

Course Title :

Population Dynamics [Environmental Sciences]

Environmental Management and Policy III

(Advanced course of)

The Theory in Bio-Demography

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Basic population metrics I

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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

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I. The Nature of Inheritance
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The consequences of the blending theory, as drawn by Darwin. Difficulties felt by Darwin. Particulate inheritance. Conservation of the variance. Theories of evolution worked by mutations. Is all inheritance particulate ? Nature and frequency of observed mutations.

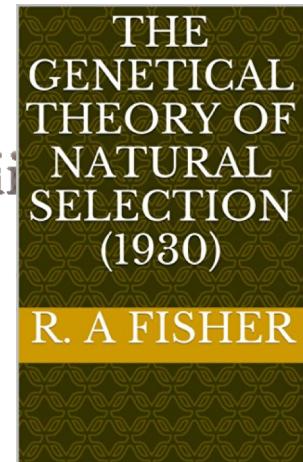
II. The Fundamental Theorem of Natural Selection .	.	.	22
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The life table and the table of reproduction. The Malthusian parameter of population increase. Reproductive value. The genetic element in variance. Natural Selection. The nature of adaptation. Deterioration of the environment. Changes in population. Summary

(logarithm of λ)

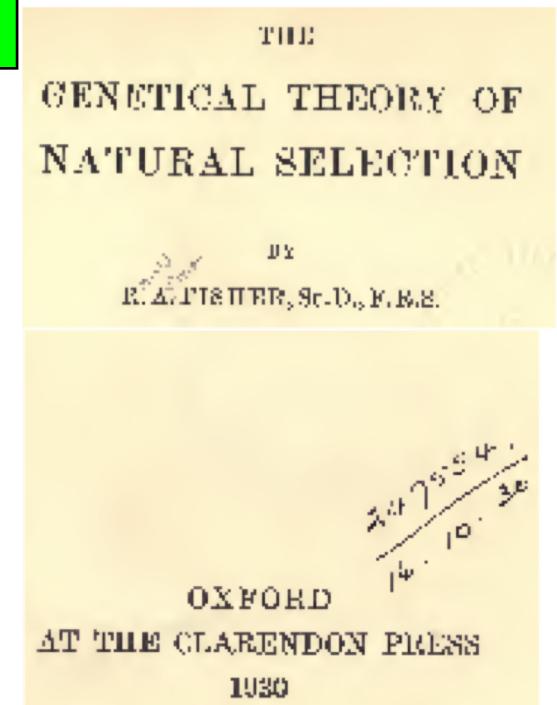
III. The Euler–Lotka Equation	reproductive value	48
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$$1 = \sum_{i=1}^n b_i l_i \lambda^{-i}$$
$$\frac{v_j}{v_1} = \frac{\lambda^j}{l_j} \sum_{i=j} b_i l_i \lambda^{-i-1}$$



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.



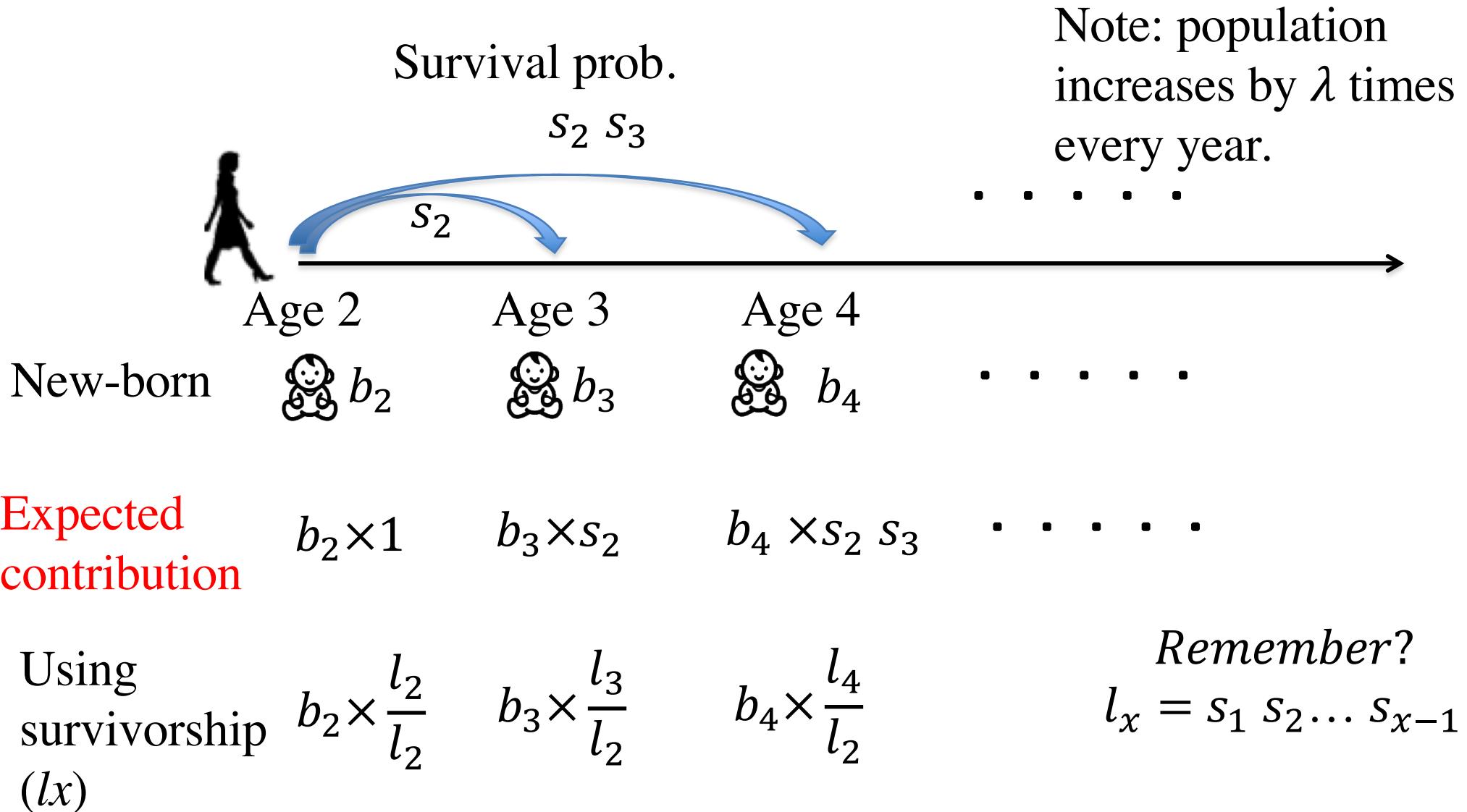
How much is the present value of your future offspring ?

Fisher did not use matrix framework

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**.



(2) The present value of expected contribution

	Survival prob.			Note: population increases by λ times every year.			
	s_2	s_3		\dots	\dots	\dots	\dots
New-born		s_2	s_3		\dots	\dots	\dots
Age 2	 b_2			\dots	\dots	\dots	\dots
Age 3		 b_3		\dots	\dots	\dots	\dots
Age 4			 b_4	\dots	\dots	\dots	\dots
Expected contribution	$b_2 \times 1$	$b_3 \times s_2$	$b_4 \times s_2 s_3$	\dots	\dots	\dots	\dots
Using survivorship (l_x)	$b_2 \times \frac{l_2}{l_2}$	$b_3 \times \frac{l_3}{l_2}$	$b_4 \times \frac{l_4}{l_2}$				
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

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

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

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

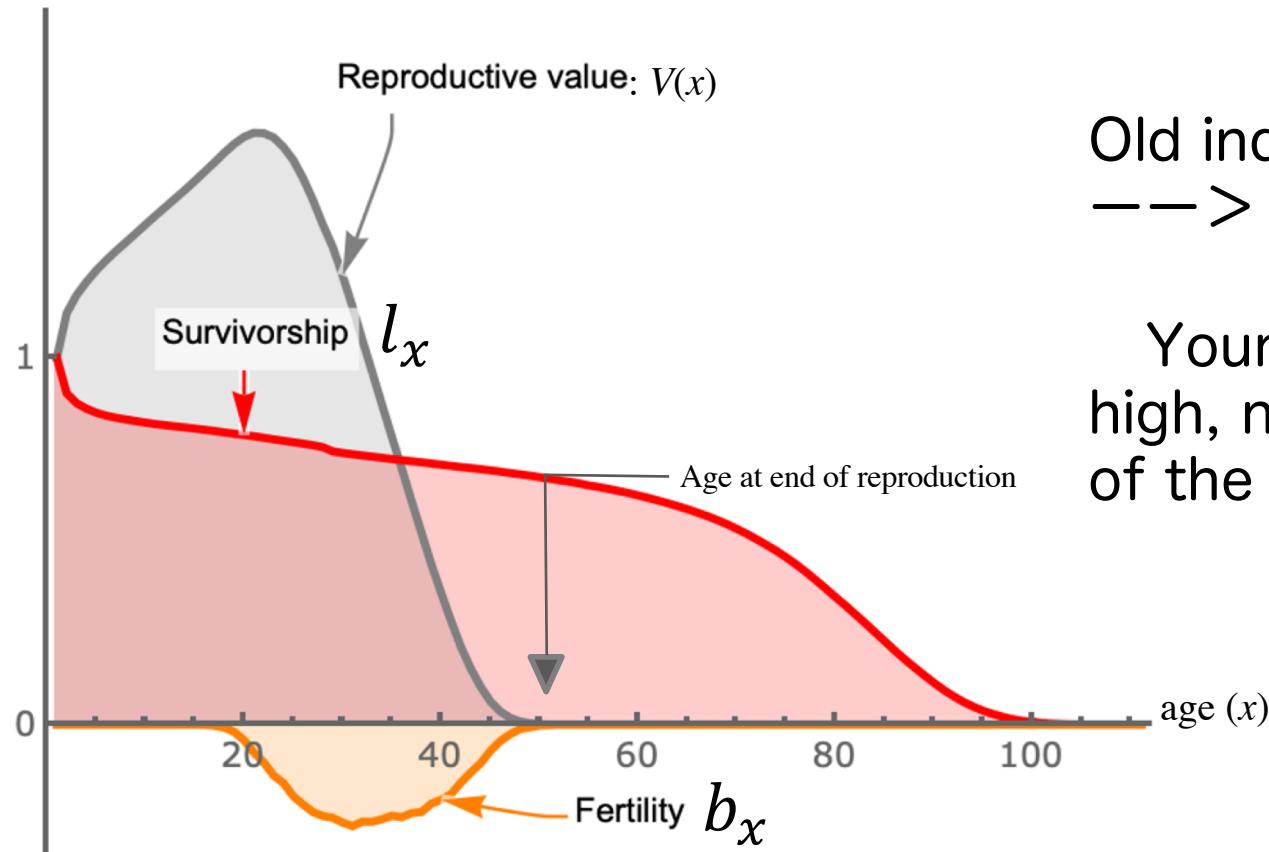
$$= \frac{\lambda^2}{l_2} (b_2 l_2 \lambda^{-2} + b_3 l_3 \lambda^{-3} + b_4 l_4 \lambda^{-4} + \dots) = \frac{\lambda^2}{l_2} \sum_{i=2} b_i l_i \lambda^{-i}$$

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

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

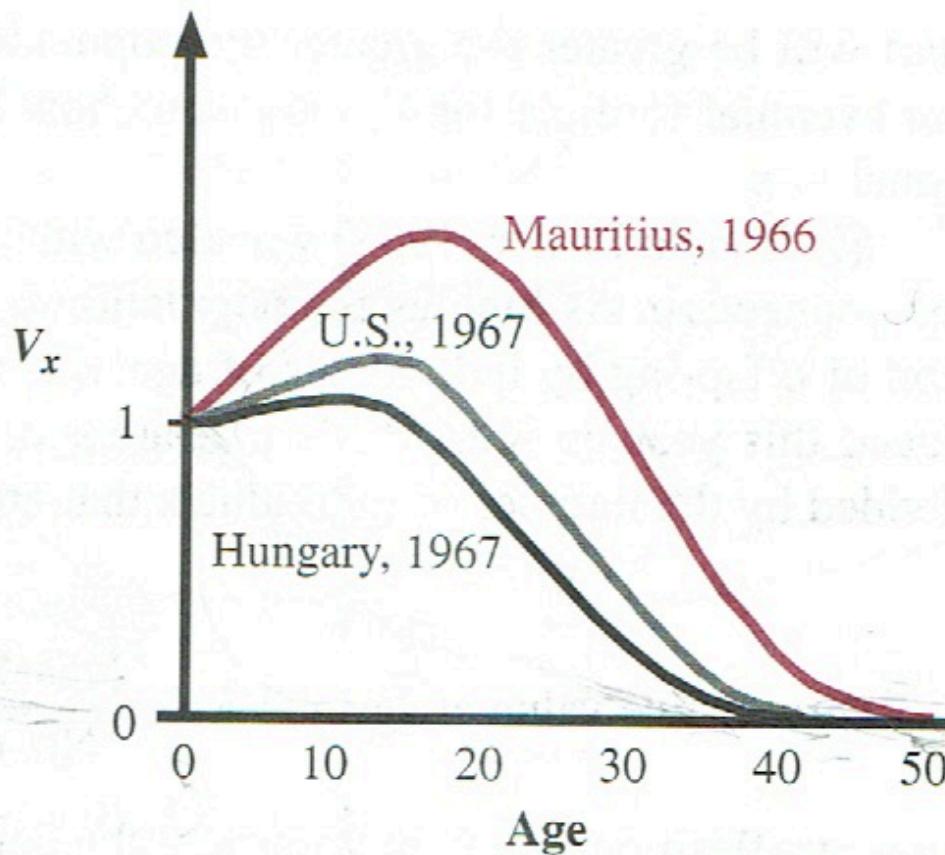


Old indi. with no fertility
---> $V_x = 0$

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

Reproductive value of age- x individual

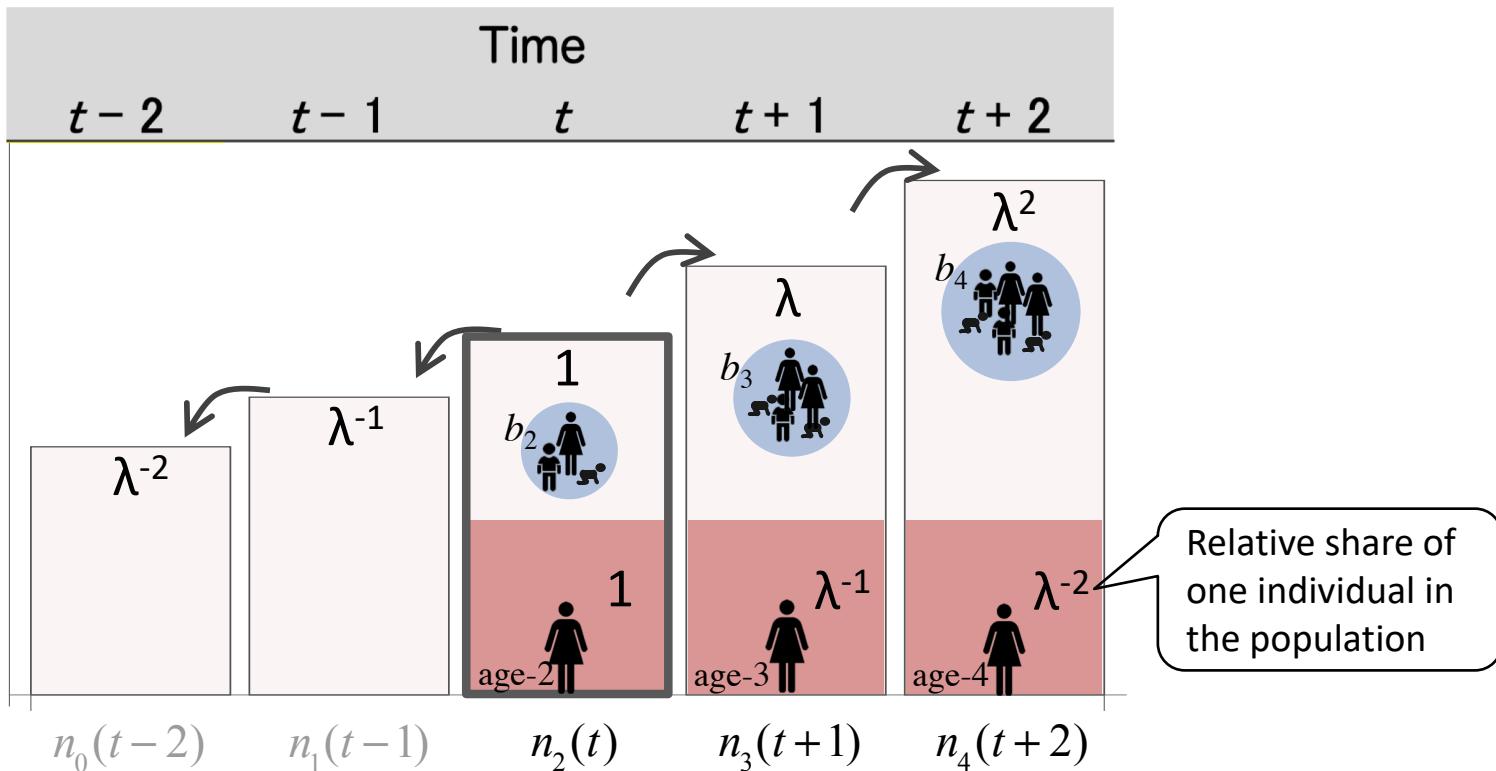
$$V_x = \frac{\lambda^x}{l_x} \sum_{i=x} b_i l_i \lambda^{-i}$$



Old indi. with no fertility
---> $V_x = 0$

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

No matrix until this slide



Sum of the relative reproductive contribution of **n_2 individuals** now and in the future

$$= b_2 \lambda^{-0} n_2(t) + \underbrace{b_3 \lambda^{-1} n_3(t+1)}_{\text{Relative reproductive contribution}} + b_4 \lambda^{-2} n_4(t+1) + \dots$$

Relativized weighting of no. of parents

Relative reproductive contribution

Left eigenvector in population matrix model

* Definition of left eigenvector in linear algebra

$$\mathbf{v}^T \mathbf{A} = \mathbf{v}^T \lambda = \lambda \mathbf{v}^T \quad T: \text{transposed}$$

Multiplied from left

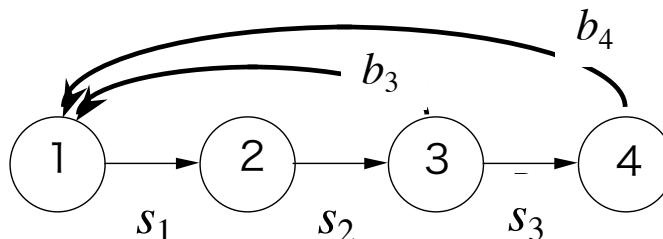
$$\mathbf{v}^T \mathbf{A} = (\nu_1 \quad \nu_2 \quad \cdots) \begin{pmatrix} & & \\ & \mathbf{A} & \\ & & \end{pmatrix} = \lambda (\nu_1 \quad \nu_2 \quad \cdots)$$

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

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

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.
- * 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:

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

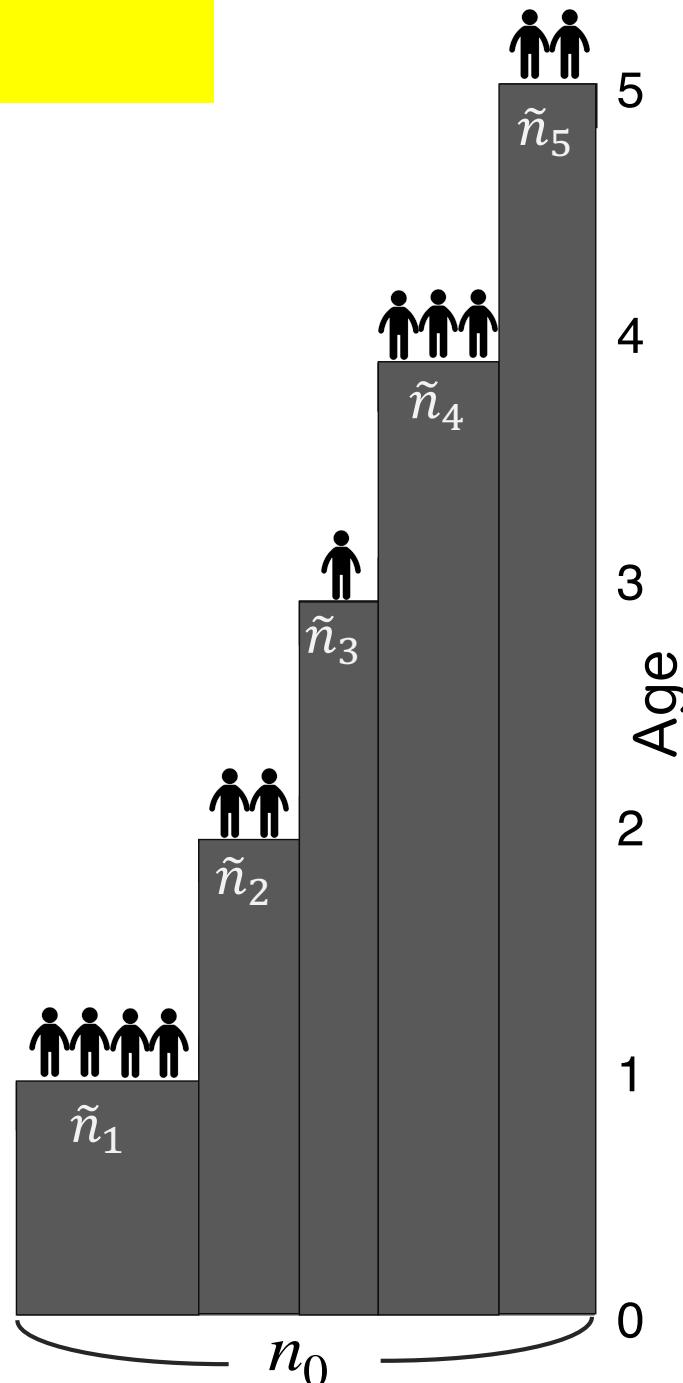
$$\mathbf{v} = \begin{pmatrix} 1 \\ v_2 \\ \vdots \end{pmatrix}$$

Left eigenvector \mathbf{v} is the right eigenvector of transposed matrix of \mathbf{A}

Population metrics from matrix models

1. Population growth rate (previously covered) λ
2. Stable stage distribution (previously covered) \mathbf{u}
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7.

Traditional
way



\tilde{n}_1 : die at age 1

\tilde{n}_2 : die at age 2

:

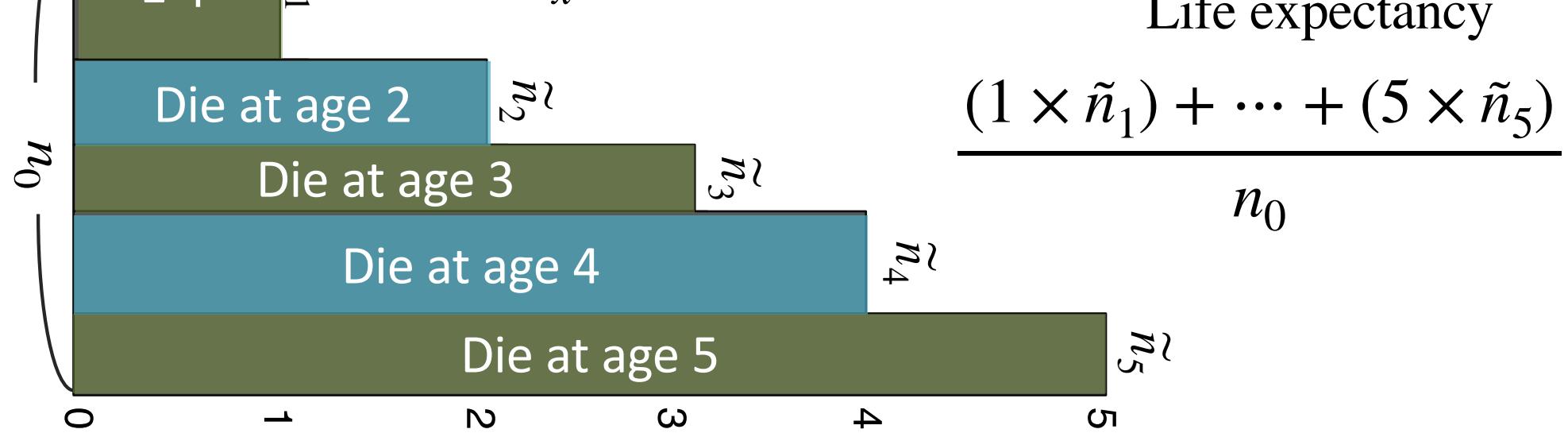
Calculation - 1

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

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

Again

Traditional way

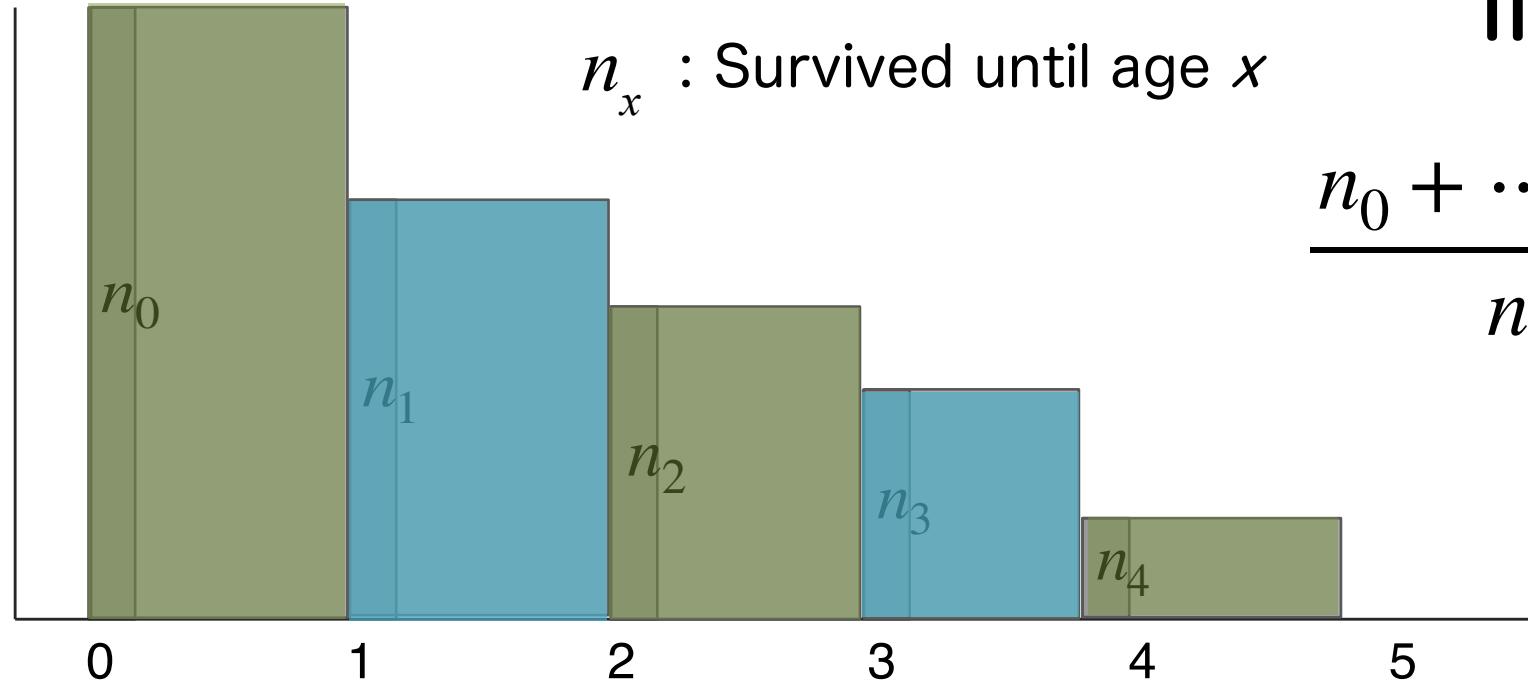


No. of indi.

n_x : Survived until age x

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

||

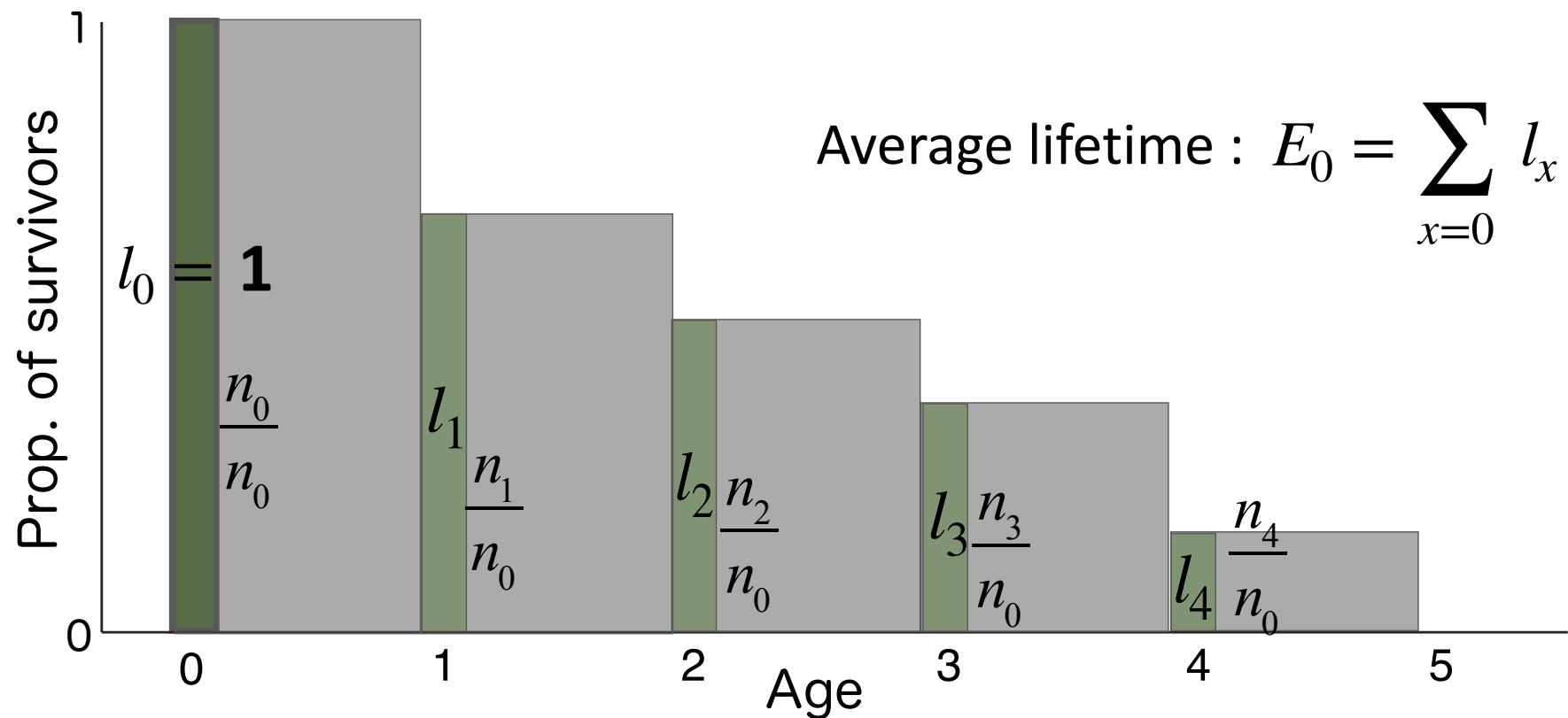


Traditional way

Again

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

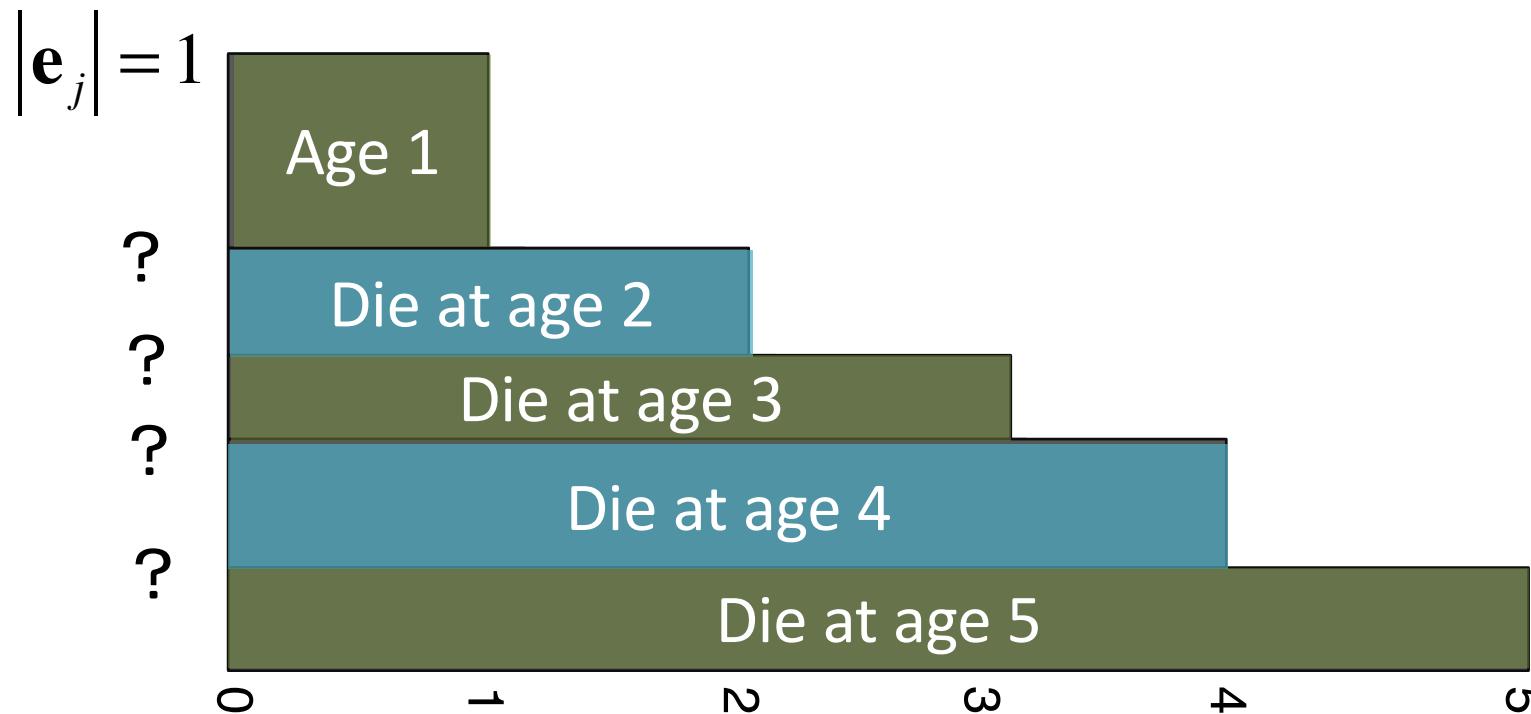
$$\text{Sum of the survivorship} = l_0 + \dots + l_4$$



- 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 $|\mathbf{e}_j|$



Matrix way

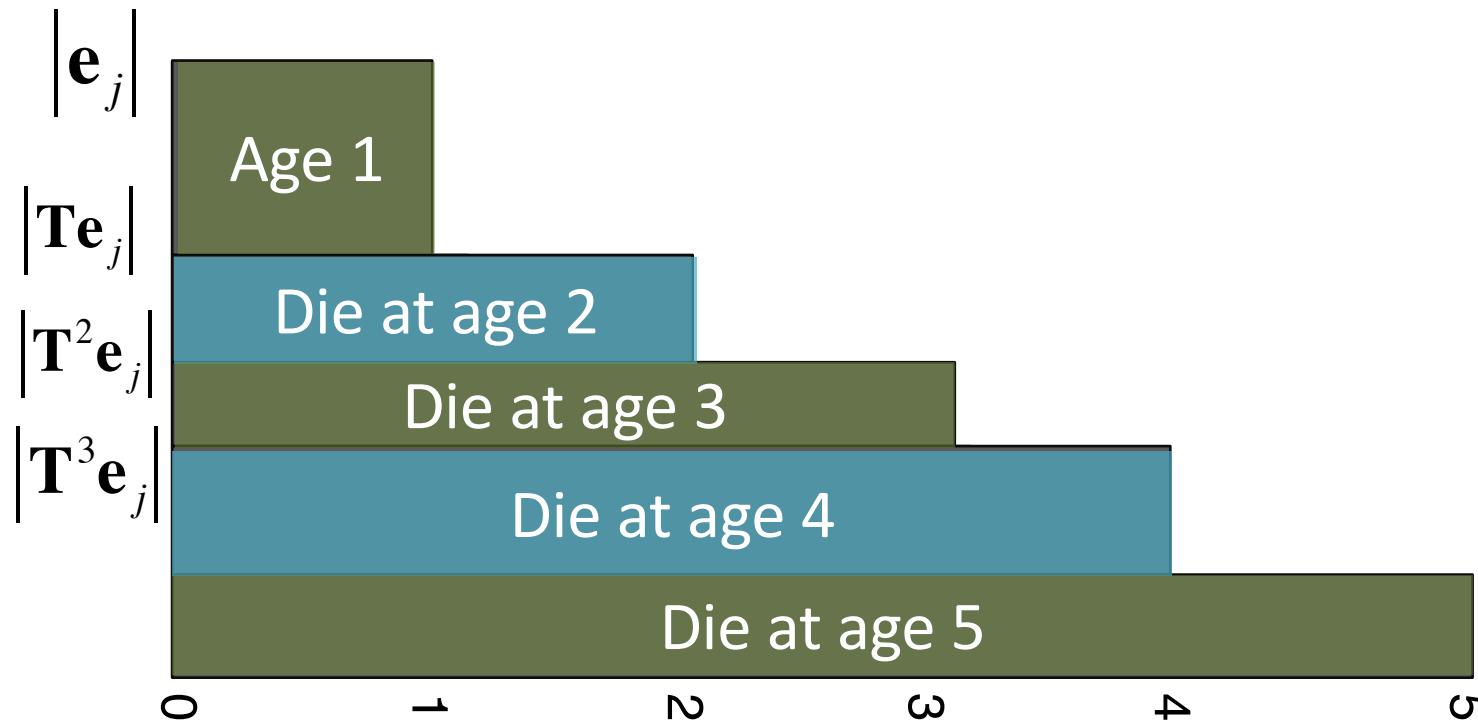
Using Transition matrix (T)

$$Te_j = \begin{pmatrix} * & * & 0 & * \\ * & * & 0.1 & * \\ * & * & 0.5 & * \\ * & * & 0.2 & * \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0.1 \\ 0.5 \\ 0.2 \end{pmatrix}$$

The survivor one year later is 0.8.

$$e_j = \begin{pmatrix} 0 \\ \vdots \\ 1 \\ \vdots \\ 0 \end{pmatrix} \leftarrow \text{Stage } j$$

$|Te_j| = 0.8$ Multiplying Matrix T n times leads to No. of survivors n years later



◆ Survival and fecundity

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



- Fecundity : Number of offspring per individual



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

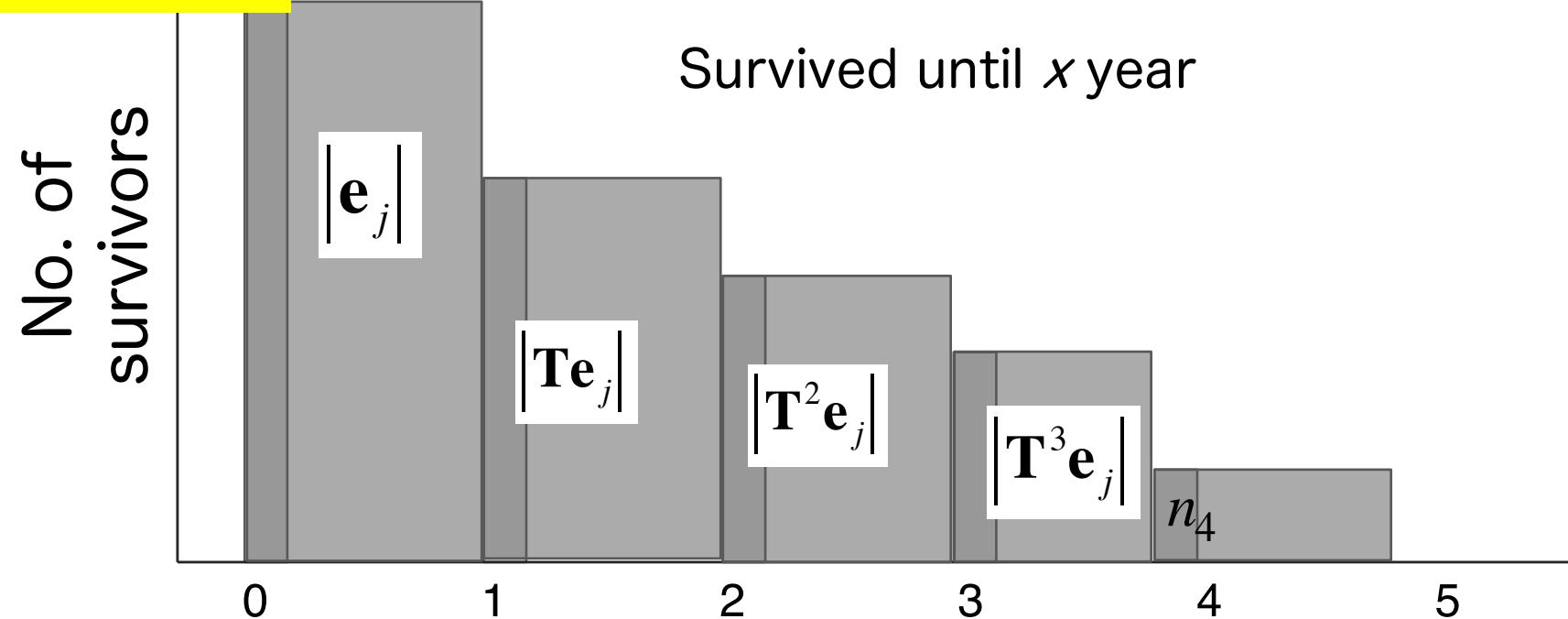
Population
Matrix A

Transition matrix
T

Reproduction matrix
F

Divided into two qualitatively different matrices.

Matrix way



Remaining lifetime at stage j : $[T^0 e_j] + [T^1 e_j] + [T^2 e_j] + \dots$
 $= \sum_{i=0}^{\infty} [T^i e_j]$

$|e_j|$: the sum of the elements in the vector
(T : Transition matrix)

Exercise

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

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

$$\begin{aligned} & [T^0 e_j] + [T^1 e_j] + [T^2 e_j] + \dots \\ &= \sum_{i=0}^{\infty} [T^i e_j] \end{aligned}$$

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

Mat T

Average lifetime
 $\sum_{i=1}^{\infty} |T^i e_j|$

T: Transition matrix

Cochran_Ellner(1992)

A (= T + F)



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

Leslie (1945)

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



Dominant eigenvalue (λ)
(Population growth rate)

Chronological table

Again

1826 Babbage

Life table

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

1910 Sharpe & Lotka

Euler-Lotka equation

Nishimura Part

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