

**"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"**

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AGE AND STAGE STRUCTURED MATRIX MODELS

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Structured Models

Why do we need structured models?

- Age is important
- Size is important
- Stage is important

Example

Let us consider a “critter” that has an offspring on its first birthday, another one on its second birthday, and dies when reaching its third birthday.

Year	0	1	2	3	4	5	6	7	8
Age 0	1	1	2	3	5	8	13	21	34
Age 1	0	1	1	2	3	5	8	13	21
Age 2	0	0	1	1	2	3	5	8	13

- Reproduction
- Aging
- Death

In mathematical terms:

$$\begin{aligned}
 N(\mathbf{0}, t+1) &= N(\mathbf{0}, t) + N(\mathbf{1}, t) \\
 &= N(\mathbf{0}, t) + N(\mathbf{0}, t-1)
 \end{aligned}$$

Age Structure

$N(a,t)$ =: # of females aged between a and $a+1$
who are alive at time t .
(including a but excluding $a+1$)

$S(a,t)$ =: probability of a female aged between a
and $a+1$ at time t to survive to age between
 $a+1$ and $a+2$ at time $t+1$.
(survivorship)

$F(a,t)$ =: # of daughters born to a female aged a
to $a+1$ at time t who will be alive at time $t+1$.
(fecundity)

Let us consider:

$$N(0, t) = \sum_{a=0}^m f(a, t) N(a, t-1)$$

= # of females aged $[0, 1)$ at time t

$$N(1, t) = s(0, t-1) N(0, t-1)$$

In general, we can write:

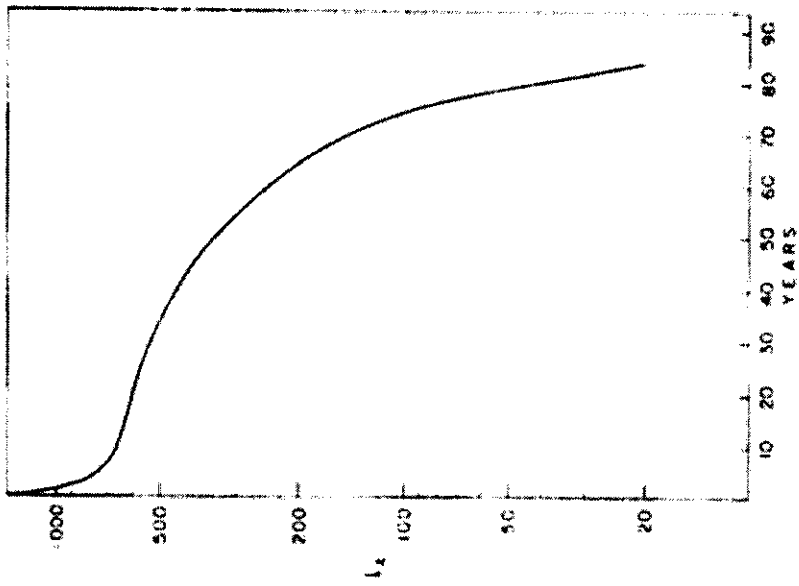
$$N(a+1, t) = s(a, t-1) N(a, t-1)$$

Age distribution vector:

$$\vec{n}(t) = \begin{pmatrix} N(0, t) \\ N(1, t) \\ \vdots \\ N(m, t) \end{pmatrix}$$

Then we can write:

$$\begin{pmatrix} N(0, t+1) \\ N(1, t+1) \\ \vdots \\ N(m, t+1) \end{pmatrix} = \begin{pmatrix} f(0, t+1) & f(1, t+1) & \cdots & f(m, t+1) \\ s(0, t) & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & s(m-1) & 0 \end{pmatrix} \begin{pmatrix} N(0, t) \\ N(1, t) \\ \vdots \\ N(m, t) \end{pmatrix}$$



Age	Survivors	Age	Survivors	Age	Survivors	Age	Survivors
0	1000	10	500	20	250	30	150
1	850	11	450	21	220	31	130
2	750	12	400	22	190	32	110
3	650	13	350	23	160	33	90
4	550	14	300	24	130	34	70
5	450	15	250	25	100	35	50
6	350	16	200	26	70	36	35
7	250	17	150	27	50	37	25
8	180	18	110	28	35	38	18
9	130	19	80	29	25	39	13
10	100	20	60	30	18	40	10
11	75	21	45	31	13	41	7
12	55	22	35	32	10	42	5
13	40	23	25	33	7	43	4
14	30	24	18	34	5	44	3
15	22	25	13	35	4	45	2
16	16	26	10	36	3	46	1.5
17	12	27	7	37	2	47	1
18	9	28	5	38	1.5	48	0.7
19	7	29	4	39	1	49	0.5
20	5	30	3	40	0.7	50	0.4
21	4	31	2.5	41	0.5	51	0.3
22	3	32	2	42	0.4	52	0.25
23	2.5	33	1.5	43	0.3	53	0.2
24	2	34	1.2	44	0.25	54	0.15
25	1.5	35	0.9	45	0.2	55	0.1
26	1.2	36	0.7	46	0.15	56	0.08
27	0.9	37	0.5	47	0.1	57	0.06
28	0.7	38	0.4	48	0.08	58	0.04
29	0.5	39	0.3	49	0.06	59	0.03
30	0.4	40	0.25	50	0.04	60	0.02
31	0.3	41	0.2	51	0.03	61	0.015
32	0.25	42	0.15	52	0.02	62	0.01
33	0.2	43	0.1	53	0.015	63	0.008
34	0.15	44	0.08	54	0.01	64	0.006
35	0.1	45	0.06	55	0.008	65	0.004
36	0.08	46	0.04	56	0.006	66	0.003
37	0.06	47	0.03	57	0.004	67	0.002
38	0.04	48	0.02	58	0.003	68	0.0015
39	0.03	49	0.015	59	0.002	69	0.001
40	0.025	50	0.01	60	0.0015	70	0.0008
41	0.02	51	0.008	61	0.001	71	0.0006
42	0.015	52	0.006	62	0.0008	72	0.0004
43	0.01	53	0.004	63	0.0006	73	0.0003
44	0.008	54	0.003	64	0.0004	74	0.0002
45	0.006	55	0.002	65	0.0003	75	0.00015
46	0.004	56	0.0015	66	0.0002	76	0.0001
47	0.003	57	0.001	67	0.00015	77	0.00008
48	0.002	58	0.0008	68	0.0001	78	0.00006
49	0.0015	59	0.0006	69	0.00008	79	0.00004
50	0.001	60	0.0004	70	0.00006	80	0.00003
51	0.0008	61	0.0003	71	0.00004	81	0.00002
52	0.0006	62	0.0002	72	0.00003	82	0.000015
53	0.0004	63	0.00015	73	0.00002	83	0.00001
54	0.0003	64	0.0001	74	0.000015	84	0.000008
55	0.0002	65	0.00008	75	0.00001	85	0.000006
56	0.00015	66	0.00006	76	0.000008	86	0.000004
57	0.0001	67	0.00004	77	0.000006	87	0.000003
58	0.00008	68	0.00003	78	0.000004	88	0.000002
59	0.00006	69	0.00002	79	0.000003	89	0.0000015
60	0.00004	70	0.000015	80	0.000002	90	0.000001
61	0.00003	71	0.00001	81	0.0000015		
62	0.00002	72	0.000008				
63	0.000015	73	0.000006				
64	0.00001	74	0.000004				
65	0.000008	75	0.000003				
66	0.000006	76	0.000002				
67	0.000004	77	0.0000015				
68	0.000003	78	0.000001				
69	0.000002	79	0.0000008				
70	0.0000015	80	0.0000006				
71	0.000001	81	0.0000004				
72	0.0000008	82	0.0000003				
73	0.0000006	83	0.0000002				
74	0.0000004	84	0.00000015				
75	0.0000003	85	0.0000001				
76	0.0000002	86	0.00000008				
77	0.00000015	87	0.00000006				
78	0.0000001	88	0.00000004				
79	0.00000008	89	0.00000003				
80	0.00000006	90	0.00000002				
81	0.00000004						
82	0.00000003						
83	0.00000002						
84	0.000000015						
85	0.00000001						
86	0.000000008						
87	0.000000006						
88	0.000000004						
89	0.000000003						
90	0.000000002						

FIG. 28. Age-specific survivorship curve for the city of Breslau in Wrocław from the table here and reproduced, corrected by Edmund Hiley, from the data of Caspar Neumann, Hiley gives the base year mortality in the first year, which has been used in compiling the graph.

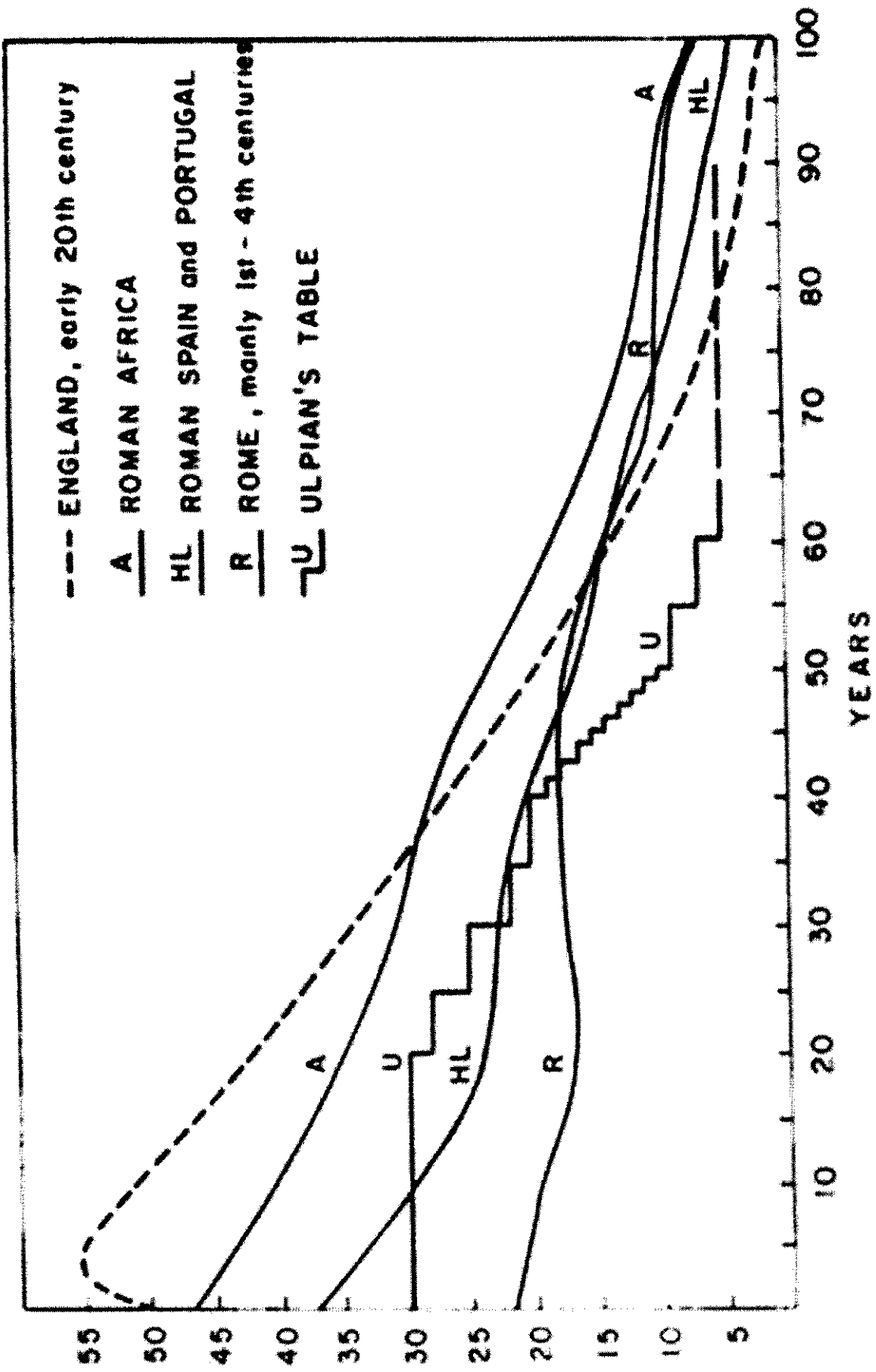


FIGURE 25. Expectation of life in the ancient Roman Empire. All except Ulpien's table from Macdonald, smoothed to remove effect of using 5 year bins in recording ages.

Survivorship

$\ell(x) = P[\text{surviving from birth until age } x]$

is a monotonous, non-increasing function and

$$\ell(0) = 1$$

The probability of surviving from x until $x+dx$ is

$$\frac{\ell(x + dx)}{\ell(x)}$$

Hence, using a truncated Taylor expansion:

$$\frac{\ell(x + dx)}{\ell(x)} = \frac{\ell(x) + dx \frac{\partial \ell(x)}{\partial x}}{\ell(x)}$$

Instantaneous mortality rate $\mu(x)dx$ is defined as

P[death in $(x, x+dx)$ /survived until x] =

$$= 1 - \frac{\ell(x) + dx \frac{\partial \ell(x)}{\partial x}}{\ell(x)} = - \frac{1}{\ell(x)} dx \frac{\partial \ell(x)}{\partial x} =$$

$$= - \frac{\partial \ln \ell(x)}{\partial x} dx = \mu(x)dx$$

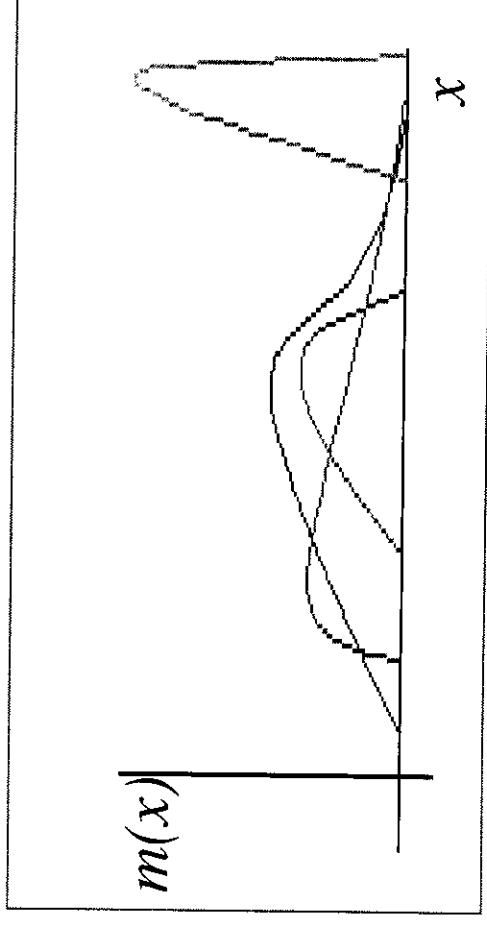
We can use the expression $e^{-\mu(x)dx} = \frac{\ell(x+dx)}{\ell(x)}$

if we suppose μ constant over $(x, x+dx)$.

Reproduction

A maternity function:

$m(x)$ = # of female offspring produced by each female aged x .



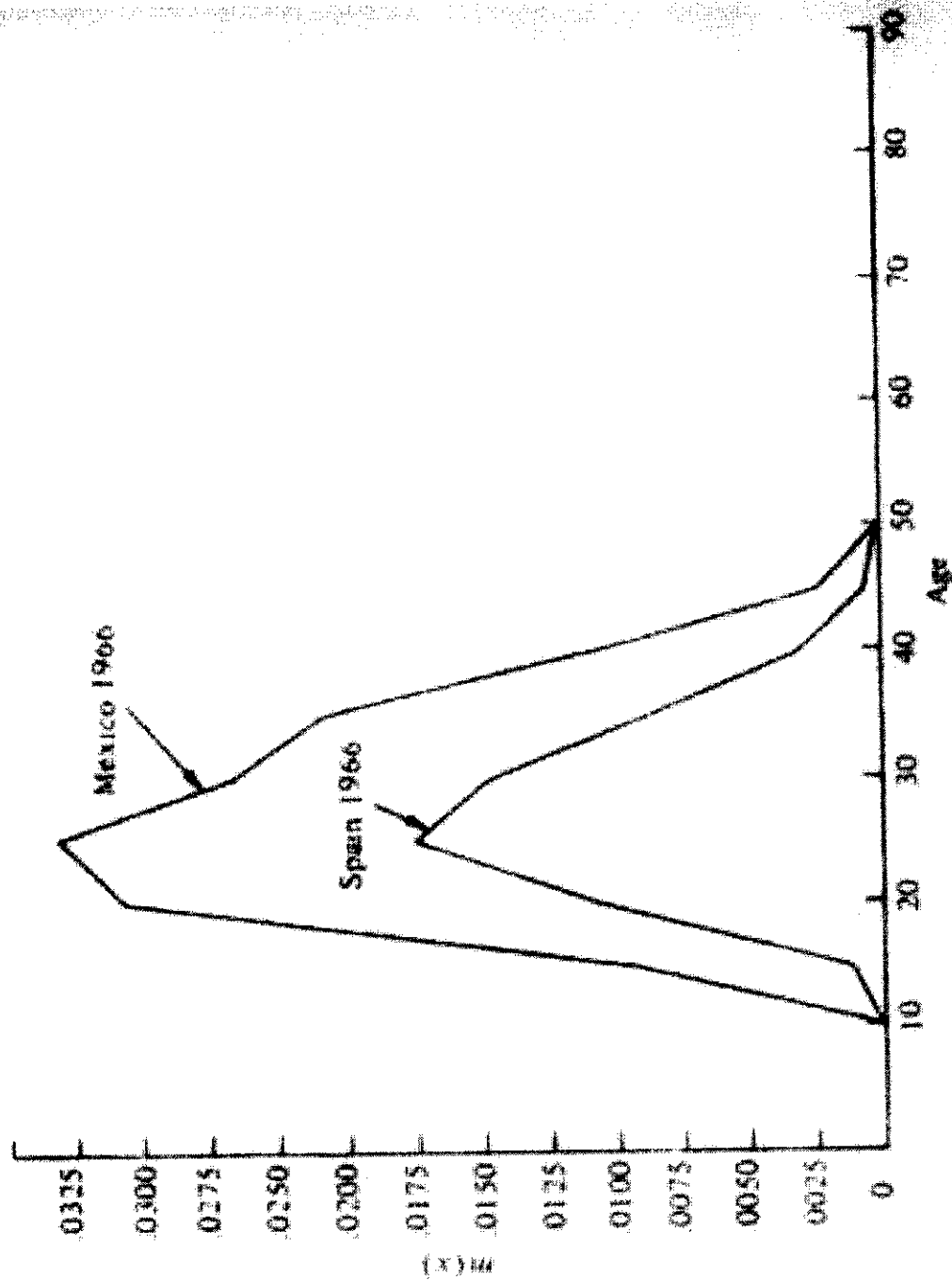
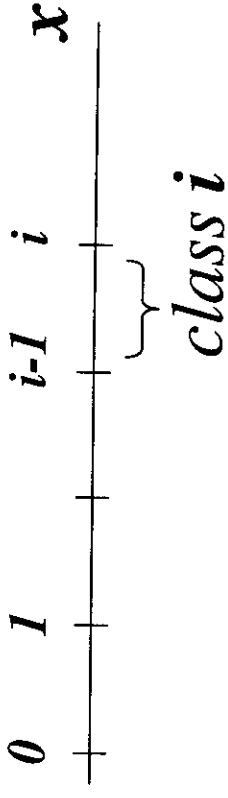


FIGURE 18.6. *Maternity function, $m(x)$, for female offspring in Spain and Mexico during 1966.* [Data from N. Keyfitz, and W. Flieger (1971), *Population, Facts and Methods of Demography*, W. H. Freeman and Company, Publishers, San Francisco.]

Projection Matrix



Class $i = \{\text{ages in } (i-1, i)\}$

Let $n_i(t)$ be the number of individuals in class i at t .
Then

$$n_i(t+1) = P_{i-1} n_{i-1}(t)$$

where P_i = probability of surviving from class i
to class $i+1$.

Individuals in class 1 are generated by individuals in other classes

$$N_i(t+1) = F_1 \cdot n_1(t) + F_2 \cdot n_2(t) + \dots + F_m \cdot n_m(t)$$

where F_i = # individuals produced by a member of class i over one time step

Projection interval is such that time step has same length as class interval.

How do we put all of this together?

Leslie Matrices

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ \vdots \\ n_m \end{pmatrix} (t+1) = \begin{pmatrix} F_1 & F_2 & F_3 & \cdots & F_{m-1} & F_m \\ P_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \ddots & 0 \\ 0 & 0 & \cdots & 0 & P_{m-1} & 0 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ \vdots \\ n_m \end{pmatrix} (t)$$

How do parameters P_i and F_i (discrete) relate to functions $\ell(x)$ and $m(x)$ (continuous)?

Birth-Flow (continuous)

✓ *Survival probability*

$P_i = P$ [probability of surviving from class i to $i+1$]

$$= \frac{\ell(x+1)}{\ell(x)}$$

But exact age of the individual in class i is not known

We can approximate $\ell(x)$ within each interval $(i-1, i)$:

✿ Arithmetic mean:

$$P_i = \frac{\int_i^{i+1} \ell(x) dx}{\int_{i-1}^i \ell(x) dx} \approx \frac{\ell(i) + \ell(i+1)}{\ell(i-1) + \ell(i)}$$

* Geometric mean:

$$P_i = \left(\frac{\ell(i) \ell(i+1)}{\ell(i-1) \ell(i)} \right)^{1/2} = \left(\frac{\ell(i+1)}{\ell(i-1)} \right)^{1/2}$$

* Average of probabilities:

$$P_i = \int_{j_{i-1}}^{j_i} \frac{\ell(x+1)}{\ell(x)} dx \approx \frac{1}{2} \left(\frac{\ell(i)}{\ell(i-1)} + \frac{\ell(i+1)}{\ell(i)} \right)$$

Comparisons for different life tables suggest that differences are small (<2%).

✓ *Fertilities*

$$B(t, t + 1) = \int_0^\infty \int_t^{t+1} m(x) n(x, \tau) d\tau$$

= total number of births in $(t, t+1)$.

Since we can approximate

$$\int_t^{t+1} n(x, \tau) d\tau \approx \frac{n(x, t) + n(x, t + 1)}{2}$$

then

$$B(t, t + 1) \approx \int_0^\infty m(x) \left(\frac{n(x, t) + n(x, t + 1)}{2} \right) dx$$

We can approximate continuous functions $m(x)$ and $n(x, t)$ over each interval $i-1 \leq x \leq i$ by constants m_i and $n_i(t)$, $1 \leq i \leq m$.

Hence

$$\begin{aligned} B(t, t+1) &\approx \frac{1}{2} \sum_1^\infty m_i \{n_i(t) + n_i(t+1)\} \\ &= \frac{1}{2} \sum_1^\infty m_i \{n_i(t) + P_{i-1} n_{i-1}(t)\} \end{aligned}$$

Reordering the terms of the sum, we get

$$B(t, t+1) \approx \frac{1}{2} \sum_1^\infty \{m_i + P_i m_{i+1}\} n_i(t)$$

Hence

$$F_i \approx \frac{m_i + P_i m_{i+1}}{2}$$

Note that

$B(t, t+1)$ is not $n_I(t+1)$

because some offspring born in the interval $(t, t+1)$ do not survive until $t+1$.

The average offspring will survive half of the projection interval with probability $\ell(0.5)$ and

$$F_i = \ell(0.5) \left(\frac{m_i + P_i m_{i+1}}{2} \right)$$

How should we estimate $\ell(0.5)$?

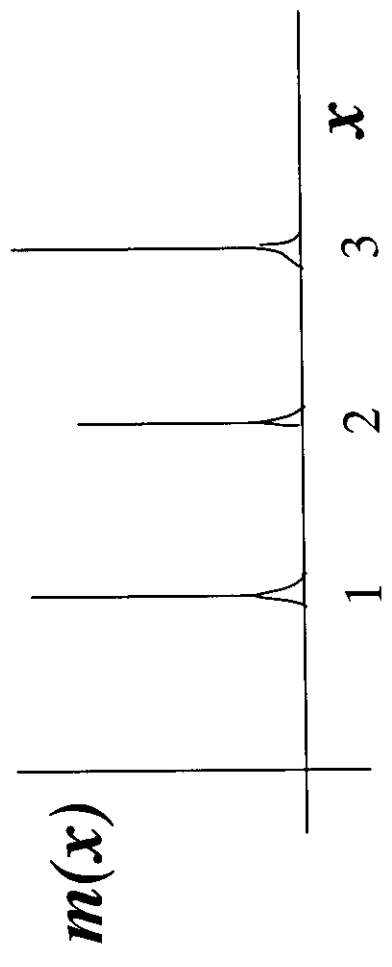
✿ We can use linear interpolation

$$\ell(0.5) \cong \frac{\ell(0) + \ell(1)}{2}$$

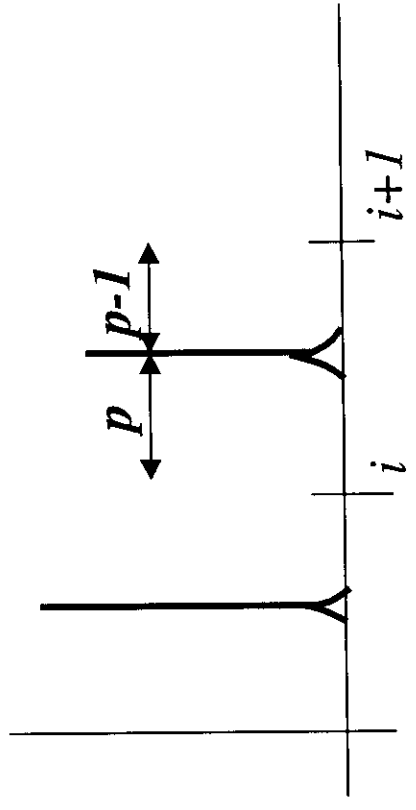
✿ In cases where mortality at birth is high, then logarithmic interpolation is more accurate

$$\ell(0.5) \cong \sqrt{\ell(0)\ell(1)}$$

Birth Pulse (discontinuous)



The expressions for P and F depend on when the pulse of breeding happens relative to the time at which the population is counted



✓ *Survival Probability*

Now every individual in class i is aged $i+p-1$, thus

$$P_i = \frac{\ell(i+p)}{\ell(i+p-1)}$$

= P [survival from age $i+p-1$ to age $i+p$]

✿ For a prebreeding census, $p \rightarrow 0$

$$P_i = \frac{\ell(i)}{\ell(i-1)}$$

✿ For a postbreeding census, $p \rightarrow 1$

$$P_i = \frac{\ell(i+1)}{\ell(i)}$$

✓ *Fertilities*

Since all the births within $(t, t+1)$ happen precisely at time $t+1$, we have

$$B(t, t+1) = B(t+1) = \sum_1^{\infty} n_i(t) m_i \phi_i$$

with m_i = # offspring per individual of exactly age i

ϕ_i = probability of survival from age $i+p-1$ to age i (survival from census to reproduction)

Unless information on seasonal mortality rates is available, a constant force of mortality over the projection interval can be assumed:

→ survival for a fraction $1-p$ of a time unit gives $\phi_i = P_i^{1-p}$

Once an individual is born, it has to survive a fraction $1-p$ of the projection interval to be counted in $n_I(t+1)$.

The probability of survival is $\ell(1-p)$ and can be estimated by interpolation.

Thus, for birth-pulse populations we compute

$$F_i = \ell(1-p)P_i^{1-p}m_i$$

✿ For a postbreeding census, $p \rightarrow 1$

$$F_i = P_i m_i$$

✿ For a prebreeding census, $p \rightarrow 0$

$$F_i = \ell(1)m_i$$

Example

Consider the following life table where individuals die by the time they reach age 4.

x	0	1	2	3	4
$l(x)$	1.0	0.8	0.5	0.1	0.0

We compute

	Birth Flow	Birth Pulse $p \rightarrow 0$	Birth Pulse $p \rightarrow 1$
P_1	$\frac{0.8+0.5}{1.0+0.8} = 0.722$	$\frac{0.8}{1.0} = 0.8$	$\frac{0.5}{0.8} = 0.625$
P_2	$\frac{0.5+0.1}{0.8+0.5} = 0.462$	$\frac{0.5}{0.8} = 0.625$	$\frac{0.1}{0.5} = 0.2$
P_3	$\frac{0.1+0.0}{0.5+0.1} = 0.167$	$\frac{0.1}{0.5} = 0.2$	$\frac{0.0}{0.1} = 0.0$
P_4	0.0	$\frac{0.0}{0.1} = 0.0$	—

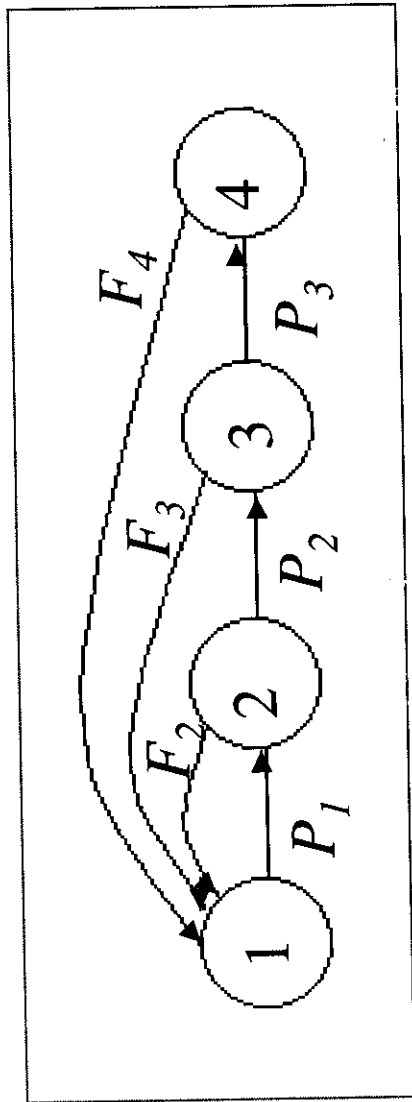
m_i	F_i	Birth Pulse	
		$p \rightarrow 0$	$p \rightarrow 1$
0	F_1	$0.9 \frac{0+2(0.722)}{2} = 0.650$	$0.8(0) = 0.0$
2	F_2	$0.9 \frac{2+6(0.462)}{2} = 2.052$	$0.8(2) = 1.6$
6	F_3	$0.9 \frac{6+3(0.167)}{2} = 2.926$	$0.8(6) = 4.8$
3	F_4	$0.9 \frac{3+0(0.0)}{2} = 1.350$	$0.8(3) = 2.4$

It becomes obvious that the resulting dynamics will depend on the how the parameters are calculated.

The projections by the three different matrices yield the following exponential growth rates:

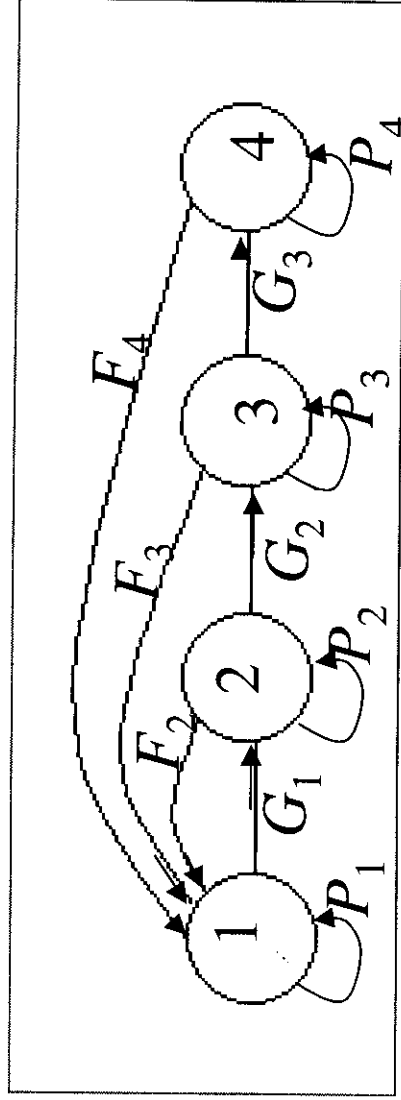
Birth flow	1.793
Birth pulse, $p \rightarrow 0$	1.221
Birth pulse, $p \rightarrow 1$	1.221

Stage Structure



(a) Age structured populations can be represented by a life cycle graph such as this.

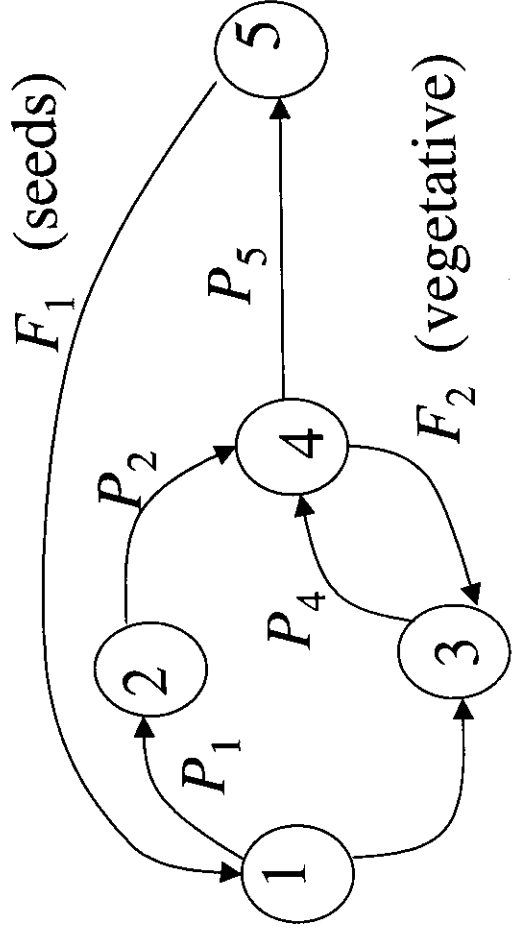
Trees, corals, sea turtles, copepods, fish populations are better classified by size rather than age.



The graph is equivalent to the transition matrix

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

We can consider a plant population in which reproduction is both sexual and vegetative



Here the matrix is

$$\begin{pmatrix} 0 & 0 & 0 & 0 & F_1 \\ P_1 & 0 & 0 & 0 & 0 \\ P_3 & 0 & 0 & F_2 & 0 \\ 0 & P_2 & P_4 & 0 & 0 \\ 0 & 0 & 0 & P_5 & 0 \end{pmatrix}$$

Life cycle graphs can be of considerable help in determining transitions taking place.

Hence:

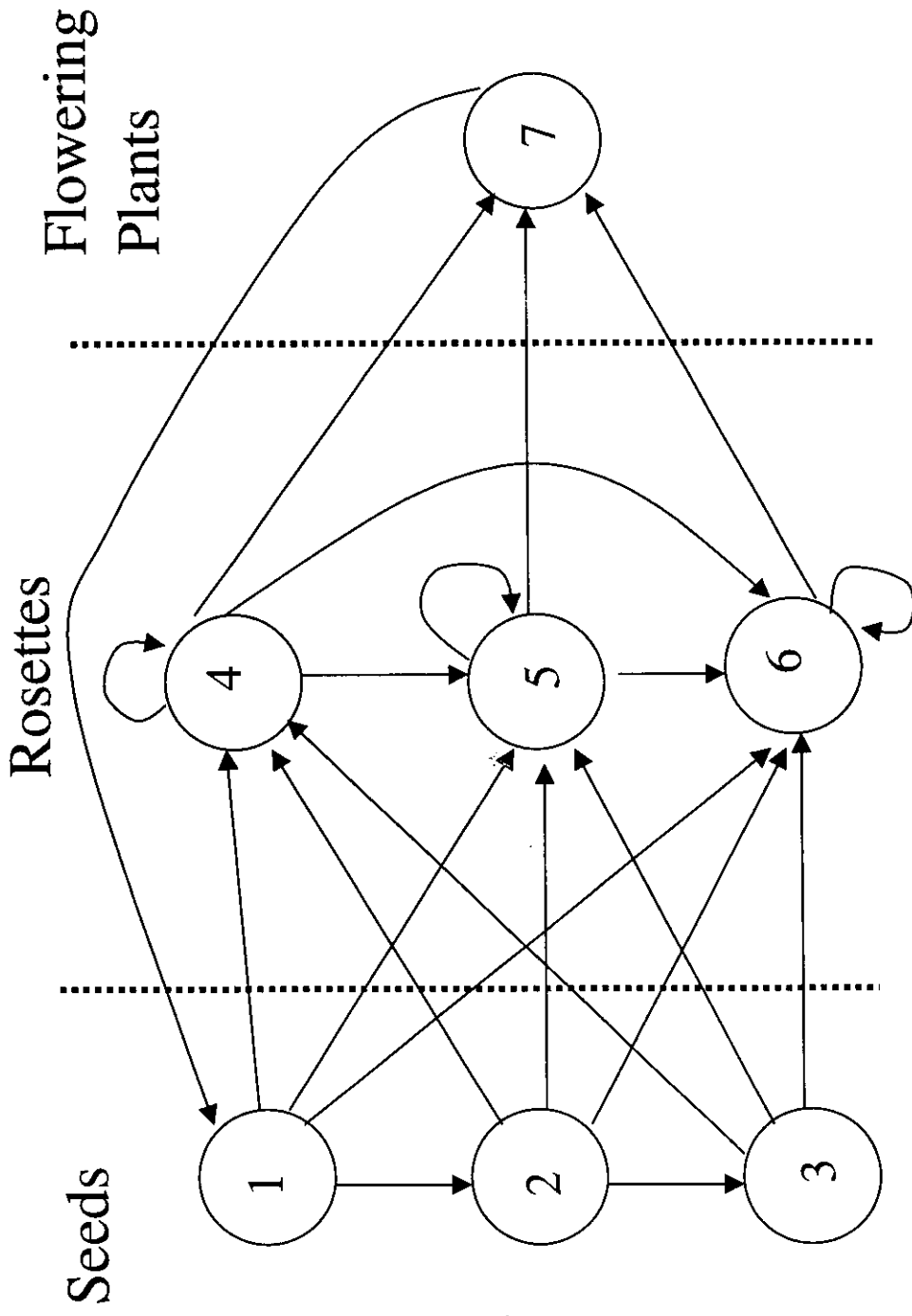
- * in defining projection intervals
- * in constructing projection matrices

Example: Werner and Caswell (1977)

Teasel Model (*Dipsacus sylvestris*)

<u>7 stages:</u>	n_1	seeds
	n_2	dormant seeds, year 1
	n_3	dormant seeds, year 2
	n_4	small rosettes
	n_5	medium rosettes
	n_6	large rosettes
	n_7	flowering plants

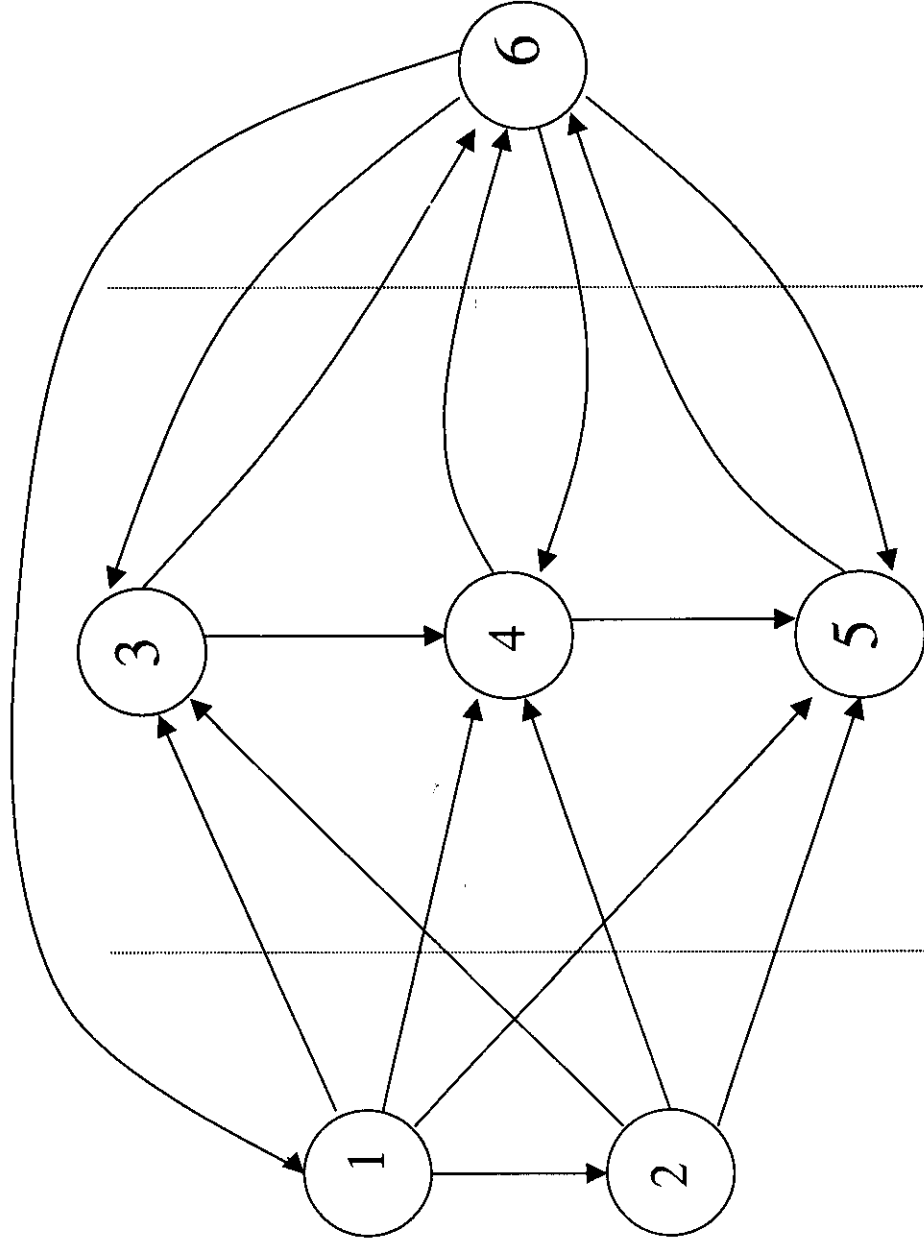
The life cycle graph:



Helps the construction of the projection matrix

$$A_1 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 4310 \\ 0.749 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.966 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.008 & 0.013 & 0.010 & 0.125 & 0 & 0 & 0 & 0 \\ 0.070 & 0.007 & 0 & 0.125 & 0.238 & 0 & 0 & 0 \\ 0.002 & 0.001 & 0 & 0.036 & 0.245 & 0.167 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.023 & 0.750 & 0 & 0 \end{pmatrix}$$

In fact stage 1 (seeds) is fictitious, since it does not take flowers one season to produce seeds an another to germinate.



Giving a new matrix:

$$A_2 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 322.380 \\ 0.966 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.013 & 0.010 & 0.125 & 0 & 0 & 0 & 0 & 3.448 \\ 0.007 & 0 & 0.125 & 0.238 & 0 & 0 & 0 & 30.170 \\ 0.008 & 0 & 0 & 0.245 & 0.167 & 0.862 & 0 & 0 \\ 0 & 0 & 0 & 0.023 & 0.750 & 0 & 0 & 0 \end{pmatrix}$$

with $a_{ij}^{(2)} = a_{1,j+1}^{(1)} \cdot a_{i+1,1}^{(1)}$

Solution of the Projection Equation

Let $\mathbf{n}(t+1) = A \mathbf{n}(t)$ with initial condition $\mathbf{n}(0)$

Let $\boldsymbol{\omega}_1, \dots, \boldsymbol{\omega}_s$ be the eigenvectors of A

We can write $\mathbf{n}(0) = c_1 \boldsymbol{\omega}_1 + \dots + c_s \boldsymbol{\omega}_s$

$$\begin{pmatrix} \vdots & \vdots & \vdots & \vdots \\ \omega_1 & \omega_2 & \dots & \omega_s \\ \vdots & \vdots & \vdots & \vdots \end{pmatrix} \begin{pmatrix} c_1 \\ \vdots \\ c_s \end{pmatrix} = Wc$$

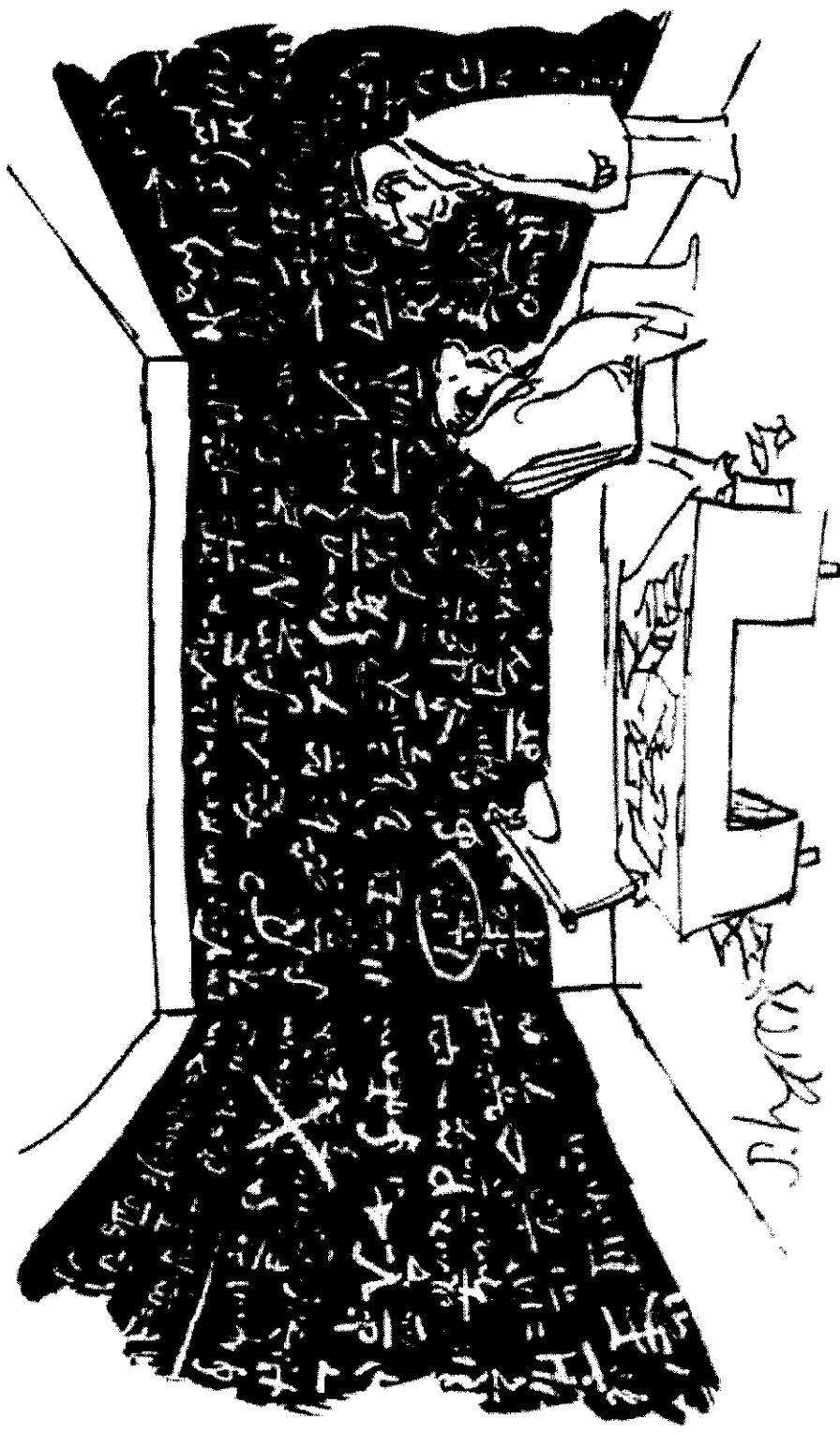
hence $c = W^{-1} \mathbf{n}(0)$

We have

$$\mathbf{n}(1) = A \mathbf{n}(0) = \sum_i c_i A \boldsymbol{\omega}_i = \sum_i c_i \lambda_i \boldsymbol{\omega}_i$$

$$\mathbf{n}(2) = A \mathbf{n}(1) = \sum_i c_i \lambda_i^2 \boldsymbol{\omega}_i$$

In general : $\mathbf{n}(t) = \sum_i c_i \lambda_i^t \boldsymbol{\omega}_i$



"Whatever happened to elegant solutions?"

The long-term behavior of $n(t)$ depends on the eigenvalues λ_i

λ_i real:

- $\lambda_i > 1 \Rightarrow \lambda_i^t$ grows exponentially
- $\lambda_i = 1 \Rightarrow \lambda_i^t = 1$
- $0 < \lambda_i < 1 \Rightarrow \lambda_i^t$ decreases exponentially
- $-1 < \lambda_i$ exhibits damped oscillations
- $\lambda_i = -1 \Rightarrow \lambda_i^t$ exhibits undamped oscillations
- $\lambda_i^t < -1 \Rightarrow \lambda_i^t$ exhibits diverging oscillations

λ_i complex:

$$\lambda_i = a + bi = |\lambda_i| (\cos \theta + i \sin \theta)$$
$$\Rightarrow \lambda_i^t = |\lambda_i|^t (\cos t\theta + i \sin t\theta)$$

A population is called **ergodic** if its long-term behavior is independent of its initial state (Cohen, 1979).

A matrix is **non-negative** if $a_{ij} \geq 0 \quad \forall i \forall j$
positive if $a_{ij} > 0 \quad \forall i \forall j$

A projection matrix is non-negative, but in general it is not positive.

A non-negative matrix V , and the associated life cycle graph, is **irreducible** if the graph is **strongly connected**, i.e., if there is a path in the graph from every node to every other node.

A non-negative **matrix** is **primitive** if it becomes positive when raised to sufficiently high powers.

Any primitive matrix is irreducible.

A **graph** is **primitive** if it is irreducible and the greatest common divisor of the length of its loops is one.

\Rightarrow A sufficient condition for **primitivity** of an irreducible age-classified model is the existence of any two adjacent age classes with positive fertility

The Perron-Frobenius Theorem

- (1) A positive, or non-negative and primitive
 $\Rightarrow \exists \lambda_1 > 0$ which is a simple root of the characteristic
equation and $\lambda_1 > |\lambda_i|$ for $i \neq 1$
The corresponding right and left eigenvectors are $\bar{w}_1 > 0$
and $v_1 > 0$.
- (2) A irreducible but imprimitive (cyclic), with index d .
 $\exists \lambda_1$ real > 0 which is a simple root of the
characteristic equation.
The corresponding eigenvectors $\bar{w}_1 > 0$ and $v_1 > 0$.
The eigenvalues λ_i satisfy $\lambda_1 \geq |\lambda_i|$ for $i \neq 1$,
but there are $d-1$ complex eigenvalues
equal in magnitude to λ_1 , $\lambda_k = \lambda_1 \exp(2k\pi i/d)$,
 $k=1, 2, \dots, d-1$

(3) A reducible

$\Rightarrow \exists \lambda_1$ real ≥ 0 with corresponding
right and left eigenvectors $\omega_1 \geq 0$ and $\nu_1 \geq 0$
and $\lambda_1 \geq |\lambda_i|$ for $i \neq 1$

• λ_1 is called the **dominant eigenvalue** of A

Stable Stage Distribution

Perron- Frobenius theorem tells us that λ_1 completely determines the ergodic properties of the population growth.

$$n(t) = c_1 \lambda_1^t \omega_1 + c_2 \lambda_2^t \omega_2 + \dots + c_s \lambda_s^t \omega_s$$

then

$$\frac{n(t)}{\lambda_1^t} = c_1 \omega_1 + c_2 \left(\frac{\lambda_2}{\lambda_1} \right)^t \omega_2 + \dots + c_s \left(\frac{\lambda_s}{\lambda_1} \right)^t \omega_s$$

If A is positive, then

$$\lambda_1 > |\lambda_2| \geq |\lambda_3| \geq \dots \Rightarrow \lim_{t \rightarrow \infty} \frac{n(t)}{\lambda_1^t} = c_1 \omega_1$$

Independently of the initial distribution

Asymptotic Behavior of Imprimitve Matrices

An irreducible but imprimitive has d eigenvalues with same absolute magnitude

$$\lim_{t \rightarrow \infty} \frac{n(t)}{\lambda_1^t} = c_1 \omega_1 + \sum_k c_k (\cos \theta_k t + i \sin \theta_k t) \omega_k$$

$$\text{with } \theta_k = \frac{2\pi k}{d}$$

\Rightarrow the limit is periodic with period d

The average population vector, taken over the period of oscillation, converges to ω_1 and grows at a rate λ_1 .

$$\lim_{t \rightarrow \infty} \frac{1}{d} \sum_{j=1}^d \frac{n(t+j)}{\lambda_1^{t+j}} = c_1 \omega_1$$

Sensitivity Analysis

- Measuring “how important” a given vital rate is.
- Evaluating the effect of errors in estimation.
- Evaluating alternative management strategies.
- Predicting the intensity of natural selection since vital rates are part of the phenotype

Perturbation of matrix elements

We have: $A\omega_i = \lambda_i\omega_i \quad \forall i$

$$v_i^T A = \lambda_i v_i^T$$

Taking the differential on both sides

$$A(d\omega) + (dA)\omega = \lambda(d\omega) + (d\lambda)\omega$$

where $dA = (da_{ij})$

$$\langle A(d\omega)|v\rangle + \langle (dA)\omega|v\rangle = \lambda\langle (d\omega)|v\rangle + \langle (d\lambda)\omega|v\rangle$$

$$\Rightarrow d\lambda = \frac{\langle (dA)\omega|v\rangle}{\langle \omega|v\rangle}$$

Suppose only one element a_{ij} is changed while the others remain constant:

$$d\lambda = \frac{v_i\omega_j da_{ij}}{\langle \omega|v\rangle} \Rightarrow \frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i\omega_j}{\langle \omega|v\rangle}$$

Sensitivity and Age

The eigenvectors ω and ν for an age-structured model are:

$$* \quad \omega_1 = 1 \quad \text{and} \quad \omega_i = P_1 P_2 \dots P_{i-1} \lambda^{1-i} \quad \text{for } i > 1$$

$$* \quad \nu_1 = 1 \quad \text{and} \quad \nu_i = F_i \lambda^{-1} + P_i \nu_{i+1} \quad \text{for } i > 1$$

We can compute the sensitivity of λ to changes

- * In fertility at successive ages:

$$\frac{\frac{\partial \lambda}{\partial F_j}}{\frac{\partial \lambda}{\partial F_{j+1}}} = \frac{\omega_j}{\omega_{j+1}} = \frac{\lambda}{P_j}$$

* In survival at successive ages:

$$\frac{\partial \lambda}{\partial P_j} = \frac{\omega_j v_{j+1}}{\omega_{j+1} v_{j+2}} = \frac{\lambda}{P_j} \left(\frac{F_{j+1} \lambda^{-1} + P_{j+1} v_{j+2}}{v_{j+2}} \right) =$$

$$= \lambda \frac{P_{j+1}}{P_j} + \frac{F_{j+1}}{P_j v_{j+2}} \geq \frac{P_{j+1}}{P_j} \rightarrow \lambda \geq 1$$

* Relative to fertility and survival with age :

$$\frac{\partial \lambda}{\partial P_j} = \frac{v_{j+1} w_j}{v_1 w_j} = \frac{v_{j+1}}{v_1}$$

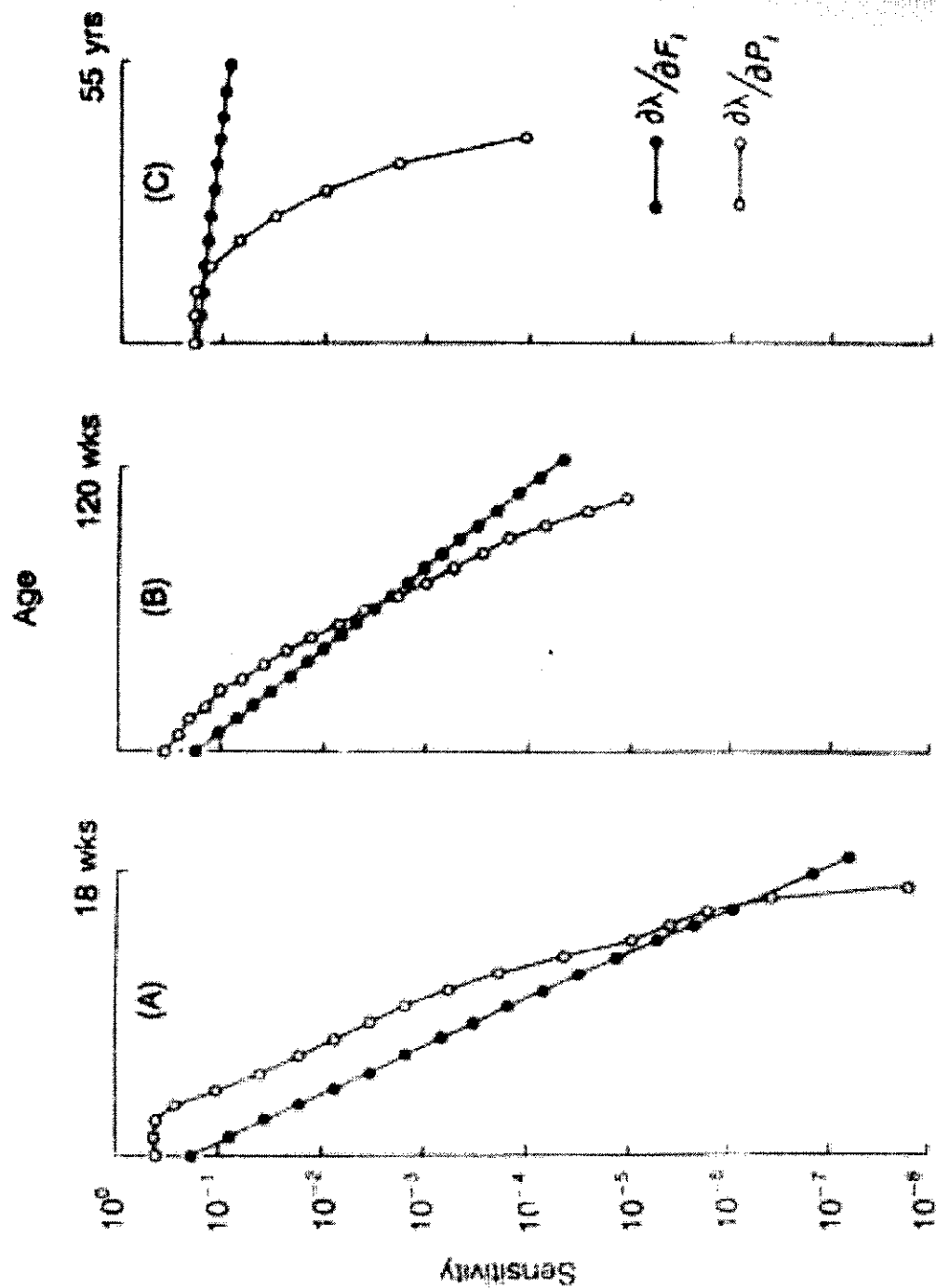


Figure 6.1: The sensitivity of the dominant eigenvalue λ to changes in age-specific fertility F_i and survival probability P_i for (A) a laboratory population of the flour beetle *Calandra oryzae* (Birch 1948), (B) a laboratory population of the vole *M. croesus orcadensis* (Leslie et al. 1955), and (C) the human population of the United States in 1965 (Keyfitz and Flieger 1968). From Caswell (1978).

Size-structured populations

Instead of using the parameters F_i , G_i and P_i we can consider:

σ_i = survival probability of size class i
 γ_i = growth probability for a survival individual of size class i

Then we can write

$$\begin{aligned} G_i &= \sigma_i \gamma_i \\ P_i &= \sigma_i (1 - \gamma_i) \end{aligned}$$

Hence

$$\begin{aligned}\frac{\partial \lambda}{\partial \sigma_i} &= \frac{\partial \lambda}{\partial G_i} \frac{\partial G_i}{\partial \sigma_i} + \frac{\partial \lambda}{\partial P_i} \frac{\partial P_i}{\partial \sigma_i} \\ &= \frac{\omega_i (\nu_i + \gamma_i (\nu_{i+1} - \nu_i))}{\langle \omega | \nu \rangle}\end{aligned}$$

and

$$\begin{aligned}\frac{\partial \lambda}{\partial \gamma_i} &= \frac{\partial \lambda}{\partial G_i} \frac{\partial G_i}{\partial \gamma_i} + \frac{\partial \lambda}{\partial P_i} \frac{\partial P_i}{\partial \gamma_i} \\ &= \frac{\omega_i (\sigma_i (\nu_{i+1} - \nu_i))}{\langle \omega | \nu \rangle}\end{aligned}$$

\Rightarrow λ is reduced by increasing the growth rate from n_i to n_{i+1} if stage $i+1$ has a lower reproductive value than stage i ($\nu_{i+1} < \nu_i$)

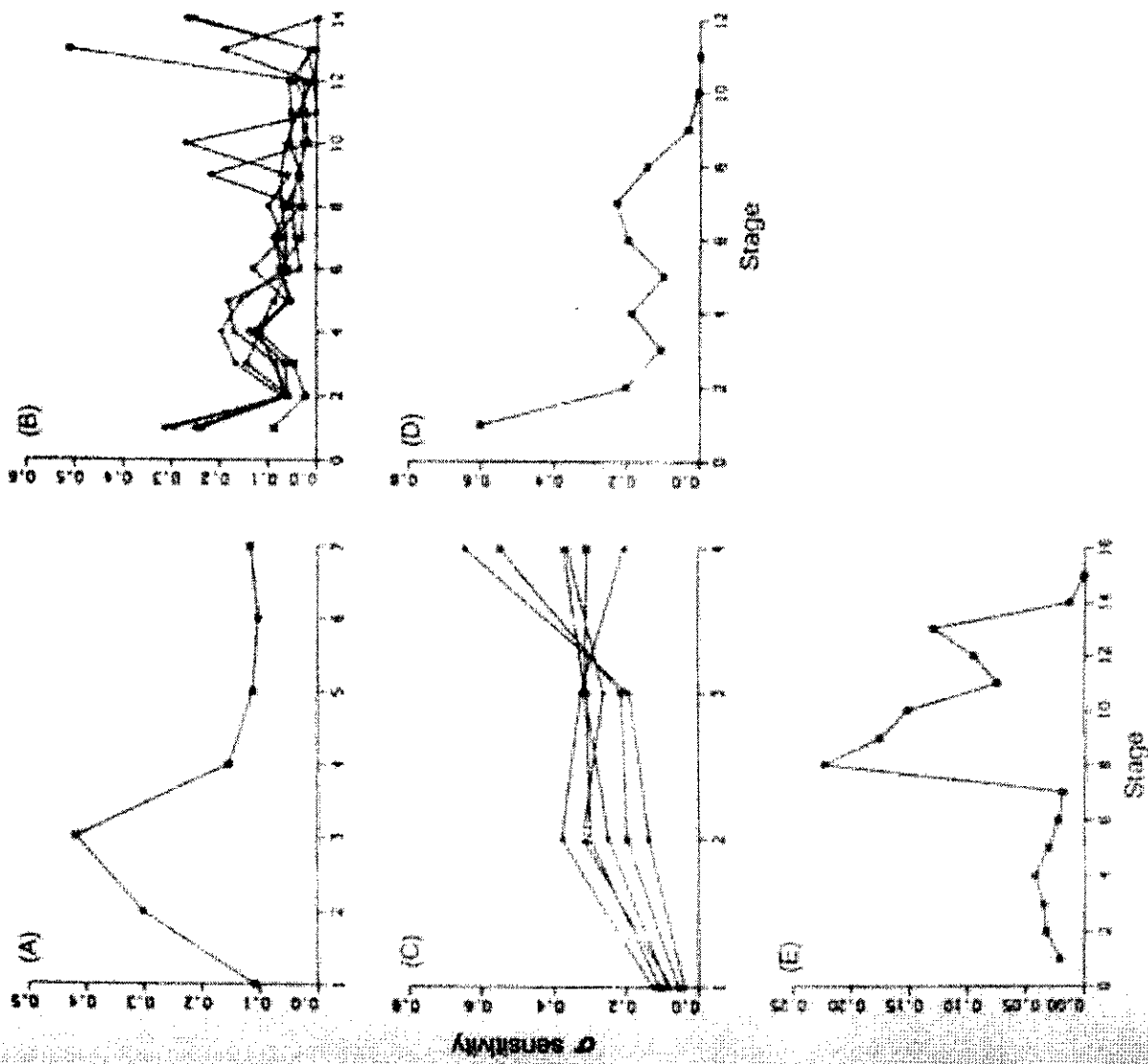


Figure 6.6: The sensitivities of λ to changes in the survival probability σ_i as a function of size class i , for five tree populations. From Caswell (1986).

Elasticity

Transition probabilities belong to $[0, 1]$ but the fertilities are not restricted to this interval

\Rightarrow different scales

\Rightarrow comparison becomes difficult.

Elasticity of λ with respect to a_{ij} is defined as

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial \log \lambda}{\partial \log a_{ij}}$$

This gives the proportional change in λ resulting from a proportional change in a_{ij}

Example: the Teasel population

Werner and Caswell find

$$\frac{\partial \lambda}{\partial a_{17}} = 0.001$$

a_{17} = fertility of flowering plants.

The sensitivities of λ to changes in growth and survival among small, medium and large rosettes range from 0.01 to 1.28.

\Rightarrow growth and survival are 10 to 1000 times as important

as fertility (although $a_{17} = 431$)

However: $e_{17} = 0.249$

is the largest elasticity of the matrix.

From this perspective fertility is the most important coefficient in the life cycle.

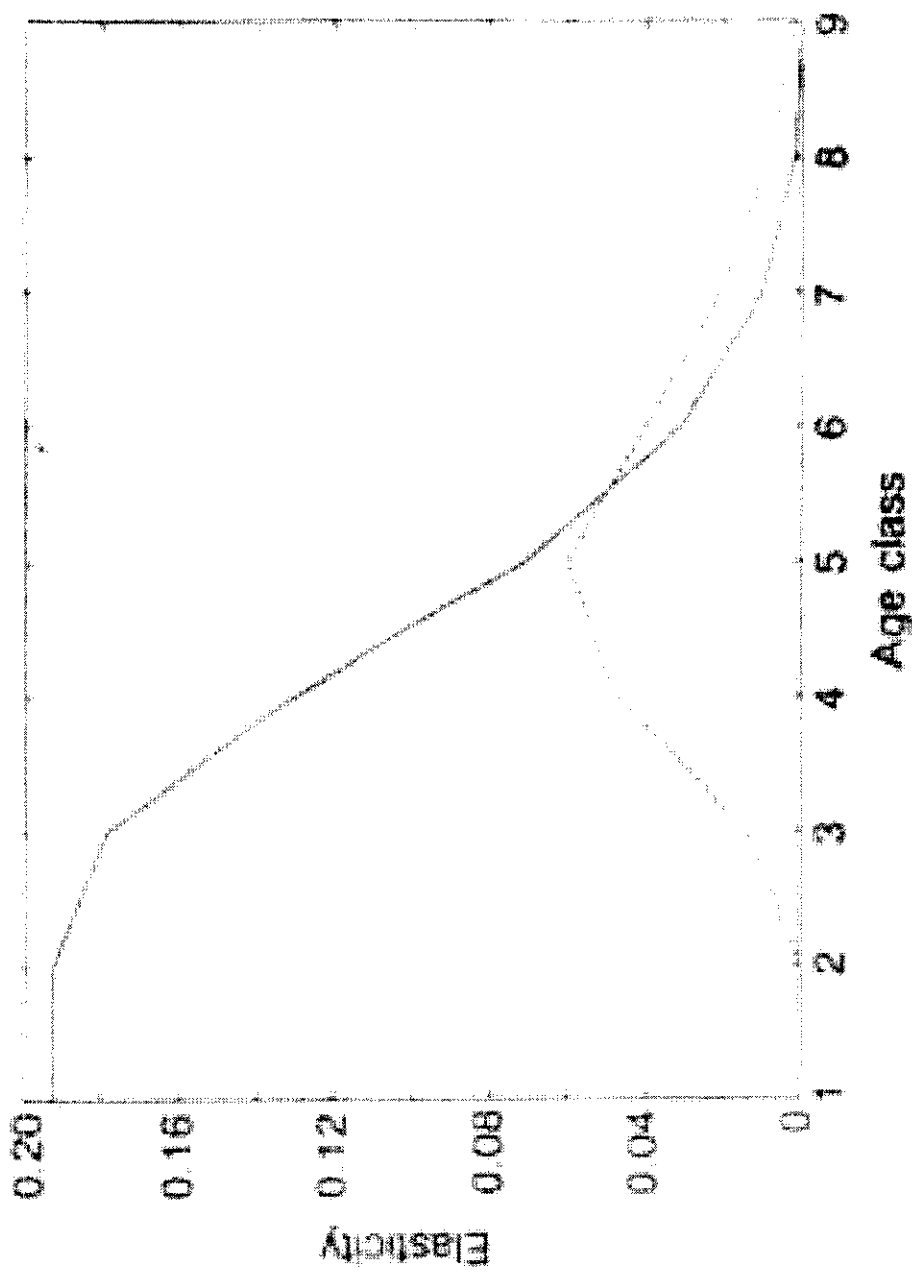


Figure 6.8: The elasticities of λ with respect to changes in age-specific survival probability F_t (solid line) and fertility F_t (dashed line) for the population of the United States, 1965.

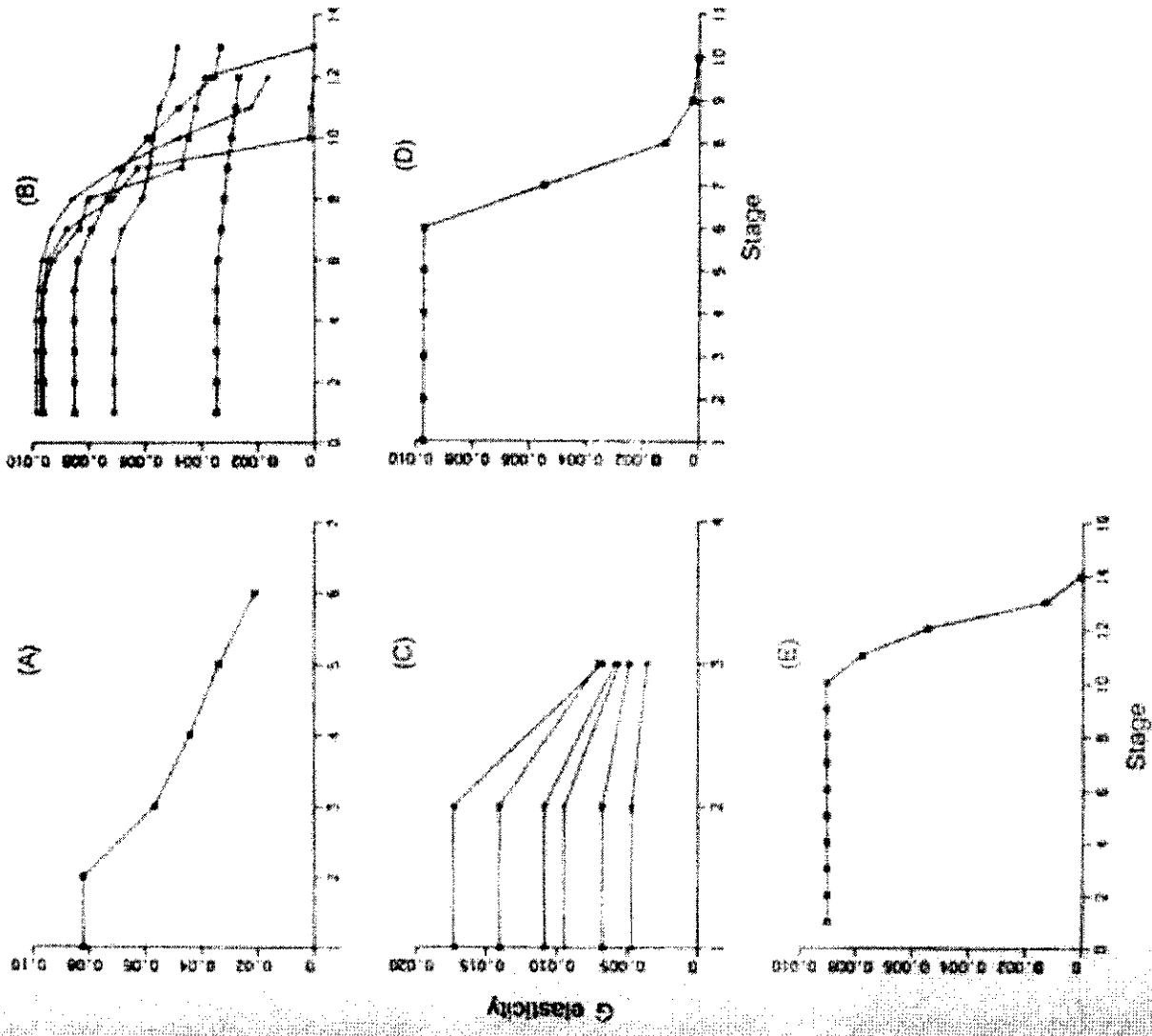


Figure 6.1.1: The elasticities of A with respect to G, as a function of size class i, for five tree populations. From Caswell (1986).

Eigenvector sensitivities

Consider λ_i , ω_i and v_i .

Let ω_i , v_i be scaled so that $\langle \omega_i | v_i \rangle = 1$

Note that $\langle \omega_i | v_j \rangle = 0$ for $i \neq j$

Consider $A\omega_i = \lambda_i\omega_i$

then

$$(dA)\omega_i + A(d\omega_i) = (d\lambda_i)\omega_i + \lambda_i(d\omega_i)$$

After some calculations we obtain

$$\frac{\partial \omega_i}{\partial a_{ke}} = \sum_{j \neq i} \frac{\omega_e^{(i)} \bar{v}_k^{(j)}}{\lambda_i - \lambda_j} \omega_j = \omega_e^{(i)} \sum_{j \neq i} \frac{\bar{v}_k^{(j)}}{\lambda_i - \lambda_j} \omega_j$$

$$\frac{\partial v_i}{\partial a_{ke}} = v_k^{(i)} \sum_{j \neq i} \frac{\bar{\omega}_e^{(j)}}{\lambda_i - \lambda_j} v_j$$

LEAGUE