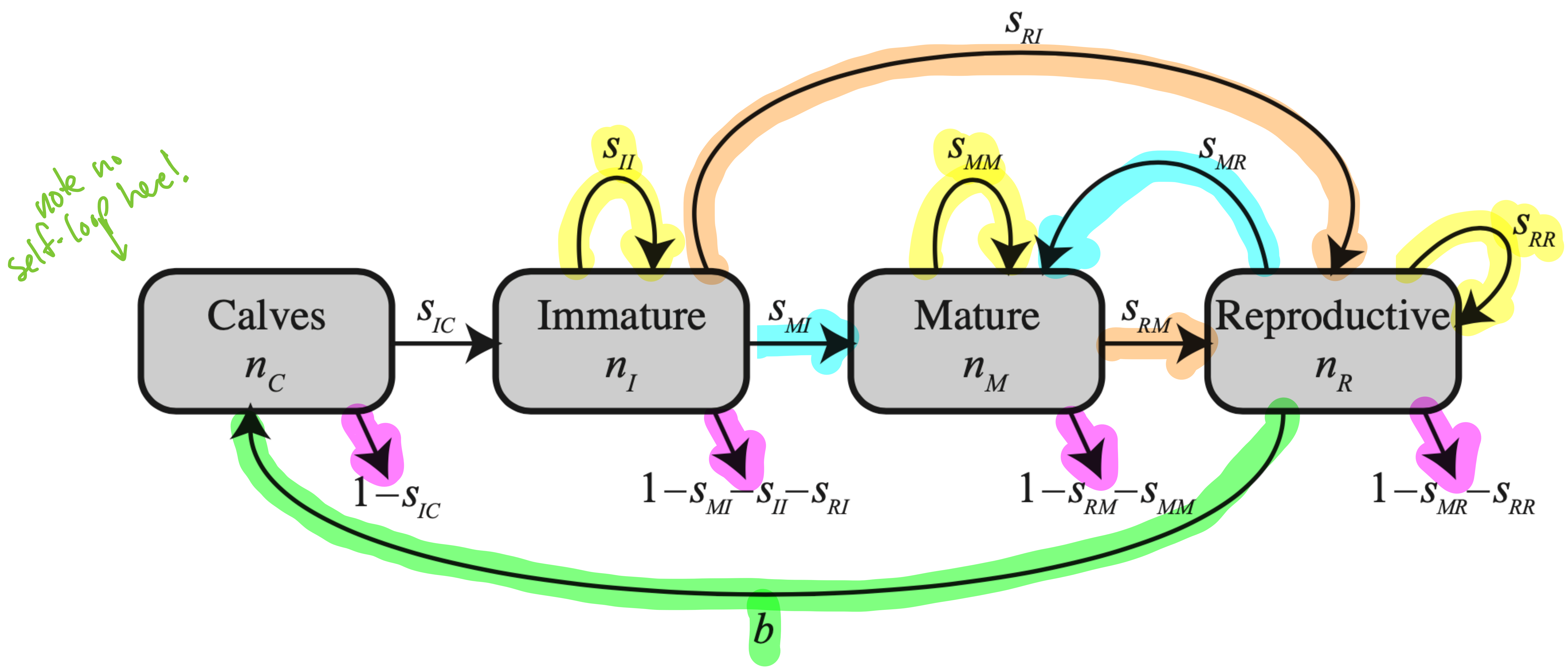
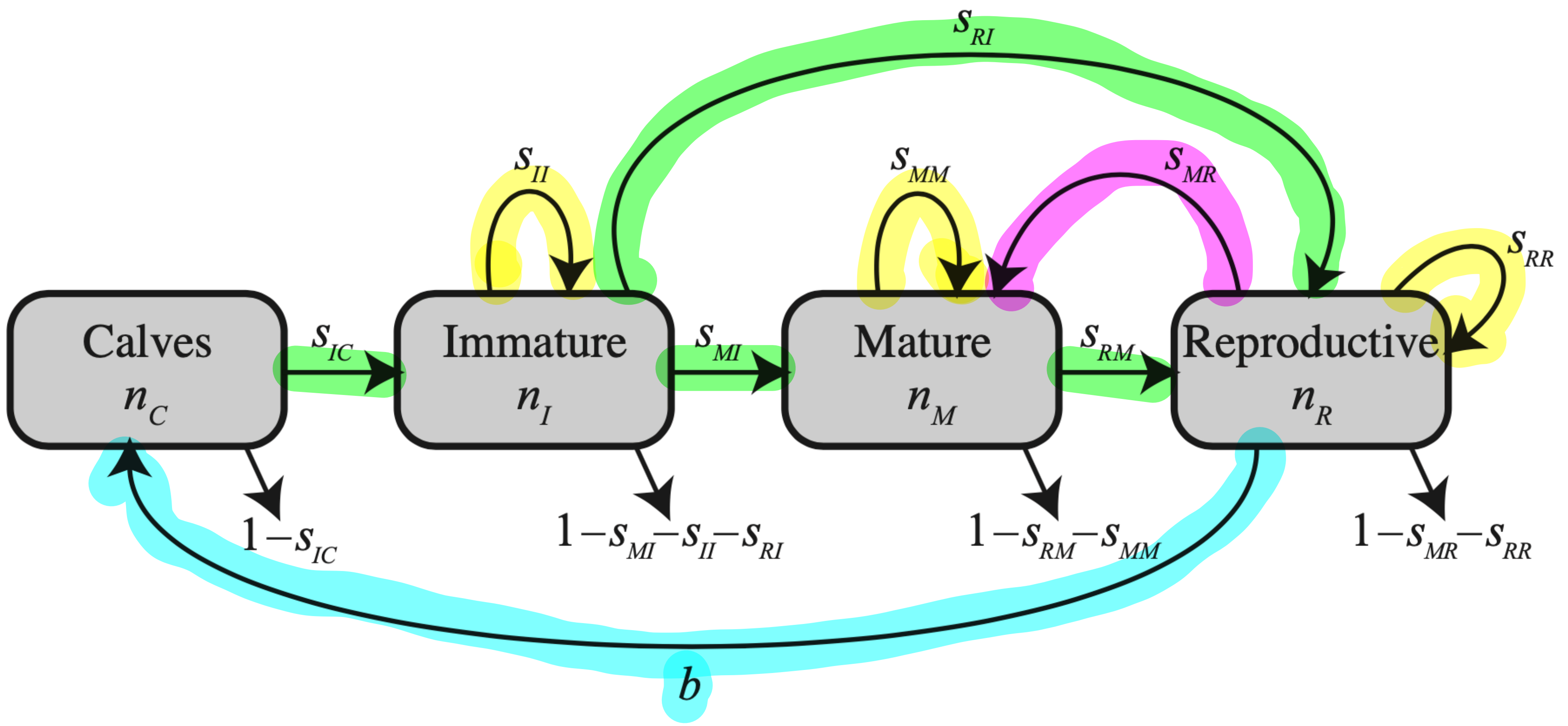


Figure 10.1: A flow diagram for the discrete-time model of right whales. The parameters, s_{ij} give the probabilities of an individual moving from j to i, and b is the fecundity of a reproducing female.

Expect a 4x4 matrix!

Class structured populations: right whales

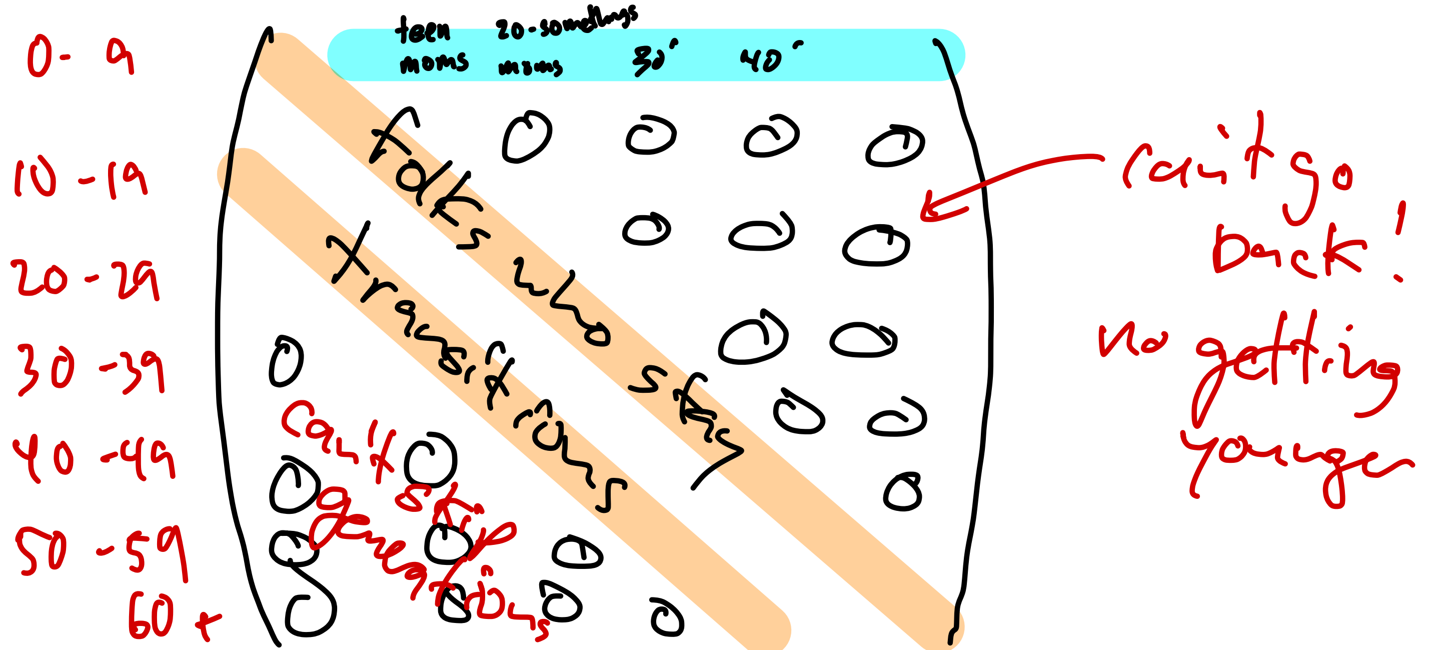


$$n_C(t+1) = 0 + 0 + 0 + b\, n_R(t)$$

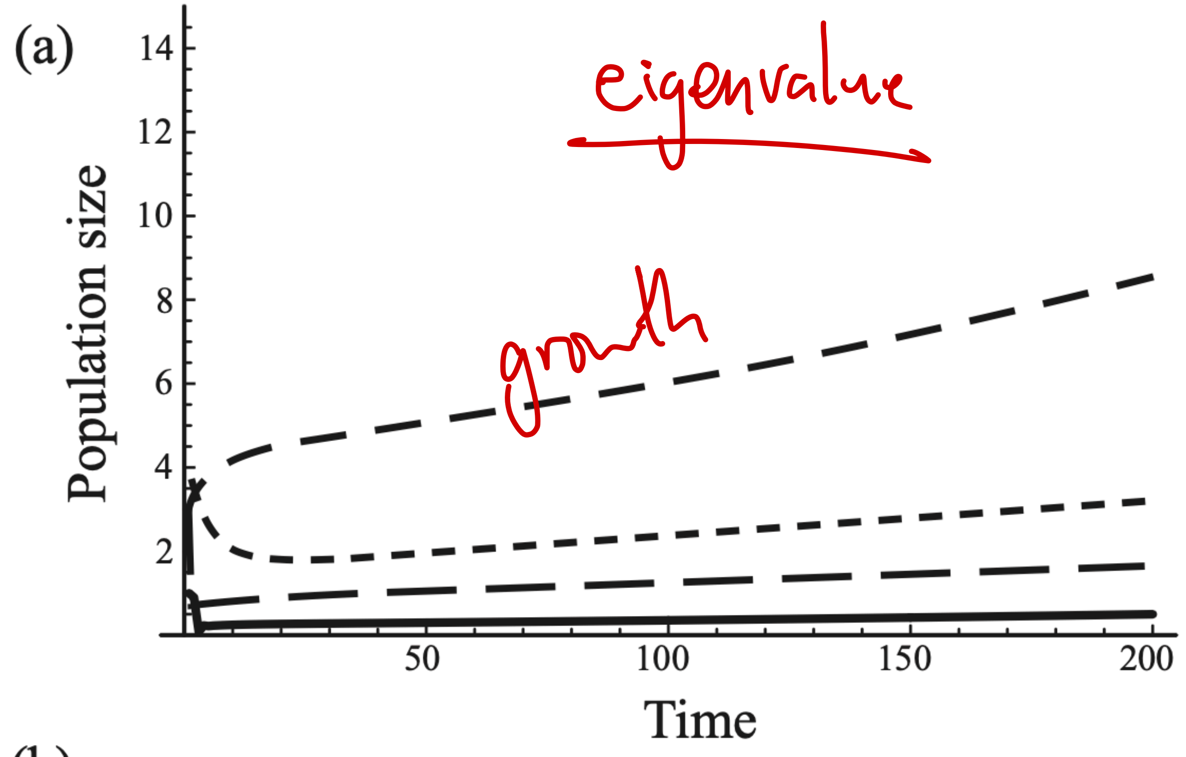
$$\begin{pmatrix} n_C(t+1) \\ n_I(t+1) \\ n_M(t+1) \\ n_R(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & b \\ s_{IC} & s_{II} & 0 & 0 \\ 0 & s_{MI} & s_{MM} & s_{MR} \\ 0 & s_{RI} & s_{RM} & s_{RR} \end{pmatrix} \begin{pmatrix} n_C(t) \\ n_I(t) \\ n_M(t) \\ n_R(t) \end{pmatrix}.$$

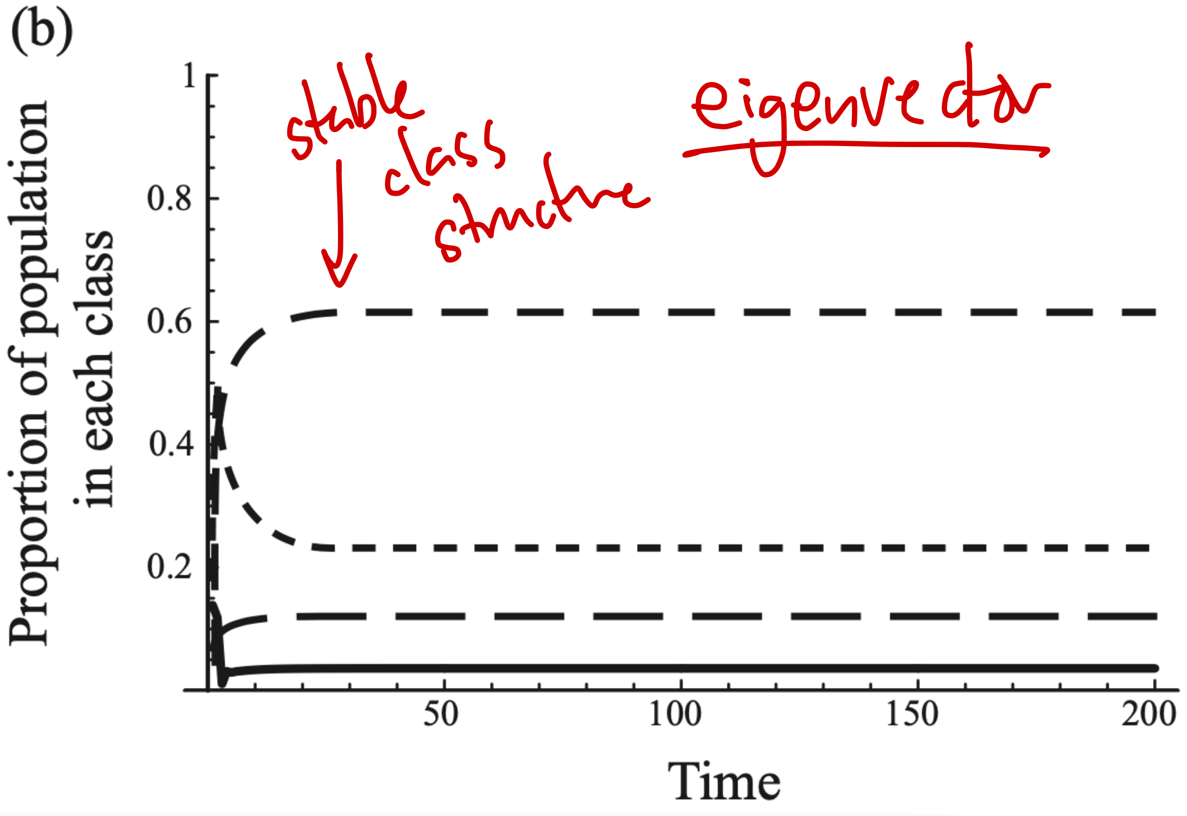
Leslie Matrix

Age Demography

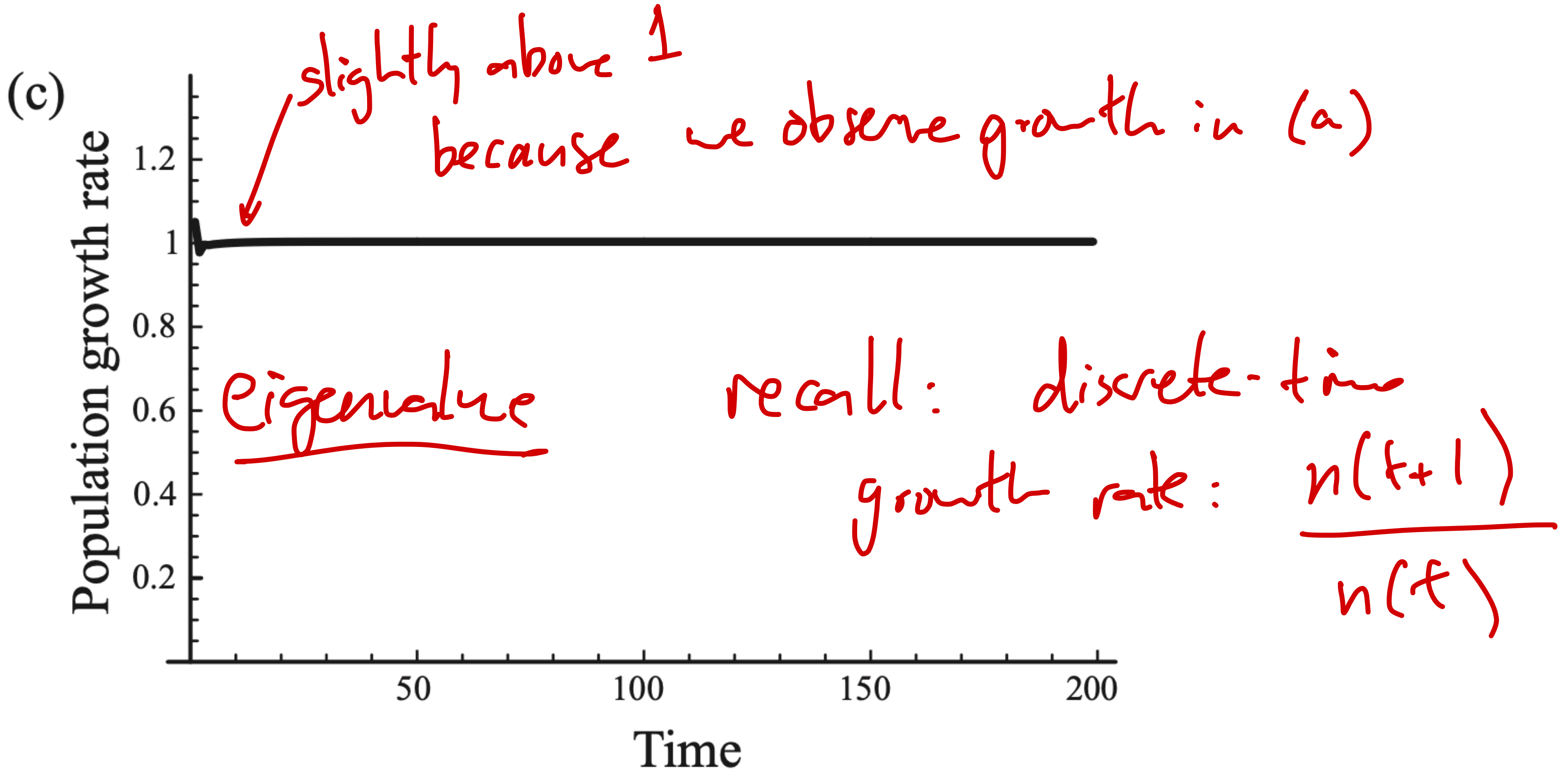


Class structured populations: right whales



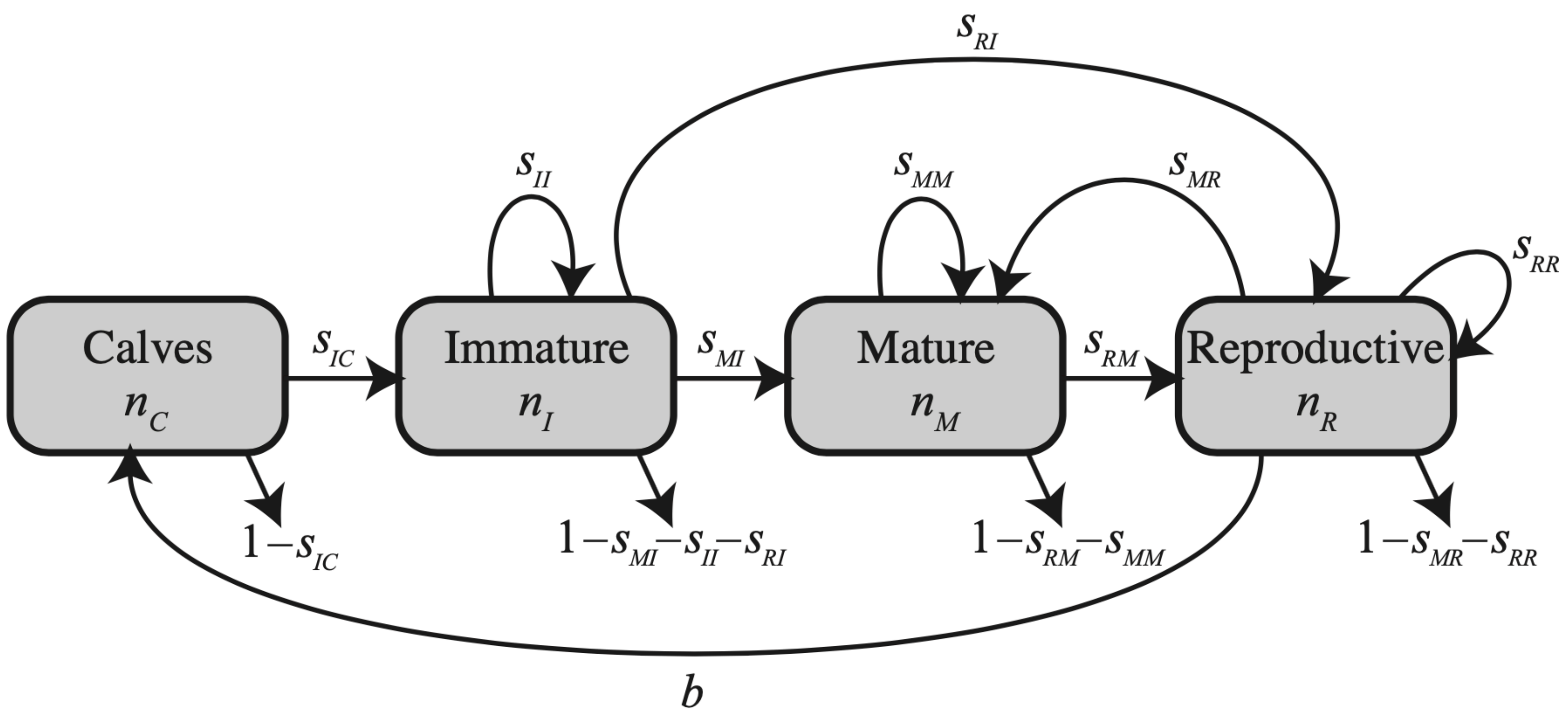


1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?



Class structured populations: right whales

Assume $\lambda_1 > \lambda_2 \geq \lambda_3 \geq \lambda_4 \dots$



$$\begin{pmatrix} n_C(t+1) \\ n_I(t+1) \\ n_M(t+1) \\ n_R(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & b \\ s_{IC} & s_{II} & 0 & 0 \\ 0 & s_{MI} & s_{MM} & s_{MR} \\ 0 & s_{RI} & s_{RM} & s_{RR} \end{pmatrix} \begin{pmatrix} n_C(t) \\ n_I(t) \\ n_M(t) \\ n_R(t) \end{pmatrix}.$$

Diagonal w/ eigenvalues

IC

$$\begin{pmatrix} n_C(t) \\ n_I(t) \\ n_M(t) \\ n_R(t) \end{pmatrix} = \mathbf{A}\,\mathbf{D}^t\mathbf{A}^{-1} \begin{pmatrix} n_C(0) \\ n_I(0) \\ n_M(0) \\ n_R(0) \end{pmatrix},$$

columns are eigenvectors

1. What is the **long-term growth rate** of a population? λ_1
2. What is the **long-term class structure** of a population? $\vec{x}_1$

where $M\vec{x}_1 = \lambda_1 \vec{x}_1$

General rules for class-structured populations

L T G R

1. What is the **long-term growth rate** of a population?

If there exists one eigenvalue of M which is larger than all others,

then LTGR is λ_1.

L T C S

2. What is the **long-term class structure** of a population?

In scenario above, LTCS given by $\vec{x}_1$.

$M\vec{x}_1 = \lambda_1 \vec{x}_1$

let $\vec{p} = \frac{\vec{x}_1}{\sum \vec{x}_1} = \frac{\vec{x}_1}{\vec{1}^T \vec{x}}$ ensures $\vec{p}$ sums to 1.

$M(s\vec{x}_1) = \lambda_1 (s\vec{x}_1)$

$M\vec{v} = \lambda_1 \vec{v}$ $\quad \vec{v} = s\vec{x}_1$

3. Which **classes contribute most** to the long-term growth rate of a population.

stay tuned.

Perron Frobenius

Population **transition matrices** have interesting properties:

1. All entries are ≥ 0.
2. The matrix is square.

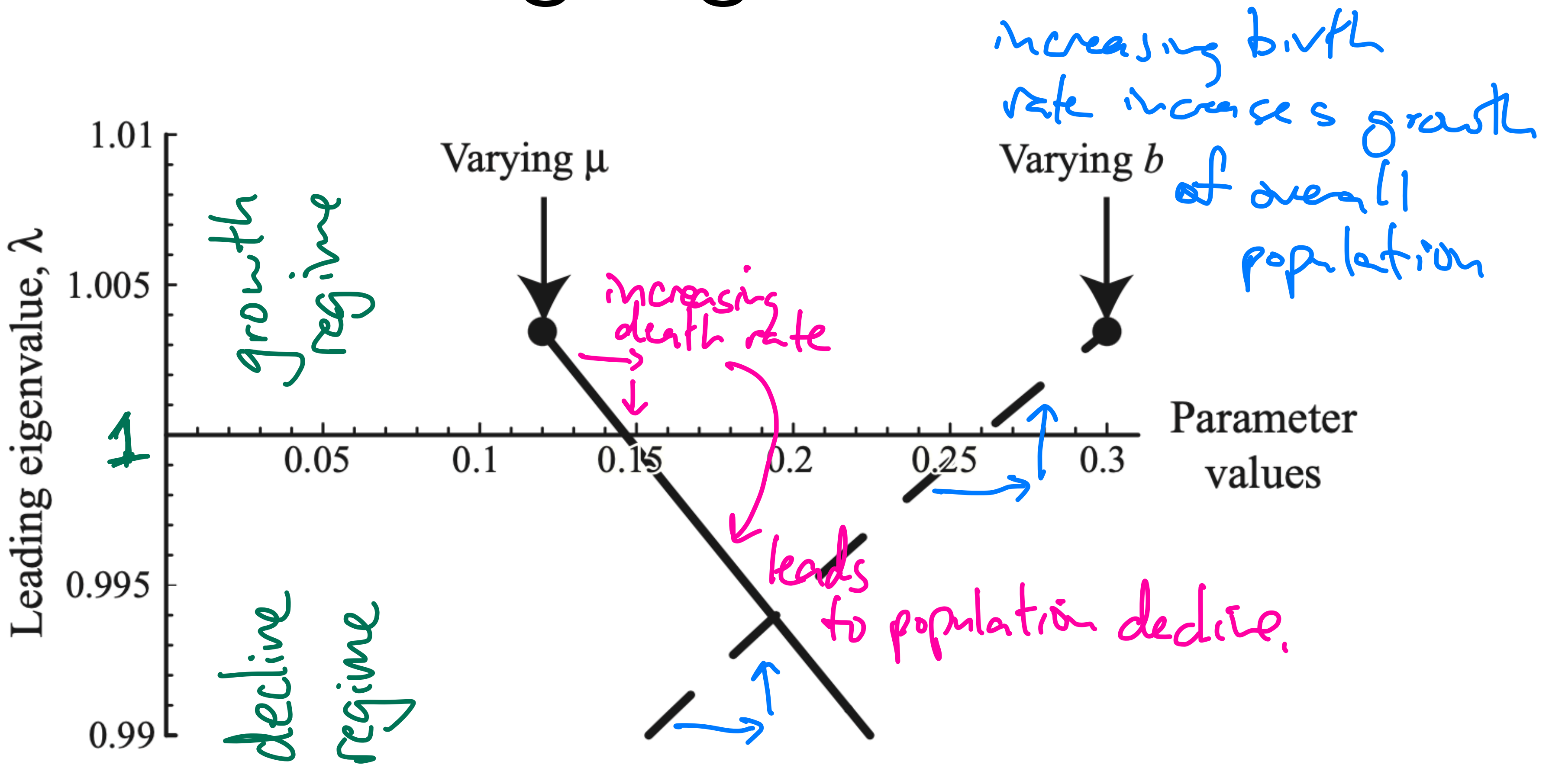
When these conditions are met, the **Perron-Frobenius Theorem** tells us that:

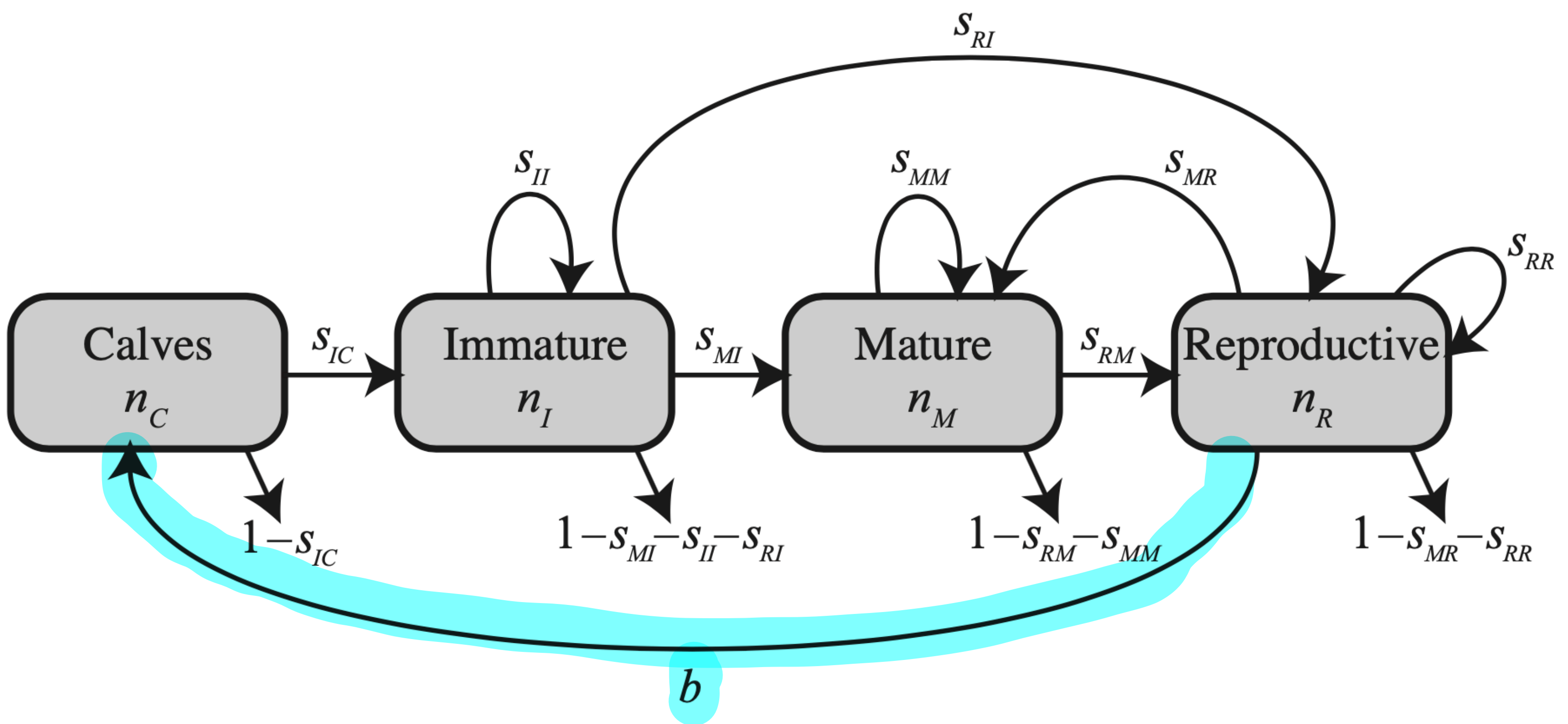
1. The eigenvalue with largest magnitude λ_1 will *never be negative*.
2. This eigenvalue will also *always be real*.
3. The eigenvector $\vec{x}_1$ associated with this eigenvalue will *also* be non-negative and real.

This means that we can ask how λ_1 is affected by the model's parameters!

How do parameters affect the leading eigenvalue?

Figure 10.4: The influence of the unknown parameters on the growth rate of the right whale population. The right whale population grows over the long term as long as the leading eigenvalue is greater than one (above the horizontal axis). The solid and dashed lines show how the leading eigenvalue depends on the unknown parameters, μ and b, respectively, holding all other parameters at their values in Figure 10.3. The dots show the leading eigenvalue when $\mu = 0.12$ and $b = 0.3$ as in Figure 10.3.





fecundity b

death rate $\mu = 1 - s_{MR} - s_{RR}$

General rules for class-structured populations

Def'n of y: $(y^T M)^T = (\lambda y^T)^T$

$M^T y = \lambda y$

this means y is a right eigenvector of M^T!

1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?
3. Which **classes contribute most** to the long-term growth rate of a population.

Alternative phrasing: you are a conservation biologist and you can introduce 1 new right whale. What age whale would be best to introduce, in terms of future population size?

The values of adding population in each bin are called **reproductive values**.

Right Eigenvectors

$Mx = \lambda x$

Left eigenvectors

$y^T M = \lambda y^T$

1. λs are same
2. If M is symmetric, xs and ys are same
3. If M not symmetric xs and ys not same.
4. $\vec{x}_1 \rightarrow$ LTCS

$\vec{y}_1 \rightarrow$ reproductive values

General rules for class-structured populations

Discrete time

$\vec{n}(t+1) = \vec{n}(t)$

growth: $\frac{\vec{n}(t+1)}{\vec{n}(t)} = 1$

$\Rightarrow \lambda_1 = 1$

Eigenvalues of M = Eigenvalues of M^T

1. What is the **long-term growth rate** of a population?

   The **long-term growth rate** of a population is given by the **leading eigenvalue**.

2. What is the **long-term class structure** of a population?

   The **stable class distribution** describes the long-term proportion of individuals in each class; these proportions are given by the leading **right eigenvector**.

3. Which **classes contribute most** to the long-term growth rate of a population.

   The **reproductive value** of each class is proportional to the **left eigenvector** associated with the leading eigenvalue.

All left eigenvectors of M are right eigenvectors of M^T.

right $\quad M \quad$ left $\quad M^T$