Age-Structured Population Models

Exponential and Logistic growth models assumed all individuals equivalent, no age structure, not so for many organisms of interest

Fecundity and survival often differ with age (or size), so age structure of population matters for the number of newborns next time unit

Age and stage-based models include information about the members of the same species tallied separately by groups.

N was a scalar (single value) in previous models, it becomes a vector $\boldsymbol{N_{age}}$ of numbers of individuals of each age class

Age-Structured Population Models

We will use 2 facts to develop age-based demography:

- How do you get to be 30?
    - You had to be 29 one year before and survive
- Every newborn has a mom, and that mom had an age

And lots of math!

Age-Structured Population Models

What we will develop:

How to predict the population size $\boldsymbol{N_{age}}$ at some time in the future;

How to determine if an age-structured population is growing or declining (and measure its rate of growth);

How natural selection might shape schedules of age-specific fecundity and survival (life histories).

Age-Structured Population Models

Pitfalls:

Powerful mathematical tools, and simple concepts, but the notation is horrid! (and not standardized)

Corollary is that many early papers have one or more equations wrong, and even textbooks still mess up on the exponents (or mis-define reproductive value)

Age-Structured Population Models

Discrete time steps (e.g., years) and age classes:

What age class are "Young of Year"?   0 or 1

Goodman noted that old Fortran compilers didn't like 0 as array subscript, so settled on YoY age class = 1

Gotelli (mostly) uses YoY=age class 0

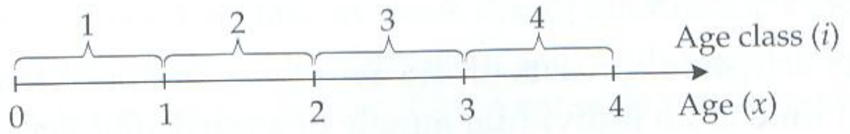


Figure 3.1 The relationship between age (x) and age class (i) in population growth models. (From Caswell 2001.)

Gotelli. 2001. A Primer of Ecology, 3rd ed. Sinauer

Age-Structured Population Models

Vital Rates (“life rates”)

---

x = age or stage class (0 to k or ω; or 1 to k or ω)

N_x = number of age class x individuals in population (Gotelli uses S_x for no known reason)

s_x = probability of survival from age class x to age class x+1 (Gotelli uses g_x)

b_x = average fecundity per female of age class x; measured as YoY offspring alive at next census (**b** for birth, also often $\mathbf{f_x}$ for fecundity or $\mathbf{m_x}$ for maternity)

US: fertility=potential fecundity=realized

UK: fecundity=potential fertility=realized

Age-Structured Population Models

From Fact 1:
$N_x(t+1) = N_{x-1}(t) \cdot s_{x-1}$

(subscripts are age class, parentheses are time)

↘ S_x (plus aging)

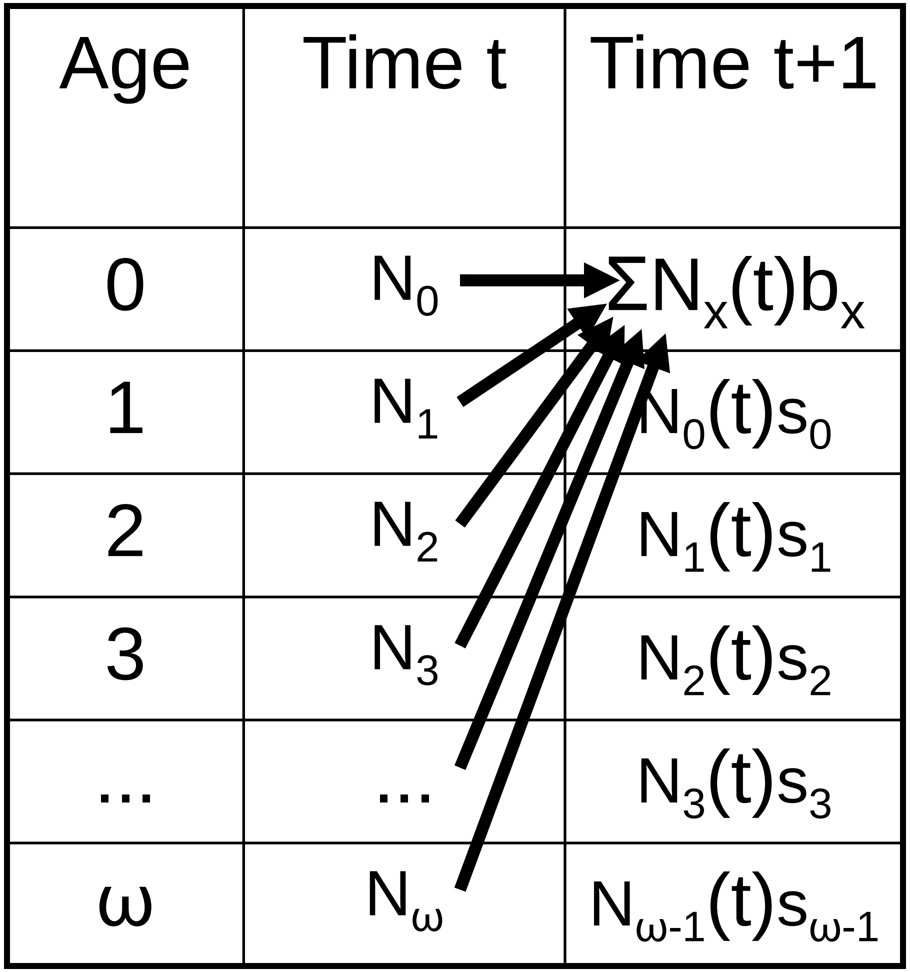
Age	Time t	Time t+1
0	N_0	?
1	N_1	$N_0(t)s_0$
2	N_2	$N_1(t)s_1$
3	N_3	$N_2(t)s_2$
...	...	$N_3(t)s_3$
ω	N_ω	$N_{\omega-1}(t)s_{\omega-1}$

Age-Structured Population Models

From Fact 2 (each YoY had a mom of an age):

$$N_0(t+1) = \sum_{age=0}^{age=\omega} N_{age}(t)\, b_{age}$$

$\longrightarrow b_x$



Age	Time t	Time t+1
0	N_0	$\Sigma N_x(t) b_x$
1	N_1	$N_0(t) s_0$
2	N_2	$N_1(t) s_1$
3	N_3	$N_2(t) s_2$
...	...	$N_3(t) s_3$
ω	N_ω	$N_{\omega-1}(t) s_{\omega-1}$

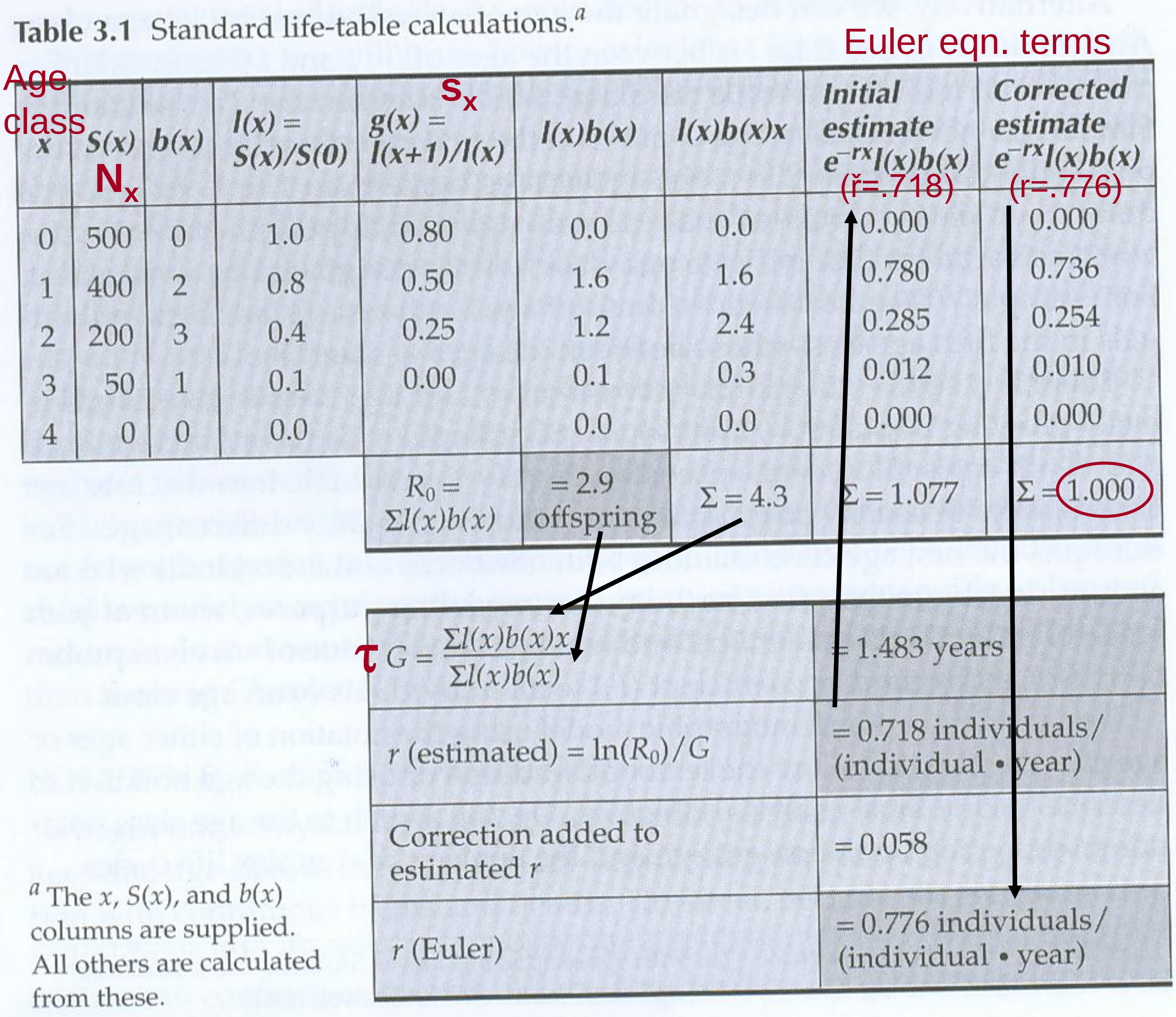


Table 3.1 Standard life-table calculations.[a]

Euler eqn. terms

x Age class	S(x) N_x	b(x)	l(x) = S(x)/S(0)	g(x) = l(x+1)/l(x) s_x	l(x)b(x)	l(x)b(x)x	Initial estimate $e^{-rx}l(x)b(x)$ (ř=.718)	Corrected estimate $e^{-rx}l(x)b(x)$ (r=.776)
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	Σ = 4.3	Σ = 1.077	Σ = 1.000

τ $G = \frac{\Sigma l(x)b(x)x}{\Sigma l(x)b(x)}$	= 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.

Gotelli. 2001. A Primer of Ecology, 3rd ed. Sinauer

Stable age distribution

- An emergent property of demographic schedules that are constant through time
- Expected for populations at ‘equilibrium’
- An explicit assumption of many ecological models; an implicit assumption of many empirical studies (doh!)

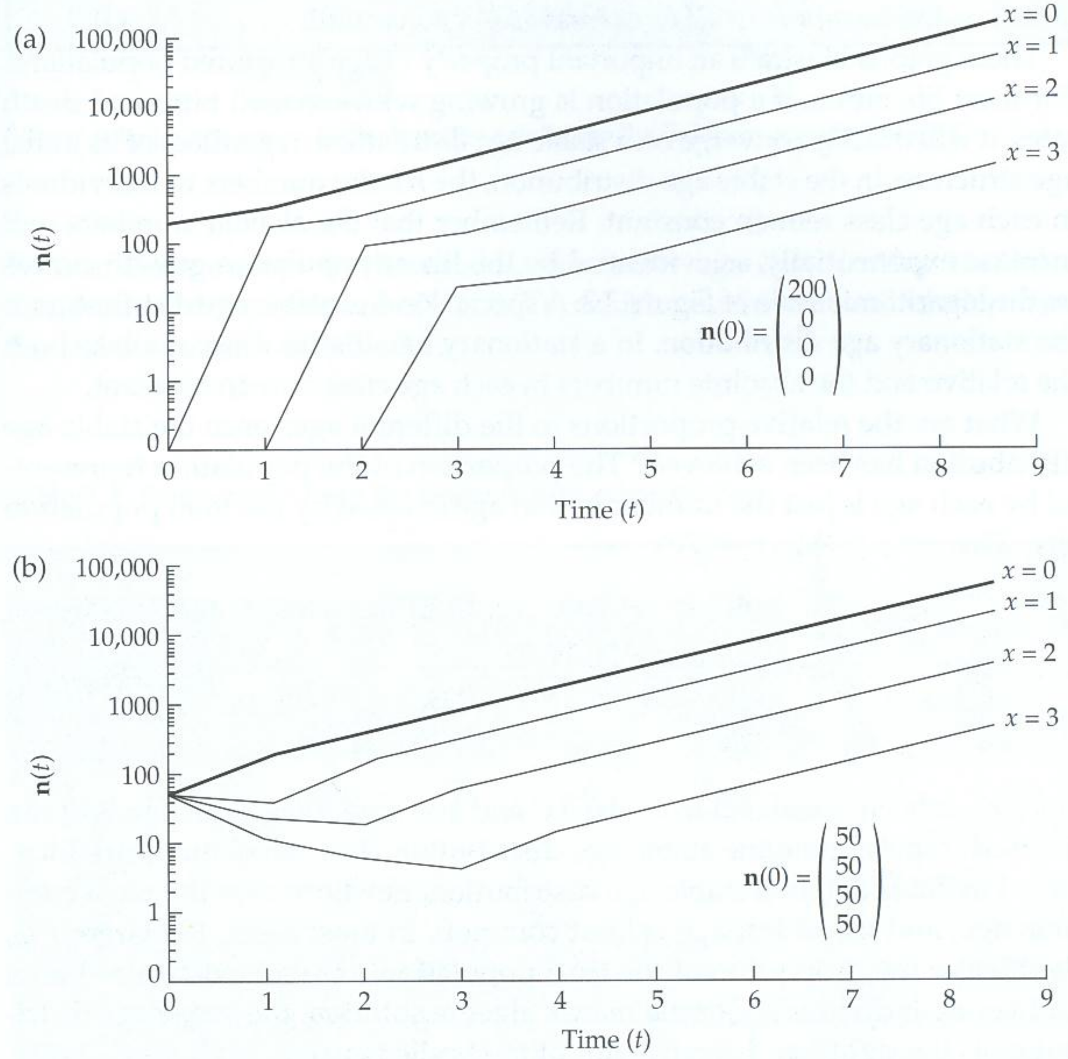


Figure 3.3 Stable age distributions, showing the effects of initial age structure on population growth. Each line represents a different age class, growing according to the birth and death schedules of Table 3.1. In (a), the initial age distribution was 200 newborns. In (b), the initial age distribution was 50 individuals in each age class. After some initial fluctuations, both populations settle into identical stable age distributions. On the logarithmic scale, the straight line for each age class indicates exponential increase.

Age-Structured Population Models

Derived Vital Rates ("life rates")

ℓ_x = (should be script "L") cumulative survivorship from age class 0 to age x; ℓ_0=1

R_0 = replacement rate: expected number of (female) offspring produced over a lifetime (not discounted by time!)

τ = (should be Greek tau) the generation time; across mom's expectation of lifetime fecundity, the average age of mom at birth. (Gotelli uses G for generation time)

r = Population growth rate at SAD (also $\lambda=e^r$, so $r=\ln(\lambda)$)

ν = (should be Greek nu, but often lowercase "v") reproductive value. Will be defined (correctly) later!

Age-Structured Population Models

From Fact 1: $N_x(t+1) = N_{x-1}(t) \cdot s_{x-1}$

(For cumulative survivorship we don't care about time)

$\ell_0 \equiv 1$

$\ell_1 = \ell_0 \cdot s_0 = s_0$

$\ell_2 = \ell_1 \cdot s_1 = s_0 s_1$

$\ell_3 = \ell_2 \cdot s_2 = s_0 s_1 s_2$

Age-Structured Population Models

From Fact 1: $N_x(t+1) = N_{x-1}(t) \cdot s_{x-1}$

(For cumulative survivorship we don't care about time)

$\ell_0 \equiv 1$

$\ell_1 = \ell_0 \cdot s_0 = s_0$

$\ell_2 = \ell_1 \cdot s_1 = s_0 s_1$

$\ell_3 = \ell_2 \cdot s_2 = s_0 s_1 s_2$

$$\ell_x = \prod_{age=0}^{x-1} s_{age}$$

Age-Structured Population Models

Derived Vital Rates (“life rates”)

R_0 = replacement rate: expected number of (female) offspring produced over a lifetime (not discounted by time!)

$$R_0 = \sum_{age=0}^{\omega} \ell_{age} b_{age}$$

Age-Structured Population Models

Derived Vital Rates ("life rates")

τ = (should be Greek tau) the generation time; across mom's expectation of lifetime fecundity, the average age of mom at offspring's birth. (Gotelli uses G for generation time)

$$\tau = \frac{\sum_{age=0}^{\omega} age \cdot \ell_{age} b_{age}}{\sum_{age=0}^{\omega} \ell_{age} b_{age}}$$

Age-Structured Population Models

Derived Vital Rates (“life rates”)

---

r = Population growth rate at SAD (also $\lambda = e^r$, so $r = \ln(\lambda)$)

Euler equation:

$$1 = \sum_{age=0}^{\omega} e^{-r\cdot(age+1)} \ell_{age} b_{age}$$

Age-Structured Population Models

Euler equation:

$$1 = \sum_{age=0}^{\omega} e^{-r \cdot (age+1)} \ell_{age} b_{age}$$

Can't solve analytically

Guess answers until ≈ 1

Starting guess:

$$r \approx \frac{\ln(R_0)}{\tau}$$

Age-Structured Population Models

"Types" of life tables (how do we estimate s_x and b_x parameters):

Cohort (horizontal) – follow a cohort of females through time; permits direct estimation of vital rates. Fecundity can be difficult.

Static (vertical) – characterize demographic parameters of population at one point in time (to estimate vital rates, must assume SAD). Fecundity is impossible without assumptions about shape of age-dependence.

Hybrid or Piecewise (what ecologists really do) – measure population 2 or more times, possibly marking individuals for individual survival tracking. Fecundity can be difficult unless there is parental care.

Age-Structured Population Models

Idealized survivorship curves

I – Organisms with developed parental care; humans

II – Constant mortality rate through life; probably not common, suggested for some birds

III – High juvenile mortality; egg-scattering fish; many seed-producing plants, etc

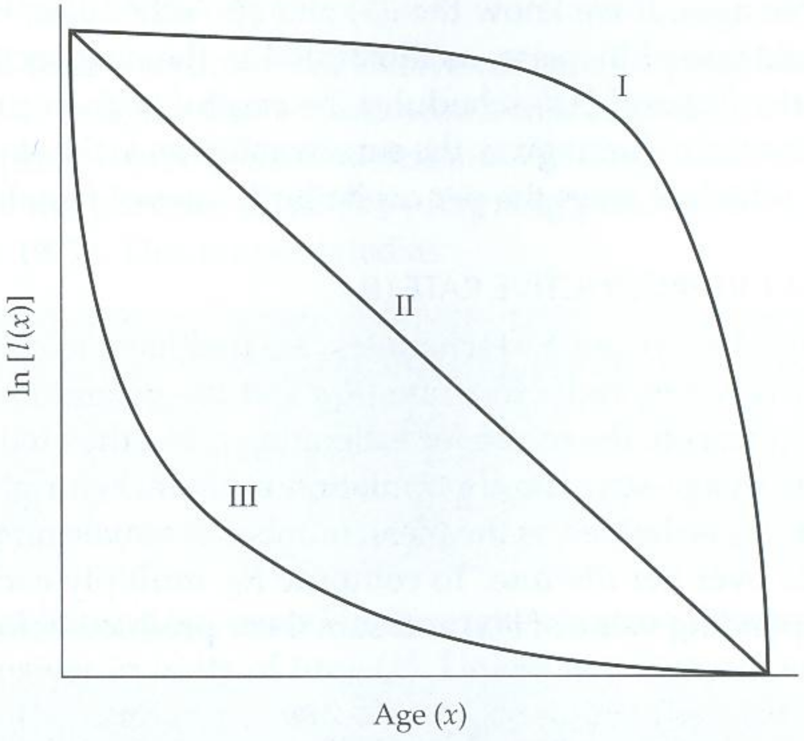


Figure 3.2 Type I, II, and III survivorship curves. Note the logarithmic transformation of the y axis.

Gotelli. 2001. A Primer of Ecology, 3rd ed. Sinauer

Age-Structured Population Models

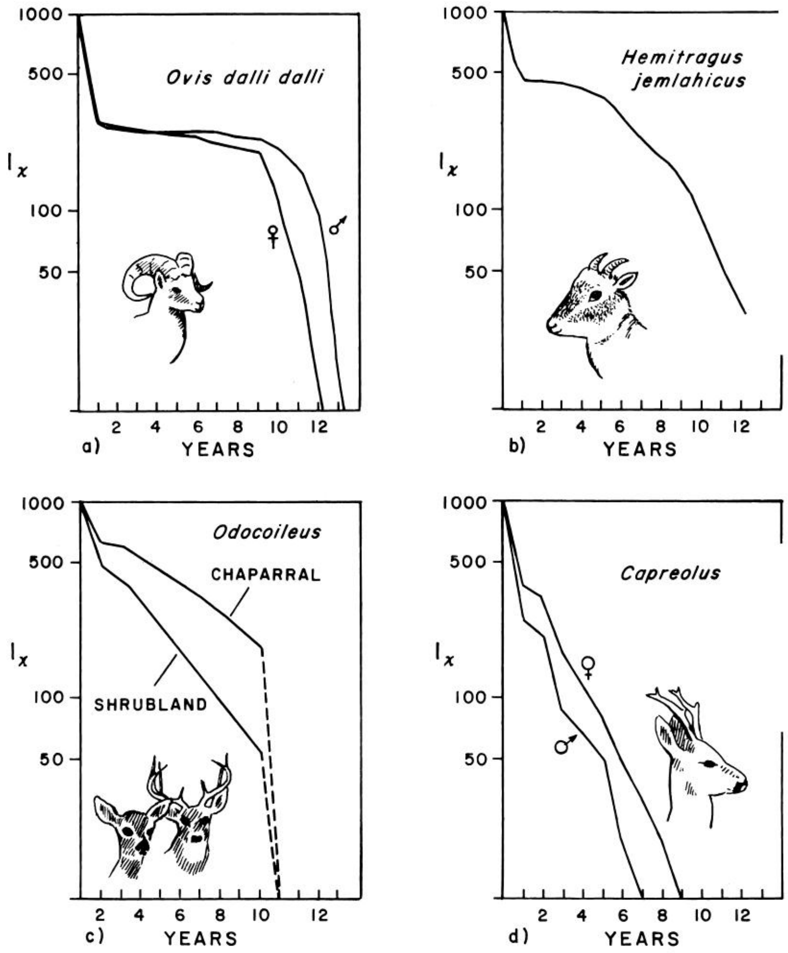


FIGURE 41. Survivorship curves of (a) the Dall sheep (*Ovis d. dalli*) in Alaska ♂ and ♀; (b) the that (*Hemitragus jemlahicus*), introduced into New Zealand; (c) the Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in Lake County, California; and (d) the roebuck (*Capreolus capreolus*) in Denmark (data from Murie, Caughley, Taber and Dasmann, and Andersen).

- "Interesting ways of thinking about death"
- Hutchinson 1978 An Introduction to Population Ecology

Age-Structured Population Models

Reproductive Value ν

The expected contribution to future population size of an individual of age class x, relative to that of other age classes

Which population is "bigger": 5 huge abalone or 1000000 fertilized eggs?

Age-Structured Population Models

Reproductive Value ν

The expected contribution to future population size of an individual of age class x, relative to that of other age classes

Any initial population will eventually reach SAD

Compare "populations" of descendants of 10 age *i* individuals to 10 age *j* individuals

What will their relative sizes be once both reach SAD?

Which has a bigger head start?

Age-Structured Population Models

Derived Vital Rates (“life rates”)

ν_x = (should be Greek nu, but often lowercase "v") reproductive value. A vector: each age class x has a reproductive value ν_x

The expected contribution to future population size of an individual of age class x, relative to that of other age classes

$\nu_0 \equiv 1$, so defined as relative to that of a YoY

$$\frac{\nu_x}{\nu_0} = \frac{e^{rx}}{\ell_x} \sum_{y=x}^{\omega} e^{-ry} \ell_y b_y$$

$\boldsymbol{\nu_x}$ discounts future offspring by the population growth rate, survival and reproduction in future ages, and survival to age x

Age-Structured Population Models

What's Cool about ν:

Can be partitioned into 2 components: current reproduction and (discounted) future reproduction (aka residual reproductive value)

$$\frac{\nu_x}{\nu_0} = \underbrace{b_x}_{\text{Current Reproduction}} + \underbrace{\sum_{y=x+1}^{\omega} e^{-r(y-x)} \frac{\ell_y}{\ell_x} b_y}_{\text{Discounted Future Reproduction}}$$

Conditional
prob. survival
to age y given
alive at age x

Age-Structured Population Models

What's Cool about ν:

Can be partitioned into 2 components: current reproduction and (discounted) future reproduction (aka residual reproductive value)

$$\frac{\nu_x}{\nu_0} = b_x + \sum_{y=x+1}^{\omega} e^{-r(y-x)} \frac{\ell_y}{\ell_x} b_y$$

Very useful way to analyze optimal life histories (schedules of s_x and b_x)

Age-Structured Population Models

Note: r is an especially important parameter in ecology because of its use in evolutionary biology

Generally calculate r from life-table data using Euler's equation (assumes stable age distribution obtains):

Where there are k age classes

$$1 = \sum_{x=0}^{k} e^{-rx} l(x) b(x)$$

Age-Structured Population Models

Background: measures of population growth

λ = finite rate of increase; rate of increase as function of absolute time

r = instantaneous rate of increase; per capita rate of population growth over short time interval (generally used as empirical value for fitness)

$$r = \ln(\lambda) \text{ and } \lambda = e^r$$

R_o = net reproductive rate; mean number of female offpsring produced by an average female over her lifetime, units are no. of offspring per generation

$$r \cong \ln(R_o)/G \qquad R_o = \sum_{x=0}^{k} l(x)b(x)$$

Age-Structured Population Models

From age x at time t

To age x at time t+1

$$\begin{array}{|c|c|c|c|c|c|} \hline b_0 & b_1 & b_2 & b_3 & b_4 & b_5 \\ \hline s_0 & & & & & \\ \hline & s_1 & & & & \\ \hline & & s_2 & & & \\ \hline & & & s_3 & & \\ \hline & & & & s_4 & \\ \hline \end{array}$$

Leslie Matrix

(matrices = bookkeeping)

A (sometimes **L**)

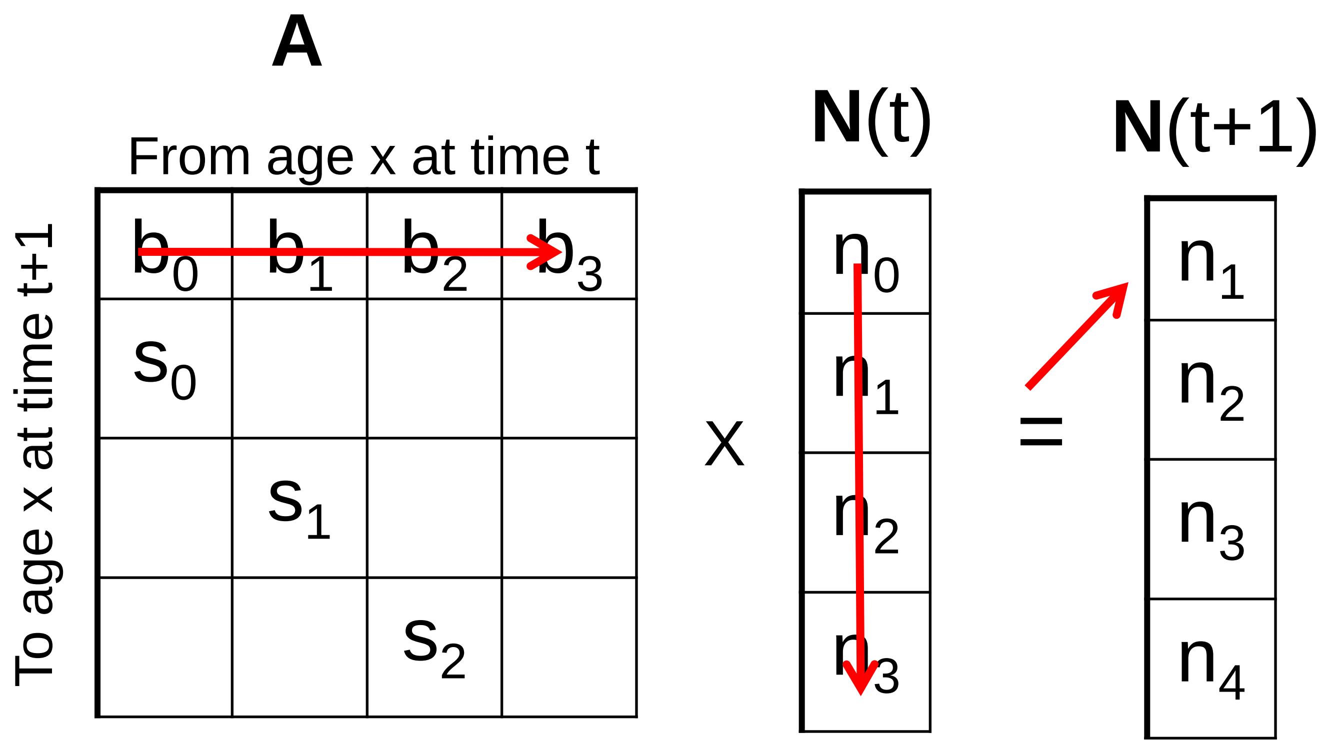
Projects population vector **N**(t) 1 time step:

N(t+1)=**AN**(t)

(order matters: vector multiplication is not commutative)

Example of to multiple a matrix and a vector

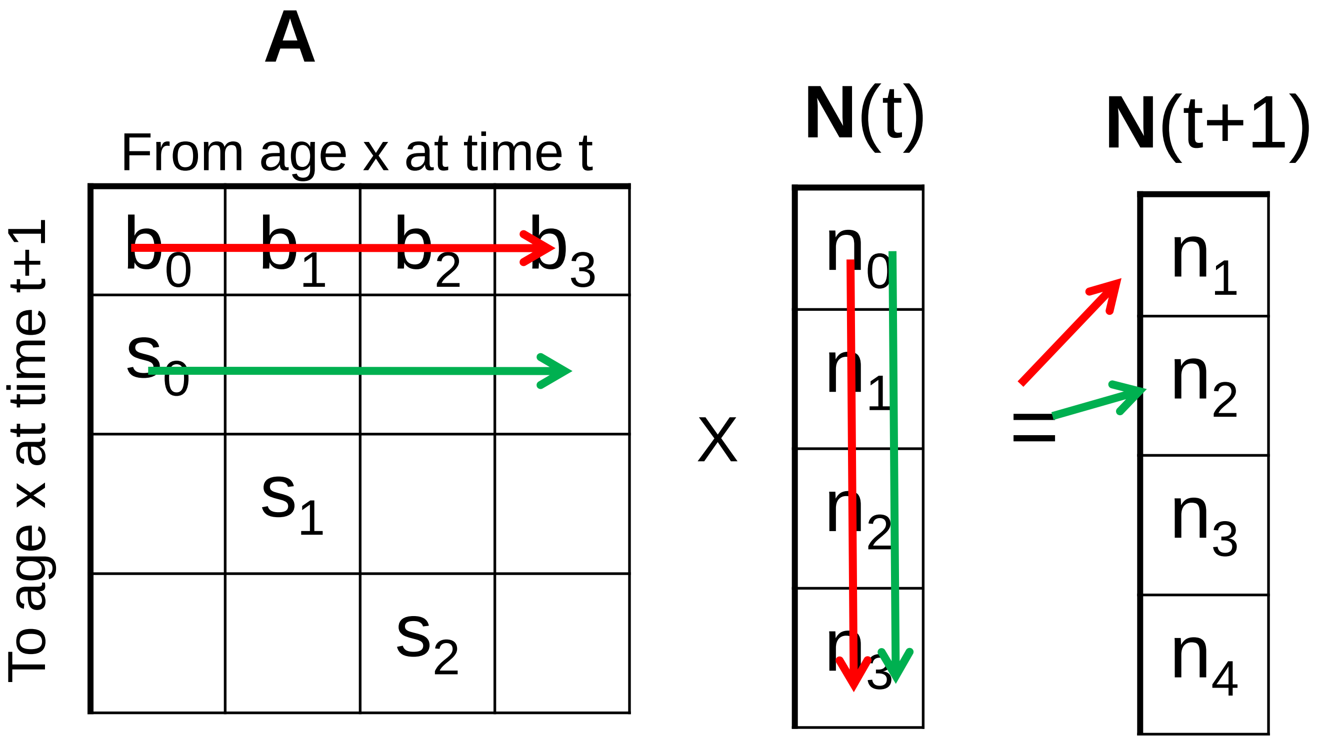
$$\mathbf{N}(t+1)=\mathbf{A}\mathbf{N}(t)$$



$$\begin{array}{c} \mathbf{A} \\ \begin{array}{c|cccc} & \multicolumn{4}{c}{\text{From age x at time t}} \\ \hline \text{To age x at time t+1} & b_0 & b_1 & b_2 & b_3 \\ & s_0 & & & \\ & & s_1 & & \\ & & & s_2 & \end{array} \end{array} \text{ X } \begin{array}{c} \mathbf{N}(t) \\ \hline n_0 \\ n_1 \\ n_2 \\ n_3 \end{array} = \begin{array}{c} \mathbf{N}(t+1) \\ \hline n_1 \\ n_2 \\ n_3 \\ n_4 \end{array}$$

Example of to multiple a matrix and a vector

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



A

From age x at time t

To age x at time t+1

N(t)

N(t+1)

$$\begin{array}{|c|c|c|c|} \hline b_0 & b_1 & b_2 & b_3 \\ \hline s_0 & & & \\ \hline & s_1 & & \\ \hline & & s_2 & \\ \hline \end{array} \times \begin{array}{|c|} \hline n_0 \\ \hline n_1 \\ \hline n_2 \\ \hline n_3 \\ \hline \end{array} = \begin{array}{|c|} \hline n_1 \\ \hline n_2 \\ \hline n_3 \\ \hline n_4 \\ \hline \end{array}$$

Age-Structured Population Models

$$\mathbf{A}=\begin{array}{|c|c|c|c|c|c|}\hline b_0 & b_1 & b_2 & b_3 & b_4 & b_5 \\ \hline s_0 & & & & & \\ \hline & s_1 & & & & \\ \hline & & s_2 & & & \\ \hline & & & s_3 & & \\ \hline & & & & s_4 & \\ \hline \end{array}$$

Leslie Matrix **A**

Can project Z steps:

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

$\mathbf{N}(t+2)=\mathbf{A}\mathbf{N}(t+1)=\mathbf{A}^2\mathbf{N}(t)$

$\mathbf{N}(t+z)=\mathbf{A}\mathbf{N}(t+z-1)=\mathbf{A}^z\mathbf{N}(t)$

Age-Structured Population Models

If $b_i>0$ and $b_j>0$, then the population will eventually reach a Stable Age Distribution (SAD), where the relative sizes of the age classes remain constant

Each time step every age class is larger by a factor of λ:

$N_{age}(t+1)=\lambda N_{age}(t)$

In full vector notation:

$\mathbf{N}_{SAD}(t+1)=\lambda \mathbf{N}_{SAD}(t)$

$\mathbf{N}_{SAD}(t+z)=\lambda^z \mathbf{N}_{SAD}(t)$

Exponential (density independent) population growth

From age x at time t

To age x at time t+1

b_0	b_1	b_2	b_3	b_4	b_5
s_0					
	s_1				
		s_2			
			s_3		
				s_4	

Age-Structured Population Models

(a) **Insect**

$$\begin{matrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{matrix}$$

(b) **Forest tree**

$$\begin{matrix} P_{11} & F_{21} & F_{31} & F_{41} & F_{51} \\ P_{12} & P_{22} & 0 & 0 & 0 \\ 0 & P_{23} & P_{33} & 0 & 0 \\ 0 & 0 & P_{34} & P_{44} & 0 \\ 0 & 0 & 0 & P_{45} & P_{55} \end{matrix}$$

(c) **Coral**

$$\begin{matrix} P_{ss} + F_{ss} & P_{ms} + F_{ms} & P_{ls} + F_{ls} \\ P_{sm} & P_{mm} & P_{lm} \\ P_{sl} & P_{ml} & P_{ll} \end{matrix}$$

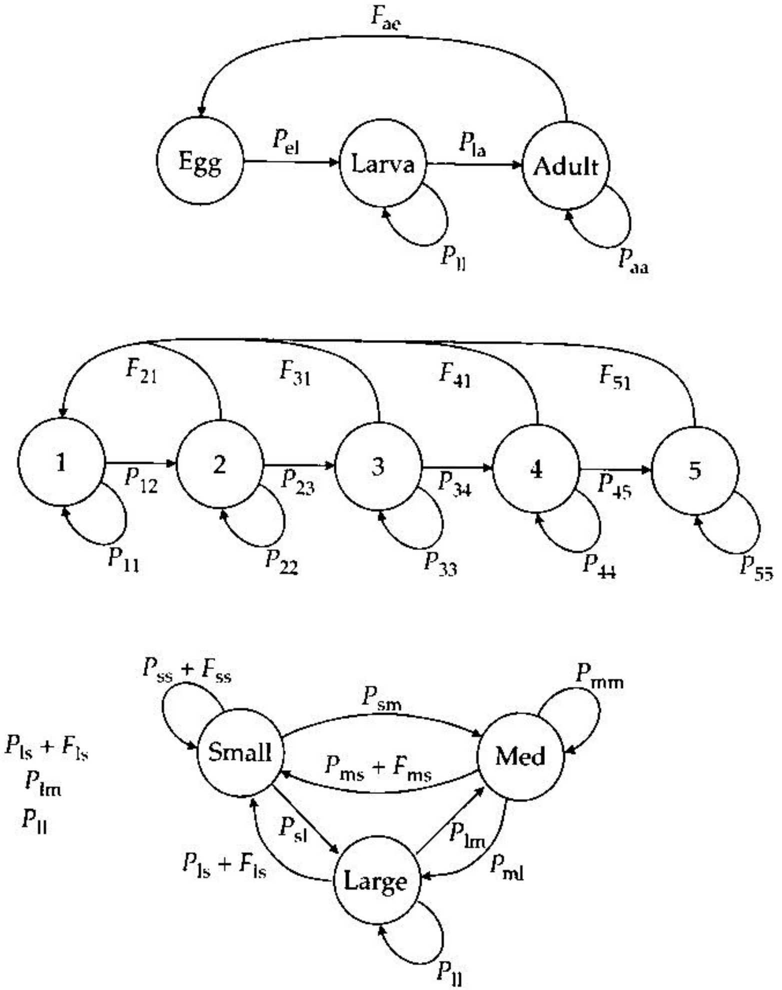


Figure 3.4 Stage-transition matrices and loop diagrams for different life histories. (a) Simplified insect life history. (b) Long-lived forest tree life history. (c) Coral life history, with sexual and asexual reproduction.