Population Growth

"Populační ekologie živočichů"

Stano Pekár

Ecological Models

- aim: to simulate (predict) what can happen
- model is tested by comparison with observed data

- realistic models - complex (many parameters), realistic, used to simulate real situations
- strategic models - simple (few parameters), unrealistic, used for understanding the model behaviour

- a model should be:

1. a satisfactory description of diverse systems
2. an aid to enlighten aspects of population dynamics
3. a system that can be incorporated into more complex models

- deterministic models - everything is predictable
- stochastic models - including random events

- <u>discrete models:</u>

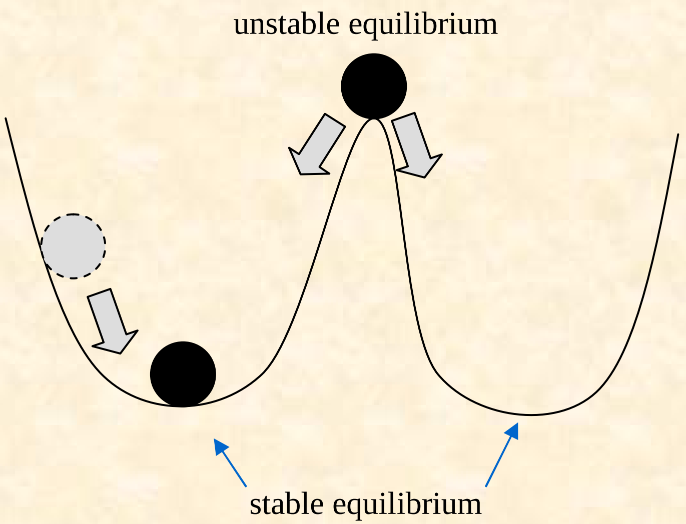
- time is composed of discrete intervals or measured in generations
- used for populations with synchronised reproduction (annual species)
- modelled by difference equations

- <u>continuous models:</u>

- time is continual (very short intervals) thus change is instantaneous
- used for populations with asynchronous and continuous overlapping reproduction
- modelled by differential equations

STABILITY

- how population changes in time
- stable equilibrium is a state (population density) to which a population will move after a perturbation



Population processes

- focus on rates of population processes

- number of cockroaches in a living room increases:

- influx of cockroaches from adjoining rooms → <u>immigration</u> [***I***]
- cockroaches were born → <u>birth</u> [***B***]

- number of cockroaches declines:

- dispersal of cockroaches → <u>emigration</u> [***E***]
- cockroaches died → <u>death</u> [***D***]

Blatta orientalis

$$N_{t+1} = N_t + I + B - D - E$$

- population increases if $I + B > E + D$

- rate of increase is a summary of all events ($I + B - E - D$)

- growth models are based on ***B*** and ***D***
- spatial models are based on ***I*** and ***E***

Density-independent population increase

Population processes are independent of its density

Assumptions:

- immigration and emigration are none or ignored
- all individuals are identical
- natality and mortality are constant
- all individuals are genetically similar
- reproduction is asexual
- population structure is ignored
- resources are infinite
- population change is instant, no lags

Used only for

- relative short time periods
- closed and homogeneous environments (experimental chambers)

Discrete (difference) model

- for population with discrete generations (annual reproduction), no generation overlap
- time (t) is discrete, equivalent to generation
- exponential (geometric) growth
- Malthus (1834) realised that any species can potentially increase in numbers according to a geometric series

N_0 .. initial density

b .. birth rate (per capita)

d .. death rate (per capita)

$$b = \frac{B}{N}$$

$$d = \frac{D}{N}$$

$$\Delta N = bN_{t-1} - dN_{t-1}$$

$$N_t - N_{t-1} = (b-d)N_{t-1}$$

$$N_t = (1+b-d)N_{t-1}$$

$$1+b-d=\lambda$$

$$b-d=R$$

$$\lambda=1+R$$

R .. **demographic growth rate**
-shows proportional change (in percentage)

λ .. **finite growth rate**, per capita rate of growth

λ = 1.23 then R = 0.23
.. 23% increase

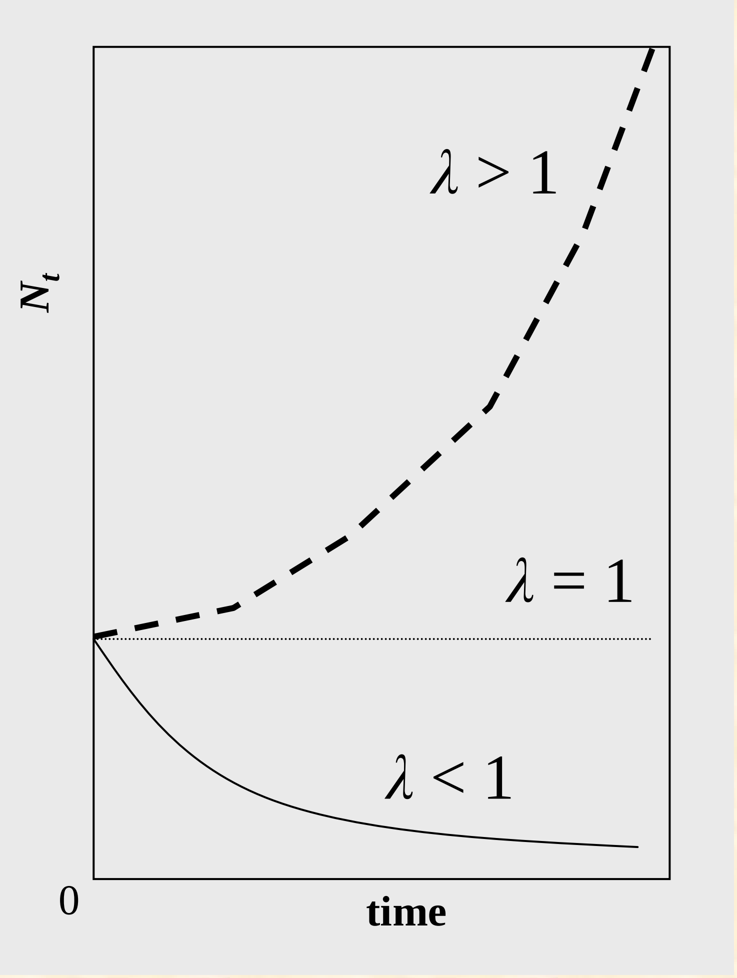
- number of individuals is multiplied each time - the larger the population the larger the increase

▸ if λ is constant, population number in generations ***t*** is equal to

$$N_t = N_{t-1}\lambda$$

$$N_2 = N_1\lambda = N_0\lambda\lambda$$

$$N_t = N_0\lambda^t$$



Average of finite growth rates
- estimated as geometric mean

$$\bar{\lambda} = \left(\prod_{i=1}^{t}\lambda_i\right)^{\frac{1}{t}} = (\lambda_1\lambda_2\ldots\lambda_t)^{\frac{1}{t}}$$

Continuous (differential) model

- populations that are continuously reproducing, with overlapping generations
- when change in population number is permanent
- derived from the discrete model

$$N_t = N_0 \lambda^t$$

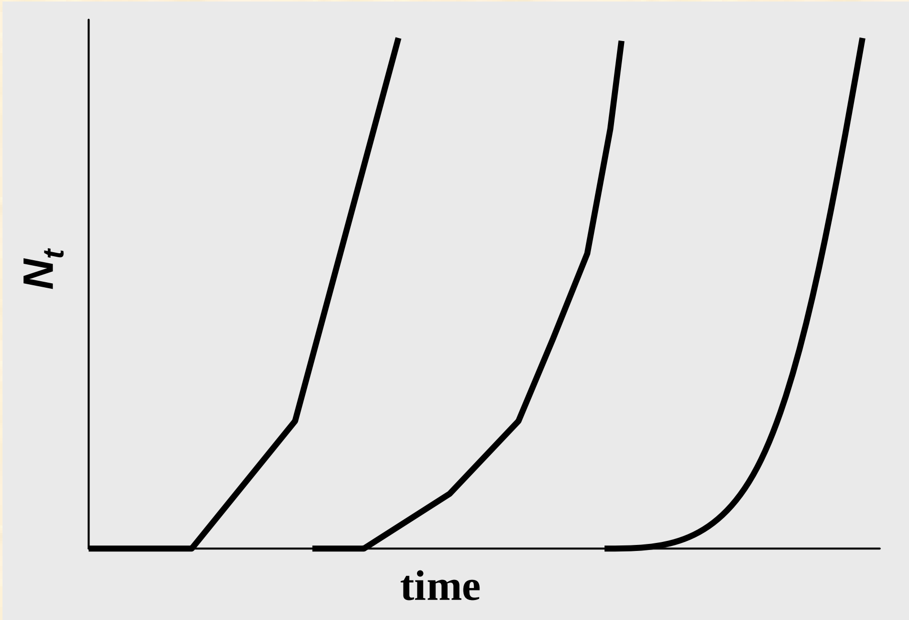
$$\ln(N_t) = \ln(N_0) + t\ln(\lambda)$$

$$\ln(N_t) - \ln(N_0) = t\ln(\lambda)$$

$$\frac{\mathrm{d}N}{\mathrm{d}t}\frac{1}{N} = \ln(\lambda)$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N\ln(\lambda)$$

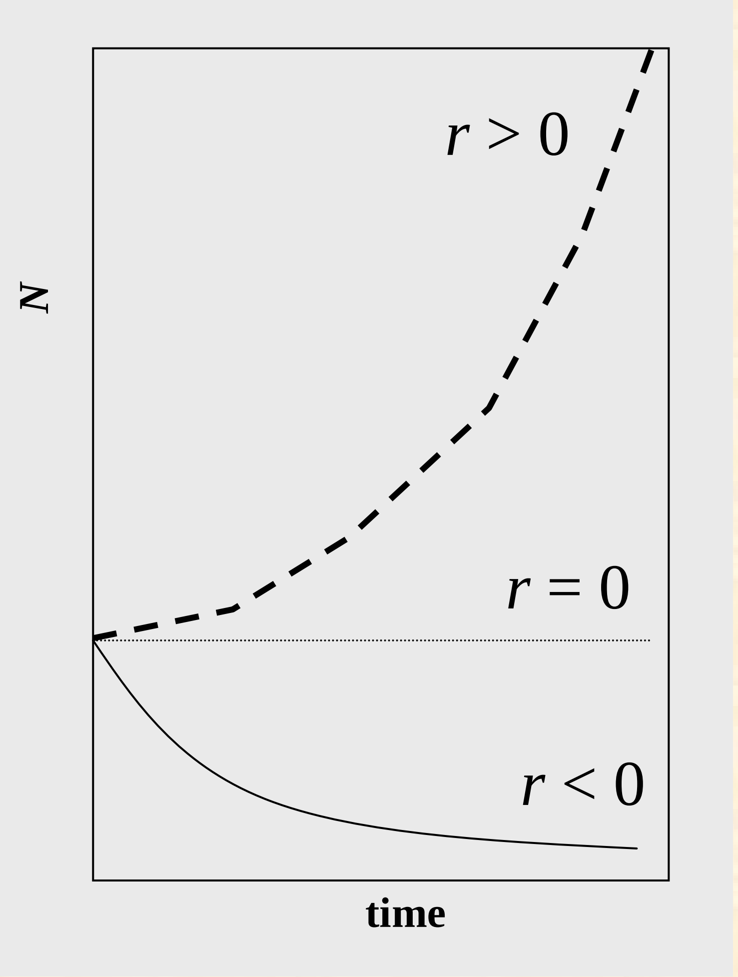
Comparison of discrete and continuous generations



if $r = \ln(\lambda)$

r .. **intrinsic rate of natural increase**,
instantaneous per capita growth rate

$$\frac{dN}{dt} = Nr$$



<u>Solution of the differential equation:</u>

- analytical or numerical

▸ at each point it is possible to determine the rate of change by differentiation (slope of the tangent)

▸ when t is large it is approximated by the exponential function

$$\frac{\mathrm{d}N}{\mathrm{d}t} = Nr$$

$$\frac{\mathrm{d}N}{\mathrm{d}t}\frac{1}{N} = r$$

$$\int_0^T \frac{1}{N}\mathrm{d}N = \int_0^T r\mathrm{d}t$$

$$\ln(N_T) - \ln(N_0) = r(T - 0)$$

$$\ln\left(\frac{N_T}{N_0}\right) = rT$$

$$\frac{N_T}{N_0} = e^{rT}$$

$$N_t = N_0 e^{rt}$$

- doubling time: time required for a population to double

$$t = \frac{\ln(2)}{r}$$

r versus *λ*

$$N_t = N_0 \lambda^t \qquad N_t = N_0 e^{rt}$$

$$\lambda^t = e^{rt}$$

$$r = \ln(\lambda)$$

- r is symmetric around 0, λ is not

r = 0.5 ... λ = 1.65

r = -0.5 ... λ = 0.61

Population structure

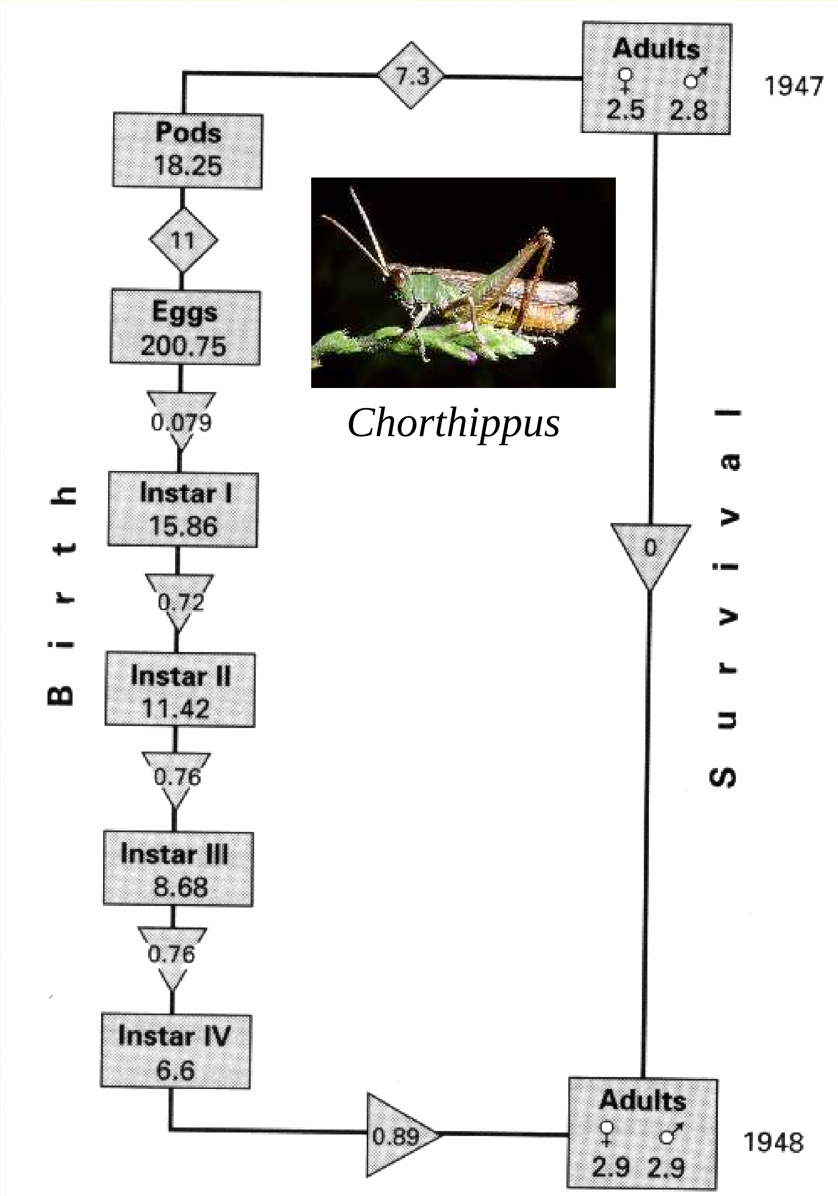
- **Demography** - study of organisms with special attention to stage or age structure
- processes are associated to age, stage or size

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)

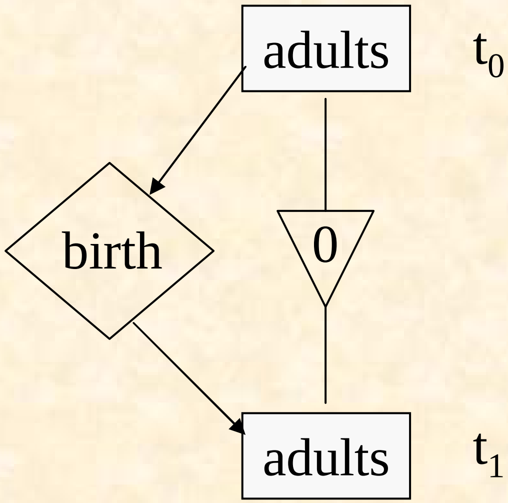


Richards & Waloff (1954)

- main focus on births and deaths
- immigration & emigration is ignored
- no adult survive
- one (not overlapping) generation per year

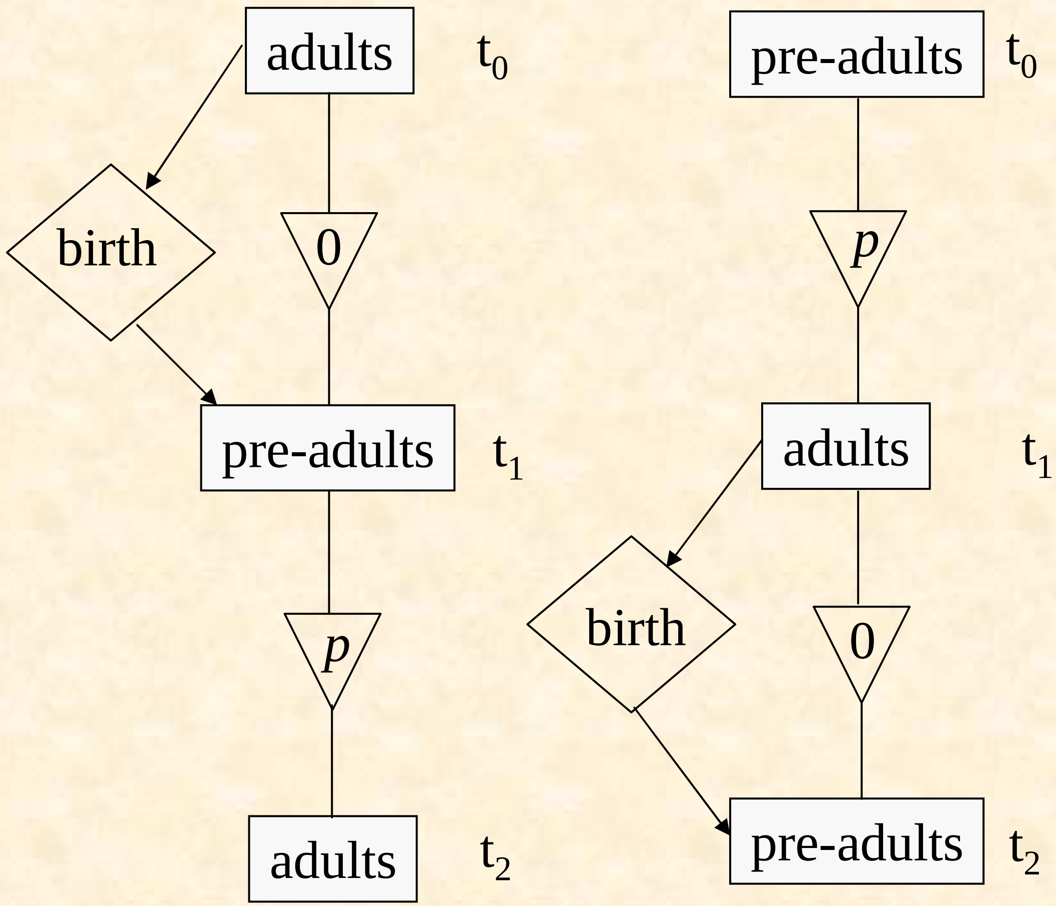
- egg pods over-winter
- despite high fecundity they just replace themselves

Annual species



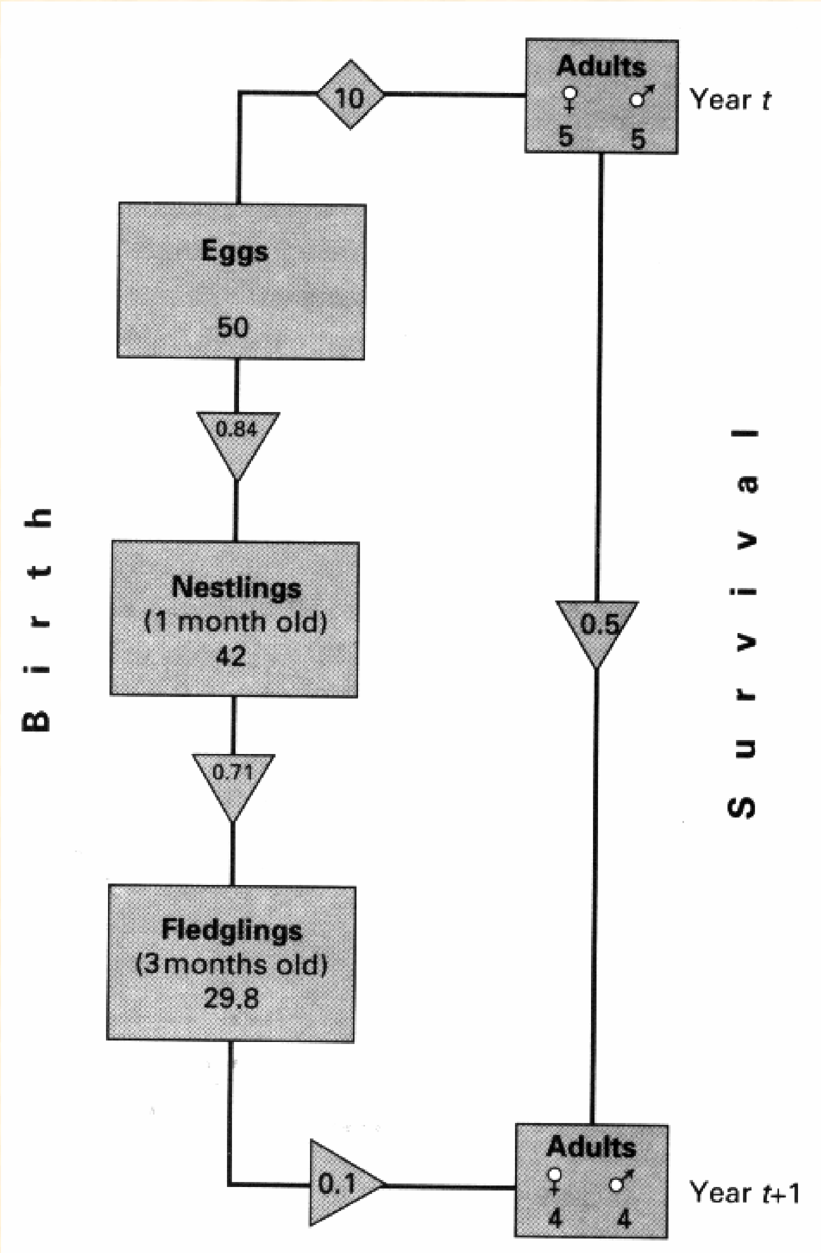
- breed at discrete periods
- no overlapping generations

Biennal species



- breed at discrete periods
- adult generation may overlap

Perins (1965)



Perennial species

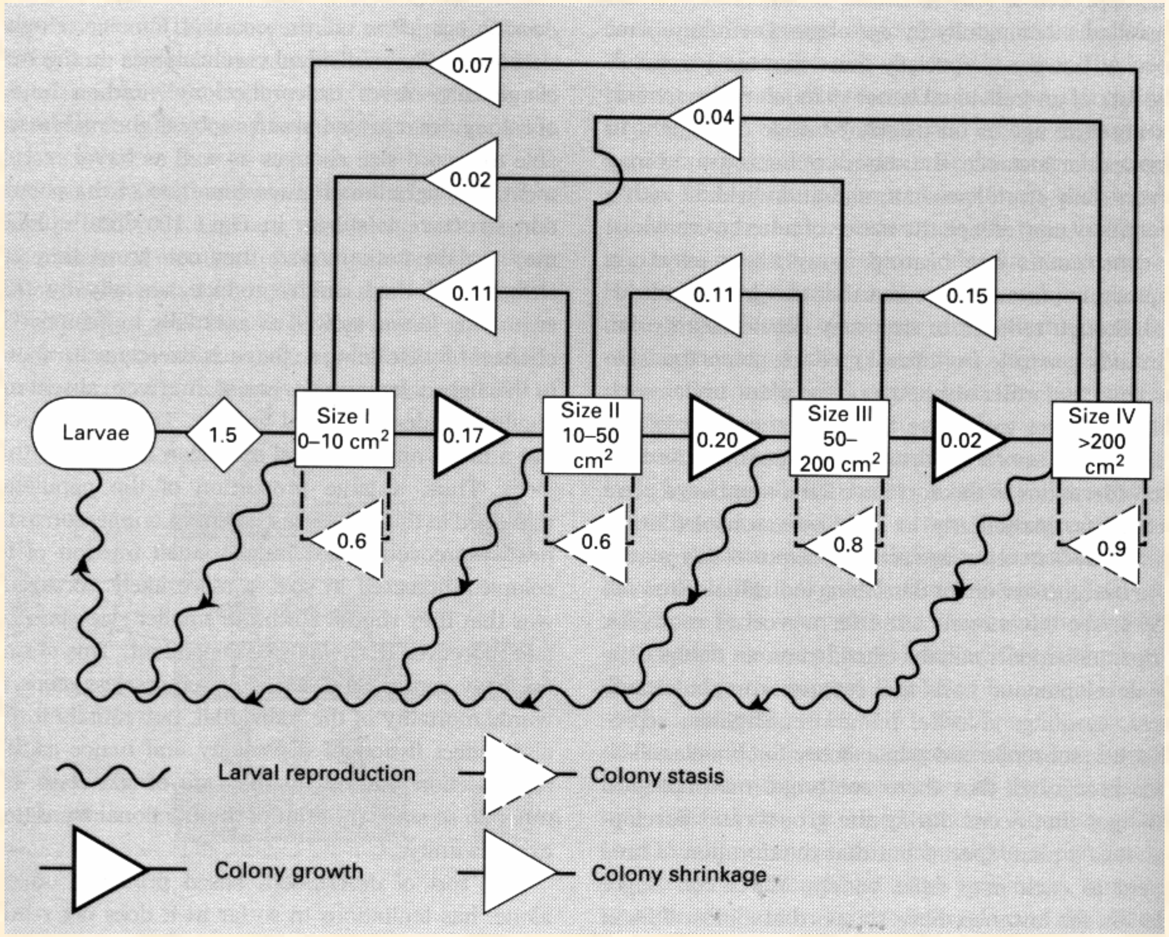
- breed at discrete periods
- breeding adults consist of individuals of various ages (1-5 years)
- adults of different generations are equivalent
- overlapping generations

Parus major

Age-size-stage life-table

- age/stage classification is based on developmental time
- size may be more appropriate than age (fish, sedentary animals)
- Hughes (1984) used combination of age/stage and size for the description of coral growth

Agaricia agaricites

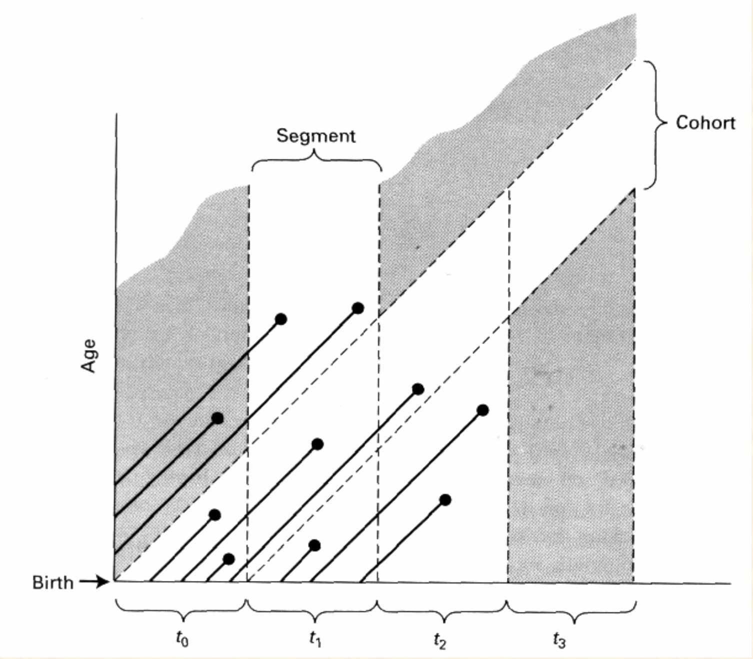


Age-dependent life-tables

- 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

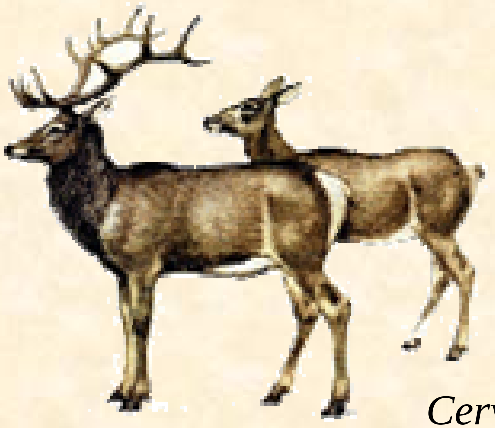


- ASSUMPTIONS:
- Birth rate and survival are constant over time
- population does not grow

- 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

$\boldsymbol{S_x}$ .. number of survivors

$\boldsymbol{D_x}$ .. number of dead individuals

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

$\boldsymbol{l_x}$ .. standardised number of survivors

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

$\boldsymbol{q_x}$ .. age-specific mortality

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

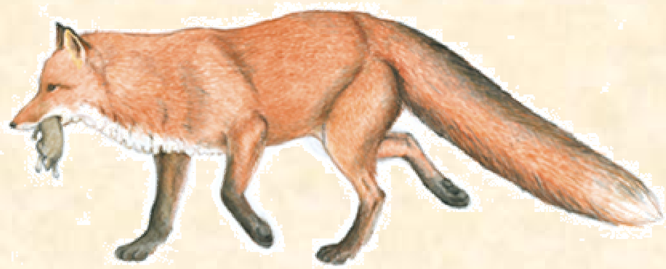
$\boldsymbol{p_x}$ .. age-specific survival

$$p_x = \frac{l_{x+1}}{l_x}$$

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

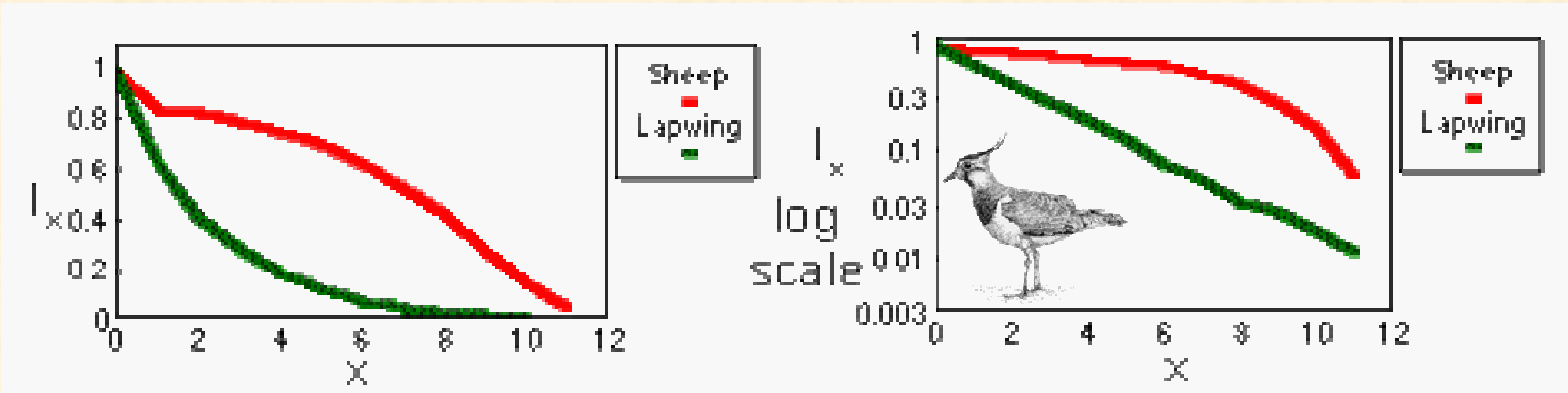
Campbell (1981)

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

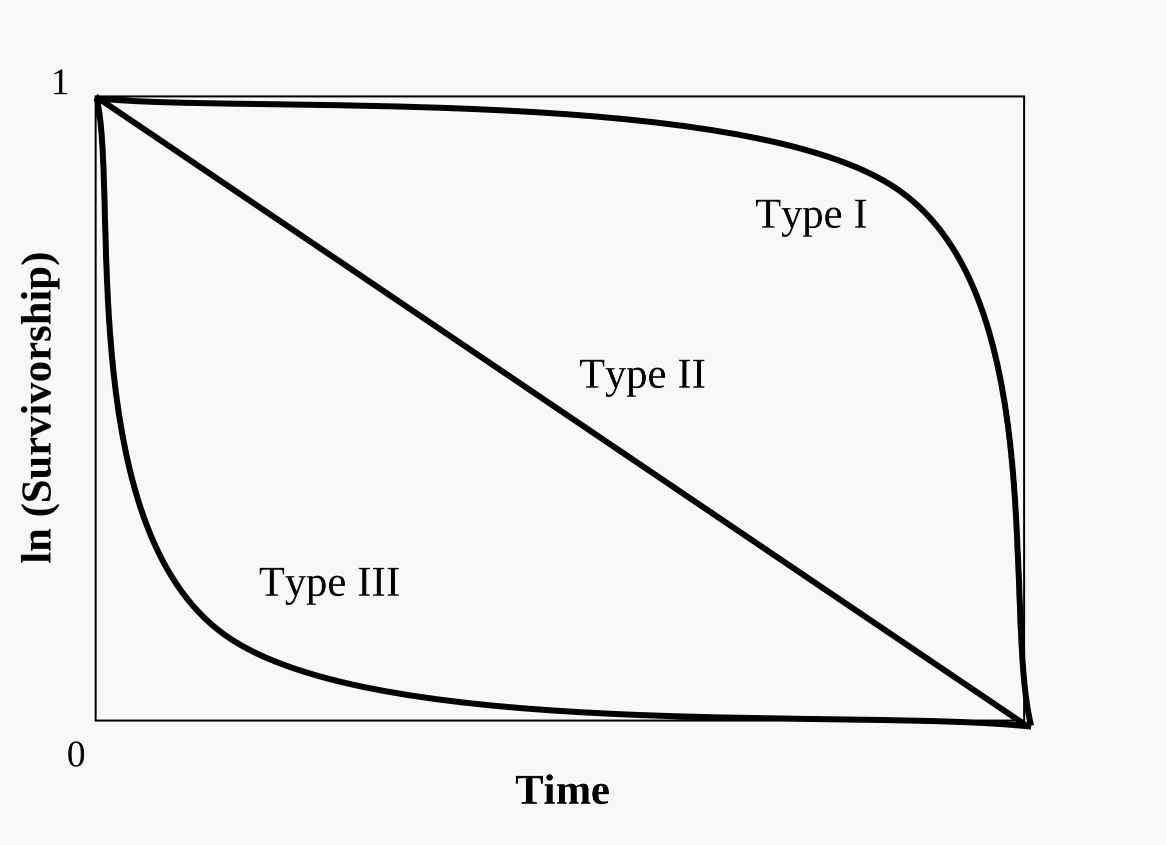
Survivorship curves

- display change in survival by plotting log($\boldsymbol{l_x}$) against age ($\boldsymbol{x}$)
- sheep mortality increases with age
- survivorship of lapwing (*Vanellus*) is independent of age but survival of sheep is age-dependent



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)

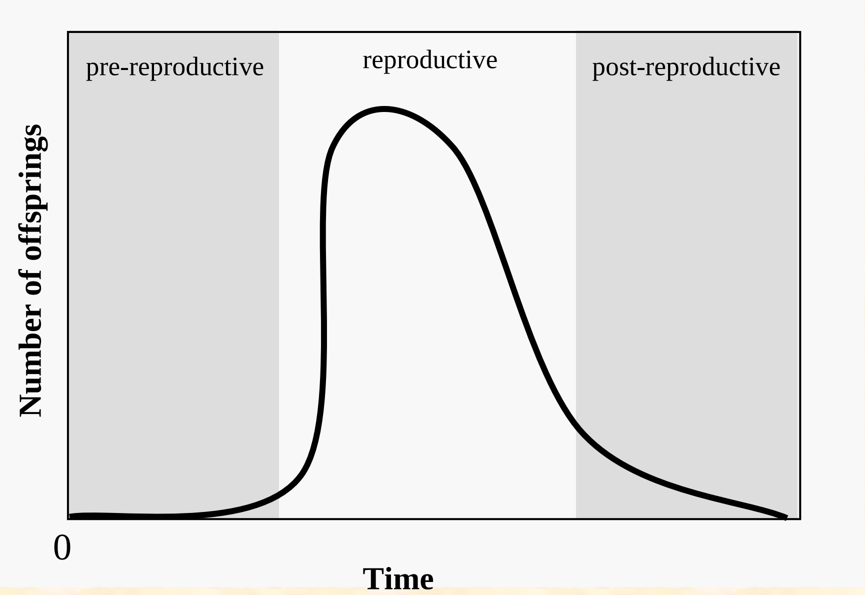


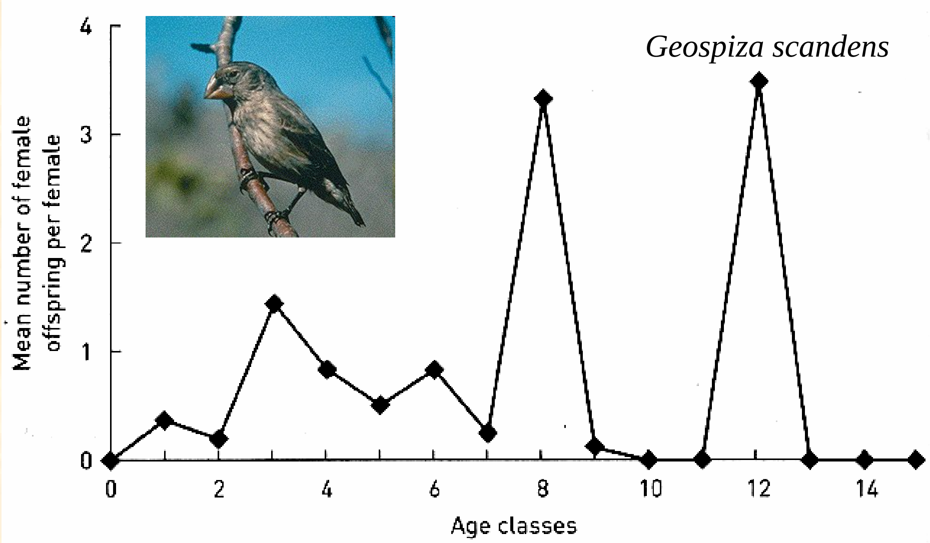
Birth rate curves

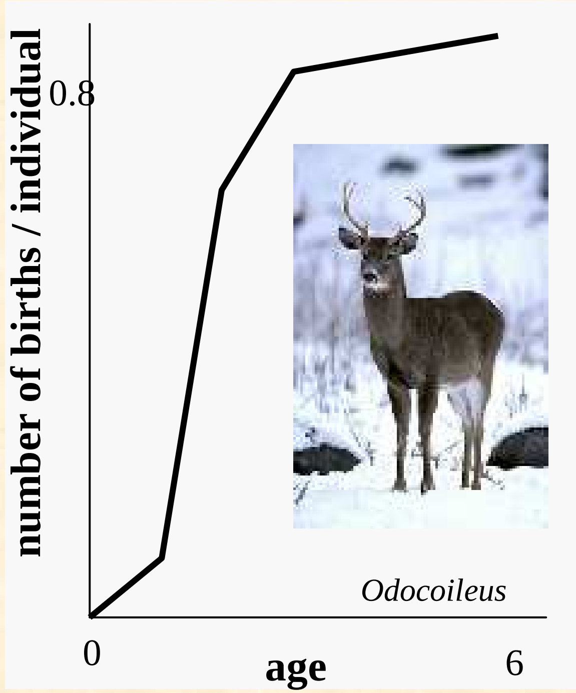
- fecundity - potential number of offspring
- fertility - real number of offspring

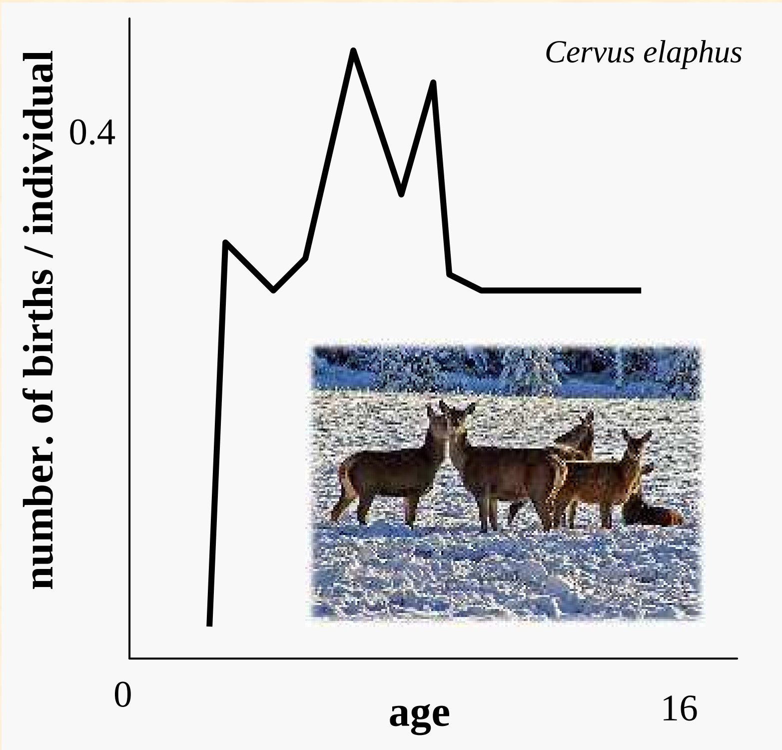
- semelparous .. reproducing once a life
- iteroparous .. reproducing several times during life

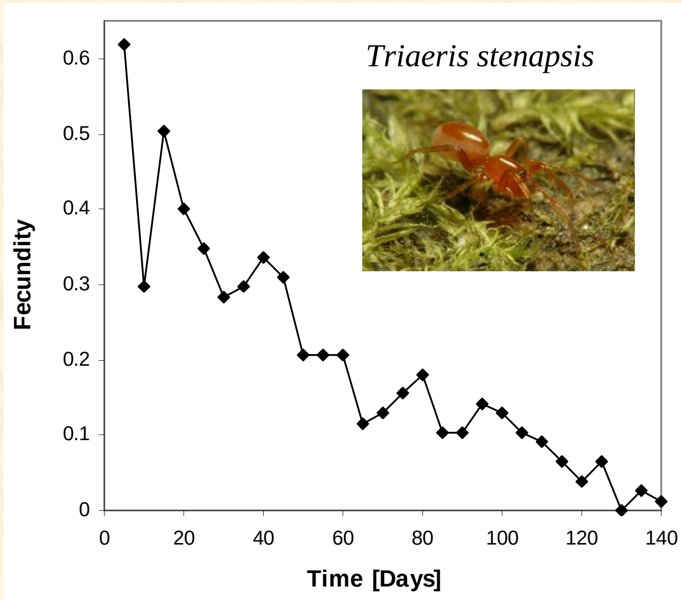
- birth pulse .. discrete reproduction (seasonal reproduction)
- birth flow .. continuous reproduction




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


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 $\log(N)$

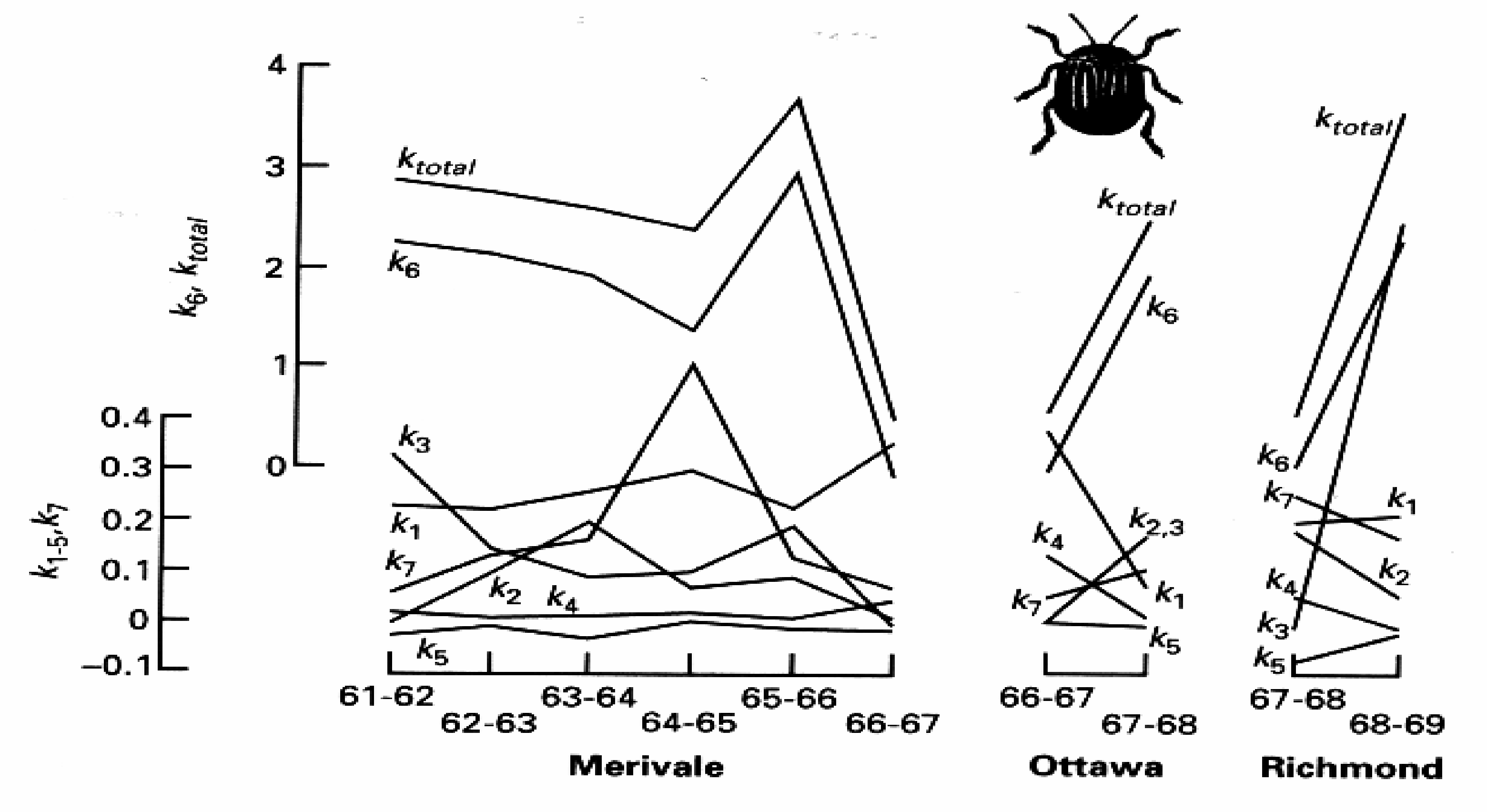
Leptinotarsa decemlineata

- 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 natality and mortality
- generations are not overlapping
- reproduction is asexual
- used for modelling of density-independent processes (exponential growth)

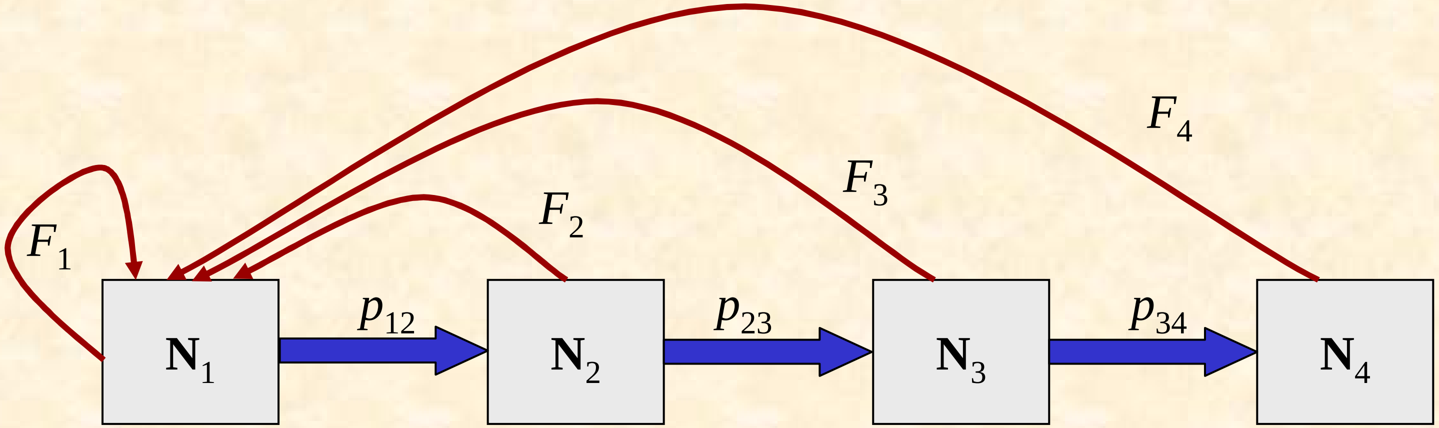
$\mathbf{N}_{x,t}$ .. no. of organisms in age *x* and time *t*

G_{x} .. probability of persistence in the same size/stage

F_{x} .. age/stage specific fertility (average no. of offspring per female)

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 census and reproduction

- populations with discrete pulses post-reproductive census

$$p_x = \frac{l_{x+1}}{l_x} \qquad F_x = p_x m_{x+1}$$

includes *p* of reproductive stages

- populations with discrete pulses pre-reproductive census

$$p_x = \frac{l_{x+1}}{l_x} \qquad F_x = p_0 m_{x+1}$$

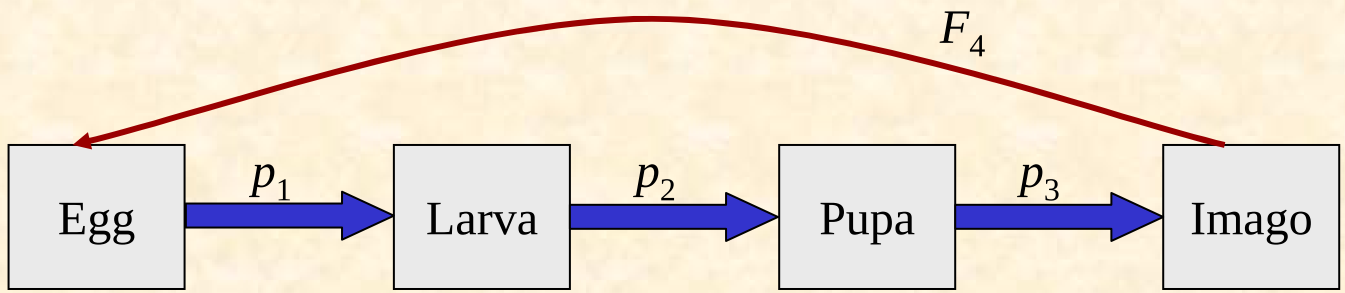
includes *p* of the youngest stage

- for pre-reproductive census 0 age is omitted

- for populations with continuous reproduction

$$p_x = \left(\frac{l_x + l_{x+1}}{l_{x-1} + l_x} \right) \qquad F_x = \frac{\sqrt{l_1}\left(m_x + p_x m_{x+1}\right)}{2}$$

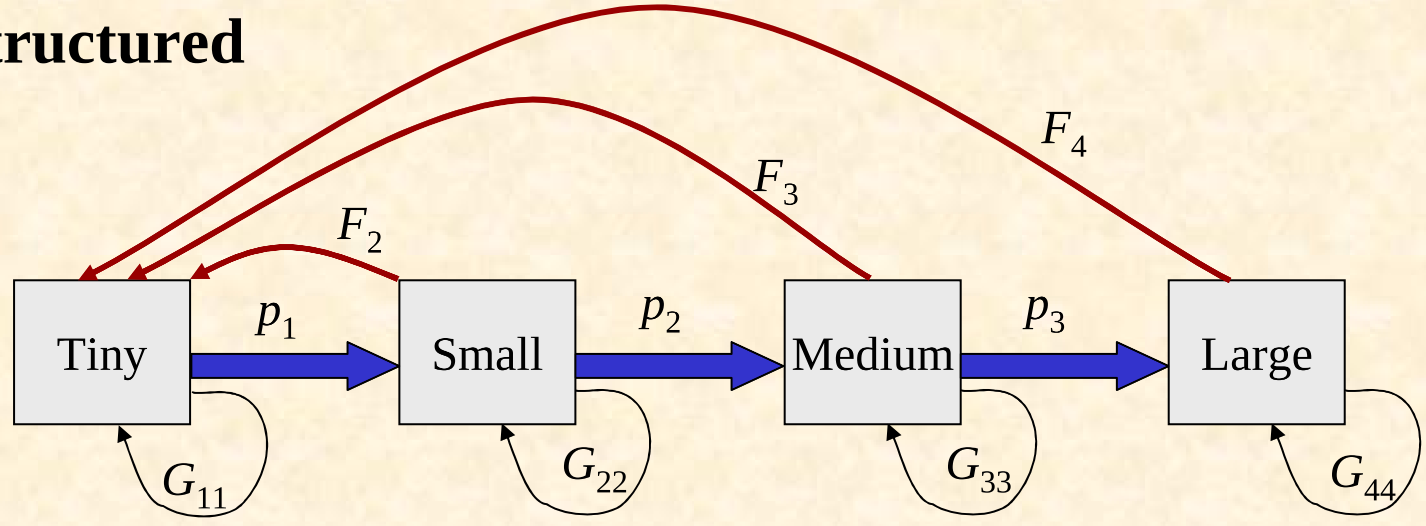
Stage-structured



- 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

- 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

$$\begin{bmatrix} 2 & 3 \\ 5 & 7 \end{bmatrix} \times \begin{bmatrix} 4 \\ 5 \end{bmatrix} = \begin{bmatrix} 2\times4+3\times5 \\ 5\times4+7\times5 \end{bmatrix} = \begin{bmatrix} 23 \\ 55 \end{bmatrix}$$

- determinant

$$\begin{bmatrix} 2 & 3 \\ 4 & 7 \end{bmatrix} = 2\times7-4\times3 = 2$$

- eigenvalue (λ)

$$\mathbf{Au} = \lambda\mathbf{u}$$

$$\det(\mathbf{A}-\lambda\mathbf{I}) = 0$$

$$\begin{bmatrix} 2 & 4 \\ 0.25 & 0 \end{bmatrix}$$

$$\begin{bmatrix} 2-\lambda & 4 \\ 0.25 & 0-\lambda \end{bmatrix} = (2-\lambda)\times(0-\lambda)-(0.25\times4) = \lambda^2-2\lambda-1=0$$

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

$\lambda_1 = 2.41$

$\lambda_2 = -0.41$

$$N_2 = AN_1$$

$$N_3 = AN_2$$

$$N_{t+2} = AAN_t = A^2 N_t$$

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

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