Matrix formulation:

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_A(t+1) \end{bmatrix} = \overbrace{\begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_A \\ p_0 & 0 & 0 & & 0 \\ 0 & p_1 & 0 & \cdots & 0 \\ & & \cdots & & \\ 0 & 0 & 0 & p_{A-1} & 0 \end{bmatrix}}^{A \quad \text{[write later]}} \begin{bmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_A(t) \end{bmatrix}$$

Implements rule 1: $n_a(t) = p_{a-1}\, n_{a-1}(t-1)$; $a \geq 1$

rule 2: $n_0(t+1) = \sum_{a=0}^{A} f_a\, n_a(t-1)$

✓

WRITE: $\underset{\sim}{n}(t+1) = A\, \underset{\sim}{n}(t)$

def: A: projection matrix.

NOTE: Lin. Alg. review in Sec. 2.2.1 or 2.4.1 – or OH.

or posted simoncelli notes

Solution:

$$\underset{\sim}{n}(t+1) = A\,\underset{\sim}{n}(t) \longrightarrow \underset{\sim}{n}(t) = \underbrace{A \cdot A \cdot A \cdot \ldots}_{t}\ \underset{\sim}{n}(0)$$

$$= A^t\,\underset{\sim}{n}(0)$$

Simulate in matlab... or R

Same choices as before...

$P_0 = .5$ $\quad f_0 = 0$

$P_1 = .25$ $\quad f_1 = 1$

$\qquad\qquad f_2 = 5$

$$A = \begin{bmatrix} 0 & 1 & 5 \\ .5 & 0 & 0 \\ 0 & .25 & 0 \end{bmatrix}$$

Say $\underset{\sim}{n}(0) = \begin{pmatrix} 10 \\ 100 \\ 500 \end{pmatrix}$

Solve via pop1_eulot_and_leslie_iterate.ipynb

Claim: $n_0(t) = c\,\lambda^t$

$$\log n_0(t) = \log c + t(\log \lambda)$$

[Fit line to $\log n_0(t)$ in [illegible]

Get: $\log \lambda \approx .0464$

$$\rightarrow \lambda \approx 1.0475$$

As from Euler-Lotka formula.

• DISCUSS ... fitting commands in each language...

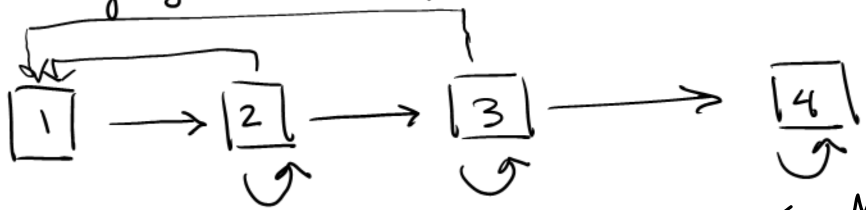
More general formulation: "STAGES NOT AGES"

STAGE CLASS MODELS: $n_a(t)$ = number individuals in stage a

STAGES chosen to best-predict the f_a, based on available data.

Ex 1.1. Life-cycle stage
WA-state orca . . . [Brault + Caswell 1993; E+L Ex. 2.13]
Yearling - juvenile - reproductive - postreproductive

STAGE:



Note: yearling is newborn stage.

← Matrix Formulation (next pg.)

ass models : N stages

Matrix formulation:

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_N(t+1) \end{bmatrix} = \overbrace{\begin{array}{c} \begin{bmatrix} a_{11} & a_{12} & a_{13} & \cdots & a_{1N} \\ a_{21} & a_{22} & & \cdots & \\ a_{31} & a_{3} & & \cdots & \\ \vdots & & & & \\ a_{N1} & & & \cdots & a_{NN} \end{bmatrix} \\ \begin{array}{cc} \underset{\sim}{c_1} & \underset{\sim}{c_2} \end{array} \end{array}}^{A} \begin{bmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_N(t) \end{bmatrix}$$

POPULATION DYNAMICS:

$$\boxed{\underset{\sim}{n}(t+1) = A\,\underset{\sim}{n}(t)}$$

A: projection matrix.

ALSO WRITE AS:

$$n_i(t+1) = \sum_j a_{ij}\, n_j(t-1)$$

Key Interpretation: → $\underset{\sim}{a_{ij}}$ = # stage-i individuals at $t+1$ per " j " " t.

$$\underset{\sim}{n}(t+1) = \sum_{j=1}^{N} n_j(t)\, \underset{\sim}{c_j}$$

; matrix columns c_j

Solution to population dynamics:

initial state vector

$$\underset{\sim}{n}(t) = \underbrace{A \cdot A \cdot A \cdot}_{t} \cdots \underset{\sim}{n}(0)$$

$$= A^t\, \underset{\sim}{n}(0)$$

... Returning to Ex. 1:

More general formulation: "STAGES NOT AGES"

STAGE CLASS MODELS: $n_a(t)$ = number individuals in stage a

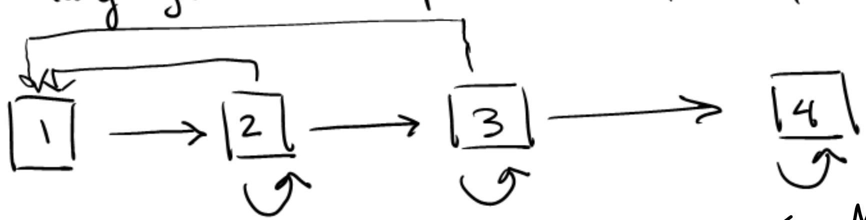
STAGES chosen to best-predict the f_a, based on available data.

Ex 1.1: Life-cycle stage

WA-state orca ... [Brault + Caswell 1993; E+L Ex. 2.13]

Yearling - juvenile - reproductive - postreproductive

STAGE:



Note: yearling is newborn stage.

LIFE-CYCLE GRAPH.

← Matrix Formulation (next pg.)

births

$$A = \begin{bmatrix} 0 & .0043 & .1132 & 0 \\ .9775 & .9111 & 0 & 0 \\ 0 & .0736 & .9534 & 0 \\ 0 & 0 & .0452 & .9804 \end{bmatrix}$$

a_{21} Frac. STAGE-2 at t+1 per STAGE-1 at t.

a_{33}: ... STAGE 3 per STAGE 3

— . —

Message: STAGE-STRUCTURED MODELS have more general projection matrices A:

- generalization 1: $a_{jj} \neq 0$: fraction of individuals stay in same stage from t to t+1

Ex 21 Size (plant Primula vulgaris - p. 39 E+a)
[Valverde and Silvertown, 1998]

$$A = \begin{bmatrix} 0 & 0 & 0.03 & 0.1 & 0.18 \\ .25 & .35 & .12 & .02 & 0 \\ .04 & .45 & .65 & .33 & .19 \\ 0 & 0 & .16 & .58 & .38 \\ 0 & 0 & 0 & .05 & .38 \end{bmatrix}$$

- generalization 2 : can skip more than 1 stage

$$a_{j(j+2)} \neq 0$$

- generalization 3: can move to "lower" stage

Skip this page,

Eigenvalues (evl^s) and Eigenvectors (evr^s) of Proj. Matrix A

See Sect. 2-2-1 +

Eigenvalues (evl$\underline{s}$) and Eigenvectors (evr$\underline{s}$) of Proj. Matrix A

<u>Def</u>: λ is eigenvalue of A if there exists $\underset{\sim}{w} \neq 0$ s.t.

$$A\underset{\sim}{w} = \lambda \underset{\sim}{w}.$$

<u>Fact</u>: Let A be $n \times n$ matrix. Then "typically" n has n distinct eigenvalues $\{\lambda_1, \lambda_2, \ldots, \lambda_n\}$ with assoc. eigenvectors $\{\underset{\sim}{w}_1, \underset{\sim}{w}_2, \ldots, \underset{\sim}{w}_n\}$. $[A\underset{\sim}{w}_1 = \lambda_1 \underset{\sim}{w}_1]$

Means: choose one at "random".

<u>Fact</u>: If $\underline{\lambda_i \neq \lambda_j}$, then $\underset{\sim}{w}_i$ and $\underset{\sim}{w}_j$ are <u>linearly indep.</u>

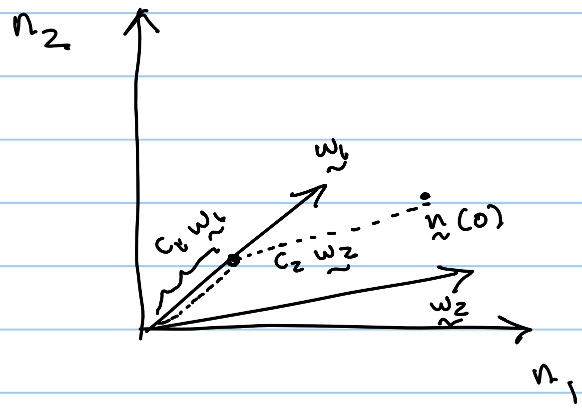
(point in diff. directions).

<u>Result</u>: for typical A, have n linearly indep. eigenvectors $\{\underset{\sim}{w}_j\}$. Therefore ... initial population

(**) vector $\underset{\sim}{n}(0) = c_1 \underset{\sim}{w}_1 + c_2 \underset{\sim}{w}_2 + c_3 \underset{\sim}{w}_3 + \cdots + c_n \underset{\sim}{w}_n$.

$\{c_i\}$ are "initial constants."

Example with $n=2$:



"Travel along each vector distance c_j to reach $\underset{\sim}{n}(0)$"

How to find the $\underset{\sim}{c}_j$ numerically.

$$\underset{\sim}{n}(0) = \sum_j c_j \underset{\sim}{w}_j$$

Looks like – and is – matrix multiplication.

$$\begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_N \end{bmatrix} = \underbrace{\begin{bmatrix} | & | & & | \\ w_1 & w_2 & \cdots & w_N \\ | & | & & | \end{bmatrix}}_{V} \begin{bmatrix} c_1 \\ \vdots \\ c_N \end{bmatrix}$$

Linear combination of columns.

$$\underset{\sim}{n}(0) = V \underset{\sim}{c}$$

Want to solve for $\underset{\sim}{c}$.

" Solve Matrix Equation " :

```
c = la.solve (V , n_0)
```

$\underset{\sim}{n}(1) = A\underset{\sim}{n}(0) =$

$$c_1 A \underset{\sim}{w_1} + c_2 A \underset{\sim}{w_2} + \ldots + c_n A \underset{\sim}{w_n}$$

$$= c_1 \lambda_1 \underset{\sim}{w_1} + c_2 \lambda_2 \underset{\sim}{w_2} + \ldots + c_n \lambda_n \underset{\sim}{w_n}$$

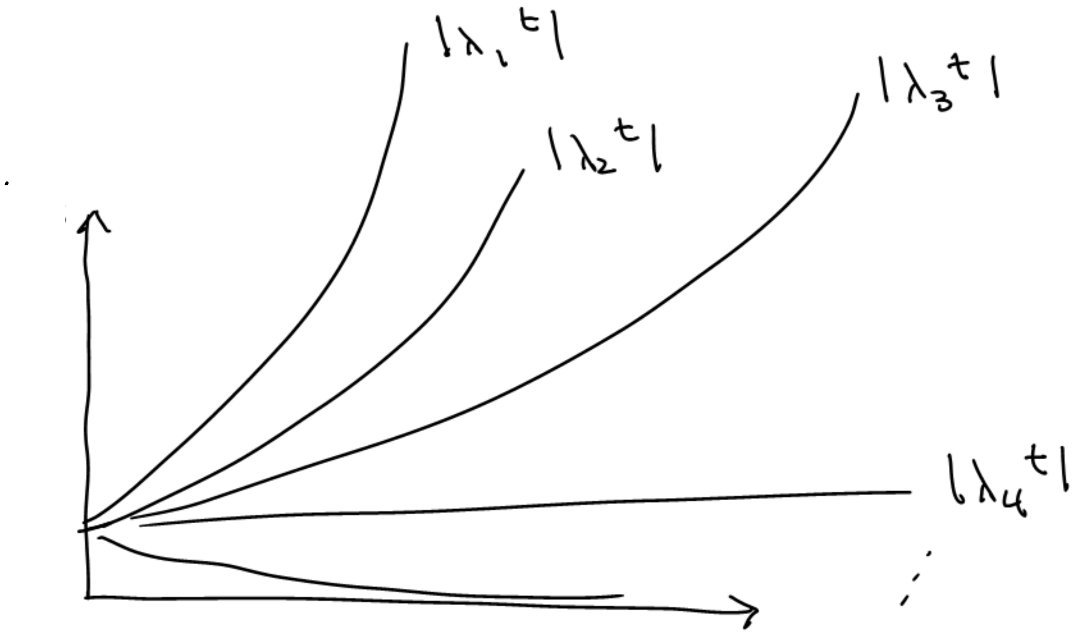
← Implications of (**) for population DYNAMICS

$$\underset{\sim}{n}(t) = c_1 \lambda_1^t \underset{\sim}{w_1} + \ldots + c_n \lambda_n^t \underset{\sim}{w_n}$$

What happens as $t \to \infty$?

ORDER eigenvalues so that $|\lambda_1| \geq |\lambda_2| \geq \ldots$

Typical picture...



IMPORTANT CONCLUSION: If there exists SINGLE dominant eigenvalue λ_1 such that $|\lambda_1| > \lambda_j, \forall j \neq 1$,

$$\text{as } t \to \infty, \ \underset{\sim}{n}(t) \sim c_1 \lambda_1^t \underset{\sim}{w_1}$$

- If $|\lambda_1| > 1$ then pop. grows exponentially
- If $|\lambda_1| < 1$ then pop. shrinks "
- If $|\lambda_1| = 1$ then pop. tends to const. size

(Note: same conclusion holds if A does not have n distinct eigenvalues: it is <u>general</u>)

— · —

Also: as $t \to \infty$, $\underset{\sim}{n}(t)$ is proportional to $\underset{\sim}{w}_1$ ...
so that $\underset{\sim}{w}_1$ gives <u>relative</u> proportions of individuals in various stages.

— · —

Aside: meaning of "$\sim$": Relative error $\to 0$ as $t \to \infty$.

<u>i.e.</u>

$$\frac{|\lambda_2^t| + |\lambda_3^t| + \cdots + |\lambda_n^t|}{|\lambda_1^t|} \leq (n-2)\left(\frac{|\lambda_2|}{|\lambda_1|}\right)^t \to 0$$

$\leftarrow$ left-off terms

<u>Think:</u> $\lambda_i = re^{i\theta} \to |\lambda^t| = |r^t| = |r|^t$

— · —

<u>Illustration:</u> Popl_Rulot_and_Leslie_iterate.ipynb

<u>Key Syntax:</u> `w, v = la.eig(A)`