Quantitative Modeling

Structured Populations

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Bio534

Announcements & Assignments

Labs

- For each task (1) describe what you did, (2) the results (include graphs), and (3) describe what it means.
- Make sure to address all questions posed in the initial assignment
- put code in an appendix
- Lab 4 due on Friday

Project Topic Selection

- 1 page description – see assignment
- proposed due date Oct 19.

Exam

~10 multipart questions (short answer, sketch, essay)

- cover material up to generalized control functions.

Meeting Objectives

- Distinguish structured population models from unstructured population models
- Discuss age and more general class structured populations
- Contrast r and K selected life history characteristics
- Use life table technique to estimate structured population growth rates
- Use Matrix population models to forecast future population size and stable age distribution.

Why Structured Populations?

Unstructured Population Models

- Assume all individuals are genetically and ecologically equivalent (Identical Individuals II)
- Overlapping generations with births and deaths at any time (continuous models)

Structured Models

- Individual Distribution Models
  - Represent differences among individuals by placing them into different classes (e.g. age, sex, size)
  - Still assuming II within a class
- Individual Configuration Models (IBM, ABM)
  - Each individual is modeled computationally
  - No II assumption

individual distribution models

matrix population models

For more information see

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates, Inc. Publishers. Sunderland, MA.

Age Structured Model

- Partition population into classes based on a trait that influences the process rates (e.g. age)
- Choose a projection interval (Δt)
  - Width of classes may equal the projection interval so that all individuals in a class move on the next time step, but this may not be true

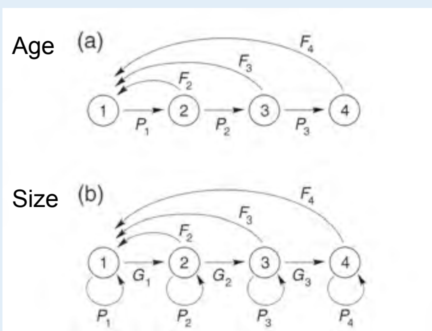


Figure 4.1: (a) A life cycle graph for an age-classified life cycle, in which the width of the age classes equals the projection interval. (b) A life cycle graph for the standard size-classified model. Nodes represent size classes, and an individual can grow no more than a single size class in the interval $(t, t+1)$.

$$\mathbf{A}_a = \begin{pmatrix} 0 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix}$$

$$\mathbf{A}_b = \begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Caswell 2001

Leslie Matrix

When we partition the population into *a = 0,…,A* age classes, then we can calculate the future population density of any age class as

$$n_a(t+1) = p_{a-1}n_{a-1}(t) \text{ for } a > 0$$

Where

$p_x =$ the probability that an x-year-old survives to be age $x+1$

If we assume that per individual birth rates are only a function of age, then

$f_a =$ the average number of newborns next year, per age-a female this year

$$n_0(t+1) = \sum_{a=0}^{A} f_a n_a(t)$$

We can summarize the whole population dynamics as

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ \vdots \\ n_A(t+1) \end{bmatrix} = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_A \\ p_0 & 0 & 0 & \cdots & 0 \\ 0 & p_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & & \vdots \\ 0 & 0 & & p_{A-1} & 0 \end{bmatrix} \begin{bmatrix} n_0(t) \\ n_1(t) \\ \vdots \\ n_A(t) \end{bmatrix}$$

Ellner & Gukenhimer 2006

$$\longrightarrow \mathbf{n}(t+1) = \mathbf{Ln}(t)$$

Where **L** is the Leslie matrix

Assumptions, Caveats, and Warnings

This is a linear, time-invariant model

- It is also a discrete-time, exponential or geometric model

Caswell's (2001, p 30) distinction between

- Forecasting – predict what *will* happen
- Projection - what *would* happen , given certain hypotheses

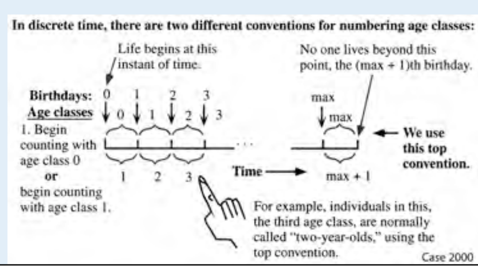
Counting everyone or just females

- Just females is common
- Assumes males are not limiting reproduction

When to census: prebreeding vs. postbreeding

- Pulse birth populations
- Post: $f_a = p_a \times m_{a+1}$
- Pre: $f_a = m_a \times p_0$

Numbering schemes



Generalization: Stage Classes

Populations can be partitioned using any relevant trait

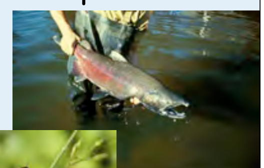
- Age (Leslie Matrix)
- Developmental Stage (L. Lefkovitch 1965)
- Movement between patches (space)
- …or any combination!

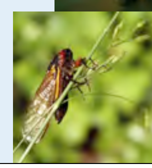
Thus, the "individual distribution" structured population model is quite general

This is also a useful approach when modeling semelparous species

semelparous

organism that reproduces just once in its lifetime (e.g., salmon, cicadas)





iteroparous

organism that reproduces many times

Solution to the Projection Equation

Let **A** represent the general projection matrix, where a_{ij} is the probability that an individual in the type-*j* (compartment *j*) will move to type-*i* during *Δt*

Then our model is

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

As we saw with the scalar discrete time model,

we can find the general solution as …

$$\begin{aligned} \mathbf{n}(1) &= \mathbf{A}\mathbf{n}(0) \\ \mathbf{n}(2) &= \mathbf{A}\mathbf{n}(1) = \mathbf{A}(\mathbf{A}\mathbf{n}(0)) = \mathbf{A}^2\mathbf{n}(0) \\ \mathbf{n}(3) &= \mathbf{A}\mathbf{n}(2) = \mathbf{A}(\mathbf{A}^2\mathbf{n}(0)) = \mathbf{A}^3\mathbf{n}(0) \\ &\vdots \\ \mathbf{n}(t) &= \mathbf{A}^t\mathbf{n}(0) \end{aligned}$$

Thus, given **A** and an initial population distribution **n**(0) we can project the future population at time *t*

Matrix Time Series: Levels of Analysis

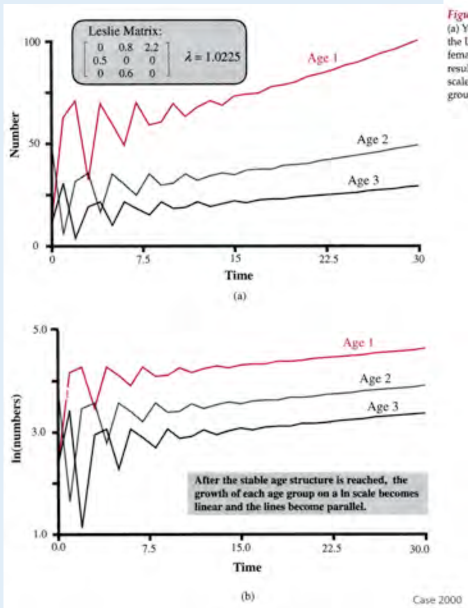
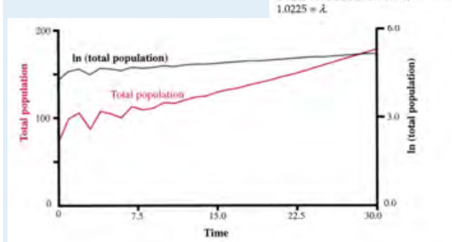


Figure 3.5
(a) Yearly changes in age structure for the Leslie matrix shown and 100 females of age 1 at time 0. (b) The results of Figure 3.5(a) plotted on a ln scale for the numbers of each age group.

Figure 3.6
Total population size, *N*, over time for the population in Figure 3.5. The slope of the ln *N* line near the end of this time series is 0.0221; $e^{0.0221} = 1.0225 = \lambda$.



Analysis

We can analyze the projection matrix A to learn the following

1. Asymptotic rate of population growth → dominant eigenvalue
2. Stable stage distribution → right dominant eigenvector
3. Reproductive value of a stage → left dominant eigenvector

The dynamics of $\mathbf{A}^t$ are determined by the characteristic polynomial

$$\pi(\lambda) = det(\lambda\mathbf{I} - \mathbf{A})$$

Where

$\mathbf{I}$ is the matrix identity matrix

λ_i are the roots of the characteristic polynomial where $\pi(\lambda) = 0$

The eigenvalues λ_i must satisfy $\mathbf{AW} = \mathbf{\Lambda W}$ and $\mathbf{VA} = \mathbf{V\Lambda}$

$$\mathbf{A}^t = \mathbf{W} \times \mathbf{\Lambda}^t \times \mathbf{W}^{-1},$$

$$\mathbf{A}^t = \mathbf{W} \times \begin{bmatrix} \lambda_1^t & 0 & \cdots & 0 \\ 0 & \lambda_2^t & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \lambda_n^t \end{bmatrix} \times \mathbf{W}^{-1}$$

The columns of W are the corresponding right eigenvectors

The columns of V are the corresponding left eigenvectors

Example: USA Population

Example 4.3 An age-classified population

Keyfitz and Flieger (1971) give an age-classified matrix, with 5-year age classes and a projection interval of 5 years, for the United States population in 1966. The entries are

i	F_i	P_i
1	0	0.99670
2	0.00102	0.99837
3	0.08515	0.99780
4	0.30574	0.99672
5	0.40002	0.99607
6	0.28061	0.99472
7	0.15260	0.99240
8	0.06420	0.98867
9	0.01483	0.98274
10	0.00089	

The eigenvalues of this matrix (in decreasing order of absolute magnitude), their magnitudes, and the angle θ (as a fraction of π) defined in the complex plane by each are

Caswell 2001

λ_i	$\lvert\lambda_i\rvert$	θ/π
1.0498	1.0498	0.0000
$0.3112 + 0.7442i$	0.8067	0.3739
$0.3112 - 0.7442i$	0.8067	−0.3739
$-0.3939 + 0.3658i$	0.5375	−0.7618
$-0.3939 - 0.3658i$	0.5375	0.7618
$0.0115 + 0.5221i$	0.5223	0.4930
$0.0115 - 0.5221i$	0.5223	−0.4930
$-0.4112 + 0.1204i$	0.4284	−0.9093
$-0.4112 - 0.1204i$	0.4284	0.9093
−0.0852	0.0852	1.0000

Figure 4.6 shows this spectrum plotted in the complex plane. (The computation of eigenvalues and eigenvectors is discussed in Section 4.8.)

The largest eigenvalue is real and positive. The second largest is a complex conjugate pair at angles of about $\theta = \pm 0.37\pi$ in the complex plane. This pair would generate oscillations with a period $2\pi/\theta \approx 5.4$ projection intervals. Since the projection interval is 5 years, the oscillation produced by this pair of eigenvalues has a period of 27 years.

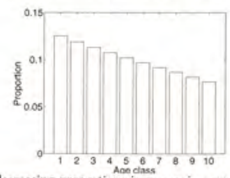
Caswell 2001

Stable Stage Distribution (right ev)

Example 4.4 An age-classified model

The eigenvector $\mathbf{w}_1$ corresponding to $\lambda_1 = 1.0498$ for the United States population in 1966 (Example 4.3), scaled so that $\mathbf{w}_1$ sums to 1, is

$$\mathbf{w}_1 = \begin{pmatrix} 0.1252 \\ 0.1189 \\ 0.1131 \\ 0.1075 \\ 0.1020 \\ 0.0968 \\ 0.0917 \\ 0.0867 \\ 0.0817 \\ 0.0765 \end{pmatrix}$$



The pattern shown by $\mathbf{w}_1$ — decreasing proportions in successive age classes — is typical for age-classified populations.

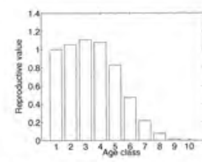
Caswell 2001

Reproductive Value (left ev)

Example 4.7 An age-classified population

The reproductive value vector $\mathbf{v}_1$ for the United States population (Example 4.3) is

$$\mathbf{v}_1 = \begin{pmatrix} 1.0000 \\ 1.0532 \\ 1.1064 \\ 1.0787 \\ 0.8293 \\ 0.4724 \\ 0.2165 \\ 0.0752 \\ 0.0149 \\ 0.0008 \end{pmatrix}$$



Note the increase in v_i from birth to a maximum in age class 3 (ages 10 – 15 years), and its subsequent decline. This pattern is typical for age-classified populations.

Caswell 2001

Analysis Assumptions

These matrix analysis assume that **A** is

- Positive (non-negative)
  - all elements of *A* are >= 0
- Irreducible
  - If $(\mathbf{I}+\mathbf{A})^{s-1}$ is positive, where *s* is size of **A**
- Primitive
  - Iff $\mathbf{A}^{(s^2-2s+2)}$ is positive

See Caswell 2001 Chapter 4 for more detail and consequences of violating these assumptions.

Generalizing the Matrix Model

- Stochastic Matrix Models
- Density-Dependent Matrix Models

  Both relax the assumption that *A* is a constant coefficient matrix

- Continuous Size Distributions

  Integral projection matrix

Additional Demographic Considerations:

How do we estimate growth rates?

demography:

the statistical study of the size and structure of populations and changes within them

Life Table Analysis

Demographic Parameters

- **Cohort**: group of individuals born at the same time
- x = age class of a population
- n_x: number of individuals of age (x)
- l_x: probability at birth of surviving to age x
- d_x: number of individuals who have died between age classes (n_x-n_{x+1})
- q_x: age specific mortality (d_x/n_x)
- b_x: age specific birth rate
- s_x: survival rate (1-q_x)

Life Table Analysis – Life History

Table 3.1 Standard life-table calculations.[a]

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$	Corrected estimate $e^{-rx}l(x)b(x)$
0	500	0	1.0	0.80	0.0	0.0	0.000	0.000
1	400	2	0.8	0.50	1.6	1.6	0.780	0.736
2	200	3	0.4	0.25	1.2	2.4	0.285	0.254
3	50	1	0.1	0.00	0.1	0.3	0.012	0.010
4	0	0	0.0		0.0	0.0	0.000	0.000
				$R_0 = \Sigma l(x)b(x)$	= 2.9 offspring	$\Sigma = 4.3$	$\Sigma = 1.077$	$\Sigma = 1.000$

Data

$G = \frac{\Sigma l(x)b(x)x}{\Sigma l(x)b(x)}$	= 1.483 years
r (estimated) = $\ln(R_0)/G$	= 0.718 individuals/(individual • year)
Correction added to estimated r	= 0.058
r (Euler)	= 0.776 individuals/(individual • year)

[a] The x, $S(x)$, and $b(x)$ columns are supplied. All others are calculated from these.

Survivorship
l(x) = prob. ind. survives to age x from x=0

Survival Probability
g(x) = prob. ind. survives to age x+1 from x

Net Reproductive Rate = R_0

Generation Time = G

Demography

Idealized Survivorship Curves

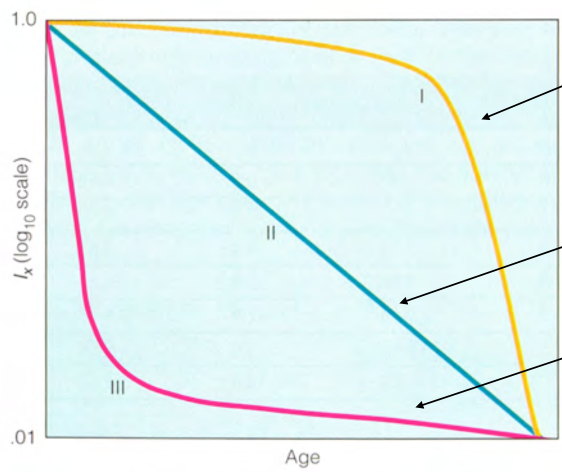


Figure 10.9 | The three basic types of survivorship curves.

Smith and Smith 2006

mammals

Adult birds, rodents

Oysters, fish, many plants

r vs. *K* selected life histories

Demography

Example Survivorship Curves

Survivorship

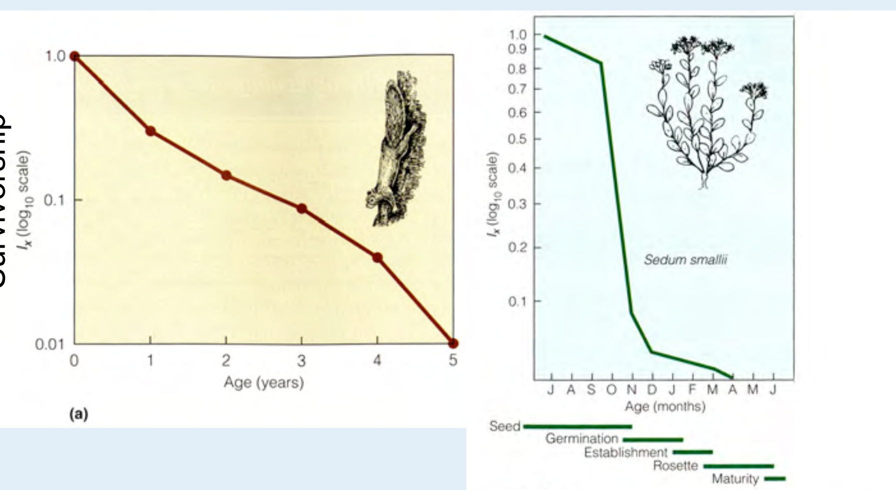


Figure 10.7 | Survivorship curve for **(a)** gray squirrel based on Table 10.1 and **(b)** *Sedum smallii* based on Table 10.3.

Smith and Smith 2006

Age Specific Survival and Fertilities for Leslie Matrix

Table 3.2 Calculation of age-specific survival probabilities and fertilities for the Leslie matrix. Data from Table 3.1. Notice that the first row of the table is blank for P_i and F_i, because we begin counting age classes at 1, not 0.

x	i	$l(x)$	$b(x)$	$P_i = l(i)/l(i-1)$	$F_i = b(i)P_i$
0		1.0	0		
1	1	0.8	2	0.80	1.60
2	2	0.4	3	0.50	1.50
3	3	0.1	1	0.25	0.25
4	4	0	0	0.00	0.00

The resulting Leslie matrix is:

$$\mathbf{A} = \begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

Table 3.1 Standard life-table calculations.[a]

x	$S(x)$	$b(x)$	$l(x) = S(x)/S(0)$	$g(x) = l(x+1)/l(x)$	$l(x)b(x)$	$l(x)b(x)x$	Initial estimate $e^{-rx}l(x)b(x)$	Corrected estimate $e^{-rx}l(x)b(x)$
0	500	0	1.0	0.80	0.0	0.0	0.000	0.000
1	400	2	0.8	0.50	1.6	1.6	0.780	0.736
2	200	3	0.4	0.25	1.2	2.4	0.285	0.254
3	50	1	0.1	0.00	0.1	0.3	0.012	0.010
4	0	0	0.0		0.0	0.0	0.000	0.000

Gotelli

Demography

Dynamic vs. Time-Specific Life Table

Dynamic life table
Follows a cohort through time.

Time-specific Life
Sample a population at a given time to obtain a distribution of age classes.

Assumes

(1) Sample each age class in proportion to its numbers

(2) constant age specific demographic rates.

Life Table Analysis

n_x = Number of individuals l_x = Survivorship d_x =Number dead

q_x = Age-specific death rate

Table 10.1 | Gray Squirrel Life Table

x	n_x	l_x	d_x	q_x
0	530	1.0	371	0.7
1	159	0.3	79	0.5
2	80	0.15	32	0.4
3	48	0.09	27	0.55
4	21	0.04	16	0.75
5	5	0.01	5	1.0

Smith and Smith 2006

Birth Rate & Fecundity Tables

Table 10.4 | Gray Squirrel Fecundity Table

x	l_x	b_x	l_xb_x
0	1.0	0.0	0.00
1	0.3	2.0	0.60
2	0.15	3.0	0.45
3	0.09	3.0	0.27
4	0.04	2.0	0.08
5	0.01	0.0	0.00
Σ		10.0	1.40

Mean number of females born in each age group

Survivorship

Birth rate (per female)

Gross reproductive rate

Net Reproductive Rate
If greater than 1 the females are replacing themselves

Projecting Population Growth

Table 10.6 | Population Projection Table, Squirrel Population

Age	Year (t)										
	0	1	2	3	4	5	6	7	8	9	10
0	20	27	34.1	40.71	48.21	58.37	70.31	84.8	101.86	122.88	148.06
1	10	6	8.1	10.23	12.05	14.46	17.51	21.0	25.44	30.56	36.86
2	0	5	3.0	4.05	5.1	6.03	7.23	8.7	10.50	12.72	15.28
3	0	0	3.0	1.8	2.43	3.06	3.62	4.4	5.22	6.30	7.63
4	0	0	0	1.35	0.81	1.09	1.38	1.6	1.94	2.35	2.83
5	0	0	0	0	0.33	0.20	0.27	0.35	0.40	0.49	0.59
Total $N(t)$	30	38	48.2	58.14	68.93	83.21	100.32	120.85	145.36	175.30	211.25
Lambda	λ	1.27	1.27	1.21	1.19	1.21	1.20	1.20	1.20	1.20	1.20

See description on p. 211,
Smith and Smith 2006

$$\lambda = \frac{N(t+1)}{N(t)}$$

Finite multiplication rate

$$\lambda = e^r$$
$$r = \ln \lambda$$

$$N(t) = N(0)\lambda^t$$

Summary

Discussed a way of building demographic information and life history into our models

Replaced a single state-variable with multiple state variables

- describe the dynamics of subpopulations

Analyzed matrix models do determine the

- geometric growth rate
- stable population distribution, and
- reproductive value

Suggested that matrix population models could be used in more general ways, including to represent meta-populations or spatial structure

Coming Up

Exam

Spatial Models

Two state-variable models
- Competition
- Consumer-resource dynamics
- Ecosystem vs. population point of view

Three state-variable models

Additional Notes

Activity

In teams work on Problem 3.2

{ (Tyler, Nikolai, Matt), (Andria, Liz), (Lisa, Ali) }

3.2. Here is a set of hypothetical life-table data for a population of snails:

Age in years (x)	*S(x)*	*b(x)*
0	500	0.0
1	400	2.5
2	40	3.0
3	0	0.0

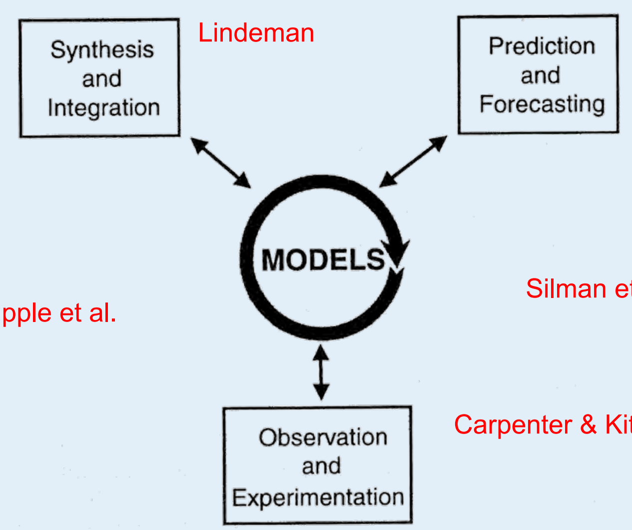
a. Complete the life-table analysis by calculating $l(x)$, $g(x)$, R_0, G, and the estimate of r. Calculate the exact value of r with the Euler equation.

b. Determine the stable age and reproductive value distributions for this life table.

Use R or Excel for life table construction

Can use Biodem package to acquire matrix multiplication or use loop

Model Use



Lindeman

Whipple et al.

Silman et al.

Carpenter & Kitchell

Analysis Assumptions

These matrix analysis assume that **A** is

- Positive (non-negative)
  - all elements of A are >= 0
- Irreducible
  - If $(\mathbf{I}+\mathbf{A})^{s-1}$ is positive, where *s* is size of **A**
- Primitive
  - Iff $\mathbf{A}^{(s^2-2s+2)}$ is positive

See Caswell 2001 Chapter 4 for more detail and consequences of violating these assumptions.

These analyses assume that A is a primitive, irreducible, and non-negative ma

A is primitive iff A^{s^2-2s+2} is positive