# Population structure

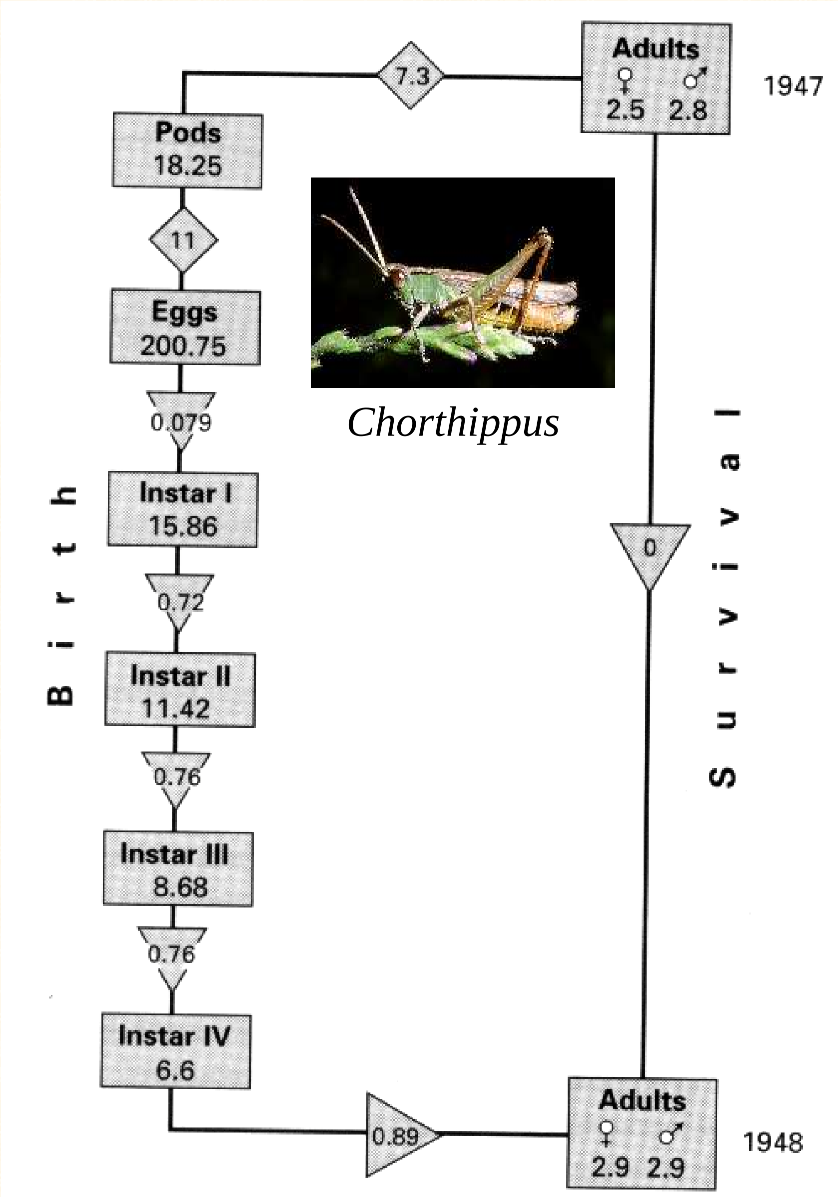
- **Demography** - study of organisms with special attention to stage or age structure
- processes associated with age, stage or size

$x$ .. age/stage/size category

$p_x$ .. age/stage/size specific survival

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

$m_x$ .. reproductive rate (expected average number of offspring per female)

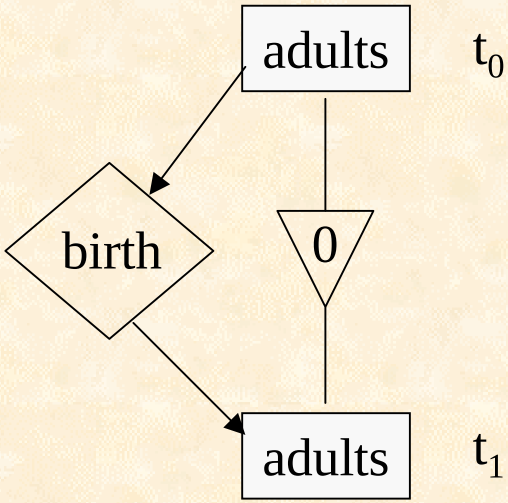



*Chorthippus*

Richards & Waloff (1954)

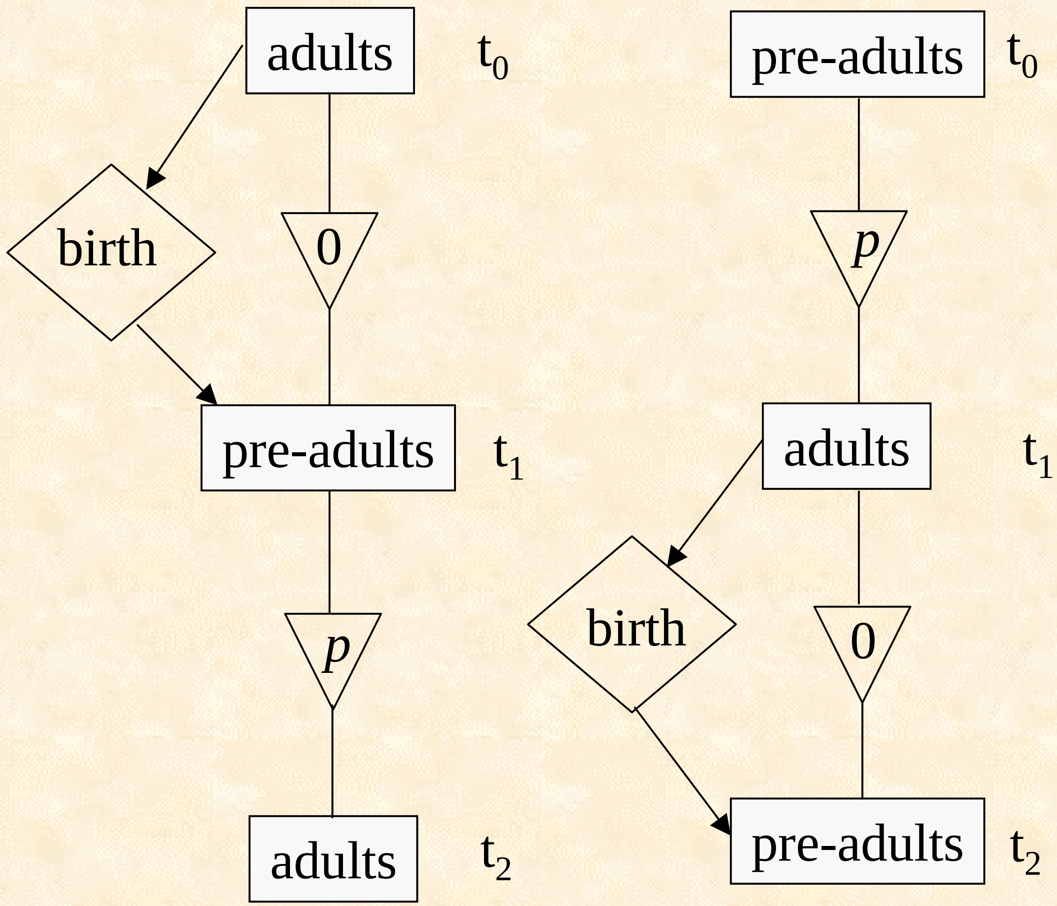
- main focus on births and deaths
- immigration & emigration is ignored
- no adult survive
- one (not overlapping) generation per year
- egg pods over-winter
- despite high fecundity they just replace themselves

# Annual species



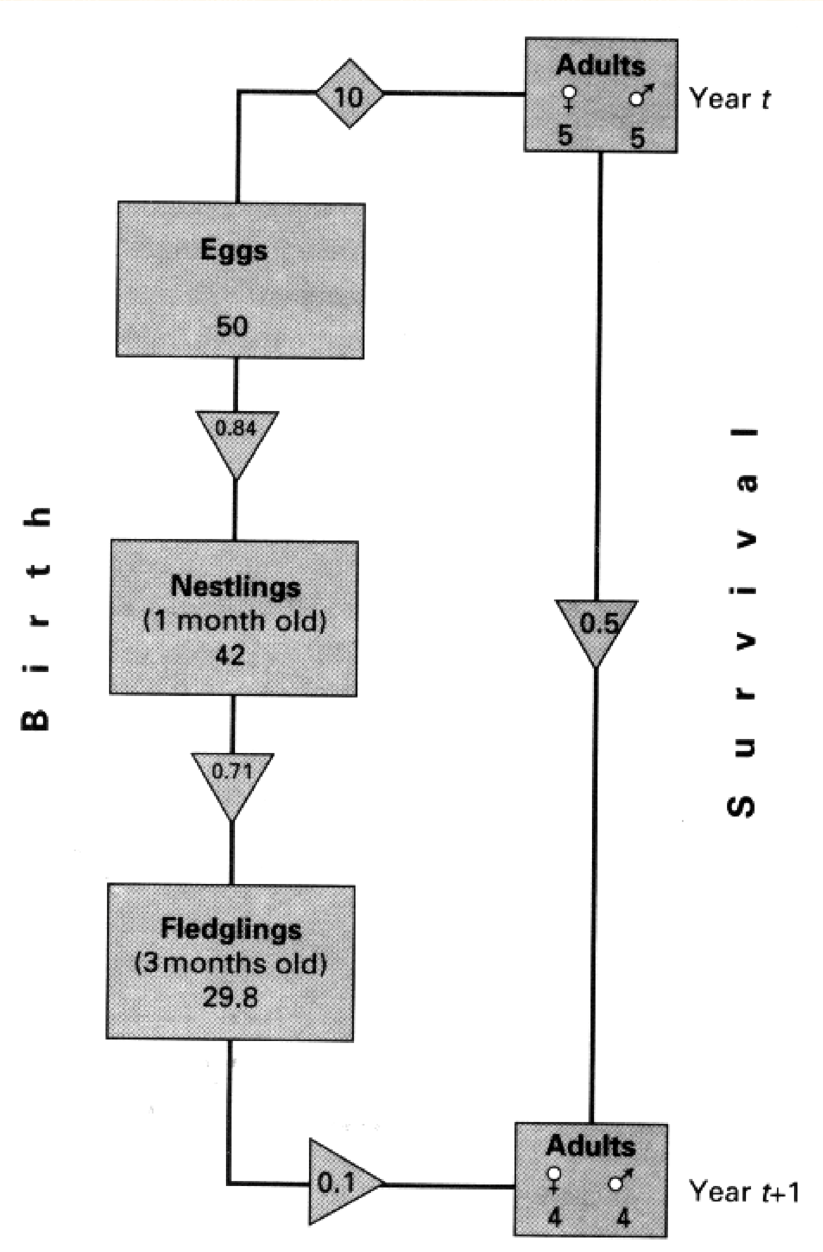

- breed at discrete periods
- no overlapping generations

# Biennal species




- breed at discrete periods
- adult generation may overlap

Perins (1965)




# Perennial species

- breed at discrete periods
- breeding adults consist of individuals of various ages (1-5 years)
- adults of different generations are equivalent
- overlapping generations

*Parus major*

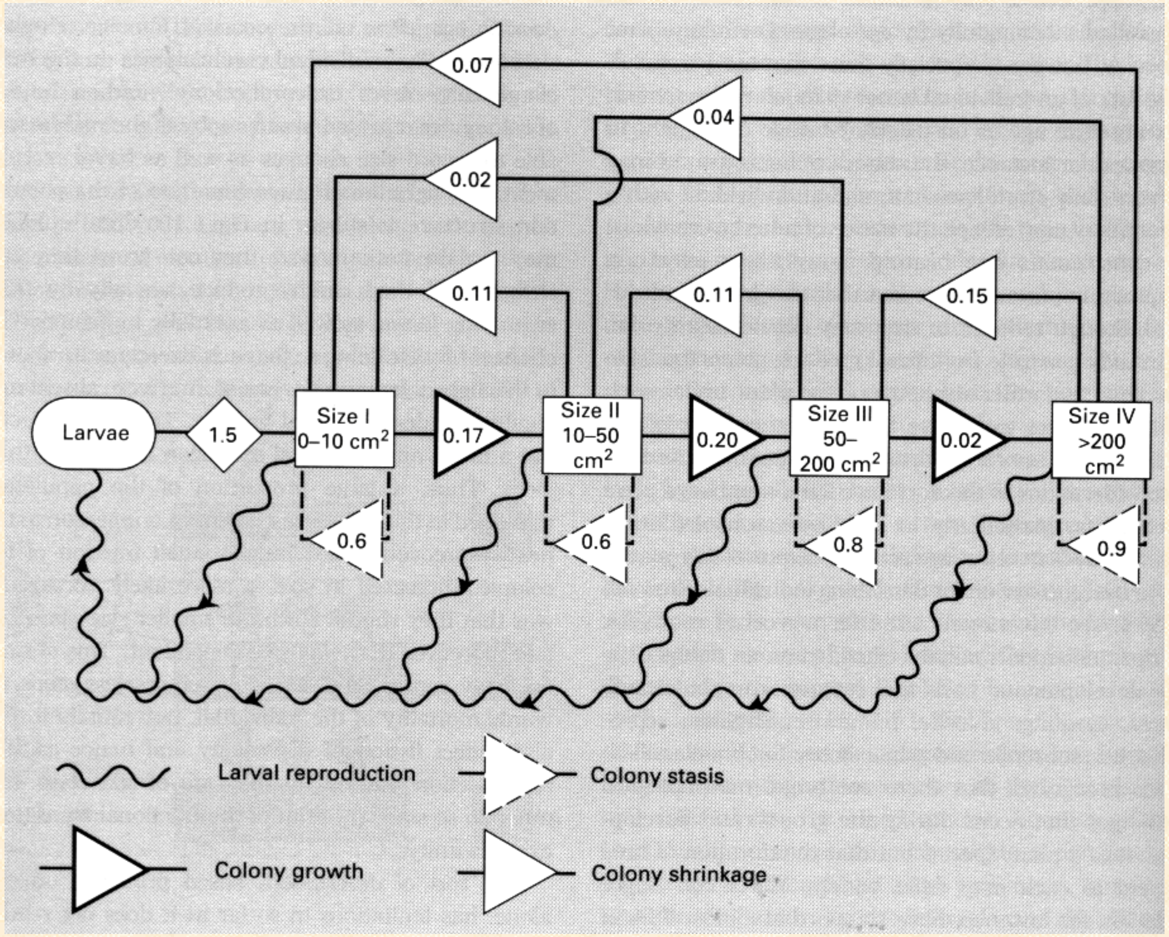
# Age-size-stage life-table

*Agaricia agaricites*

- age/stage classification is based on developmental time

- size may be more appropriate than age (fish, sedentery animals)

- Hughes (1984) used combination of age/stage and size for the description of coral growth



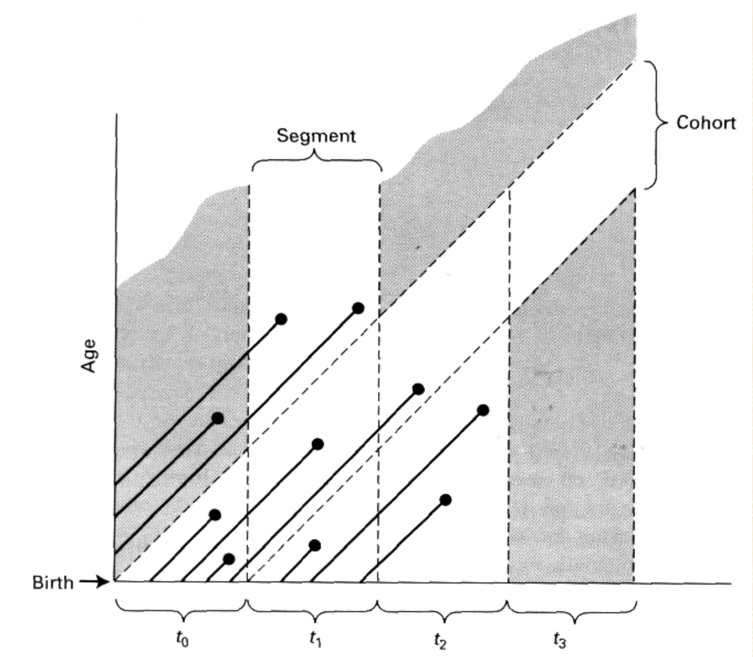
# Age-dependent life-tables

- 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



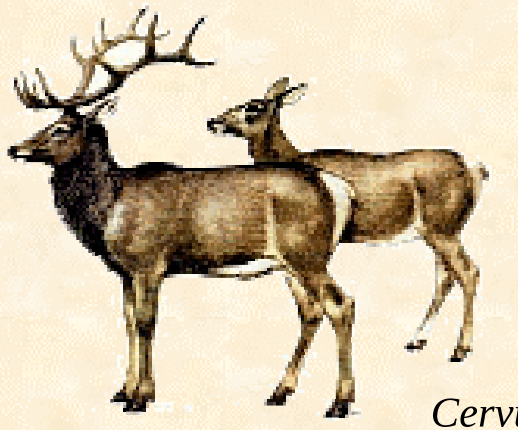

- ASSUMPTIONS:

- 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

$D_x$- number of dead individuals

$$D_x = S_x - S_{x+1}$$

$l_x$- standardised number of survivors

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

$q_x$- age specific mortality

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

# 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

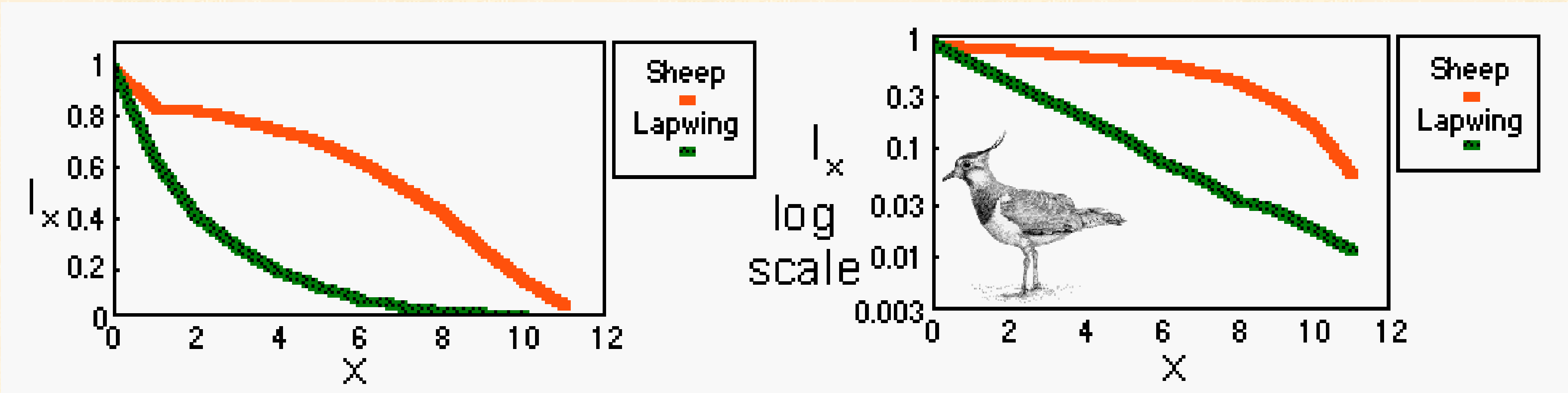
Campbell (1981)

| 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*

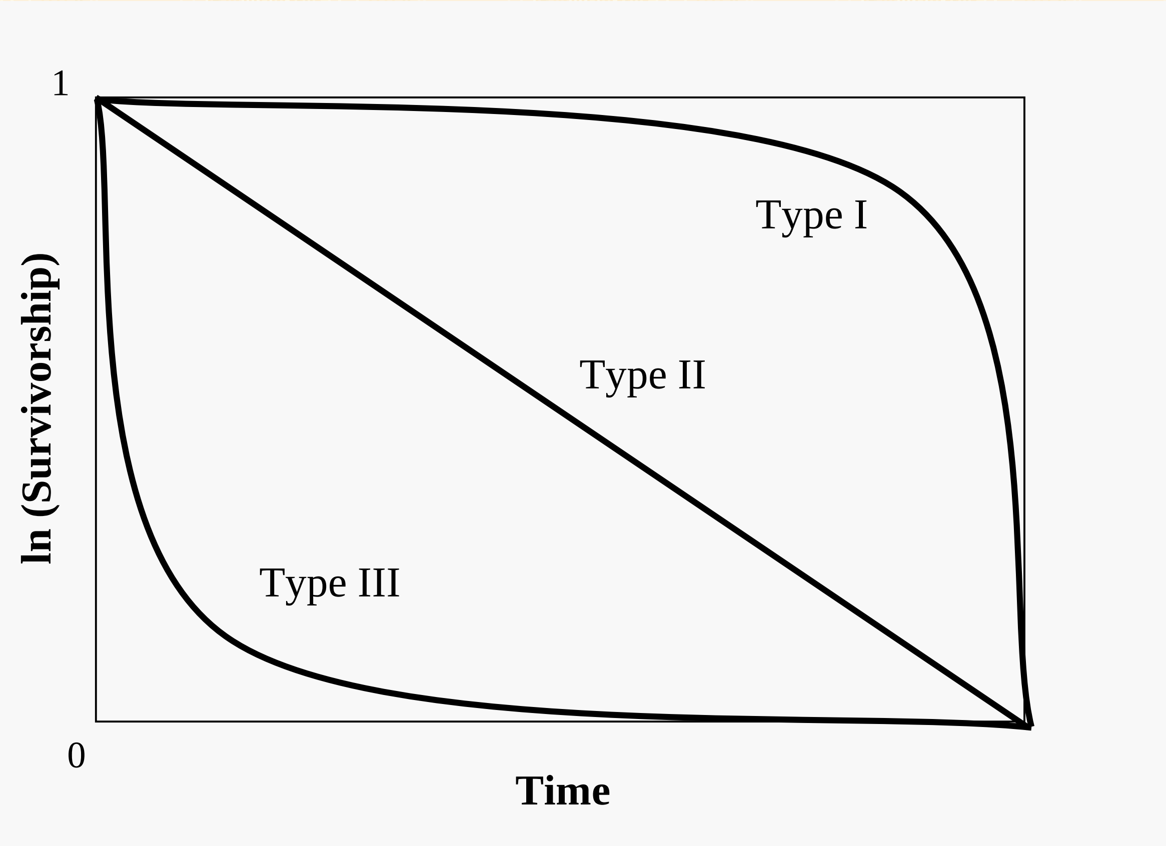
# Survivorship curves

- display change in survival by plotting log($\boldsymbol{l_x}$) against age ($\boldsymbol{x}$)
- 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 is constant over age (seeds, birds)
- Type III .. mortality is highest in the beginning of life (invertebrates, fish, reptiles)

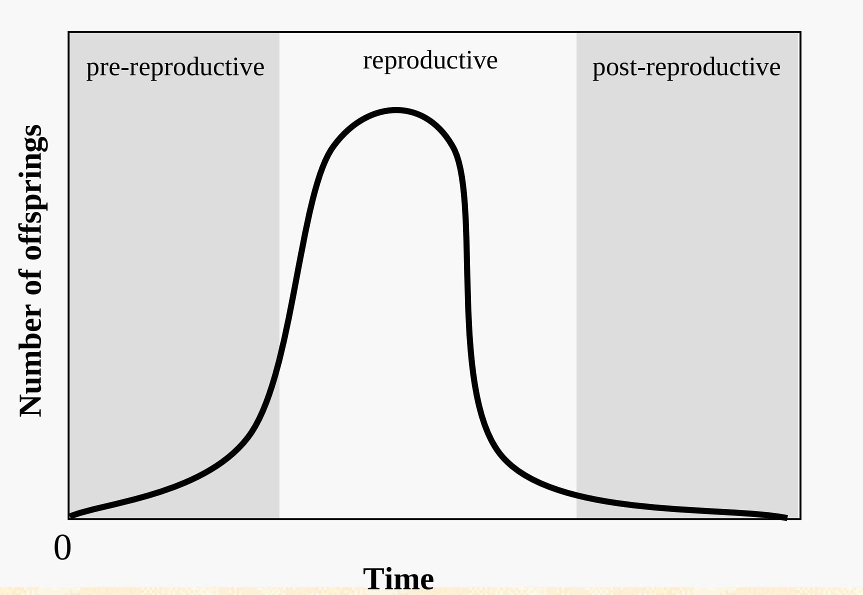


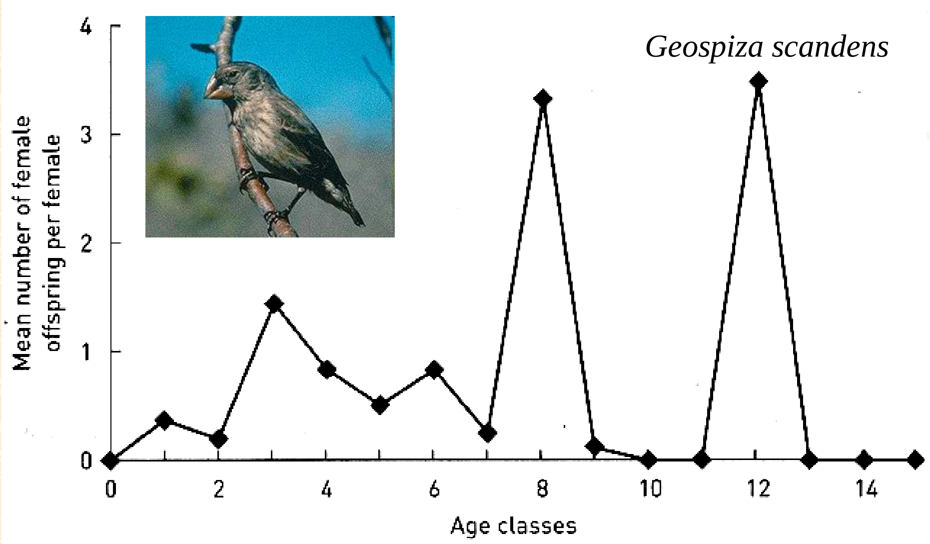
# Birth rate curves

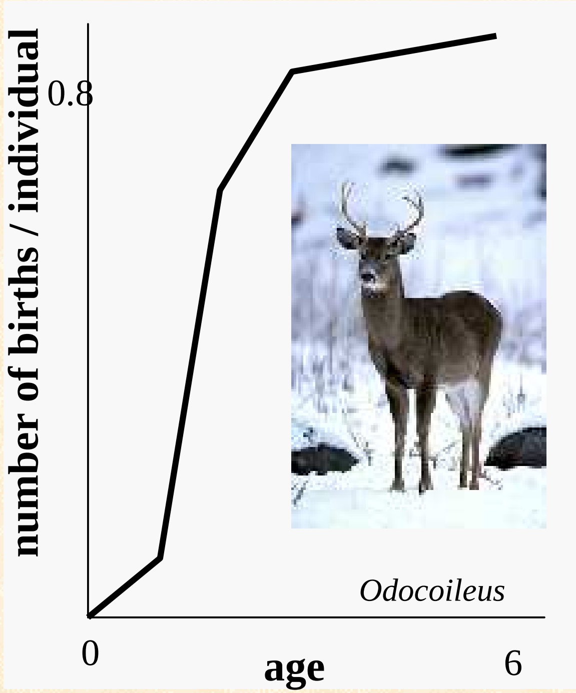
- fecundity - potential number of offspring
- fertility - real number of offspring

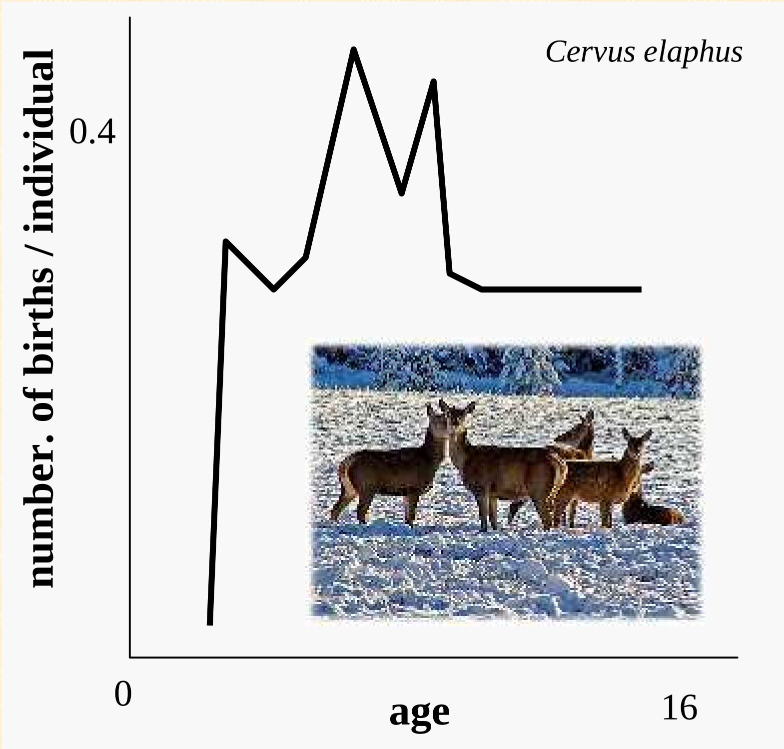
- semelparous .. reproducing once a life
- iteroparous .. reproducing several times during life

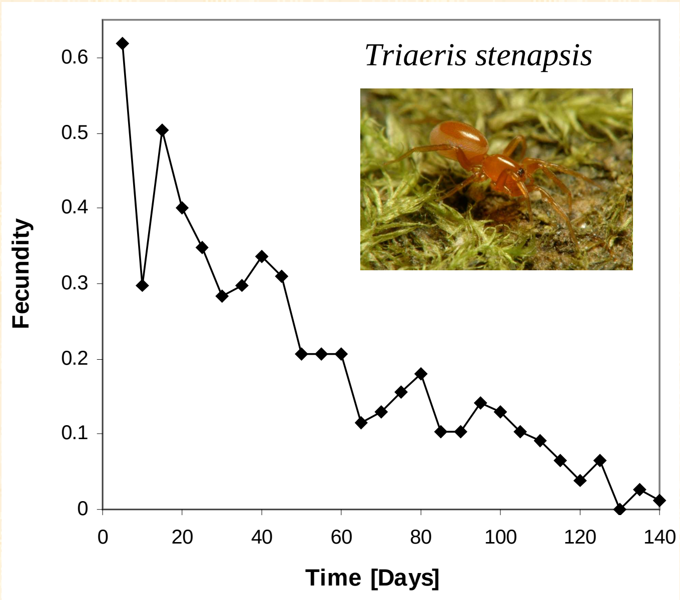
- birth pulse .. discrete reproduction (seasonal reproduction)
- birth flow .. continuous reproduction




Geospiza scandens
Mean number of female offspring per female
Age classes
0
1
2
3
4
0
2
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
0.1
0.2
0.3
0.4
0.5
0.6
0
20
40
60
80
100
120
140
Time [Days]

# Key-factor analysis

- k-value - **killing power** - another measure of mortality

$$k = -\log(p)$$

- k-values are additive unlike ***q***

$$K = \sum k_x$$

- **Key-factor analysis -** a method to identify the most important factors that regulates population dynamics

- k-values are estimated for a number of years

- important factors are identified by regressing $\boldsymbol{k_x}$ on log($N$)

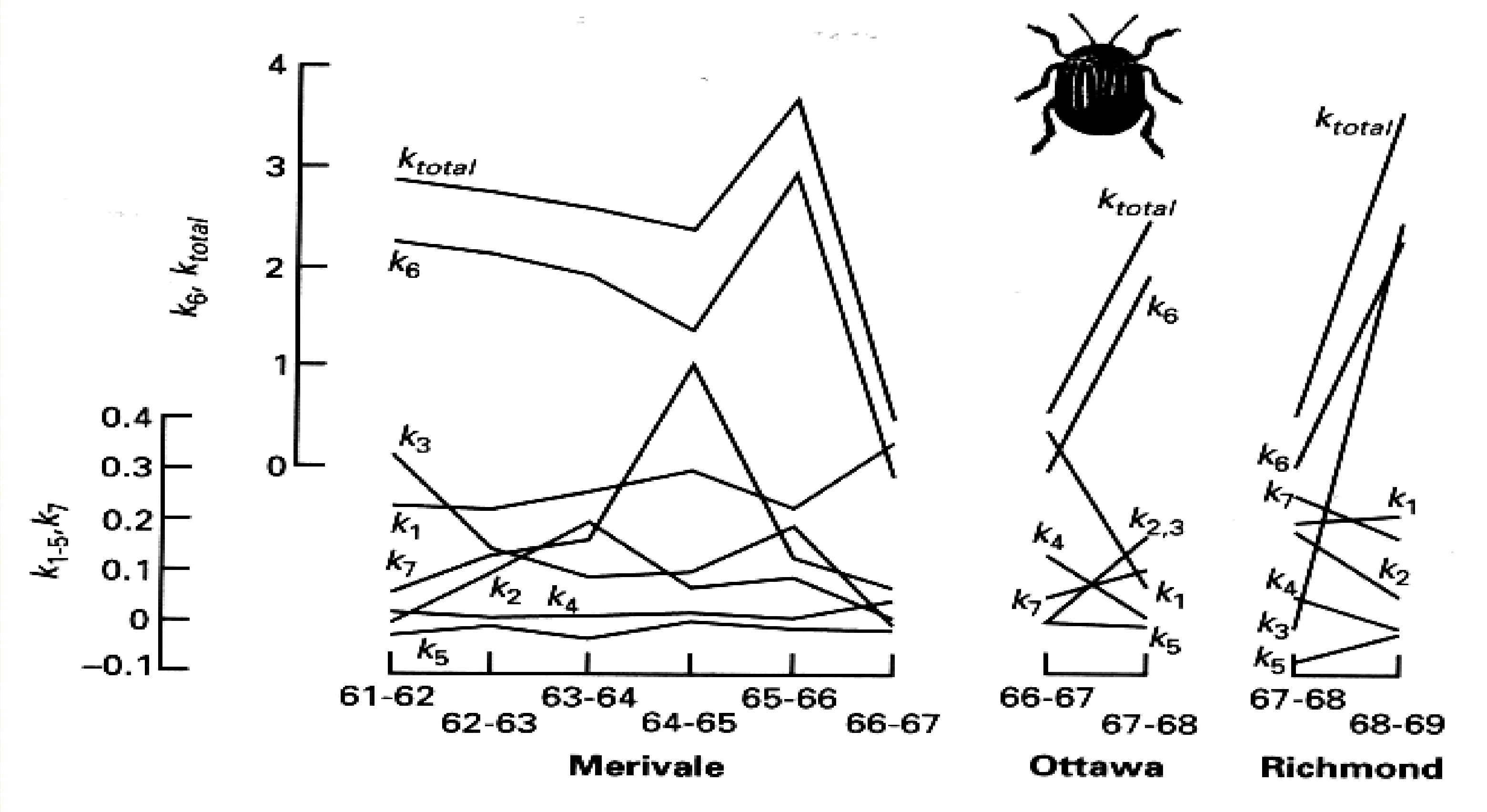
# *Leptinotarsa decemlineata*

- over-wintering adults emerge in June → eggs are laid in clusters on the lower side of leafs → larvae pass through 4 instars → form pupal cells in the soil → summer adults emerge in August → begin to hibernate in September
- mortality factors overlap

Harcourt (1971)

| Age interval | Numbers per 96 potato hills | Numbers 'dying' | 'Mortality factor' | $\log_{10} N$ | *k*-value | |
|---|---|---|---|---|---|---|
| Eggs | 11 799 | 2531 | Not deposited | 4.072 | 0.105 | ($k_{1a}$) |
| | 9268 | 445 | Infertile | 3.967 | 0.021 | ($k_{1b}$) |
| | 8823 | 408 | Rainfall | 3.946 | 0.021 | ($k_{1c}$) |
| | 8415 | 1147 | Cannibalism | 3.925 | 0.064 | ($k_{1d}$) |
| | 7268 | 376 | Predators | 3.861 | 0.024 | ($k_{1e}$) |
| Early larvae | 6892 | 0 | Rainfall | 3.838 | 0 | ($k_2$) |
| Late larvae | 6892 | 3722 | Starvation | 3.838 | 0.337 | ($k_3$) |
| Pupal cells | 3170 | 16 | *D. doryphorae* | 3.501 | 0.002 | ($k_4$) |
| Summer adults | 3154 | −126 | Sex (52% female) | 3.499 | −0.017 | ($k_5$) |
| Female × 2 | 3280 | 3264 | Emigration | 3.516 | 2.312 | ($k_6$) |
| Hibernating adults | 16 | 2 | Frost | 1.204 | 0.058 | ($k_7$) |
| Spring adults | 14 | | | 1.146 | | |
| | | | | | 2.926 | ($k_{total}$) |

# Summary over 10 years




- highest k-value indicates the role of a factor in each generation
- profile of a factor parallel with the ***K*** profile reveals the key factor
- emigration is the key-factor

# 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)

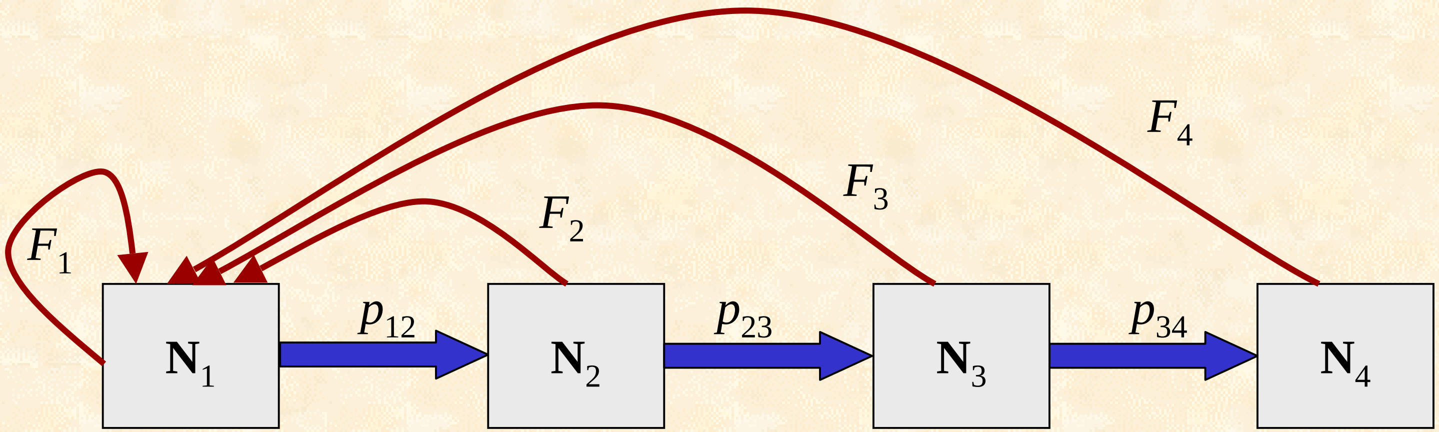
$\mathbf{N}_{x,t}$ .. no. of organisms in age *x* and time *t*

$G_x$ .. probability of persistence in the same size/stage

$F_x$ .. age/stage specific fertility

$p_x$ .. age/stage specific survival

## Age-structured




- class 0 is omitted
- number of individuals in the first age class

$$N_{1,t+1} = \sum_{x=1}^{n} N_{x,t} F_x = N_{1,t} F_1 + N_{2,t} F_2 + \ldots$$

- number of individuals in the remaining age class

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

$$\begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ p_{12} & 0 & 0 & 0 \\ 0 & p_{23} & 0 & 0 \\ 0 & 0 & p_{34} & 0 \end{bmatrix} \times \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \end{bmatrix} = \begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix}$$

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

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

- 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/fecundities ($F$) and survivals ($p$) depend on whether population has discrete or continuous reproduction

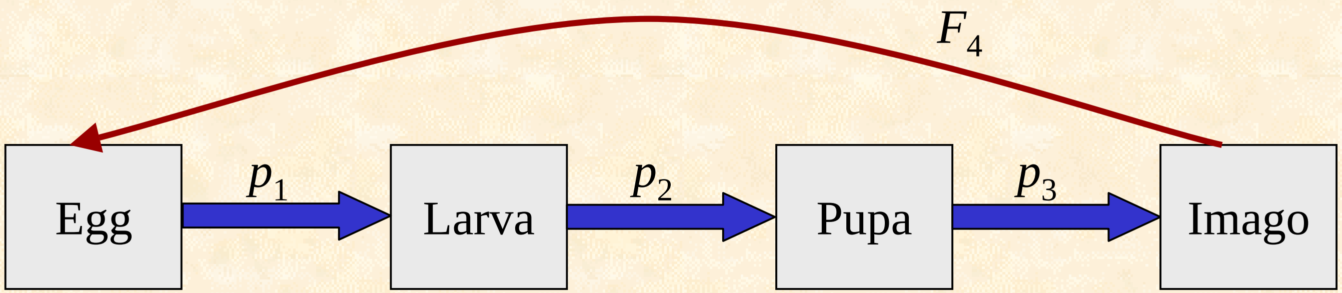
- for populations with discrete pulses post-reproductive survivals and fertilities are

$$p_x = \frac{S_{x+1}}{S_x} \qquad F_x = p_0 m_x$$

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

$$p_x \approx \left( \frac{S_x + S_{x+1}}{S_{x-1} + S_x} \right) \qquad F_x = \frac{(1 + S_1)(m_x p_0 m_{x+1})}{4}$$

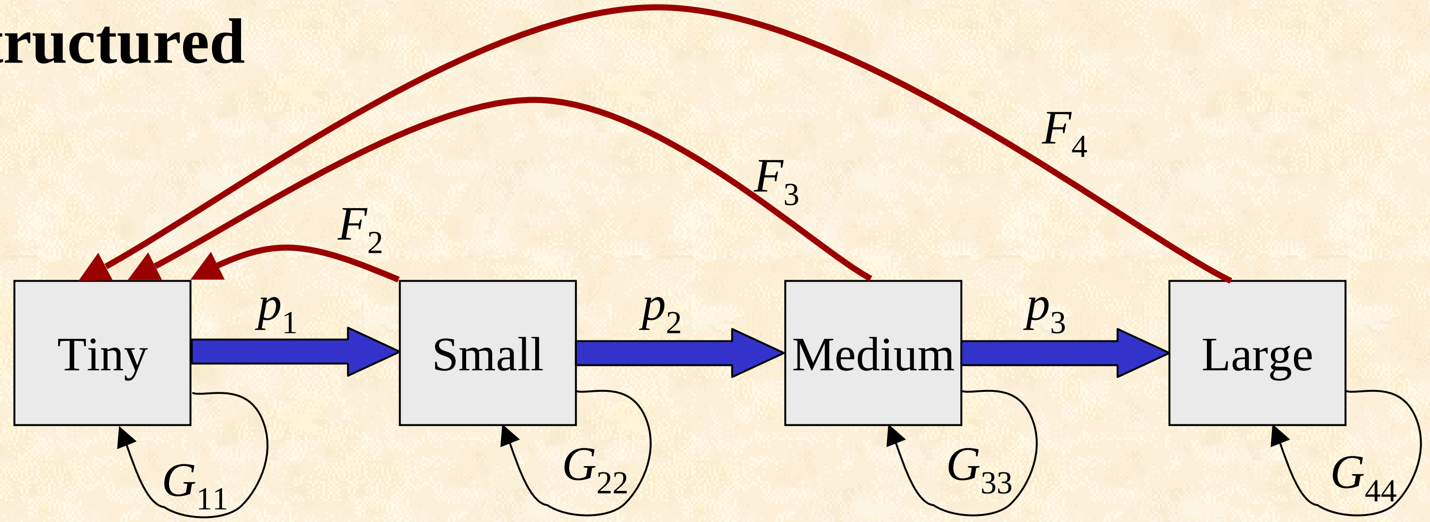
**Stage-structured**




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

$$\begin{bmatrix} 0 & 0 & 0 & F_4 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{bmatrix}$$

## Size-structured




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

$$\begin{bmatrix} G_{11} & F_2 & F_3 & F_4 \\ p_1 & G_{22} & 0 & 0 \\ 0 & p_2 & G_{33} & 0 \\ 0 & 0 & p_3 & G_{44} \end{bmatrix}$$

# 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 ($\lambda$)

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

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

$\lambda_1$ = 2.41

$\lambda_2$ = -0.41

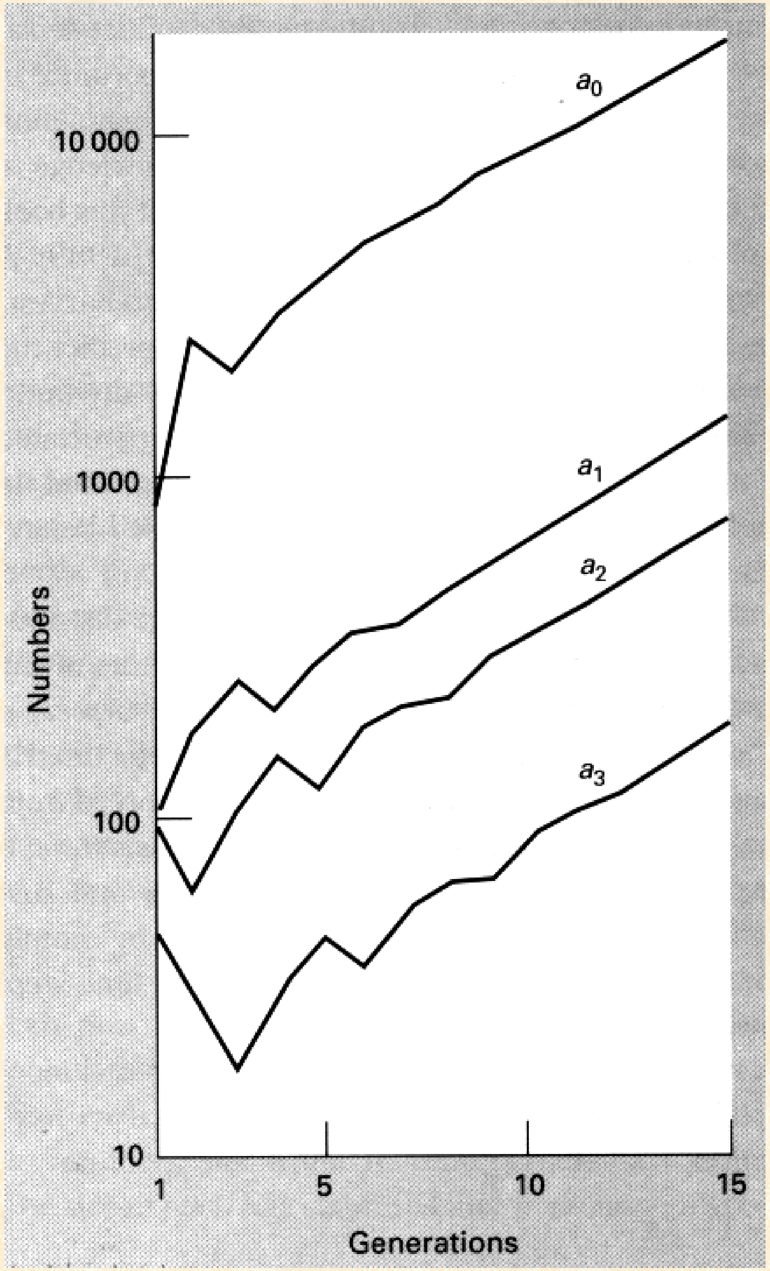
$$\mathbf{N}_2 = \mathbf{N}_1\mathbf{A}$$

$$\mathbf{N}_3 = \mathbf{N}_2\mathbf{A}$$

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

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

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



# Matrix analysis

## Net reproductive rate ($R_0$)

- average number of offspring produced by a female in her lifetime

$$R_0 = \sum_{x=0}^{n} l_x m_x$$

## Average generation time ($T$)

- average age of females when they give birth

$$T = \frac{\sum_{x=0}^{n} x l_x m_x}{R_0}$$

## Expectation of life

- age specific expectation of life
- $o$ .. oldest age

$$e_x = \frac{T_x}{l_x}$$

$$L_x = \frac{l_x + l_{x+1}}{2}$$

$$T_x = \sum_{x}^{o} L_x$$

## Intrinsic growth rate (*r* )

- when Leslie model show exponential growth the potential rate of increase can be determined from

$$r \approx \frac{\ln(R_0)}{T} \qquad \lambda \approx \frac{R_0}{T}$$

- Euler (1760) found how to estimate *r* from the life table

$$\sum_x l_x m_x e^{-rx} = 1$$

- *r* can be estimated from the only dominant positive eigenvalue of the transition matrix **A** ($\lambda_1$.. finite growth rate)

$$r = \ln(\lambda_1)$$

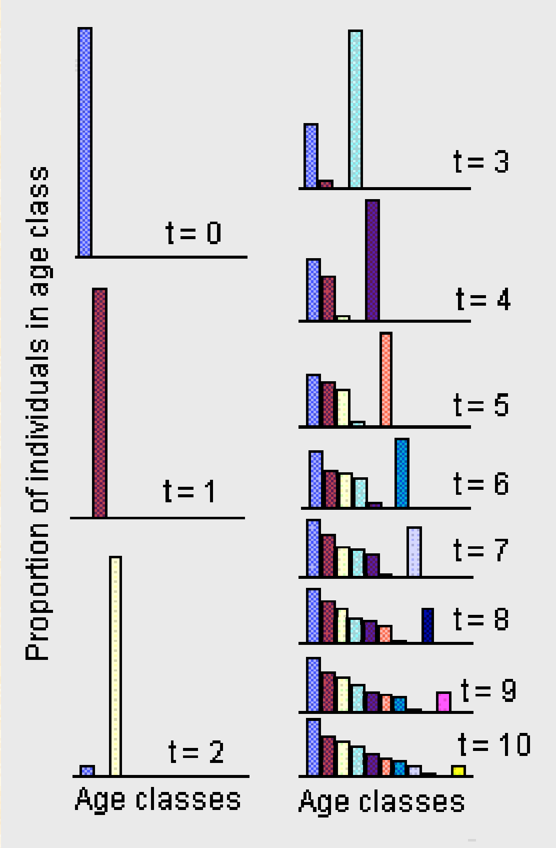
## Stable Class distribution (SCD)

- relative abundance of different life history age/stage/size categories
  - population approaches stable age distribution:

    $\mathbf{N_0} : \mathbf{N_1} : \mathbf{N_2} : \mathbf{N_3} :....:\mathbf{N}_s$ is stable

- once population reached SCD it grows exponentially
  - proportion of individuals (***c***) in age *x*

$$c_x = \frac{l_x e^{-rx}}{\sum_x l_x e^{-rx}}$$




- $\mathbf{w}_1$ .. right eigenvector of the dominant eigenvalue
- provides stable age distribution
- scale $\mathbf{w}_1$ by sum of individuals

$$\mathbf{A}\mathbf{w}_1 = \lambda_1 \mathbf{w}_1$$

$$SCD = \frac{\mathbf{w}_1}{\sum_{i=1}^{S} \mathbf{w}_1}$$

# Cvičení z Populační ekologie

S. Pekár

podzim 2011

evropský sociální fond v ČR
EVROPSKÁ UNIE
MINISTERSTVO ŠKOLSTVÍ, MLÁDEŽE A TĚLOVÝCHOVY
OP Vzdělávání pro konkurenceschopnost
UNIVERSITAS MASARYKIANA BRUNENSIS
INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

# Excercise 4

Factors causing decline in the population of a moth:

| Stage | Number | Factor |
|---|---|---|
| Eggs | 562 | Overwintering |
| Larvae | 240 | Parasites |
| Pupae | 112 | Predation |
| Imagoes | 64 | |

1. Estimate k-value for each factor.
2. Simulate change in population density given the following estimated linear models of $k_i$ on $\log(N)$:

overwintering: $k_1 = 0.48 - 0.04 \log(N_E)$

parasites: $k_2 = 0.55 - 0.09 \log(N_L)$

predation: $k_3 = 0.30 - 0.03 \log(N_P)$

The sex ratio is 1:1. Female has average fecundity 17 eggs.

# Excercise 5

Perform demographic study of the common fox using life table menu in POPULUS. The fox breeds in pulses and the data were collected using post-breeding census.

| x | lx | mx |
|---|---|---|
| 0 | 1 | 0 |
| 1 | 0.8 | 0 |
| 2 | 0.3 | 2 |
| 3 | 0.1 | 3 |
| 4 | 0.07 | 0 |

- Plot standardised survival ($l_x$) with age.
  Which survival curve type it corresponds to?
- Plot fecundity ($m_x$) and reproductive value (*RV*) with age.
- Construct Leslie transition matrix and project

it over a period of another 20 years using initial vector (25, 18, 9, 5, 4). When does the population reach stable age distribution?