Population Growth

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

"Populační ekologie živočichů"

Stano Pekár

Ecological Models

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

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

‣ <u>a model should be:</u>
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

‣ <u>deterministic models</u> - everything is predictable
‣ <u>stochastic models</u> - including random events

▶ discrete models:
- time is composed of discrete intervals or measured in generations
- used for populations with synchronised reproduction (annual species)
- modelled by difference equations
▶ continuous models:
- time is continual (very short intervals) thus change is instantaneous
- used for populations with asynchronous and continuous overlapping reproduction
- modelled by differential equations

STABILITY

▶ stable equilibrium is a state (population density) to which a population will move after a perturbation

unstable equilibrium

stable equilibrium
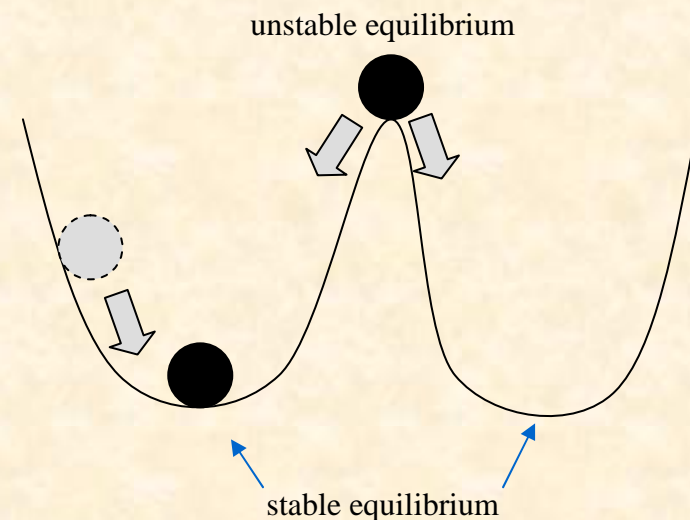
Population processes

▶ 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]

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

Blatta orientalis

▶ 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 is 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 (experiemental 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),

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

d .. death rate (per capita)

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

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

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

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

where $1+b-d = \lambda$

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

$b - d = R$

$\lambda = 1 + R$

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

$$N_2 = N_1\lambda = N_0\lambda\lambda$$
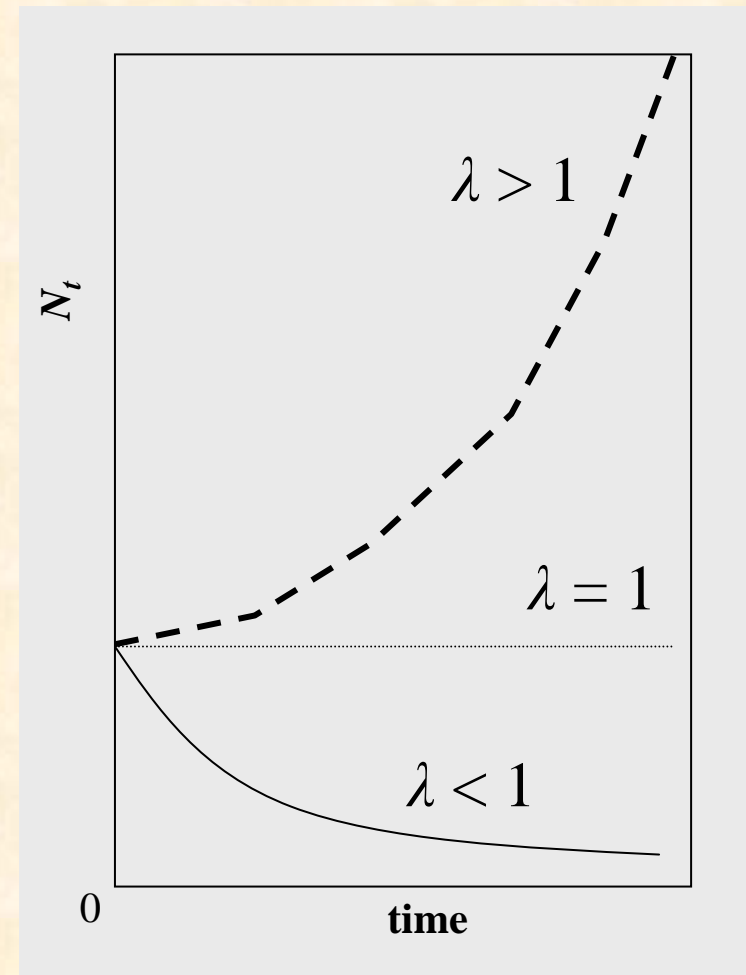
$$N_t = N_0\lambda^t$$

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

λ = finite growth-rate, per capita rate of growth
$\lambda = 1.23$ .. 23% increase

average of finite growth rates:

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

Continuous (differential) model

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

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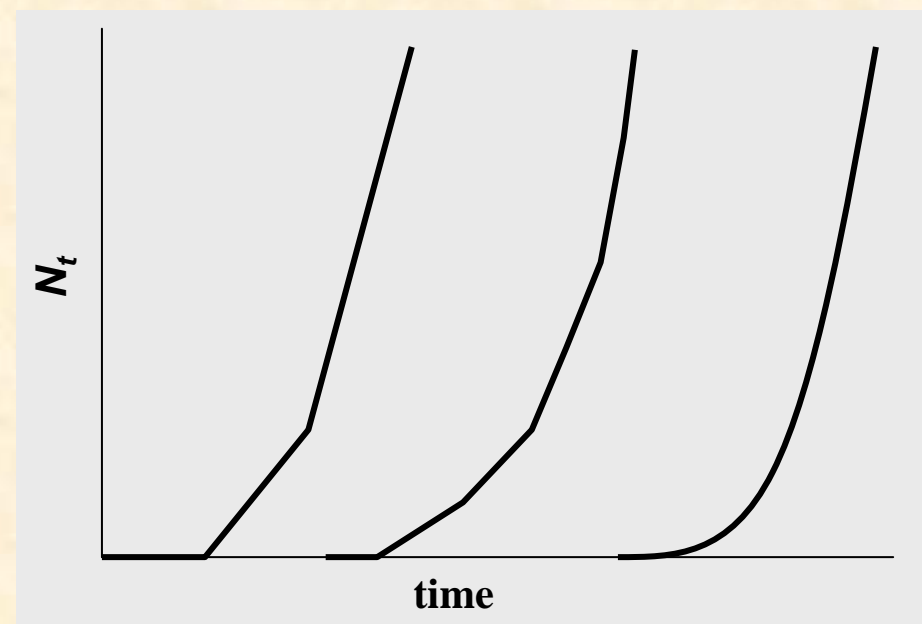
$$\ln(N_t) = \ln(N_0) + t\ln(\lambda)$$

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

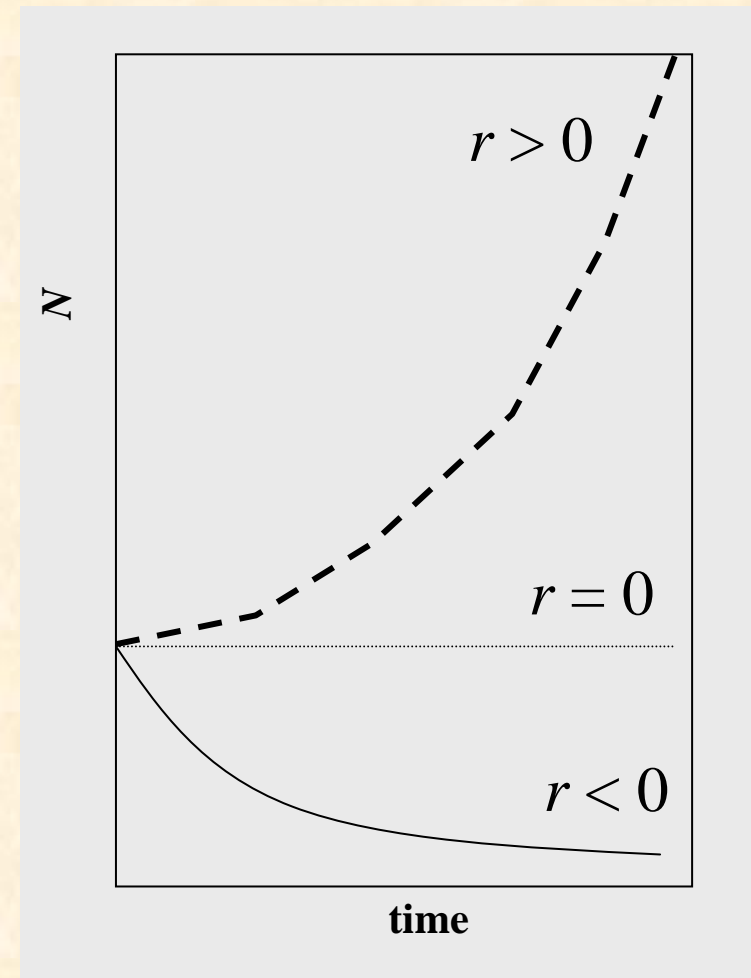$$\frac{dN}{dt}\frac{1}{N} = \ln(\lambda)$$

$$\frac{dN}{dt} = N\ln(\lambda)$$

Comparison of discrete and continuous generations

time

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

r - intrinsic rate of natural increase, instantaneous per capita growth rate

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

Solution of the differential equation:
- 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

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

$$\frac{dN}{dt}\frac{1}{N} = r$$

$$\int_0^T \frac{1}{N}dN = \int_0^T rdt$$

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

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

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

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

▸ 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

$r = 0.5 \ldots \lambda = 1.65$

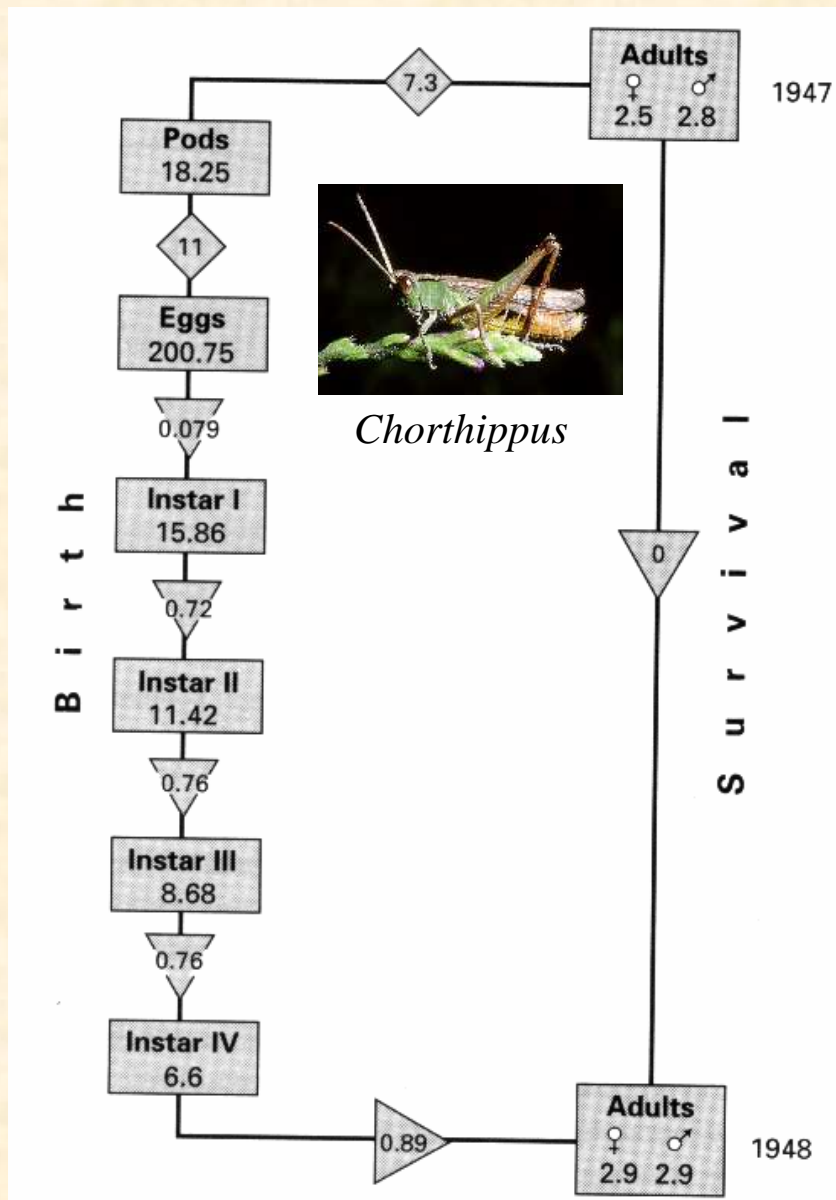$r = -0.5 \ldots \lambda = 0.61$

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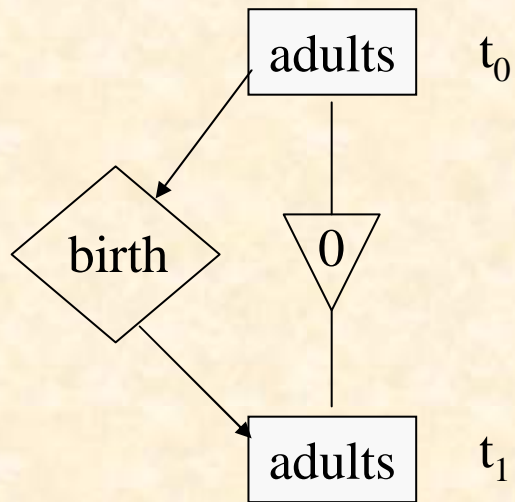
$$p_x = \frac{S_{x+1}}{S_x}$$

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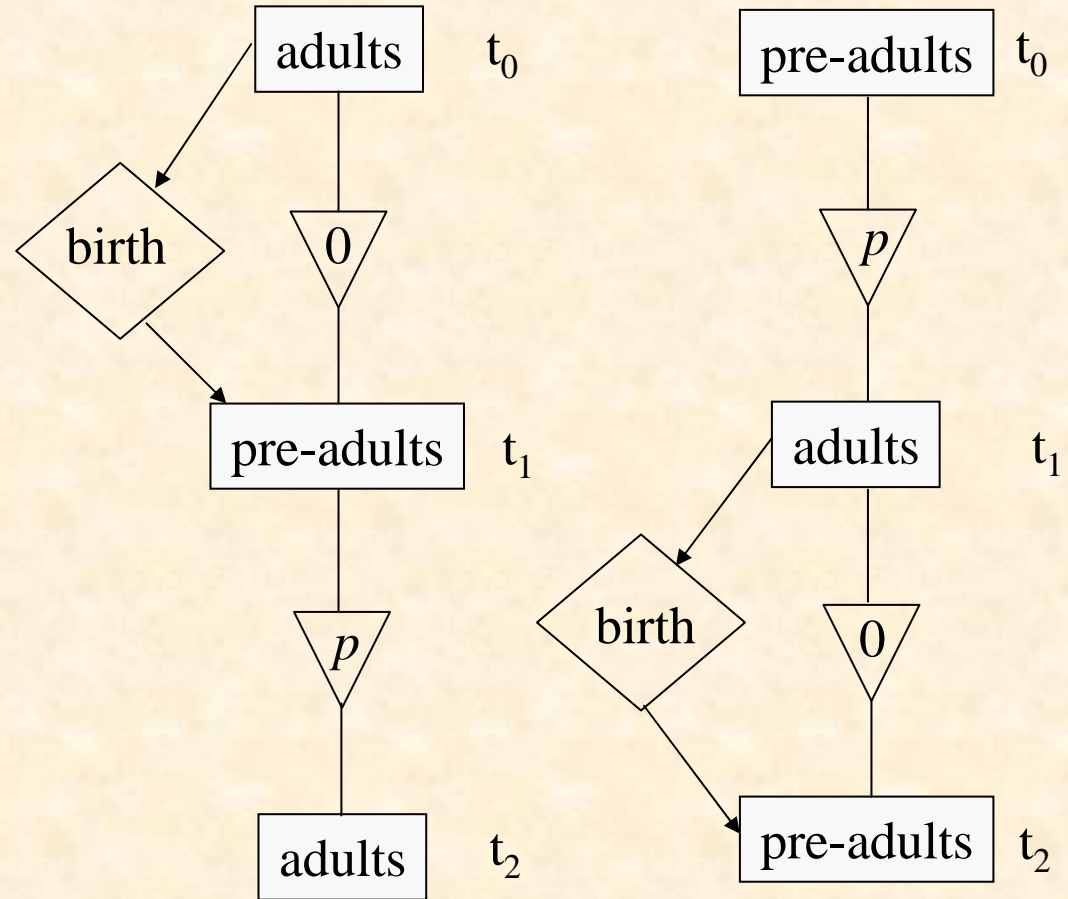
Chorthippus

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

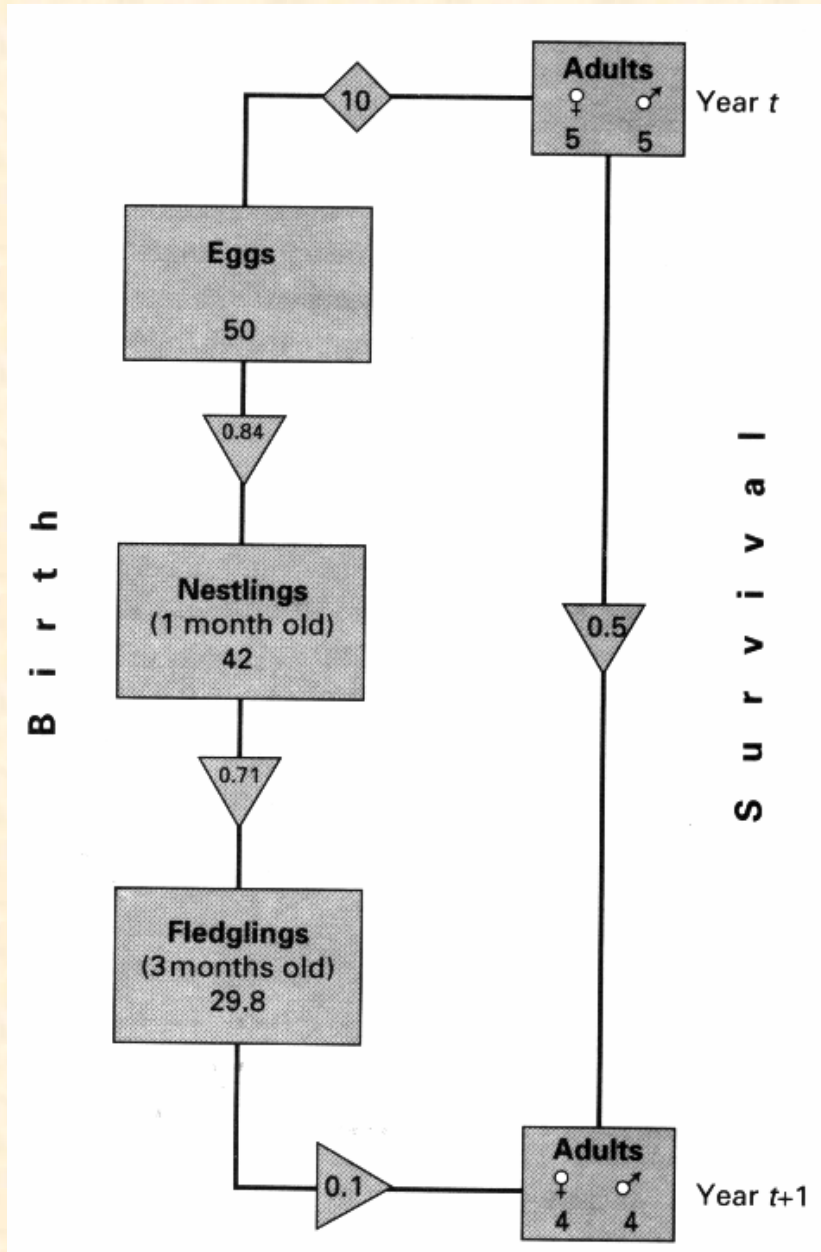▸ despite high fecundity they just replace themselves

Annual species

adults	t_0

birth 0

adults	t_1

▸ breed at discrete periods
▸ no overlapping generations

Biennal species

adults	t_0

birth 0

pre-adults	t_1

p

adults	t_2

pre-adults	t_0

p

adults	t_1

birth 0

pre-adults	t_2

▸ 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

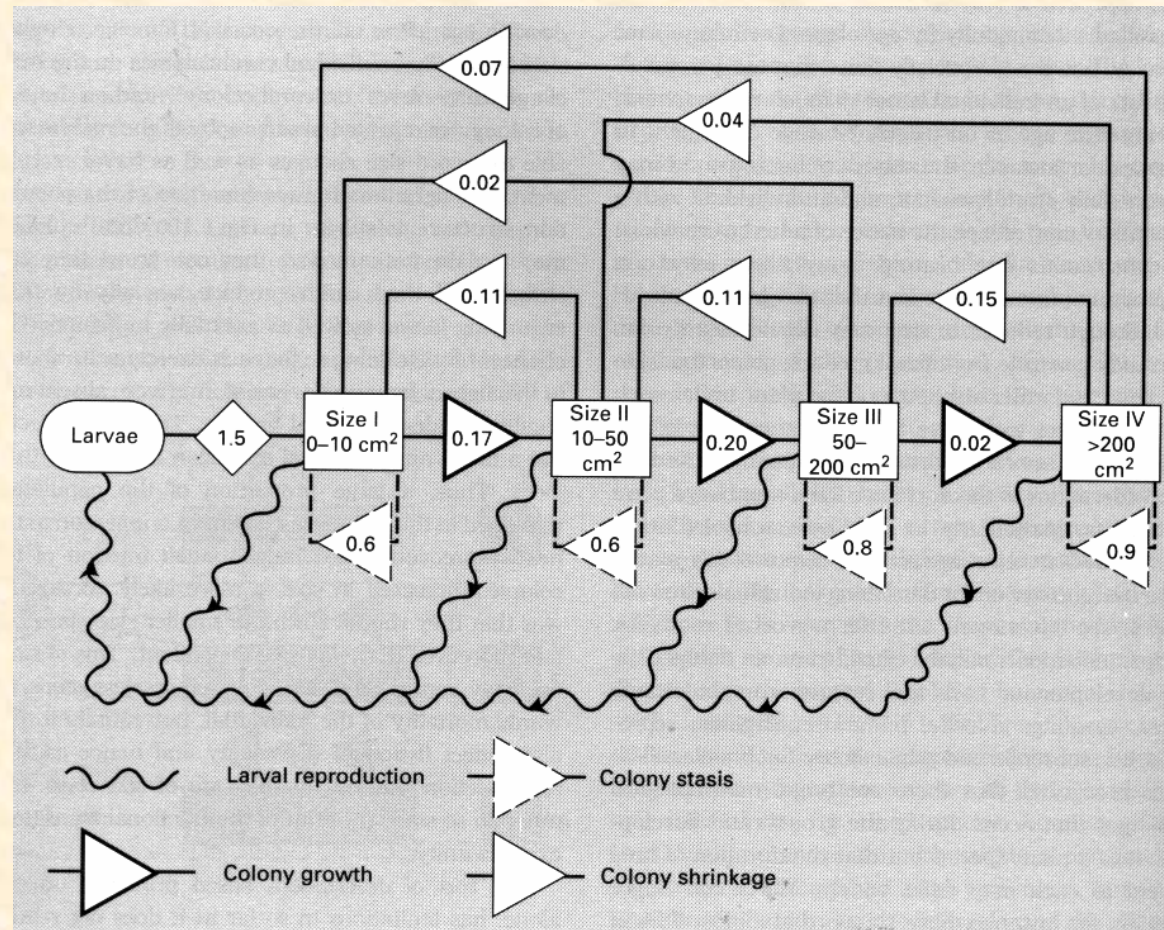*Parus major*

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-rate are constant over time
- population does not grow

▸ DRAWBACKS: confuses age-specific changes in e.g. mortality with temporal variation
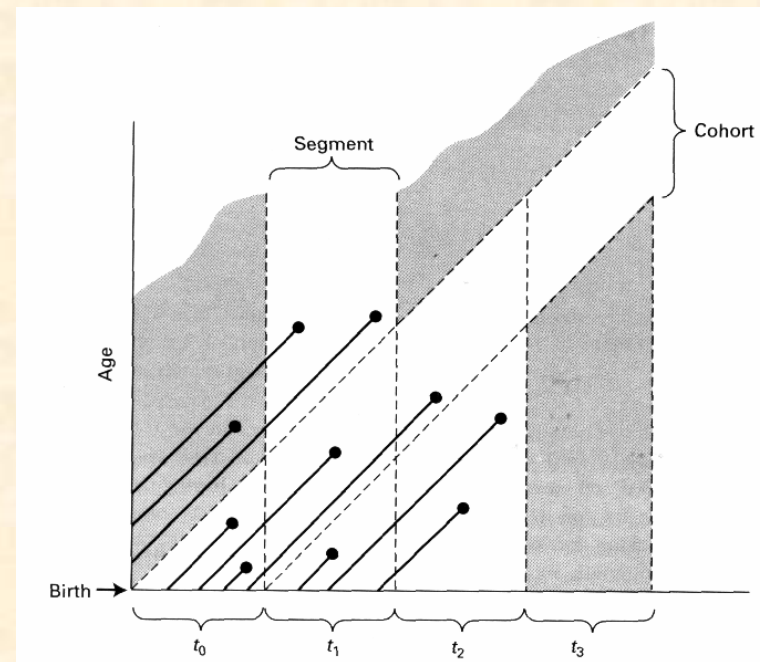
x	Sx	Dx	lx	px	qx	mx
1	129	15	1.000	0.884	0.116	0.000
2	114	1	0.884	0.991	0.009	0.000
3	113	32	0.876	0.717	0.283	0.310
4	81	3	0.628	0.963	0.037	0.280
5	78	19	0.605	0.756	0.244	0.300
6	59	-6	0.457	1.102	-0.102	0.400
7	65	10	0.504	0.846	0.154	0.480
8	55	30	0.426	0.455	0.545	0.360
9	25	16	0.194	0.360	0.640	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)
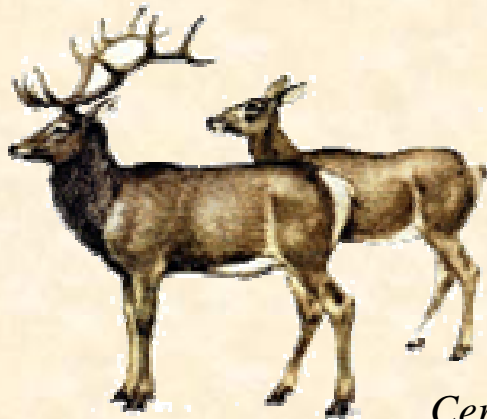
Cervus elaphus

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

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

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			
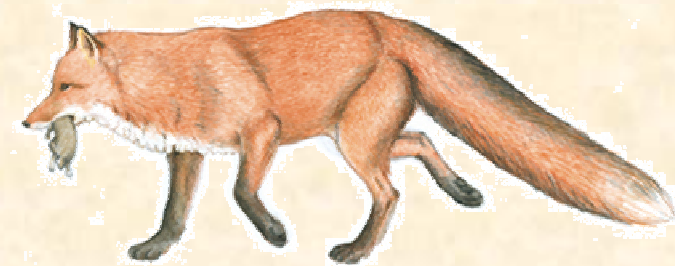
Vulpes vulpes

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 $\log(l_x)$ against age (x)

▸ sheep mortality increases with age

▸ survivorship of lapwing (*Vanellus*) is independent of age
 but survival of sheep is age-dependent
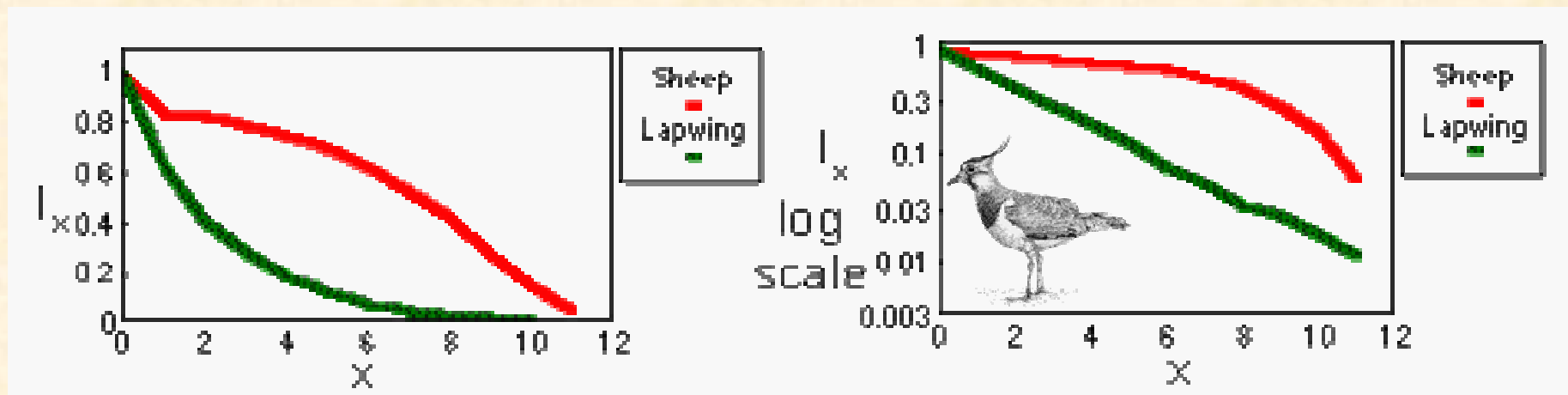
Pearls (1928) classified hypothetical age-specific mortality:

▸ Type I .. mortality is concentrated at the end of life span (humans)
▸ Type II .. mortality is constant over age (seeds, birds)
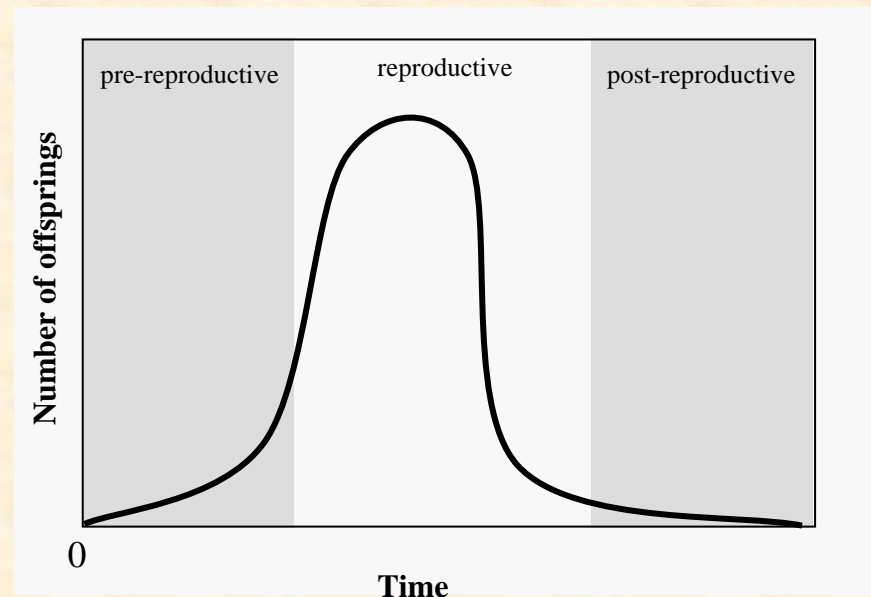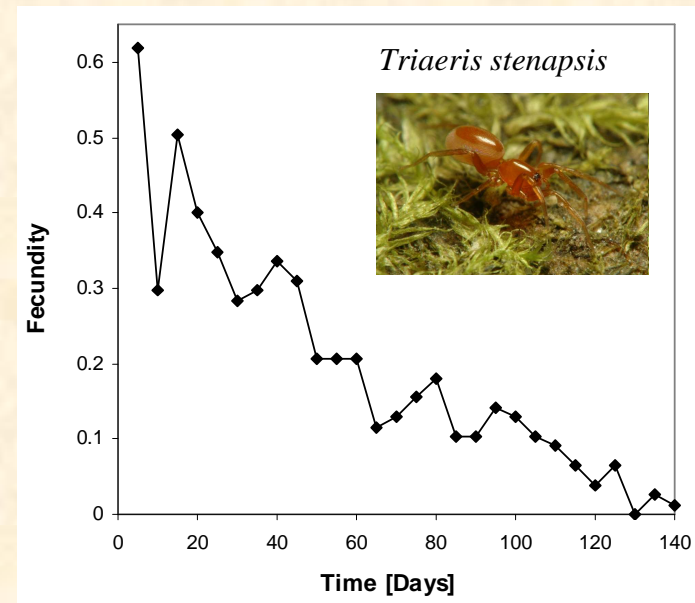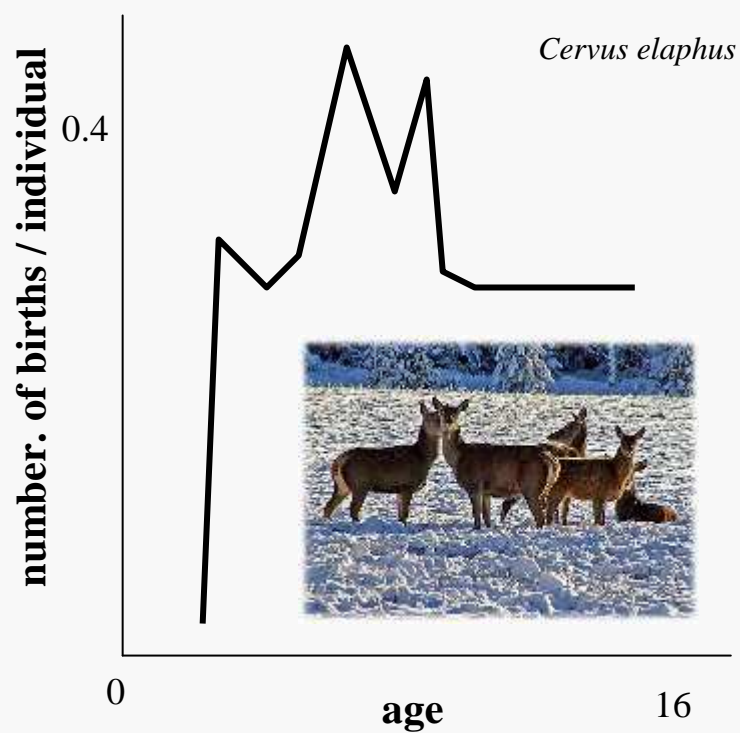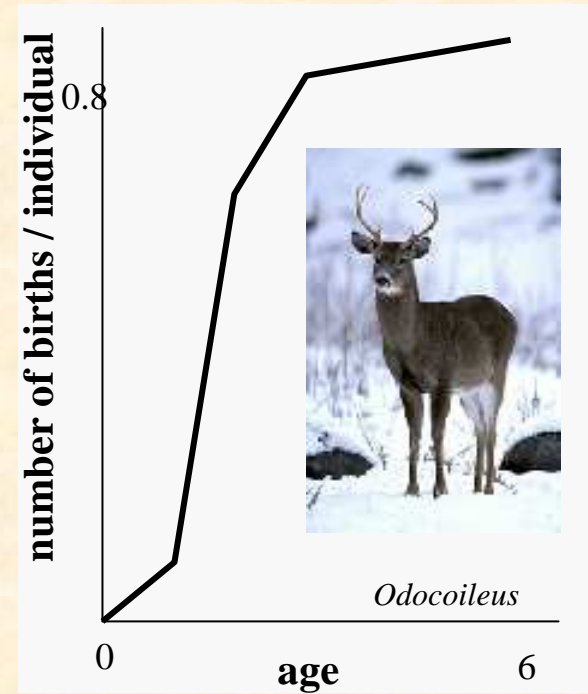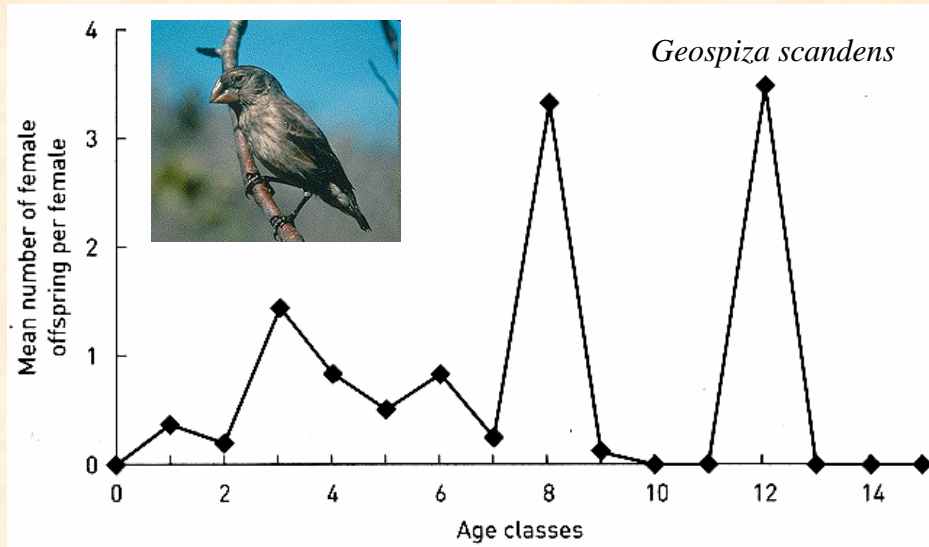▸ Type III .. mortality is highest in the beginning of life (invertebrates, fish, reptiles)
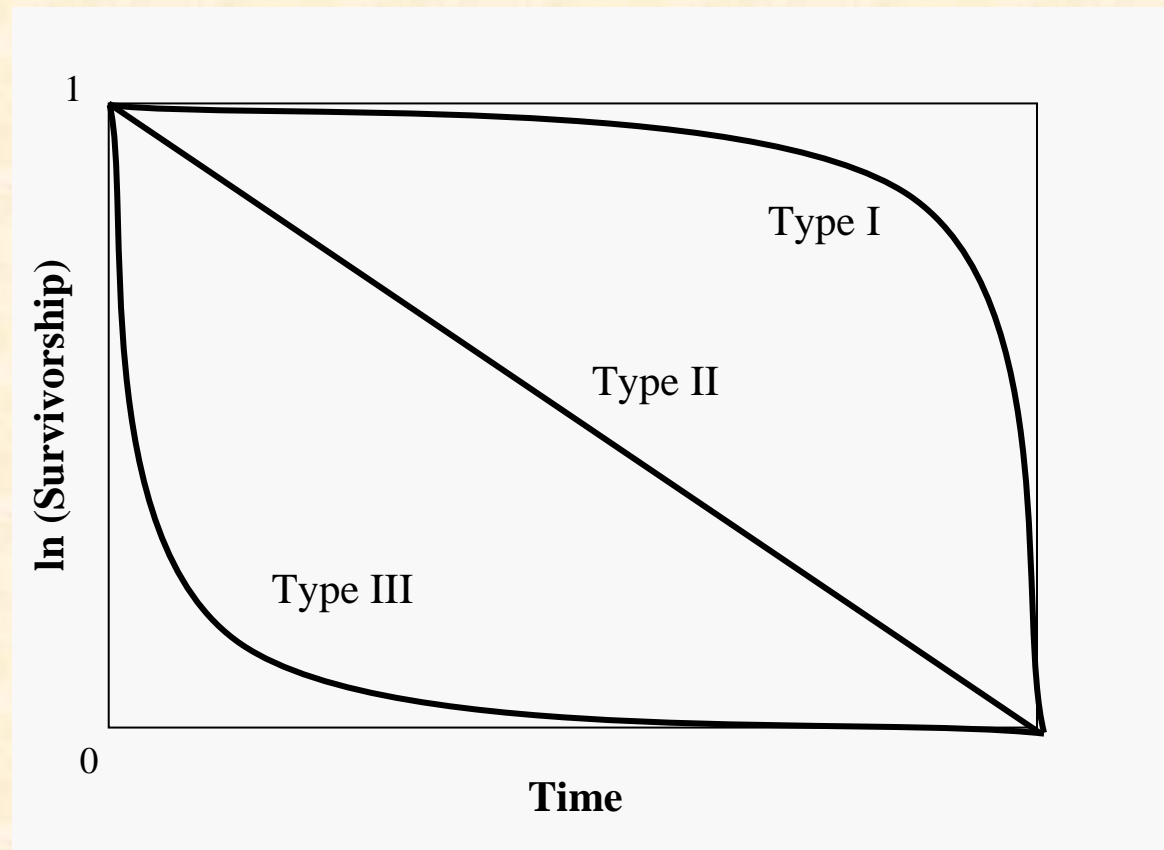
Birth rate curves

‣ 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 vs. Age classes

Odocoileus

number of births / individual vs. age (0 to 6), 0.8

Cervus elaphus

number. of births / individual vs. age (0 to 16), 0.4

Triaeris stenapsis

Fecundity vs. 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 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			4.072		
	9268	2531	Not deposited	3.967	0.105	(k_{1a})
	8823	445	Infertile	3.946	0.021	(k_{1b})
	8415	408	Rainfall	3.925	0.021	(k_{1c})
	7268	1147	Cannibalism	3.861	0.064	(k_{1d})
Early larvae	6892	376	Predators	3.838	0.024	(k_{1e})
Late larvae	6892	0	Rainfall	3.838	0	(k_2)
Pupal cells	3170	3722	Starvation	3.501	0.337	(k_3)
Summer adults	3154	16	*D. doryphorae*	3.499	0.002	(k_4)
Female × 2	3280	− 126	Sex (52% female)	3.516	−0.017	(k_5)
Hibernating adults	16	3264	Emigration	1.204	2.312	(k_6)
Spring adults	14	2	Frost	1.146	0.058	(k_7)
					2.926	(k_{total})

Summary over 10 years
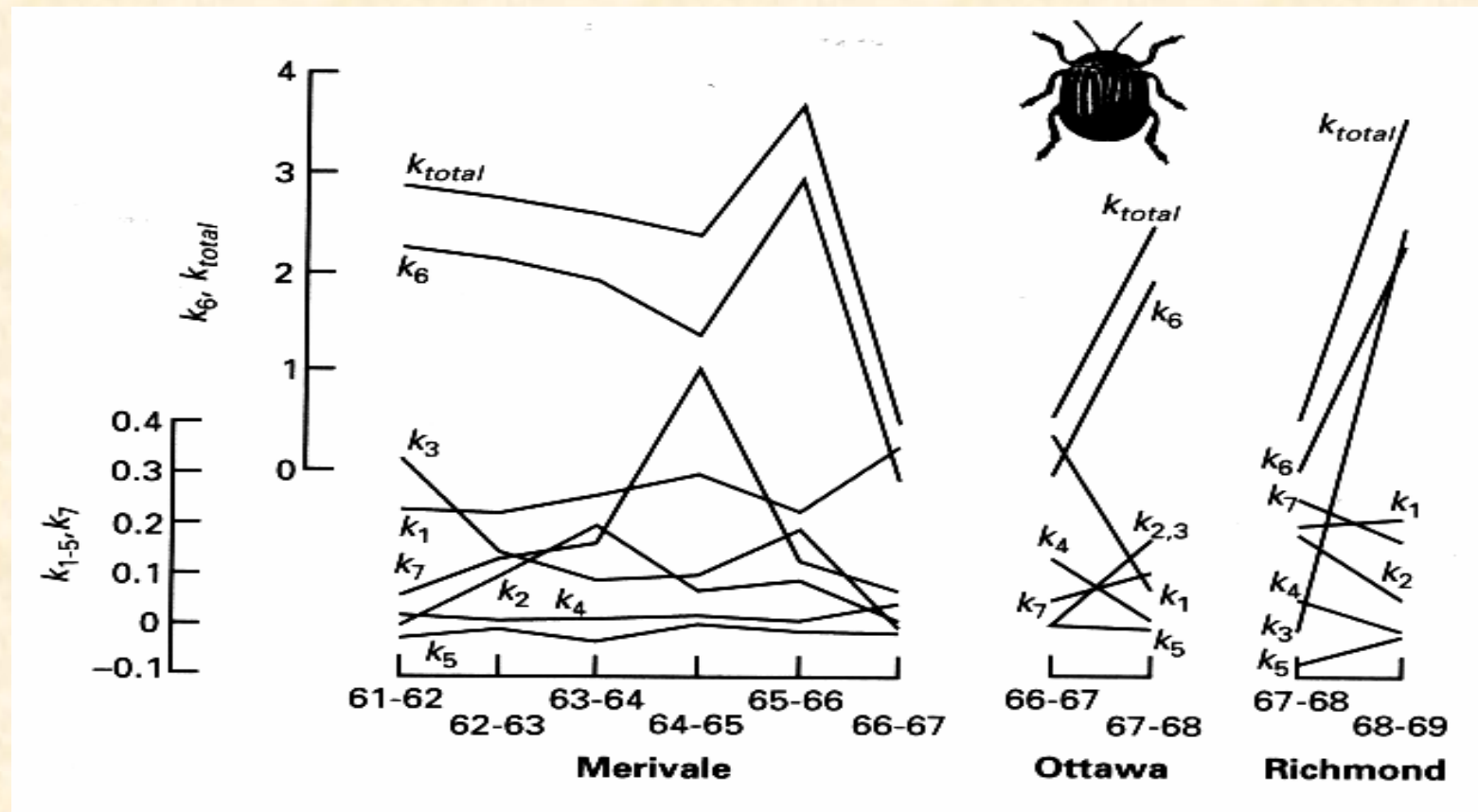
▸ highest k-value indicates the role of a factor in each generation
▸ profile of a factor parallel with the *K* profile reveals the key factor
▸ emigration is the key-factor

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
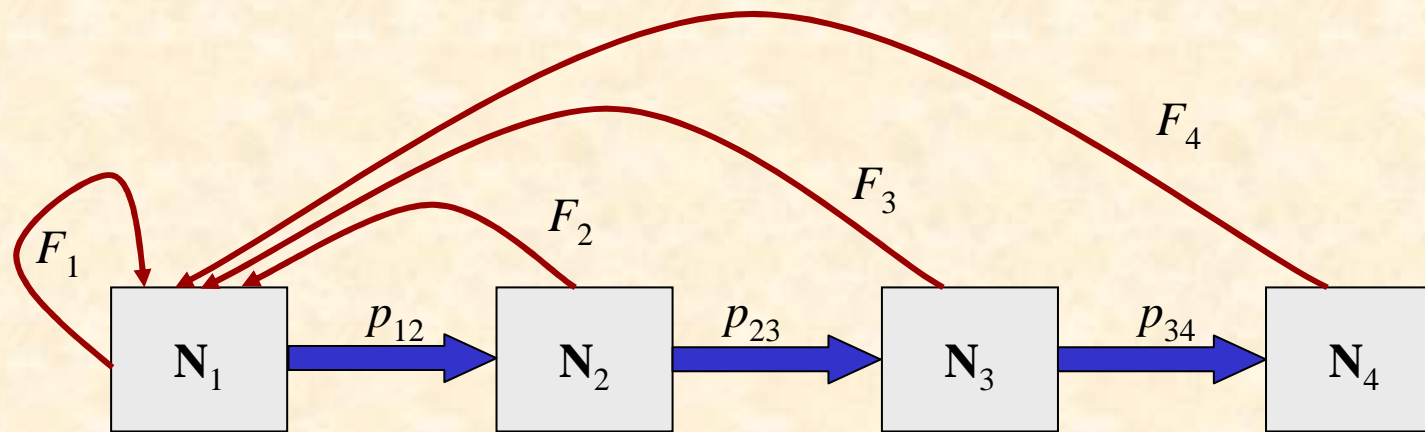‣ used for modelling of density-independent processes (exponential growth)

$N_{x,t}$ .. 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 $\mathbf{N_t}$

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

‣ each column in **A** specifies fate of an organism in a specific age: 3rd column: organism in age 2 produces F_2 offspring and goes to age 3 with probability 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

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

- populations with discrete pulses pre-reproductive census
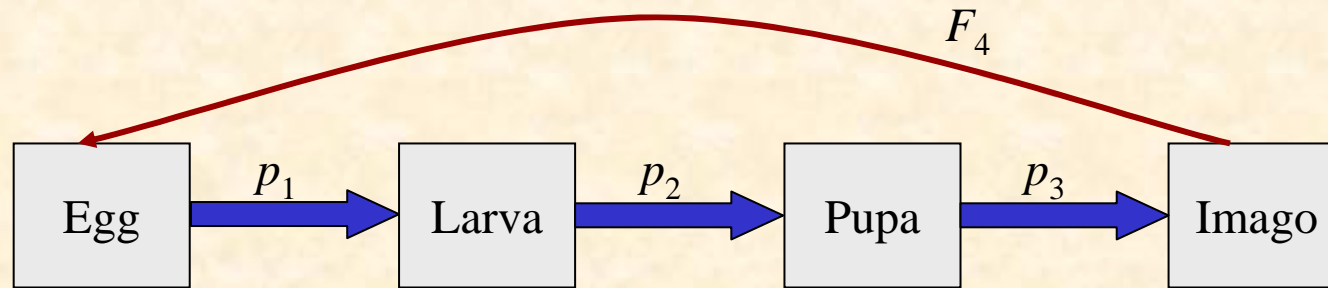
$$p_x = \frac{l_{x+1}}{l_x} \qquad\qquad F_x = p_0 m_{x+1}$$

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

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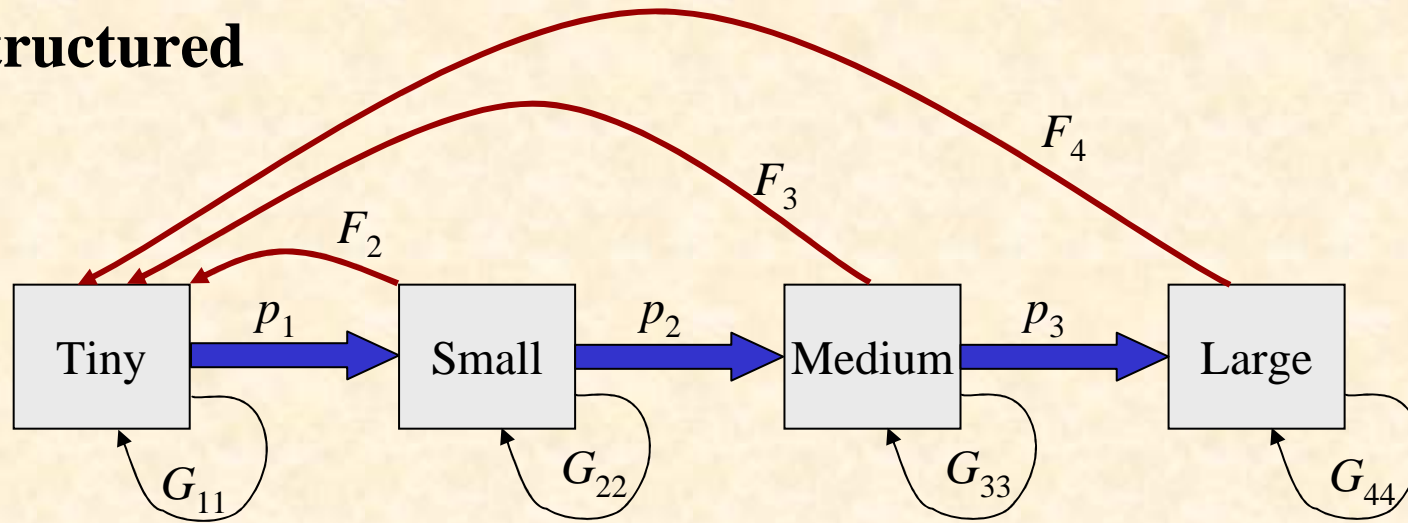
Stage-structured

▸ 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

▸ 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 vector

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

by a scalar

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

▸ determinant

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

▸ eigenvalue (λ)

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

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

$$\lambda_1 = 2.41$$
$$\lambda_2 = -0.41$$

$$N_2 = AN_1$$

$$N_3 = AN_2$$

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

$$N_t = A^t N_0$$

▶ parameters are constant over time and independent of population density

▶ follows constant exponential growth after initial damped oscillations