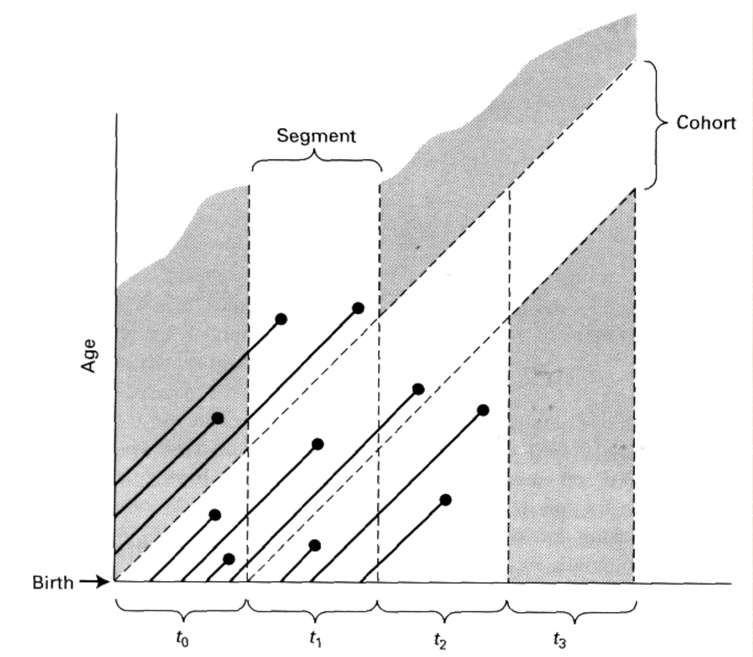
Age-dependent life-tables

- show organisms' mortality and reproduction as a function of age

Static (vertical) life-tables

- examination of a population during one segment (time interval)

- segment = group of individuals of different cohorts
- designed for long-lived organisms



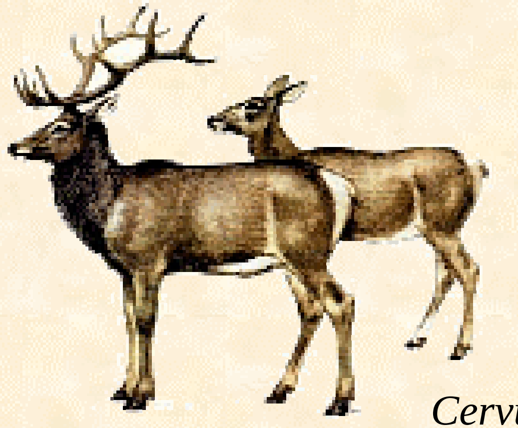
- ASSUMPTIONS:

- birth-rate and survival-rate are constant over time
- population does not grow

- DRAWBACKS: confuses age-specific changes in e.g. mortality with temporal variation

x	Sx	Dx	lx	px	qx	mx
1	129	15	1.000	0.884	0.116	0.000
2	114	1	0.884	0.991	0.009	0.000
3	113	32	0.876	0.717	0.283	0.310
4	81	3	0.628	0.963	0.037	0.280
5	78	19	0.605	0.756	0.244	0.300
6	59	-6	0.457	1.102	-0.102	0.400
7	65	10	0.504	0.846	0.154	0.480
8	55	30	0.426	0.455	0.545	0.360
9	25	16	0.194	0.360	0.640	0.450
10	9	1	0.070	0.889	0.111	0.290
11	8	1	0.062	0.875	0.125	0.280
12	7	5	0.054	0.286	0.714	0.290
13	2	1	0.016	0.500	0.500	0.280
14	1	-3	0.008	4.000	-3.000	0.280
15	4	2	0.031	0.500	0.500	0.290
16	2	2	0.016	0.000	1.000	0.280

Lowe (1969)



Cervus elaphus

S_x- number of survivors of a given age

D_x- number of dead

l_x- standardised number of survivors

q_x- age specific mortality

$$l_x = \frac{S_x}{S_0}$$

$$q_x = \frac{D_x}{S_x}$$

Cohort (horizontal) life-table

- examination of a population in a cohort = a group of individuals born at the same period
- followed from birth to death
- provide reliable information
- designed for short-lived organisms
- only females are included

x	Sx	Dx	lx	px	qx	mx
0	250	50	1.000	0.800	0.200	0.000
1	200	120	0.800	0.400	0.600	0.000
2	80	50	0.320	0.375	0.625	2.000
3	30	15	0.120	0.500	0.500	2.100
4	15	9	0.060	0.400	0.600	2.300
5	6	6	0.024	0.000	1.000	2.400
6	0	0	0.000			

Vulpes vulpes

Stage or size-dependent life-tables

- survival and reproduction depend on stage / size rather than age
- age-distribution is of no interest
- used for invertebrates (insects, invertebrates)
- time spent in a stage / size can differ

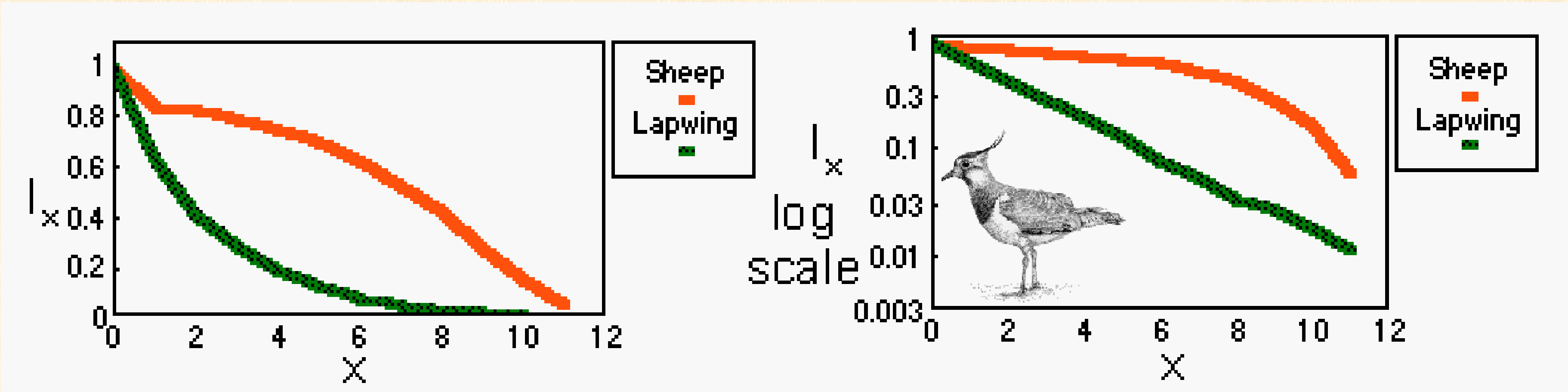
Campbell (1981)

x	Sx	Dx	lx	px	qx	mx
Egg	450	68	1.000	0.849	0.151	0
Larva I	382	67	0.849	0.825	0.175	0
Larva II	315	158	0.700	0.498	0.502	0
Larva III	157	118	0.349	0.248	0.752	0
Larva IV	39	7	0.087	0.821	0.179	0
Larva V	32	9	0.071	0.719	0.281	0
Larva VI	23	1	0.051	0.957	0.043	0
Pre-pupa	22	4	0.049	0.818	0.182	0
Pupa	18	2	0.040	0.889	0.111	0
Adult	16	16	0.036	0.000	1.000	185

Lymantria dispar

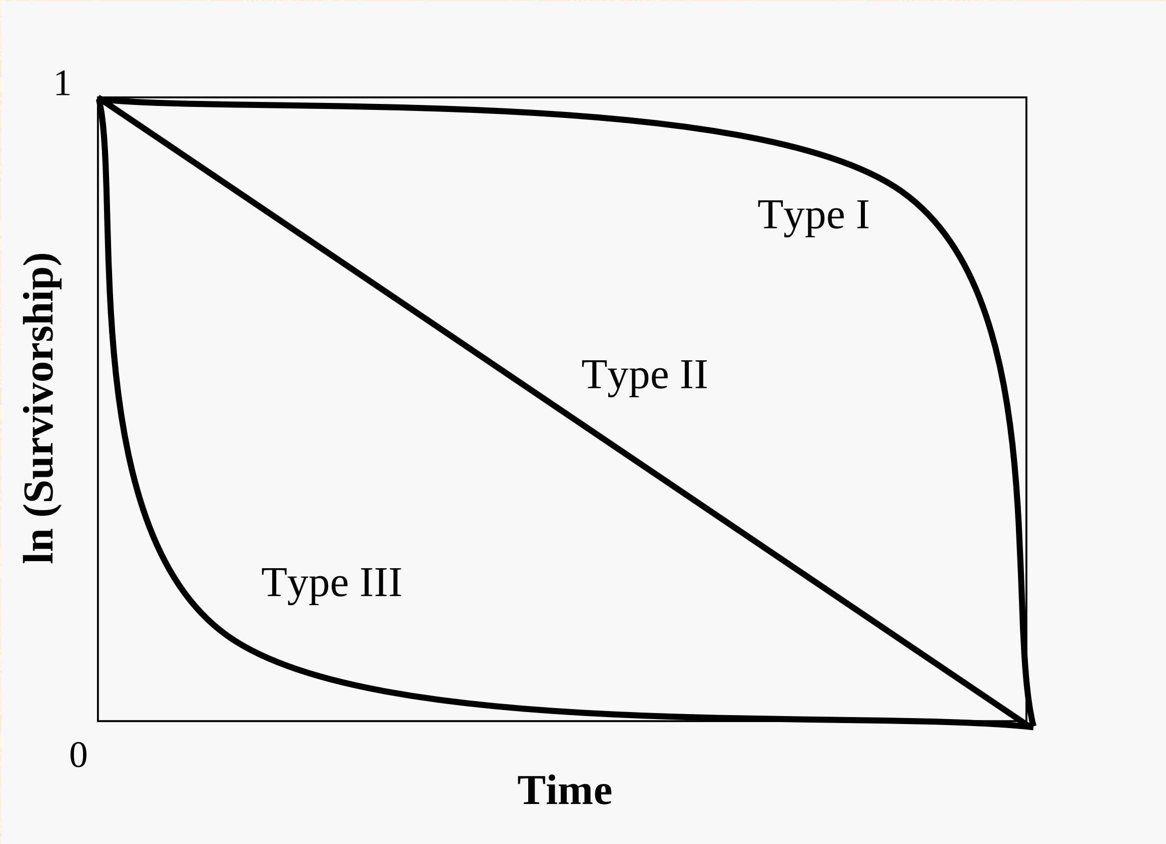
Survivorship curves

- display change in survival by plotting ln($\boldsymbol{l}_x$) against age (***x***)
- logarithmic transformation allows to compare survival based on different population size
- sheep mortality increases with age
- survivorship of lapwing (*Vanellus*) is independent of age



Pearls (1928) classified hypothetical age-specific mortality:

- Type I .. mortality is concentrated at the end of life span (humans)
- Type II .. mortality ($\boldsymbol{q_x}$) is constant over age (seeds),
- Type III .. mortality is highest in the beginning of life (invertebrates, fish, reptiles)

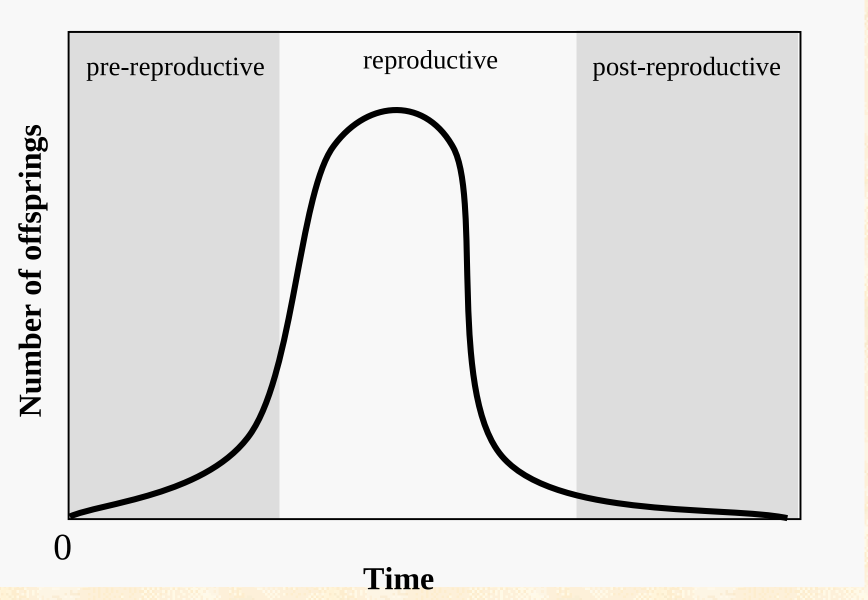


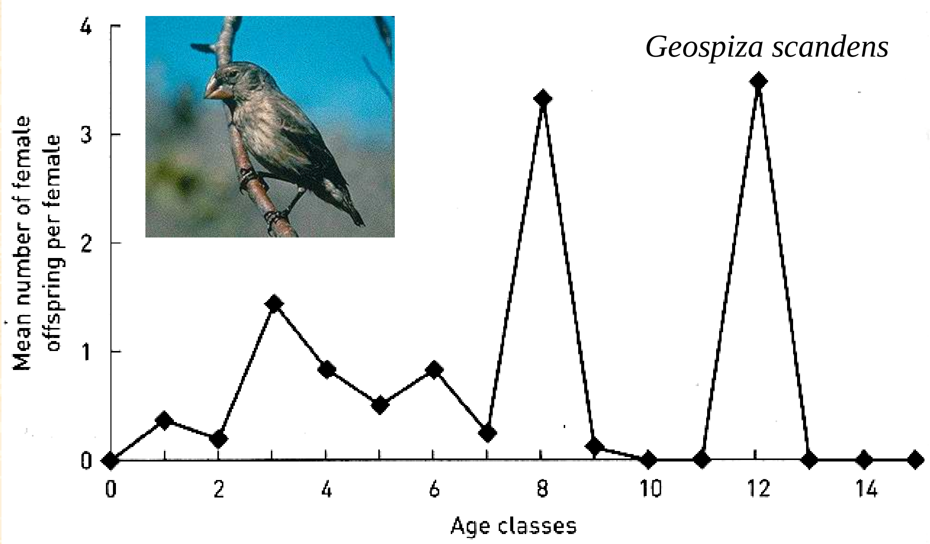
Birth rate curves

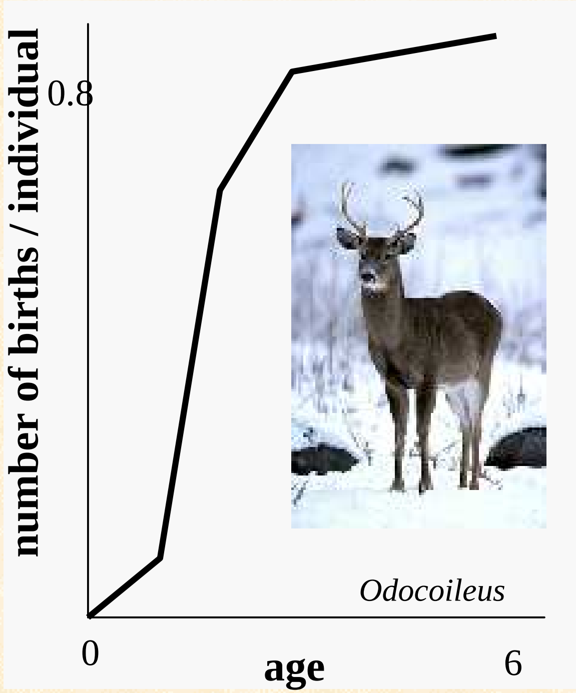
- fecundity - potential number of offspring
- fertility - real number of offspring

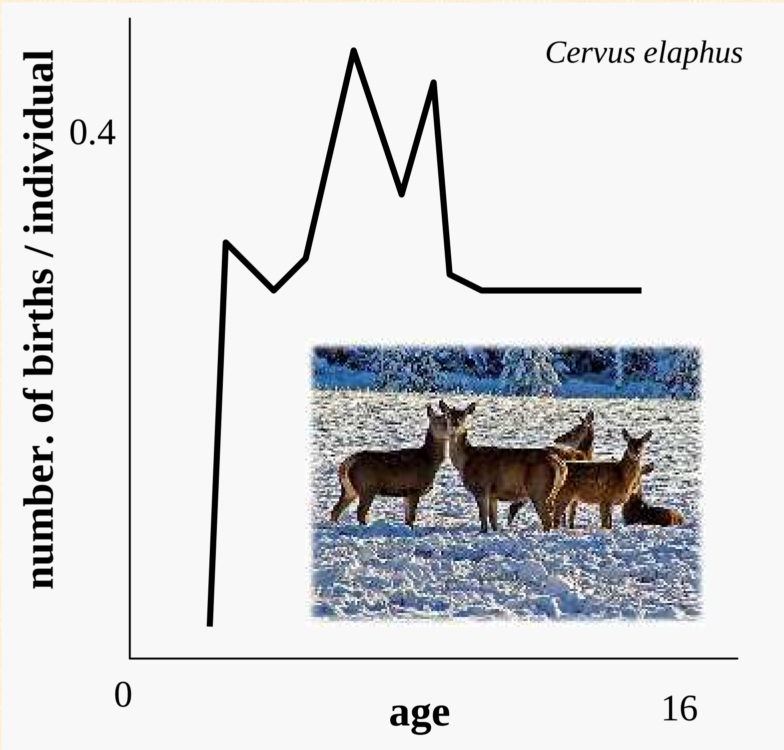
- semelparous .. reproducing once a life
- iteroparous .. reproducing several times during life

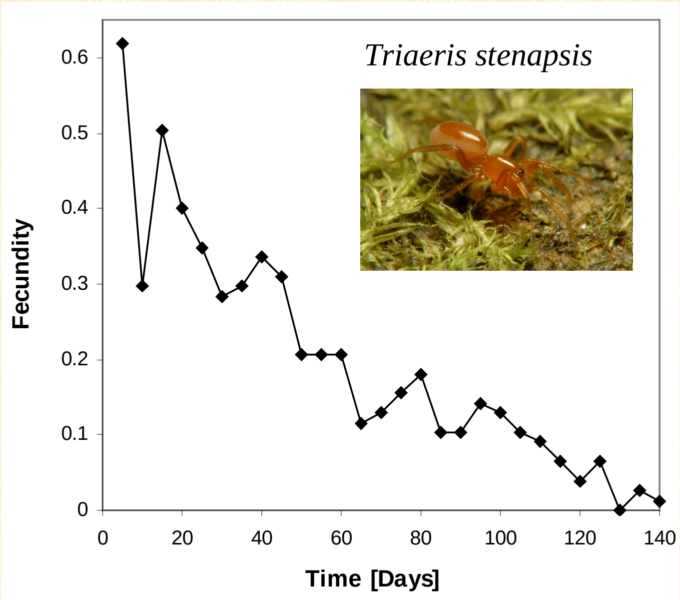
- birth pulse .. discrete reproduction (seasonal reproduction)
- birth flow .. continuous reproduction




Geospiza scandens
Mean number of female offspring per female
Age classes
0
1
2
3
4
6
8
10
12
14


number of births / individual
0.8
Odocoileus
0
age
6


Cervus elaphus
number. of births / individual
0.4
0
age
16


Triaeris stenapsis
Fecundity
0.6
0.5
0.4
0.3
0.2
0.1
0
20
40
60
80
100
120
140
Time [Days]

Matrix (structured) models

- model of Leslie (1945) uses parameters (survival and fecundity) from life-tables
- where populations are composed of individuals of different age, stage or size with specific births and deaths
- used for modelling of density-independent processes (exponential growth)

$\mathbf{N}_{x,t}$ .. no. of organisms in age x and time t
G_x .. probability of persistence in the same size/stage

- number of individuals in the first age class

$$N_{0,t+1} = \sum_{x=0}^{n} N_{x,t} F_x = N_{0,t} F_0 + N_{1,t} F_1 + \ldots$$

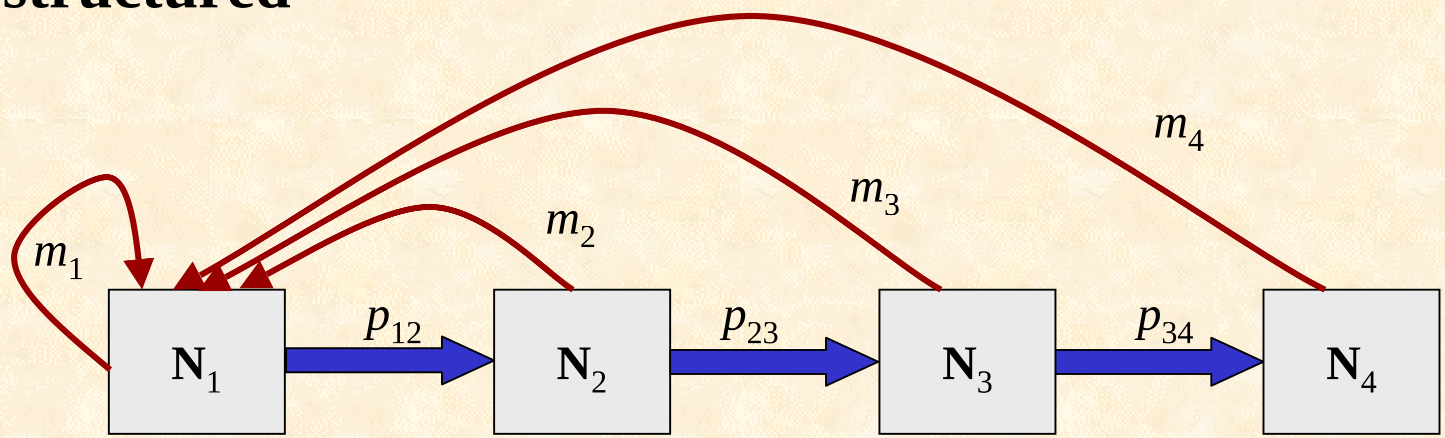
- number of individuals in the remaining age classes

$$N_{x+1,t+1} = N_{x,t} p_x$$

- combined into one matrix formula:

$$\mathbf{N}_{t+1} = \mathbf{N}_t \mathbf{A}$$

Age-structured



$$\begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ p_{12} & 0 & 0 & 0 \\ 0 & p_{23} & 0 & 0 \\ 0 & 0 & p_{34} & 0 \end{bmatrix} \times \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ N_{3,t} \end{bmatrix} = \begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \end{bmatrix}$$

transition matrix **A** — age distribution vectors $\mathbf{N_t}$

- each column in **A** specifies fate of an organism in a specific age:

3rd column: organism in age 2 produces $\boldsymbol{F_2}$ offspring and goes to age 3 with probability $\boldsymbol{p_{23}}$

- **A** is always a square matrix
- $\mathbf{N}_t$ is always one column matrix = a vector

- fertilities (*F*) and survivals (*p*) depend on whether population has discrete or continuous reproduction

- for populations with discrete pulses post-reproductive survivals and fertilities are

$$p_x = \frac{S_{x+1}}{S_x}$$

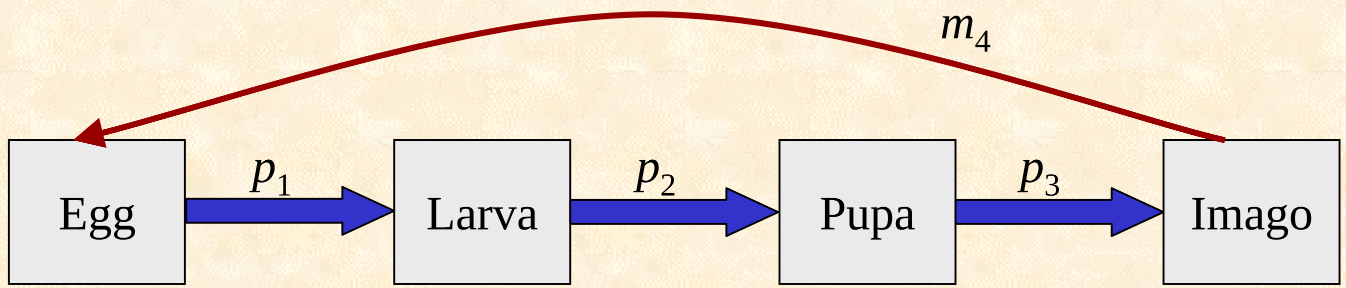
$$F_x = p_x m_x$$

- for populations with continuous reproduction post-reproductive survivals and fertilities are

$$p_x \approx \left(\frac{S_x + S_{x+1}}{S_{x-1} + S_x} \right)$$

$$F_x = \frac{(1 + S_1)(m_x p_x m_{x+1})}{4}$$

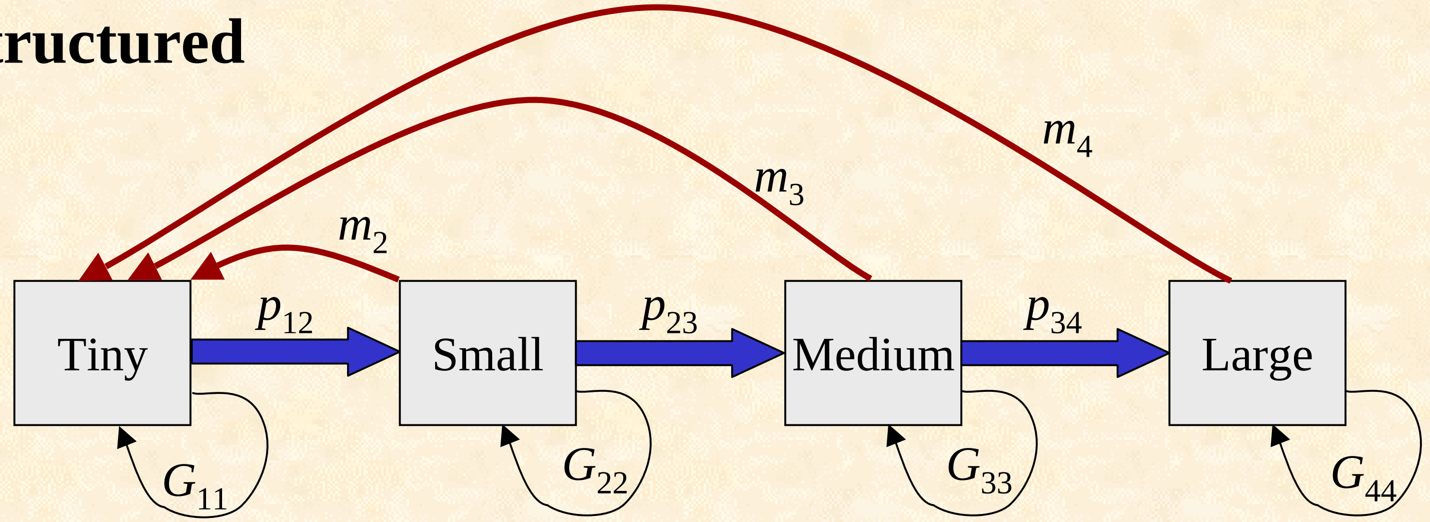
Stage-structured



- only imagoes reproduce thus $m_{1,2,3} = 0$
- no imago survives to another reproduction period: $p_4 = 0$

$$\begin{bmatrix} 0 & 0 & 0 & m_4 \\ p_{12} & 0 & 0 & 0 \\ 0 & p_{23} & 0 & 0 \\ 0 & 0 & p_{34} & 0 \end{bmatrix}$$

Size-structured



- model of Lefkovitch (1965) uses 3 parameters (mortality, fecundity and persistence)
- $F_1 = 0$

$$\begin{bmatrix} G_{11} & F_2 & F_3 & F_4 \\ p_{12} & G_{22} & 0 & 0 \\ 0 & p_{23} & G_{33} & 0 \\ 0 & 0 & p_{34} & G_{44} \end{bmatrix}$$

Matrix operations

- addition / subtraction

$$\begin{bmatrix} 2 & 3 \\ 5 & 7 \end{bmatrix} + \begin{bmatrix} 1 & 4 \\ 5 & 8 \end{bmatrix} = \begin{bmatrix} 3 & 7 \\ 10 & 15 \end{bmatrix}$$

- multiplication

by a scalar

$$\begin{bmatrix} 2 & 3 \\ 5 & 7 \end{bmatrix} \times 3 = \begin{bmatrix} 6 & 9 \\ 15 & 21 \end{bmatrix}$$

by a vector

$$\begin{bmatrix} 2 & 3 \\ 5 & 7 \end{bmatrix} \times \begin{bmatrix} 4 \\ 5 \end{bmatrix} = \begin{bmatrix} 2\times 4 + 3\times 5 \\ 5\times 4 + 7\times 5 \end{bmatrix} = \begin{bmatrix} 23 \\ 55 \end{bmatrix}$$

- determinant

$$\begin{bmatrix} 2 & 3 \\ 4 & 7 \end{bmatrix} = 2\times 7 - 4\times 3 = 2$$

- eigenvalue (λ)

$$\begin{bmatrix} 2 & 4 \\ 0.25 & 0 \end{bmatrix} = \begin{bmatrix} 2-\lambda & 4 \\ 0.25 & 0-\lambda \end{bmatrix} = (2-\lambda)\times(0-\lambda) - (0.25\times 4) = \lambda^2 - 2\lambda - 1$$

$$\lambda_{1,2} = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

$\lambda_1 = 2.41$

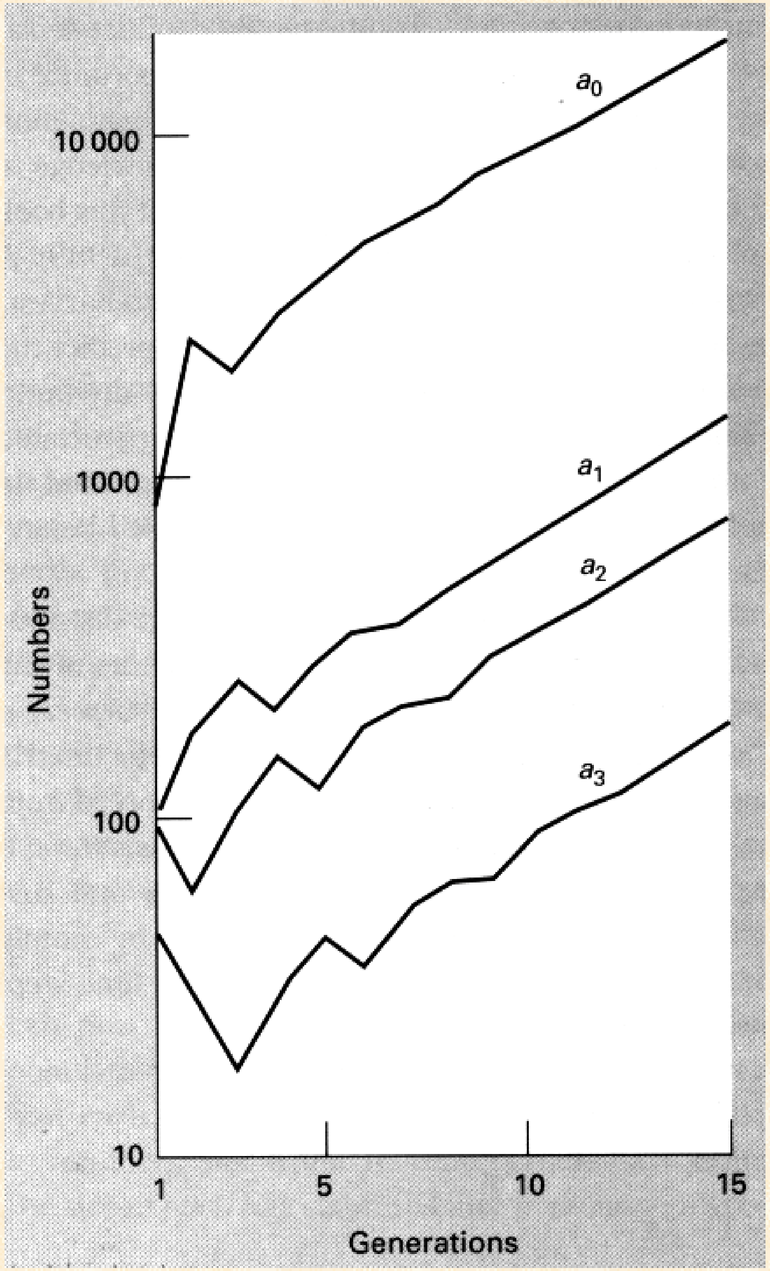
$\lambda_2 = -0.41$

$$\mathbf{N}_{t2} = \mathbf{N}_{t1}\mathbf{A}$$

$$\mathbf{N}_{t3} = \mathbf{N}_{t2}\mathbf{A}$$

$$\mathbf{N}_{t+2} = \mathbf{N}_{t1}\mathbf{A}\mathbf{A} = \mathbf{A}^2\mathbf{N}_t$$

$$\mathbf{N_t} = \mathbf{N_0}\mathbf{A^t}$$



- parameters are constant over time and independent of population density
- follows constant exponential growth after initial damped oscillations

Excercise 1

Population density of the true bugs *Coreus marginatus* was recorded for 10 years. Here are the densities:

160, 172, 188, 154, 176, 185, 168, 194, 170, 169

- Does population increase or decrease?
- What is the average population growth (R)?
- Project population for another 10 years using R and $N_0 = 90$.
- Simulate population growth for the next 20 years using observed finite-growth rates.

```
bug<-c(160, 172, 188, 154, 176, 185, 168, 194, 170, 169)
plot(bug,type="b")

lambda<-bug[-1]/bug[-10]
lambda
plot(lambda)

R<-prod(lambda)^0.1
R

time<-1:10
Nt<-90*R^time
plot(time,Nt,type="b")

sim<-sample(lambda,20,replace=T)
years<-20
N<-numeric(years+1)
N[1]<-100
for(t in 1:years) N[t+1]<-{
N[t]*sim[t]}
plot(0:years,N,type="b")
```

Excercise 2

Population density of the mite *Acarus siro* was recorded every 3 days during 28 days. The following densities were found:

165, 145, 139, 125, 105, 101, 88, 81, 73, 69

- What is the intrinsic rate of increase (*r*) and what was the initial density ?
- How long it takes for a population to decrease to half size?
- Project population growth for another 5 weeks using estimated *r* and N_0 = 69.
- What would be the estimated rate if you know the initial and final density?