Chapter 4 Lecture

Populations with Age and Stage structures

Spring 2013

4.1 Introduction

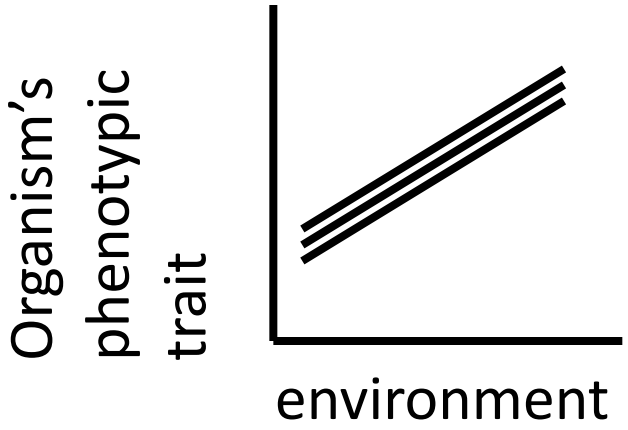
Life Table- approach to quantify age specific fecundity and survivorship data

Age (or **Size Class**) structured populations

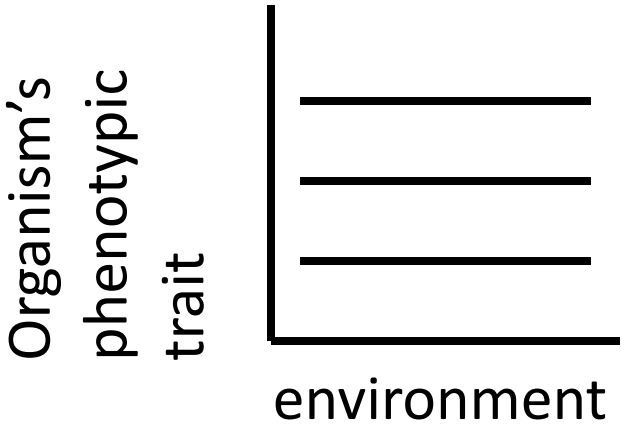
Stage structured populations

- Plant: seed, seedling, pre-reproductive, reproductive, non-reproductive
    - Genet =
    - Ramet =
- Animals: if age is not available, pre-reproductive, reproductive, post- reproductive
- Phenotypic plasticity =

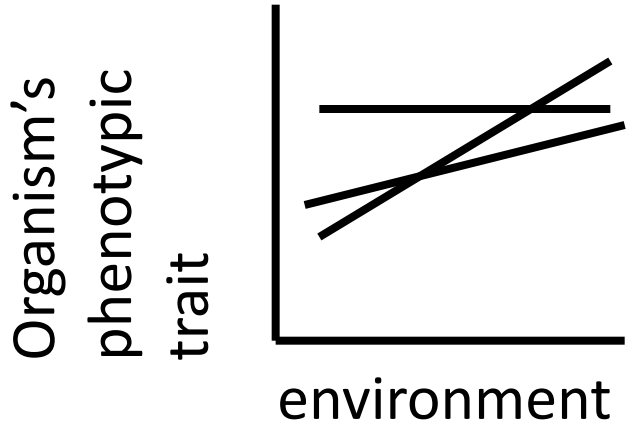
Phenotypic Plasticity Concepts



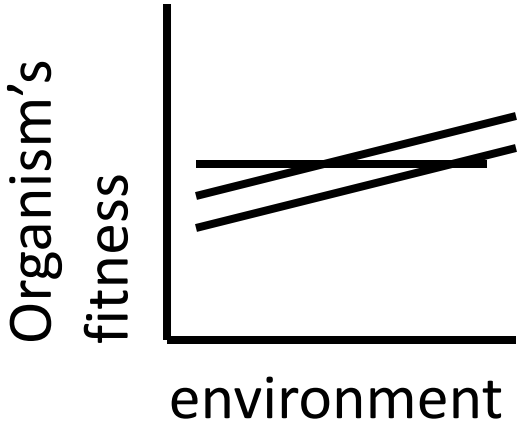
Phenotypic plasticity



Genetic variation



Genotype by environment interaction



***Each line is a genetic unit**

4.2 Survivorship l_x

1st Approach:

Cohort = individuals born at the same time (year)

Advantage: Know **exact** age of each individual

Disadvantage: lacks generality, cohorts born in different years may not respond the same way

If organisms live a LONG time one investigator could spend their whole life studying one cohort

Called a Fixed-cohort, Dynamic or Horizontal life table

Table 4.3 – we will examine shortly

4.2 Survivorship l_x

2nd Approach:

Static, Vertical or Time-specific life table

Locate all dead individuals during some time period. This approach assumes that rates of survival within a population are ~ constant

Ex., Table 4.1

OR more likely done with living organisms…..

Collect life history data from **several cohorts** over <u>one</u> time period

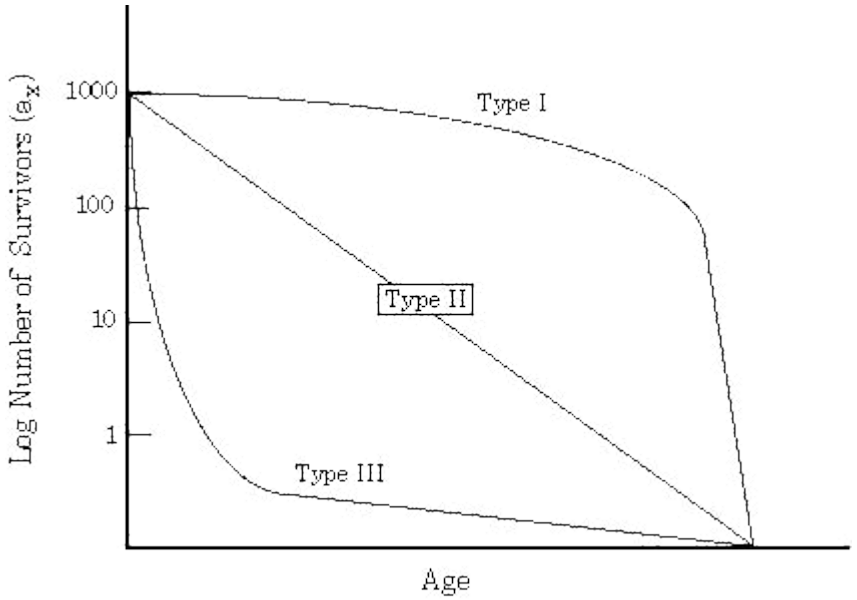
Thus cohorts are not followed in time but reconstructed using one-time observations. <u>Assumes</u> that mortality is constant across age.

3rd Approach: Collect vertical data across as many years as possible to produce a more realistic estimate of survivorship and reproduction.

GOAL: to produce an estimate of age specific survivorship and fertility

4.2 Survivorship curves l_x

Type I
Type II
Type III



Why would survivorship curves vary across years and cohorts?

Age-specific survivorship= prob. @ birth living to a given age or age class

4.3 Fertility

Fertility m_x column Table 4.2

Pre-reproductive
Reproductive
Post-reproductive

GRR = Gross reproductive rate = $\sum m_x$ *(not taking survivorship into account)*

Survivorship = l_x
$\sum l_x m_x = R_0$ = Net Reproductive Rate

Again assume that *lx* and *mx* remains constant.
Realistic? Thoughts?

Figs. 4.8: human fertility and 4.9:cactus ground finch

Table 4.3 Life Table of gray squirrel population, pg 87

Age	l_x	m_x	p_x	q_x	$l_x m_x$
0	1.000	0	0.253	0.747	0
1	0.253	1.28	0.458	0.542	0.324
2	0.116	2.28	0.767	0.233	0.264
3	0.089	2.28	0.652	0.348	0.203
4	0.058	2.28	0.672	0.328	0.132
5	0.039	2.28	0.641	0.359	0.089
6	0.025	2.28	0.880	0.120	0.057
7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0
		GRR = 14.96			R_0 = 1.119

l_x = prob. at birth of surviving to a given age

m_x = age specific fertility

$p_x = l_{x+1}/l_x$ = age specific prob. of surviving to the next age class

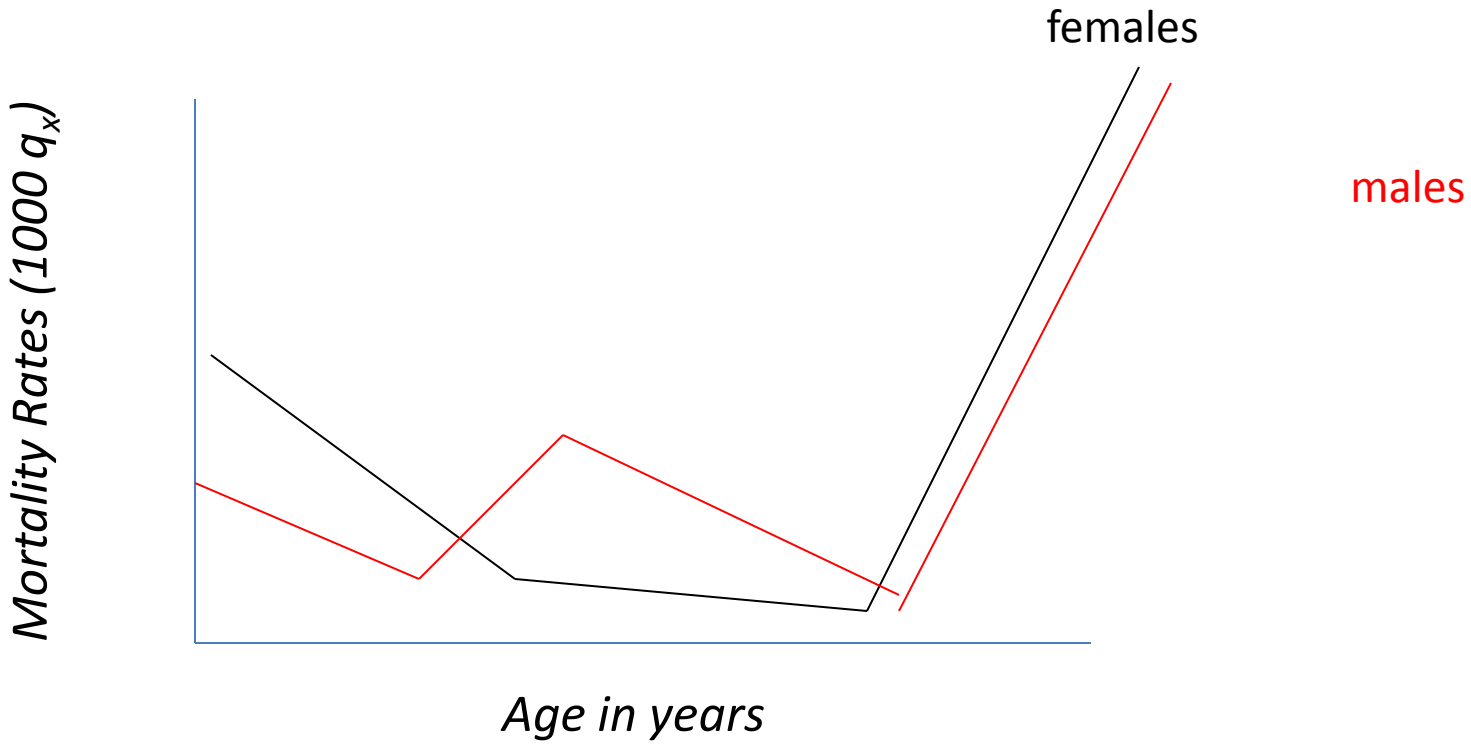
q_x = proportion of pop survived until *x*, but will die in next age class

Thus $q_x = 1 - p_x$

4.4 Mortality Curves

Mortality Curves

Fig. 4.10 Impala and 4.11 Humans - often exhibit U shaped distributions



4.5 Expectation of Life

Expectations of Life = e^x

L_x = mean survivorship for any particular age interval & assumes that on avg. an individual dies half-way between the two age classes.

Standard practical approach w/ discrete age classes:

$$L_x = l_x + l_{x+1}/2$$

T_x = area under survivorship curve for indiv. of a given age (x) to the age (w) when oldest indiv. dies $= \sum_{x}^{w} l_x + l_{x+1}/2$ (eq.4.6)

See Table 4.4 for ex.: Expectation of life = $e_x = T_x/l_x$ (eq.4.7)

4.6 Net reproductive rate (R_0), generation time (**G**) and intrinsic rate of increase (***r***)

$R_0 = \sum l_x m_x$ **Net Reproductive Rate** (eq. 4.8)

The standard approach to compare populations is to compare intrinsic rate of increase (***r*** *)* or finite rate of increase (λ) because both are estimated for a specific unit of time.

Using the "**Characteristic equation**" of demography (Lotka, Euhler)

$\sum l_x m_x e^{-rx} = 1$

- Excellent approximation for ***r***, assuming a stable age distribution:

Intrinsic rate of increase = *r* $= \ln R_0 / G$ (eq. 4.10)

G = Generation time $= \sum x\, l_x m_x / R_0 = \sum x l_x m_x / \sum l_x m_x$ (eq. 4.12)

= mean age of mothers at time of their daughter's births

Table 4.3 Life Table of gray squirrel population, pg 87

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6	0.025	2.28	0.880	0.120	0.057
7	0.022	2.28	0	1.00	0.050
8	0	0	-	-	0
		GRR = 14.96			**R_0 = 1.119**

l_x = prob. at birth of surviving to a given age

m_x = age specific fertility

$p_x = l_{x+1}/l_x$ = age specific prob. of surviving to the next age class

q_x = proportion of pop survived until *x*, but will die in next age class

Thus $q_x = 1 - p_x$

4.7 Age structure and stable age distribution

c_x = Age distribution of a population = proportion of population belonging to various age classes at a given point in time

Proportion of population belonging to a given category, ***c_x*** *and* ***n_x*** *equals the number of individuals in that age category.*

$$c_x = n_x/N = n_x/\sum n_x \qquad \text{(eq. 4.13)}$$

Stable age distribution occurs when survivorship and fertility remain constant for a period of time. The population will grow or decline at a stable state = λ

If popln has stable age distr. Then $N_{t+1}/N_t = \lambda$ And $r = \ln \lambda$

Formula predicting stable age distr.: $c_x = e^{-rx} l_x / \sum e^{-rx} l_x$ (eq. 4.14)

4.8 Projection of population growth in age structured populations

Table 4.5 Review of life table components

Table 4.6 Projection of population growth “how to”

Assignment: Work through math to project population growth for next class

Table 4.5 Review of life table components, pg 94

Age, x	lx	mx	px	qx	lxmx
0	1.0	0	0.5	0.5	0
1	0.5	2	0.4	0.6	1.0
2	0.2	1	0.5	0.5	0.2
3	0.1	1	0	1.00	0.1
4	0	0	-	-	-
Sums		GRR=4			R_0 = 1.3

mx = lx= px= qx= lxmx =

GRR = ? R_0 = ?

Table 4.6 "how to" growth projection utilizing life history table 4.5

Please review Example 4.1 for homework (pg. 96)

Table 4.6 Projected population growth based on

Table 4.5: starting with 200 individuals at age 0

Age, x	n_x, t=0	c_x, t=o	n_x, t=1	c_x, t=1	n_x, t=2	c_x, t=2	n_x, t=3	c_x, t=3	C_x =Calc. SAD
0	200	1.00	200	0.67	240	0.63	300	0.625	0.625
1	0	0	100	0.33	100	0.26	120	0.250	0.258
2	0	0	0	0	40	0.11	40	0.083	0.082
3	0	0	0	0	0	0	20	0.042	0.035
4	0	0	0	0	0	0	0	1	0
Sums	200	1.00	300	1.00	380	1.00	480	1.00	1.00

λ from t=0 to t=1 = 300/200 = 1.5
λ from t=1 to t=2 = 300/200 = 1.27
λ from t=2 to t=3 = 300/200 = 1.26
λ from t=3 to t=4 = 300/200 = 1.22 SAD reached

4.8 Projection of population growth in age structured populations

Observations from this example:

1) in the short term, population growth is greatly influenced by age distribution of the population

2) a popln with a short generation time can rapidly reach a stable age distribution (SAD)

3) finite rate of increase (λ) is influenced by age distribution, but quickly settles into the predicted value from the life history table (e^r) as pop reaches SAD.

4.9 Age structure, 1st version of Leslie projection matrix

- Leslie (1945) demonstrated that one could readily project population growth utilizing matrix algebra (please see Appendix 2 for an overview)

- Table 4.7

- This approach allows one to rapidly quantify changes in the **age** structure & population size and can calculate λ when there is a SAD.

- Matrix models allow one to describe behavior of poplns with overlapping generations of which indiv. fall into different **age** (Leslie) or **stage/size classes** (Lefkovitch).

- Matrix approach commonly used now with computer programs to estimate λ. **Excel Program posted on Website for your exploration**

Table 4.7 General matrix format

Age classes	**|A|** Matrix						t=0		t=1
0	p_0m_1	p_1m_2	p_2m_3	p_3m_4	0		n_0		n_0
1	p_0	0	0	0	0		n_1		n_1
2	0	p_1	0	0	0	x	n_2	=	n_2
3	0	0	p_2	0	0		n_3		n_3
4	0	0	0	p_3	0		n_4		n_4

- **Off diagonal** = p_x = prob (surv. from age_x to age_{x+1}) or aij
-**Surv. and fert**. columns placed in matrix form |A| - top row
- **population** itself considered a column vector, thus when:

$$N_{t+1} = |A|N_t$$

4.9 Age structure, 1st version of Leslie projection matrix

From pg 97, Tables 4.7 & 4.8 **and** Assume year begins with repro. season

Population is a column vector (@ t = 0)

Multiply **Popln Matrix, |A|** by column vector (@ t=0) **->** popln @ t=1

Popln Matrix |A|

p_x = probability of surviving from age x to x+1 in OFF diagonal

First row = p_x x (m_{x+1}) = Fertilities in top row (some refs use fecundity)

Matrix must be square with final column consisting of zeros

How to construct a matrix – w/ comparable notation

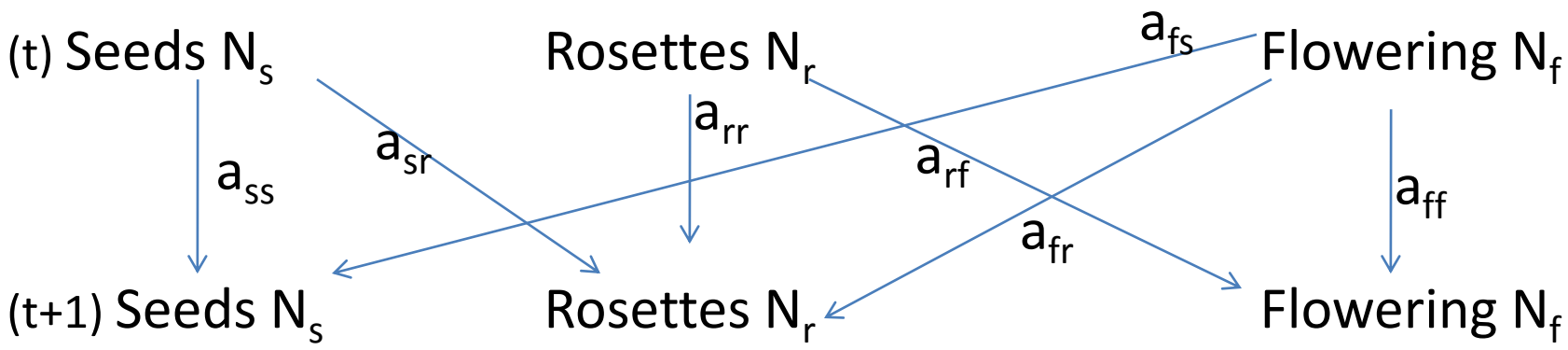
Individuals present in each **stage** (or age class) are entered in column matrix:

A column matrix of 3 classes (Lefkovitch):

Ns
Nr
Nf

Transition probability from one stage/age to the next = $\mathbf{a_{ij}}$

Transition matrix = projection matrix, perennial plant



Matrix elements ~ a_{ij}

t	Seed	rosette	flower
t+1			
Seed	a_{ss}	a_{rs}	a_{fs}
rosette	a_{sr}	a_{rr}	a_{fr}
flower	a_{sf}	a_{rf}	a_{ff}

How to matrix cont.

- Some coefficients have no biological meaning = 0 (see below)
- Each number in matrix is an element
- Ordinary single number is a called a scalar
- Single row of numbers = row vector
- Single column of numbers = column vector

A (projection matrix) x B_t Column matrix) = B_{t+1}

	Seed	rosette	flower			
Seed	a_{ss}	0	a_{fs}	x	N_s	=
rosette	a_{sr}	a_{rr}	a_{fr}		N_r	
flower	0	a_{rf}	a_{ff}		N_f	

Transition matrix iterated = repeatedly multiplied

- $A \times B_1 = B_2$; $A \times B_2 = B_3$; $A \times B_3 = B_4$……
- Then the age or stage structure of a popln eventually stabilizes at a constant ratio of classes, reach SAD, then per year rate of increase $\lambda = R_0/t$
- t= generation time; R_0 = net repro. Rate = N_{t+1}/N_t

$A_{\text{(projection matrix)}} \times B_{t\ \text{Column matrix)}} = B_{t+1}$

	Seed	rosette	flower			
Seed	a_{ss}	0	a_{fs}		N_s	
rosette	a_{sr}	a_{rr}	a_{fr}	x	N_r	=
flower	0	a_{rf}	a_{ff}		N_f	

4.9 Age structure, 1st version of Leslie projection matrix

Table 4.7

Age classes	Matrix						t=0		t=1
0	p_0m_1	p_1m_2	p_2m_3	p_3m_4	0		n_0		n_0
1	p_0	0	0	0	0		n_1		n_1
2	0	p_1	0	0	0	x	n_2	=	n_2
3	0	0	p_2	0	0		n_3		n_3
4	0	0	0	p_3	0		n_4		n_4

4.10 2nd version of Leslie projection matrix

Now assume:

1) Able to count individuals completed at least 1st year of life
2) NO count of newborn individuals, too difficult, as with seeds
3) It is possible to estimate fertility & survivorship by individuals in yr 1 onwards

Results the same!! Individuals in age class 0 do NOT reproduce, thus λ is identical. Resulting in much simpler Life Table and matrix!

Table 4.9 (based on Table 4.5) where NO count is made on zero-year age class

$$\begin{vmatrix} m_1p_0 & m_2p_0 & m_3p_0 & m_4p_0 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{vmatrix} \times \begin{vmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{vmatrix}_{t=2} = \begin{vmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{vmatrix}_{t=3} \Rightarrow \begin{vmatrix} 1.0 & 0.5 & 0.5 & 0 \\ 0.4 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{vmatrix} \begin{vmatrix} 100 \\ 40 \\ 0 \\ 0 \end{vmatrix}_{t=2} = \begin{vmatrix} 120 \\ 40 \\ 20 \\ 0 \end{vmatrix}_{t=3}$$

4.11 Stage structure or Lefkovitch projection matrix

- Noted that once indiv. becoming reproductive both their survivorship and fertility remained relatively constant

- Stage classes: juvenile, young adult, adult OR Pre-reproductive, reproductive, post-reproductive

- Lefkovitch demonstrated that in spite of lumping the age classes the finite rate of growth, λ , was conserved.

- This is because these repro. indiv. were recycled back into the SAME stage as the year before for many years (iteroparous repro.)

4.11 Stage structure or Lefkovitch projection matrix

Table 4.10 : Simplified life table of ground squirrel

Age/Stage class	m_x	p_x
Y = young adult	1.28	0.25
A = mature adult	2.28	0.80

Table 4.11: Projection of gray squirrel popln (2x2 matrix)

Stage class	Matrix		t=0	t=1	t=2	t=3
Y	0.325	0.570	50	68	86	110
A	0.80	0.80	90	112	144	184
			∑=140	∑=180	∑=230	∑=294

4.12 Dominant latent roots & the characteristic equation

If lx and mx remain constant, then able to project forward

$Nt = |A|^t N_0$

And can also project backward in time but requires Identity matrix (I):
$I|A| = |A|I = A$

Recall, in algebra each number has an inverse except zero

- $|A|\ |A|^{-1} = I$ (Identity matrix)

- If the inverse of a **square matrix** |A| is |B| then |A| |B| = I (Identity matrix)

- Then square matrix has a **determinant (D),** which is a scalar that determines the dependency among the equations that a matrix represents

- When D=0 then the # of equations is NOT equal to the # of unknowns and the equations have no unique solution

4.12 Dominant latent roots & characteristic equation

If popln is in SAD then each group grows at the same rate as the popln as a whole $\sim \lambda$

Characteristic Equation for a matrix

$|A| - \lambda I = 0$

Only exists for square matrices

λ is known as the **latent root, characteristic root, or Eigenvalue** of equation.

Leslie matrix has only **ONE** positive, **primary** or dominant latent root **= λ**

Leslie has also shown: $\lambda = e^r$

Please try out the Projection matrix program online at my website.

4.12 Eigenvalue of square projection matrix

Recall: λ is the dominant and most POSITIVE eigenvalue from projection matrix and it will grow exponentially with rate = λ

The stable age distribution and λ are independent of the initial age distribution; they depend on the projection matrix.

A row eigenvector is NOT transpose of column vector, thus have left and right eigenvectors AND they have different roles in the projection matrix.

4.12 Eigenvectors of square projection matrix:

Vectors denoted by **x** and transition matrix by **A**

A **right** eigenvector, x_R (right side of A) solves for SAD (stable age/stage distr.)

Eq 1: $A(x_R) = \lambda(x)$ or $(x)\lambda$ same since λ is scalar

A **left** eigenvector, x_L (left side of A) is defined and solves for the V, Reproductive Value (exp. contribution of each stage to pop growth):

Eq 2: $(x_L)A = (x)\lambda$ or $\lambda(x)$ same since λ is scalar

FYI: The only difference is in the actual form of A. Depending on what kind of object A is, left or right eigenvectors might not be allowed; or they might both equal each other, or be different. For example: $(x_R)A$ = undefined, as is $A(x_L)$ = undefined.

4.13 Reproductive value (V_x)

V_x =A measure of which group of individuals within the population will contribute the greatest to future reproduction.

Approach 1: Weighted avg. of present and future repro of indiv. at age x

Approach 2: Ignores current repro. , and only estimates future repro.

V_x is normalized (scaled) such that the value for the first age class is 1.0.

Approach 3: Ignores current repro., via a computer generated program, Populus with same assumptions as Approach 2.
http://www.cbs.umn.edu/populus

$$V_x = \sum_{x}^{z} e^{-rx} l_x m_x / e^{-rx} l_x$$

Fig. 4.12
Equation 4.21 (data are normally provided by computer program)
Ex. 4.2

4.14 Sensitivity Analysis

- How sensitive is a poplulation's growth (or extinction) to a particular demographic change?
- Examine how changing vital rates (survivorship or fertility) alters λ
- Table 4.12 and Fig. 4.13
- **Vital rates** = factors that have a direct impact on survival & reproduction.
- This type of examination = **perturbation** or **sensitivity analysis**
- Survivorship scales from 0 to 1, but reproduction can range from 0 – 1000s
- This approach makes it difficult to <u>compare</u> different poplns of the same species or to compare species

4.14 Sensitivity Analysis

Each transition, a_{ij} (or p) has a sensitivity, s_{ij}

Calculate sensitivity of λ between classes of ij.

SA Requires:

1) SAD
2) Repro. Value, V_x of indiv in each stage or age class
3) All transition probabilities equally likely**** likely NOT true in nature

SA = (V_i) x (% indiv in size class j)

Why perform Sensitivity Analysis?

1) Measure importance of vital rates
2) Evaluate effects of error in estimation
3) Quantify effects of environmental perturbations
4) Evaluate alternative management strategies
5) Predict intensity of natural selection

Be able to compare populations across a species range to determine vulnerability, need another metric.

Elasticity Analysis

- To facilitate being able to compare changes in vital rate with changes in λ across populations and species => **elasticity analysis**

- Utilize **proportional changes** in λ as a proportion of change in the vital rates ~ matrix coefficients (a_{ij}) (sum to 100%).

- **Standardized sensitivity = Elasticity**

- Elasticities reveal the effect of the perturbations in vital rates that are all the same relative magnitude.

- Elasticity is a refined SA

- $e_{ij} = a_{ij}/\lambda = \delta \lambda / \delta a_{ij}$
- $\delta \log \lambda / \delta \log a_{ij}$

Elasticity Analysis

Thus -> provides a proportional change in λ resulting from a proportional change in a_{ij}.

e_{ij}'s sum to 1.0

$e_{ij} = (a_{ij}/\lambda)\ x\ (s_{ij})$

e_{ij} = (transition probability/ λ) x (sensitivity of particular transition)

Therefore one could be given these values (a_{ij}, λ, and s_{ij}) and calculate e_{ij} for a given matrix.

AND compare across populations and species as well.

Example: Comparison of SA and EA

Transitions	Sensitivity	Elasticity
a_{ss}	0.20300	0.15320
a_{sr}	0.07660	0.23120
a_{rf}	0.72780	0. 38440
a_{rr}	0.61280	0. 2312
$\sum$	1.6204	~ 1.00

Highlights

An understanding of:

- Survivorship
- Fertility
- Mortality curves
- Expectation of life
- Net Reproductive rate, generation time, *r*
- Age structure and stable age distribution
- Projecting popln growth in age-structured popIns
- Leslie or population projection matrix
- Reproductive value
- Sensitivity analysis
- Elasticity analysis

Questions?

- Reference information on **website** related to a refresher of matrix algebra to be able to appreciate how computer programs can project population growth.
- Readings
- Problem set and answer key
- Excel program that you can manipulate to gain an understanding of how important age and stage structure is in estimating future population growth.