Course Title :
Population Dynamics [Environmental Sciences]
Environmental Management and Policy III

(Advanced course of)

The Theory in Bio-Demography

Kinya Nishimura & Takenori Takada

Basic population metrics I

Oct. 10 and 17

Chapter 5

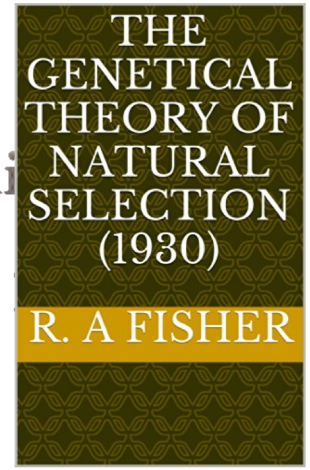
Basic population metrics I

Population metrics from matrix models

1. Population growth rate (previously covered) λ
2. Stable stage distribution (previously covered) $\mathbf{u}$
3. Reproductive value
4. Life expectancy & remaining lifetime
5. Sensitivity of population growth rate accompanied with environmental change
6. Elasticity of population growth rate accompanied with environmental change
7. ････

Fundamental theories of population ecology in 1930s

Again



CONTENTS

(logarithm of λ)

Euler–Lotka Equation

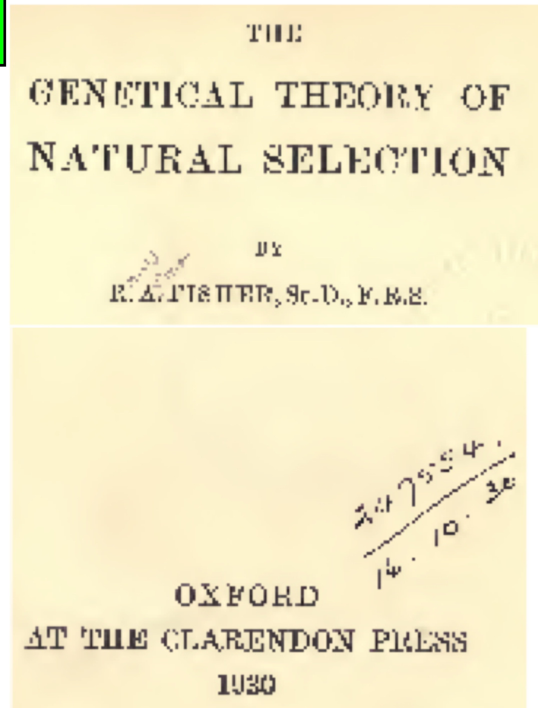
$$1 = \sum_{i=1}^{n} b_i l_i \lambda^{-i}$$

reproductive value

$$\frac{v_j}{v_1} = \frac{\lambda^j}{l_j} \sum_{i=j} b_i l_i \lambda^{-i-1}$$

Fisher's reproductive value

We may ask, not only about the newly born, but about persons of any chosen age, what is the present value of their future offspring and if present value is calculated at the rate determined as before, the question has the definite meaning-To what extent will persons of this age, on the average, contribute to the ancestry of future generations? The question is one of some interest, since the direct action of Natural Selection must be proportional to this contribution.


THE

GENETICAL THEORY OF NATURAL SELECTION

BY

R. A. FISHER, Sc.D., F.R.S.

OXFORD

AT THE CLARENDON PRESS

1930

How much is the present value of your future offspring ?

Fisher did not use matrix framework

Traditional way

Fisher's Reproductive value (V_x)

(2) The present value of
(1) expected contribution of an individual of age-x to next generation(age-dependent), **in now and in the future**.

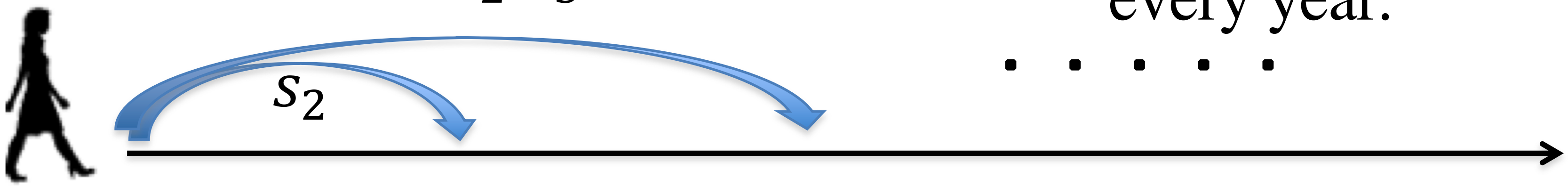
(1) expected contribution of an individual of age-x to next generation(age-dependent), **in now and in the future**.

Note: population increases by λ times every year.

Survival prob.

$s_2 \ s_3$

s_2



Age 2   Age 3   Age 4   . . . . .

	Age 2	Age 3	Age 4	
New-born	b_2	b_3	b_4	. . . . .
Expected contribution	$b_2 \times 1$	$b_3 \times s_2$	$b_4 \times s_2 \ s_3$	. . . . .
Using survivorship (lx)	$b_2 \times \frac{l_2}{l_2}$	$b_3 \times \frac{l_3}{l_2}$	$b_4 \times \frac{l_4}{l_2}$	

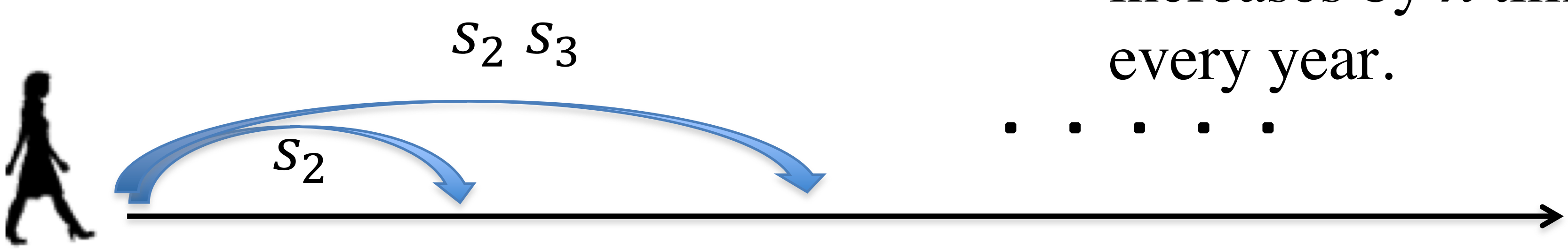
Remember?

$$l_x = s_1 \ s_2 \ldots \ s_{x-1}$$

(2) The present value of expected contribution

Survival prob.

Note: population increases by λ times every year.



	Age 2	Age 3	Age 4	
New-born	b_2	b_3	b_4	. . . . .
Expected contribution	$b_2 \times 1$	$b_3 \times s_2$	$b_4 \times s_2\ s_3$	. . . . .
Using survivorship (lx)	$b_2 \times \frac{l_2}{l_2}$	$b_3 \times \frac{l_3}{l_2}$	$b_4 \times \frac{l_4}{l_2}$	
Present value	$b_2 \times \frac{l_2}{l_2}$	$b_3 \times \frac{l_3}{l_2} \times \frac{1}{\lambda}$	$b_4 \times \frac{l_4}{l_2} \times \frac{1}{\lambda^2}$	

The value of one baby is discounted by λ to the whole population.

Sum of the present value of reproductive contribution of **one age-2 individual** now and in the future

$$= b_2\lambda^{-0}\frac{l_2}{l_2} + b_3\lambda^{-1}\frac{l_3}{l_2} + b_4\lambda^{-2}\frac{l_4}{l_2} + \cdots$$

$$= \frac{1}{l_2}\left(b_2\lambda^{-0}l_2 + b_3\lambda^{-1}l_3 + b_4\lambda^{-2}l_4 + \cdots\right)$$

$$= \frac{\lambda^2}{l_2}\left(b_2l_2\lambda^{-2} + b_3l_3\lambda^{-3} + b_4l_4\lambda^{-4} + \cdots\right) = \frac{\lambda^2}{l_2}\sum_{i=2} b_il_i\lambda^{-i}$$

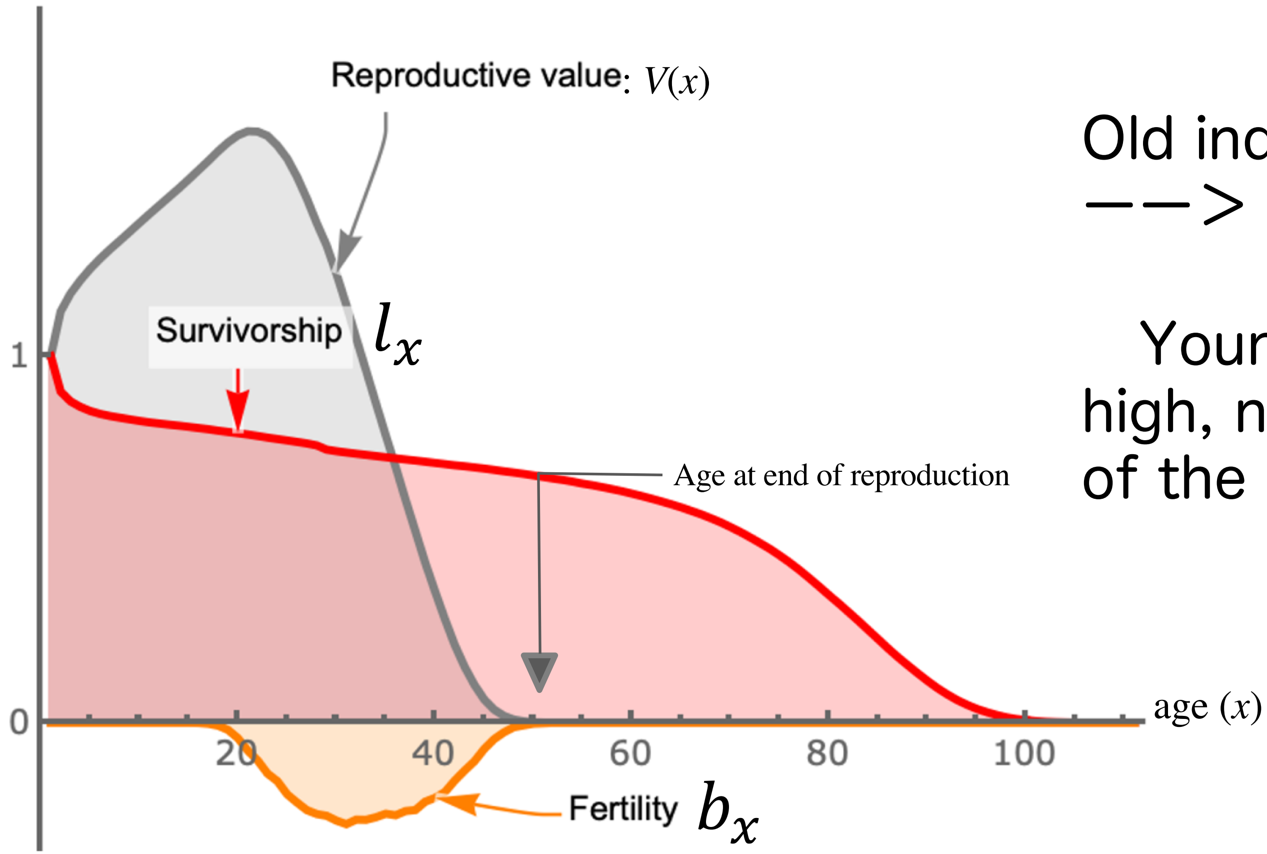
Generally, **reproductive value** of **age-*x*** individual is

$$V_x = \frac{\lambda^x}{l_x}\sum_{i=x} b_i l_i\,\lambda^{-i}$$

Reproductive value

of **age-*x*** individual

$$V_x = \frac{\lambda^x}{l_x} \sum_{i=x} b_i l_i \lambda^{-i}$$



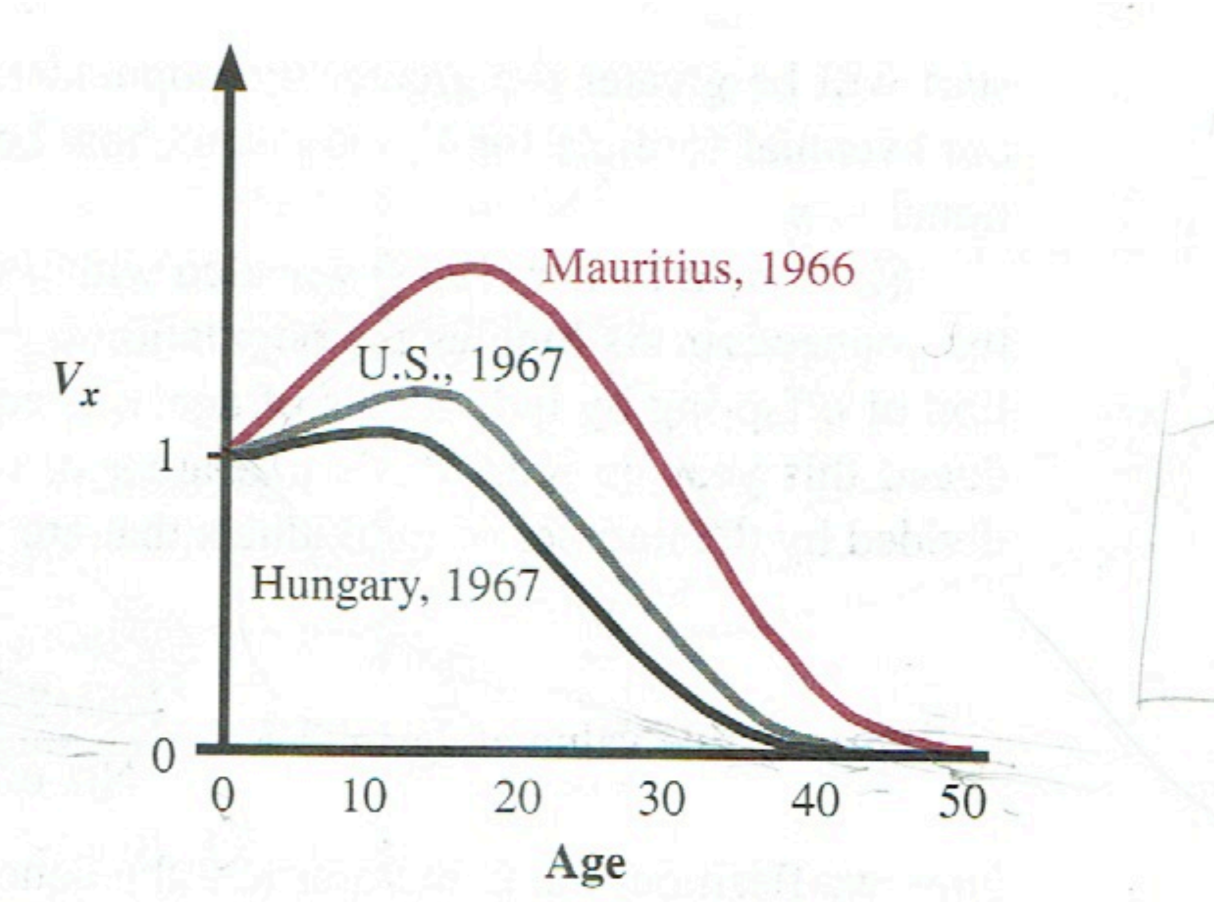
Old indi. with no fertility
---> Vx = 0

Young indi. ----> high, not maximum because of the dying possibility.

Reproductive value

of **age-*x*** individual

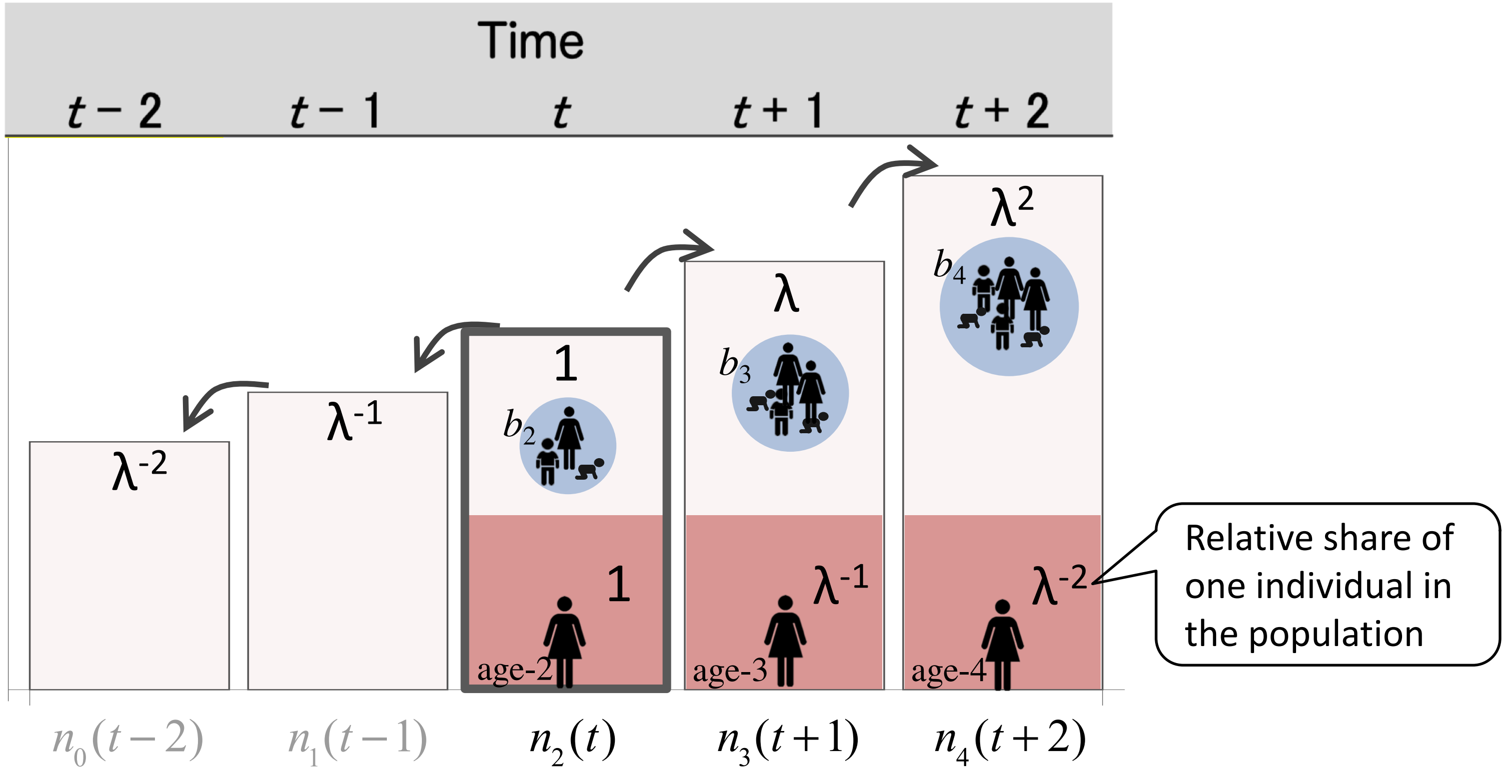
$$V_x = \frac{\lambda^x}{l_x} \sum_{i=x} b_i l_i \lambda^{-i}$$



Old indi. with no fertility
−−> Vx = 0

Young indi. −−−>
high, not maximum because
of the dying possibility.

No matrix until this slide



Sum of the relative reproductive contribution of $\boldsymbol{n_2}$ **individuals** now and in the future

$$= b_2\lambda^{-0}n_2(t) + \underbrace{b_3 \overbrace{\lambda^{-1}n_3(t+1)}^{\text{Relativized weighting of no. of parents}}}_{\text{Relative reproductive contribution}} + b_4\lambda^{-2}n_4(t+1) + \cdots$$

Matrix method

Left eigenvector in population matrix model

$$\mathbf{v} = \begin{pmatrix} v_1 \\ v_2 \\ \vdots \end{pmatrix}$$

∗ Definition of left eigenvector in linear algebra

$$\mathbf{v}^T\mathbf{A} = \mathbf{v}^T\lambda = \lambda\mathbf{v}^T$$

T: transposed

Multiplied from left

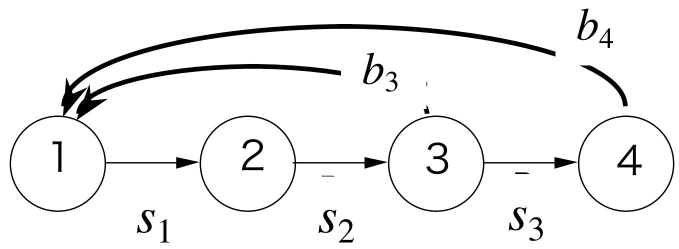
$$\mathbf{v}^T\mathbf{A} = \begin{pmatrix} v_1 & v_2 & \cdots \end{pmatrix} \begin{pmatrix} & & \\ & \mathbf{A} & \\ & & \end{pmatrix} = \lambda \begin{pmatrix} v_1 & v_2 & \cdots \end{pmatrix}$$

∗ Normalized left eigenvector (i. e. the first element = 1) is called ”Reproductive value”, which is proportional to Fisher’s reproductive value.

Actually,

Leslie matrix and traditional theory until 1930

$$\mathbf{A} = \begin{pmatrix} b_1 & b_2 & b_3 & b_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}$$



b_i: fecundity at age i

s_i: *survival at age i*

(1) Eigenvalue equation $\det(\lambda\mathbf{E} - \mathbf{A}) = 0$ ⇒ $1 = \sum_{i=1}^{n} b_i l_i \lambda^{-i}$

$l_i = \prod_{j=1}^{i-1} s_j$ survivorship

Same as Euler-Lotka Equation

(2) Left eigenvector

$$\mathbf{v} = \begin{pmatrix} 1 \\ b_2\lambda^{-1} + s_2 b_3 \lambda^{-2} + s_2 s_3 b_4 \lambda^{-3} \\ b_3 \lambda^{-1} + s_3 b_4 \lambda^{-2} \\ b_4 \lambda^{-1} \end{pmatrix}$$

Same as Fisher's reproductive value

Summary

∗ Normalized left eigenvector (i. e. the first element = 1) is "Reproductive value" in matrix population model.

$$\mathbf{v} = \begin{pmatrix} 1 \\ v_2 \\ \vdots \end{pmatrix}$$

∗ Fisher's reproductive value proposed in 1930 is proportional to the left eigenvector.

∗ Goodman (1968) mathematically proved the above statement.

∗ Reproductive value in stage-structured population is obtained by this method.

∗ How to obtain the left eigenvalue numerically:

$$\mathbf{v}^T\mathbf{A} = \mathbf{v}^T\lambda \quad \Longleftrightarrow \quad \mathbf{A}^T\mathbf{v} = \lambda\mathbf{v}$$

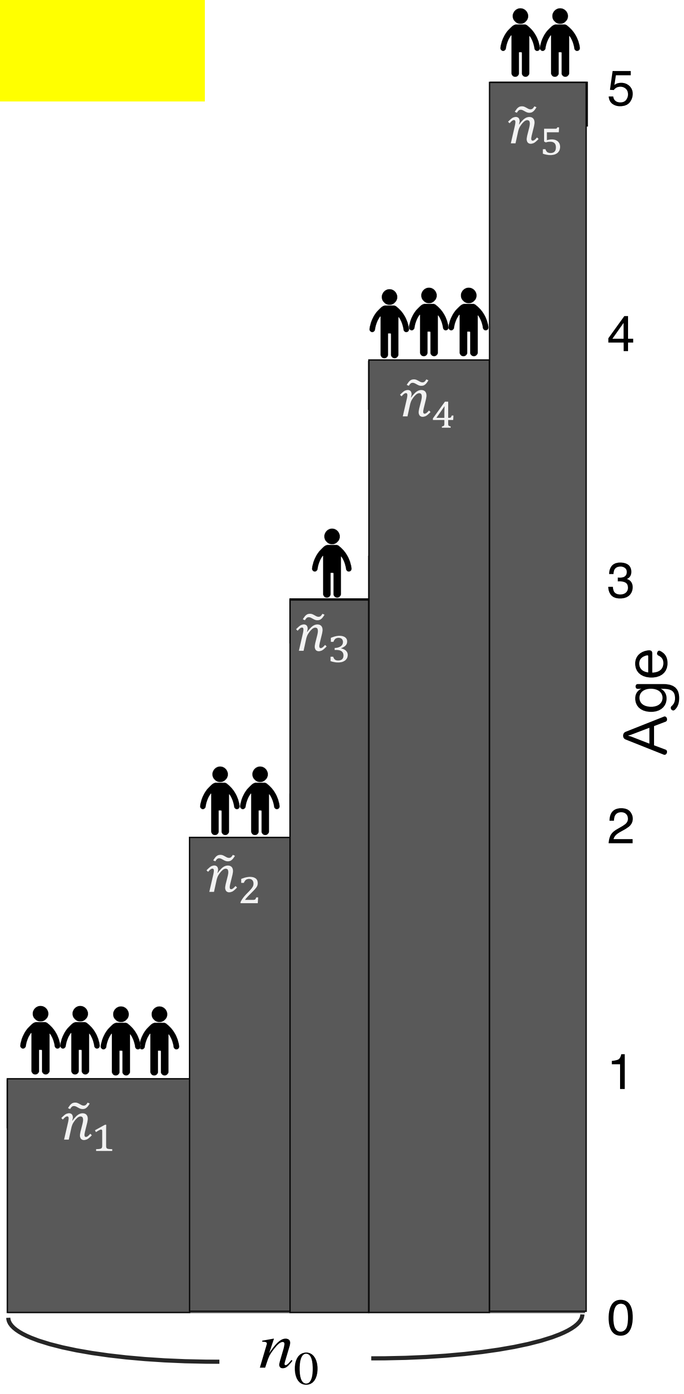
Left eigenvector **v** is the right eigenvector of transposed matrix of **A**

Population metrics from matrix models

1. Population growth rate (previously covered) λ
2. Stable stage distribution (previously covered) $\mathbf{u}$
3. Reproductive value
4. Life expectancy & remaining lifetime
5. Sensitivity of population growth rate accompanied with environmental change
6. Elasticity of population growth rate accompanied with environmental change
7. ････

Traditional way

Again



$\tilde{n}_1$: die at age 1

$\tilde{n}_2$: die at age 2

$\vdots$

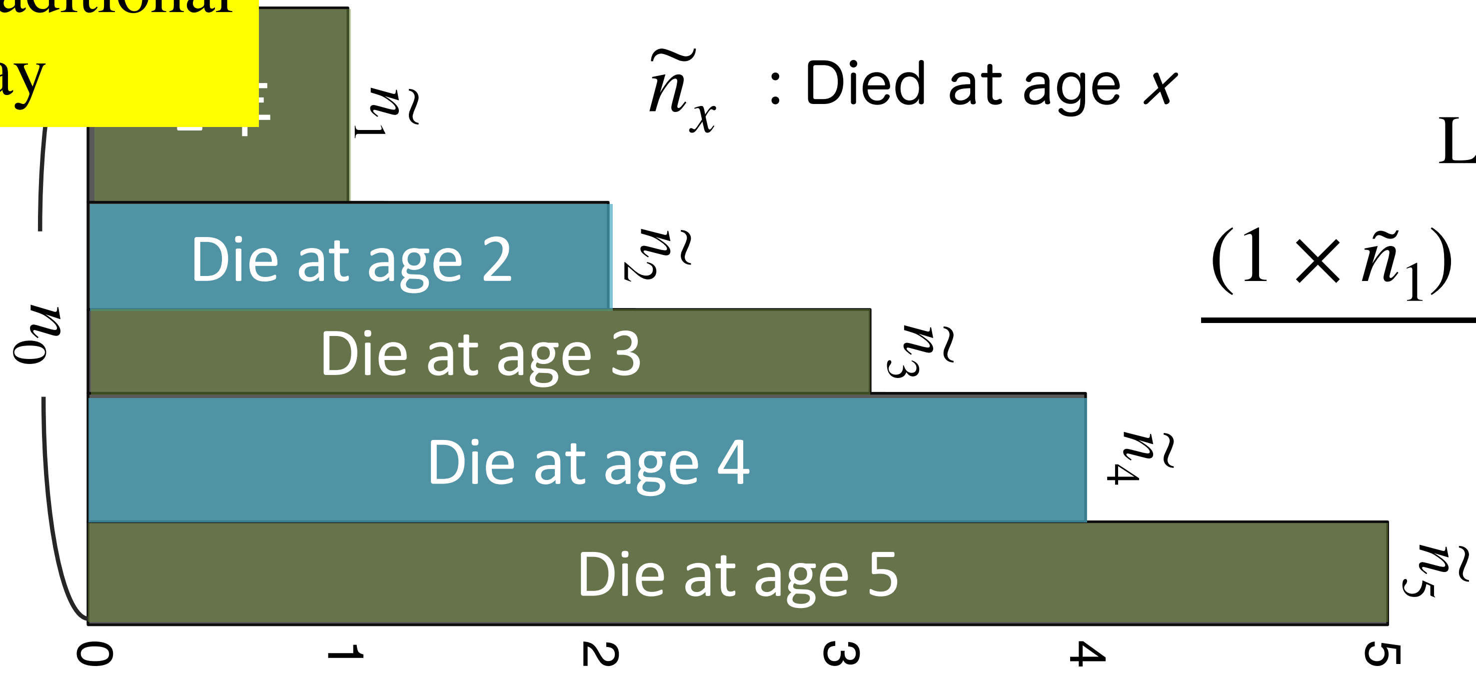
Calculation - 1

$$\text{Average lifetime} = \frac{(1 \times \tilde{n}_1) + \cdots + (5 \times \tilde{n}_5)}{\tilde{n}_1 + \cdots + \tilde{n}_5}$$

$$= \frac{(1 \times \tilde{n}_1) + \cdots + (5 \times \tilde{n}_5)}{n_0}$$

Traditional way

Again

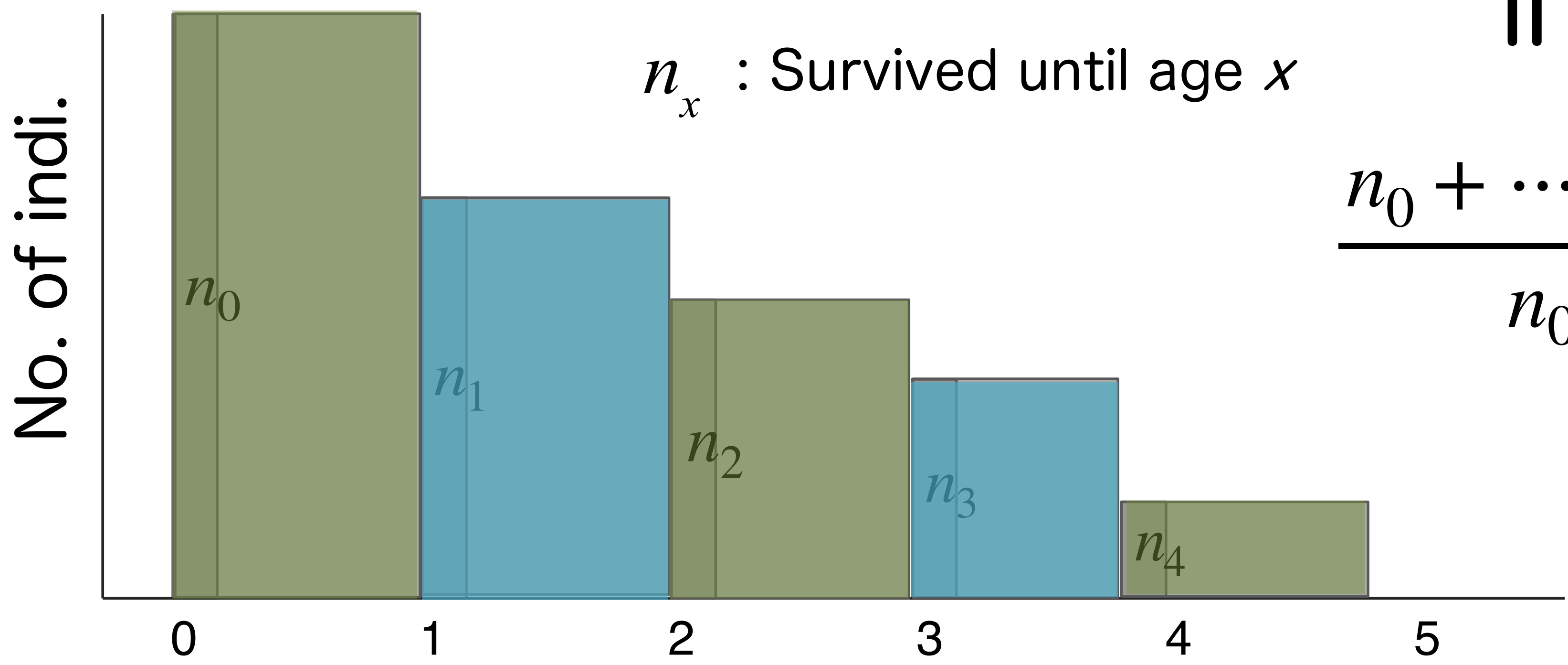


Life expectancy

$$\frac{(1 \times \tilde{n}_1) + \cdots + (5 \times \tilde{n}_5)}{n_0}$$

$$\parallel$$

$$\frac{n_0 + \cdots + n_4}{n_0}$$

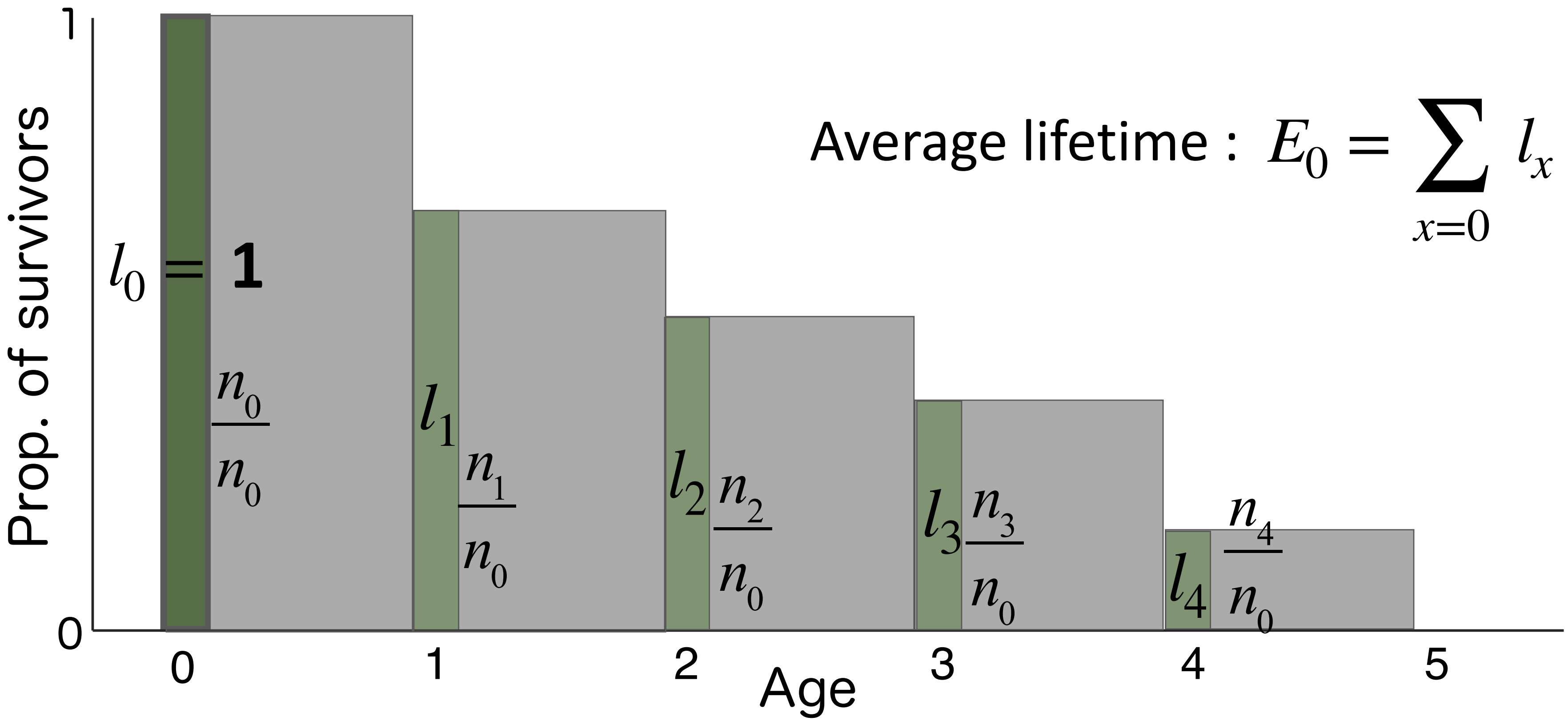


Traditional way

Again

$$\frac{(1\times\tilde{n}_1)+\cdots+(5\times\tilde{n}_5)}{n_0}=\frac{n_0+\cdots+n_4}{n_0}=\frac{n_0}{n_0}+\cdots+\frac{n_4}{n_0}$$

Sum of the survivorship $= l_0+\cdots+l_4$



Matrix way

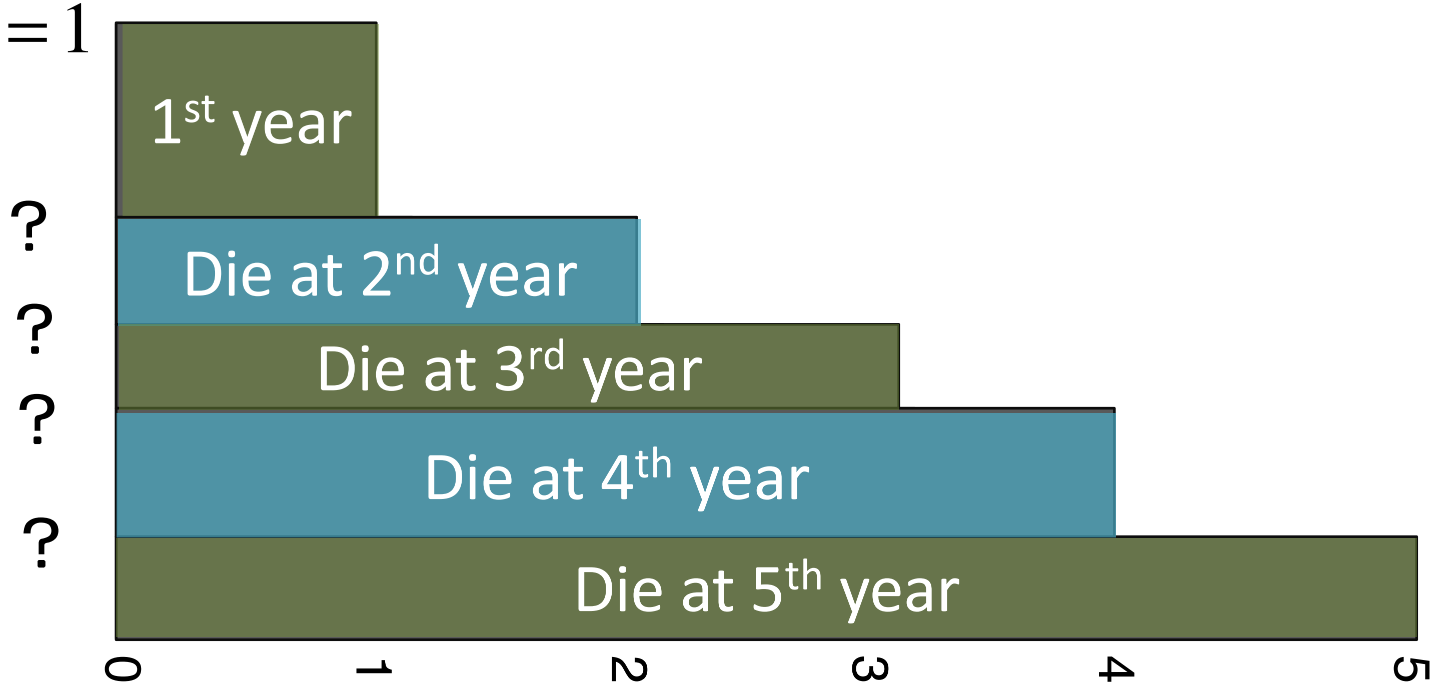
Remaining lifetime

- Suppose that there is one individual at stage j

$$\mathbf{e}_j = \begin{pmatrix} 0 \\ \vdots \\ 1 \\ \vdots \\ 0 \end{pmatrix} \leftarrow \text{Stage } j$$

Defining the sum of the elements in a vector as | **ej** |

$$|\mathbf{e}_j| = 1$$



Matrix way

Using Transition matrix (T)

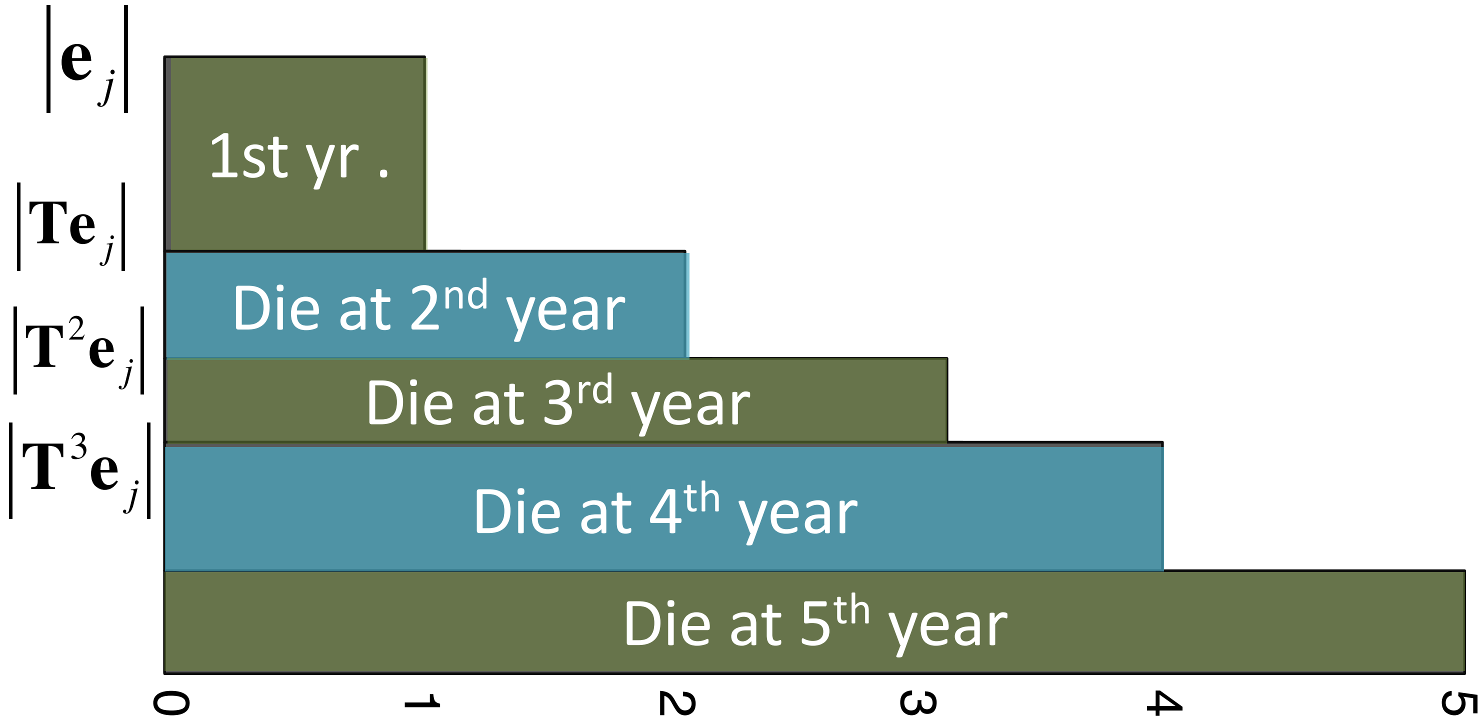
$$\mathbf{Te}_j = \begin{pmatrix} * & * & 0 & * \\ * & * & 0.1 & * \\ * & * & 0.5 & * \\ * & * & 0.2 & * \end{pmatrix}\begin{pmatrix}0\\0\\1\\0\end{pmatrix} = \begin{pmatrix}0\\0.1\\0.5\\0.2\end{pmatrix}$$

The survivor one year later is 0.8.

$$\mathbf{e}_j = \begin{pmatrix}0\\ \vdots \\ 1 \\ \vdots \\ 0\end{pmatrix} \begin{array}{l} \\ \\ \leftarrow \text{Stage } j \\ \\ \\ \end{array}$$

$$\left|\mathbf{Te}_j\right| = 0.8$$

Multiplying Matrix **T** n times leads to No. of survivors n years later



Again

◆Survival and fecundity

- Survival at a state (Calculated by the row-sum of transition prob.)

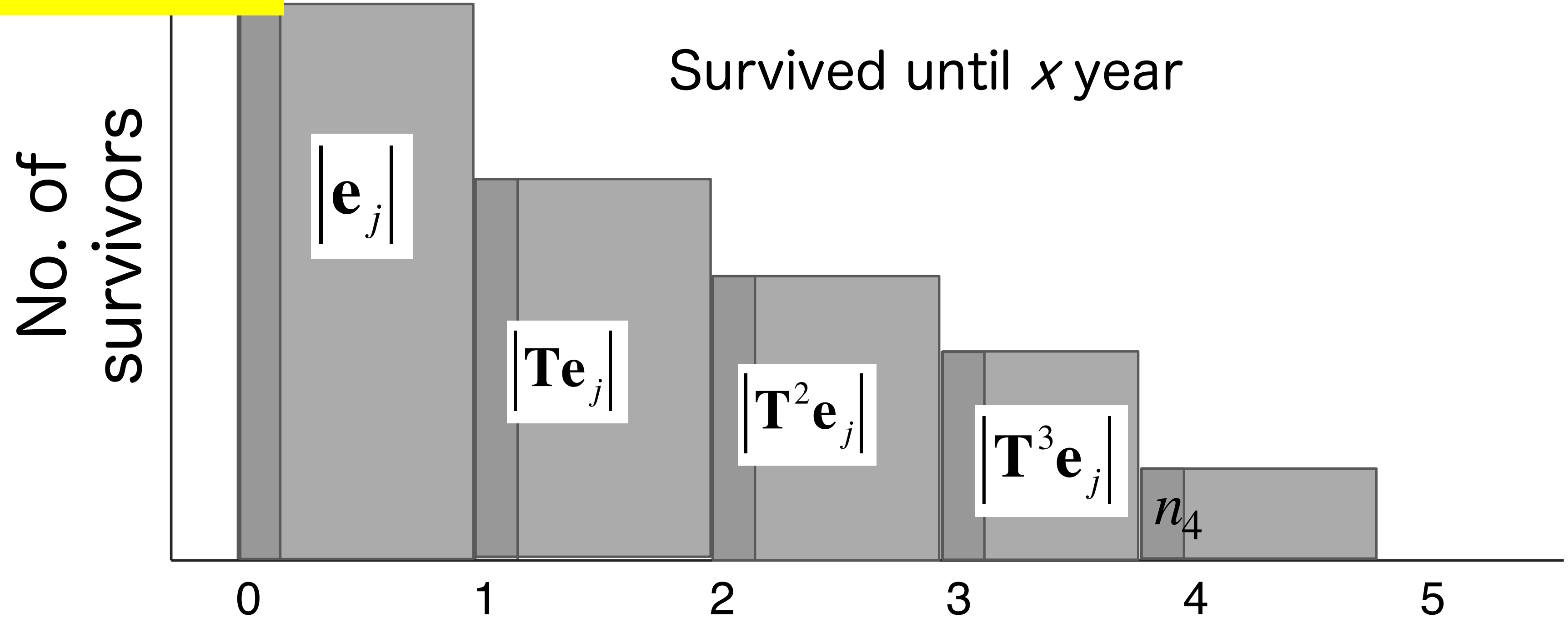
- Fecundity : Number of offspring per individual

$$
\begin{pmatrix} G_1 & 0 & F_3 & F_4 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{pmatrix} = \begin{pmatrix} G_1 & 0 & 0 & 0 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{pmatrix} + \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}
$$

Population Matrix A | Transition matrix T | Reproduction matrix F

Divided into two qualitatively different matrices.

Matrix way



Remaining lifetime at stage j: $\quad \left|\mathbf{T}^0 \boldsymbol{e}_j\right| + \left|\mathbf{T}^1 \boldsymbol{e}_j\right| + \left|\mathbf{T}^2 \boldsymbol{e}_j\right| + \cdots$

$$= \sum_{i=0}^{\infty} \left|\mathbf{T}^i \boldsymbol{e}_j\right|$$

| $\mathbf{e}_j$ |: the sum of the elements in the vector

T: Transition matrix)

Exercise

Population matrix $\mathbf{A} = \begin{pmatrix} 0 & 0 & 5 \\ 0.5 & 0.2 & 0 \\ 0 & 0.7 & 0.2 \end{pmatrix}$

Obtain the remaining lifetime of individuals at stage 2 using the formula.

$$\lfloor \mathbf{T}^0 \boldsymbol{e}_j \rfloor + \lfloor \mathbf{T}^1 \boldsymbol{e}_j \rfloor + \lfloor \mathbf{T}^2 \boldsymbol{e}_j \rfloor + \cdots$$
$$= \sum_{i=0}^{\infty} \lfloor \mathbf{T}^i \boldsymbol{e}_j \rfloor$$

Hint: Obtain the transition matrix **T** first.

Summary

Many population metrics can be obtained by using “Population matrix”.

Next two slides

Old

A series of formulae of population metrics (based on age)

l_a, b_a

Average lifetime

$$E_0 = \sum_{a=0} l_a$$

Net reproductive rate

$$R_0 = \sum_{a=0} l_a b_a$$

Euler-Lotka equation (1911)

$$1 = \sum_{i=1}^{n} b_i l_i \lambda^{-i}$$

Population growth rate (λ)

Reproductive value (1930)

$$V_x = \frac{\lambda^x}{l_x} \sum_{i=x} b_i l_i \lambda^{-i}$$

New

Matrix expression of population metrics

A (= T + F)

Average lifetime

Mat T

$$\sum_{i=1}^{\infty} \left| \mathbf{T}^i e_j \right|$$

T: Transition matrix

Cochran_Ellner(1992)

u : right eigenvector of A
(stable stage distri.)
Leslie (1945)

Eigenvalue equation
(new Euler-Lotka equation)

v : Left eigenvector of A
(reproductive value)
Goodman (1965)

Dominant eigenvalue (λ)
(Population growth rate)

Chronological table

Again

Nishimura Part

1826 Babbage Life table

A Comparative View of the various Institutions for the Assurance of Lives.

1910 Sharpe & Lotka Euler-Lotka equation

1912 Frobenius Peron–Frobenius theorem

1930 Fisher Basic theory, Defining “Reproductive value”

1941 Bernardelli Age-structured “Leslie model”

1945 Leslie Leslie matrix

1963, 1965 Lefkovitch Stage-structured “Matrix population model”

1978 Caswell Sensitivity analysis (New metrics)

1986 De Kroon et al. Elasticity analysis (New metrics)

2015 Salguero-Gomez et al. COMPADRE Plant Database