

# 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

▶ discrete models:

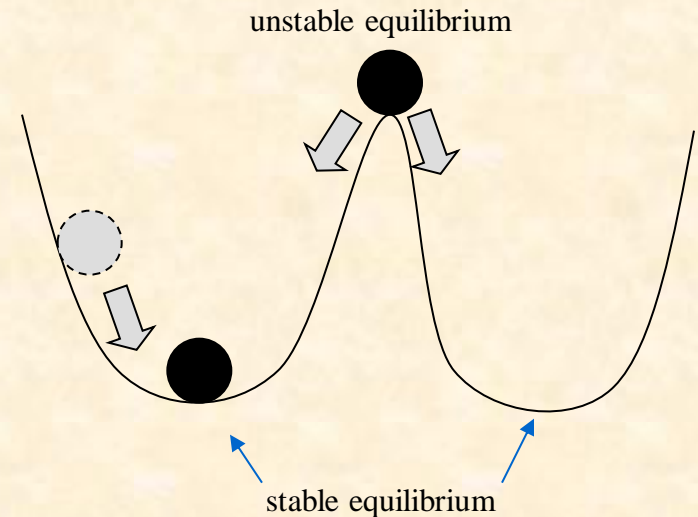
- time is composed of discrete intervals or measured in generations
- used for populations with synchronised reproduction (annual species)
- modelled by difference equations

▶ 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

- ▶ 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 → immigration [ $I$ ]
  - cockroaches were born → birth [ $B$ ]
- ▶ number of cockroaches declines:
  - dispersal of cockroaches → emigration [ $E$ ]
  - cockroaches died → death [ $D$ ]

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

- ▶ 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  $E$



*Blatta orientalis*

# 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)

**$\lambda$  .. finite growth rate**, per capita rate of growth

$\lambda = 1.23$  then  $R = 0.23$

.. 23% increase

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

► if  $\lambda$  is constant, population number in generations  $t$  is equal to

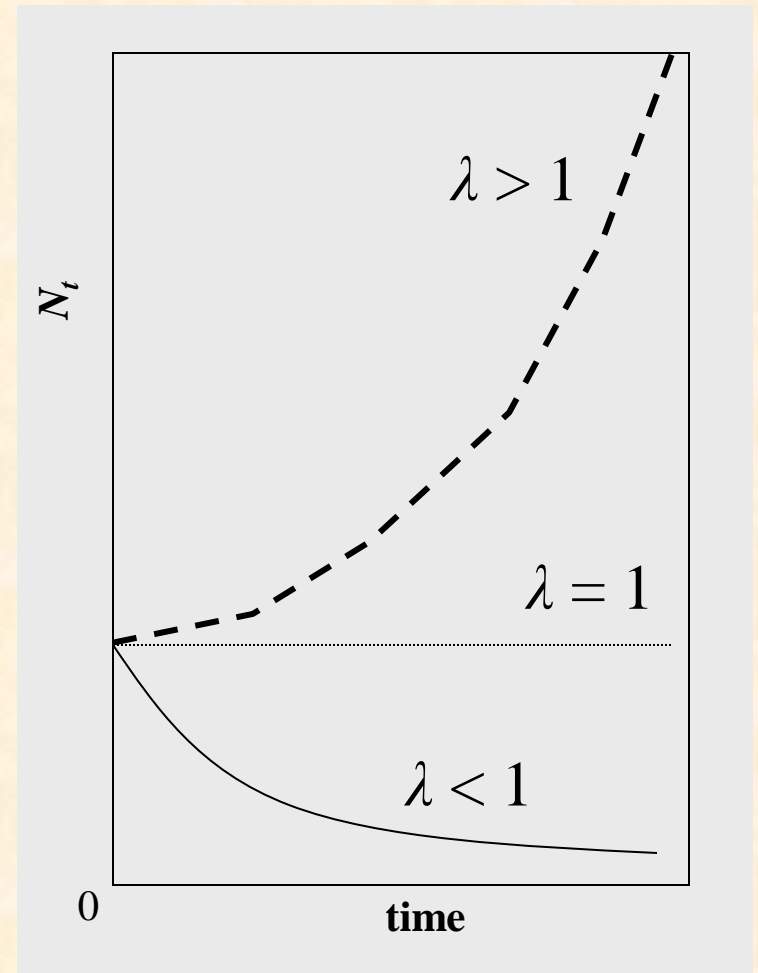
$$N_t = N_{t-1}\lambda$$

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

$$N_t = N_0\lambda^t$$

Average of finite growth rates  
- estimated as geometric mean

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





# Continuous (differential) model

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

$$N_t = N_0 \lambda^t$$

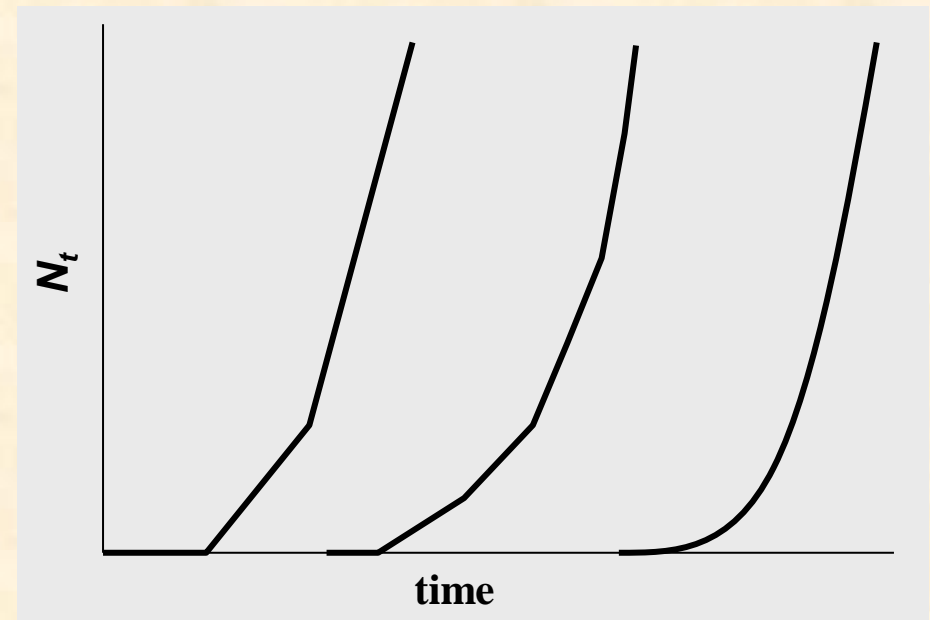
$$\ln(N_t) = \ln(N_0) + t \ln(\lambda)$$

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

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

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

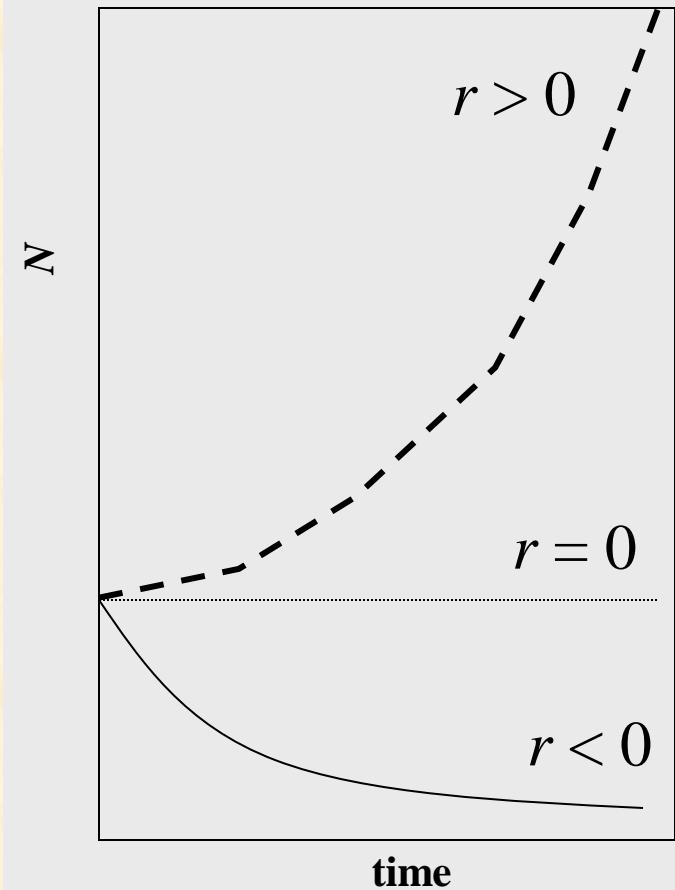
Comparison of discrete and continuous generations



if  $r = \ln(\lambda)$

$r$  .. **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

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

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

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

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

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

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

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

► doubling time: time required for a population to double

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

***r* versus  $\lambda$**

$$N_t = N_0 \lambda^t$$

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

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

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

► *r* is symmetric around 0,  $\lambda$  is not

$$r = 0.5 \dots \lambda = 1.65$$

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

# Population structure

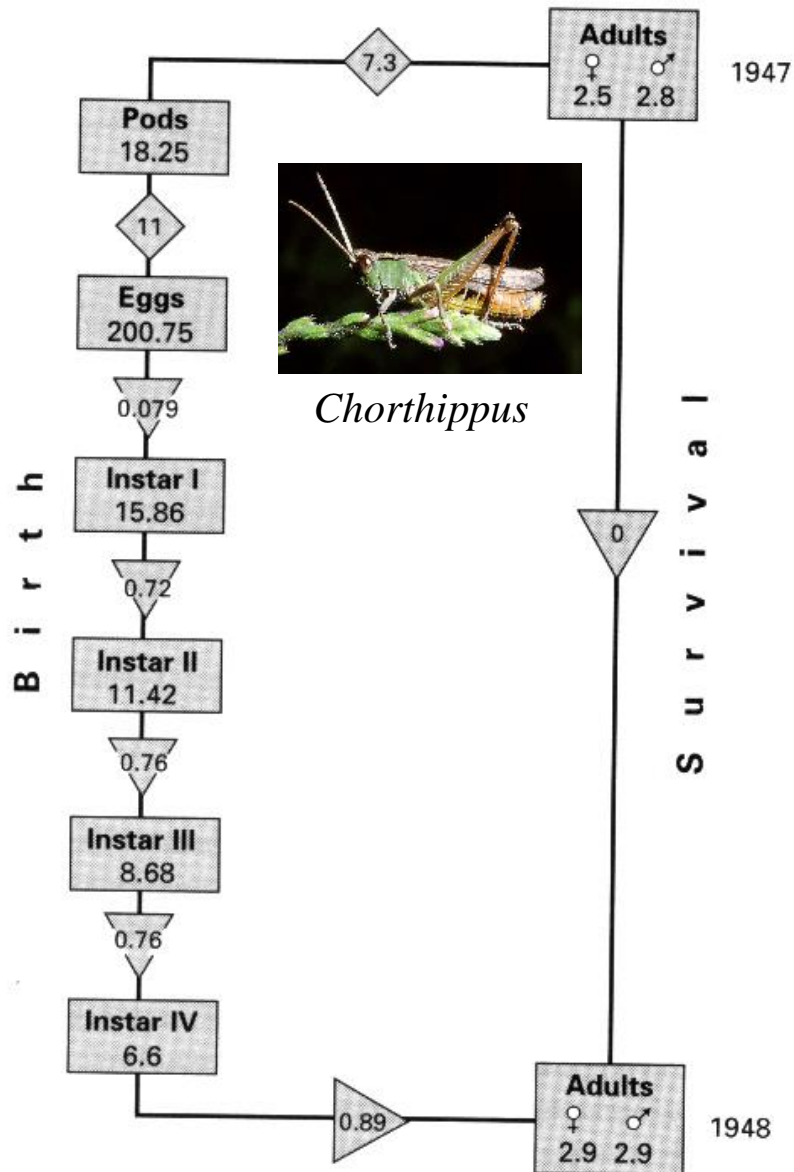
- ▶ **Demography** - study of organisms with special attention to stage or age structure
- ▶ processes are associated to age, stage or size

$x$  .. age/stage/size category

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

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

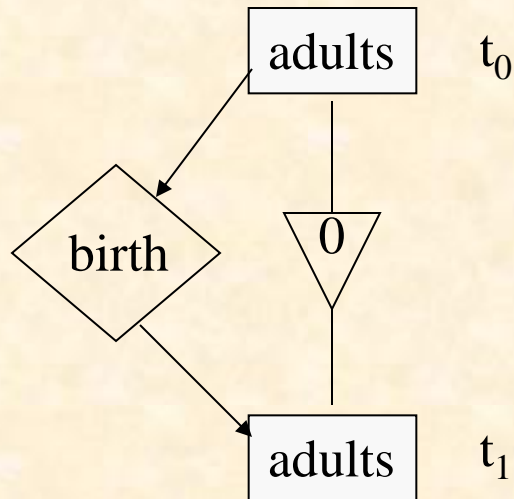
$m_x$  .. reproductive rate (expected average number of offspring per female)



Richards & Waloff (1954)

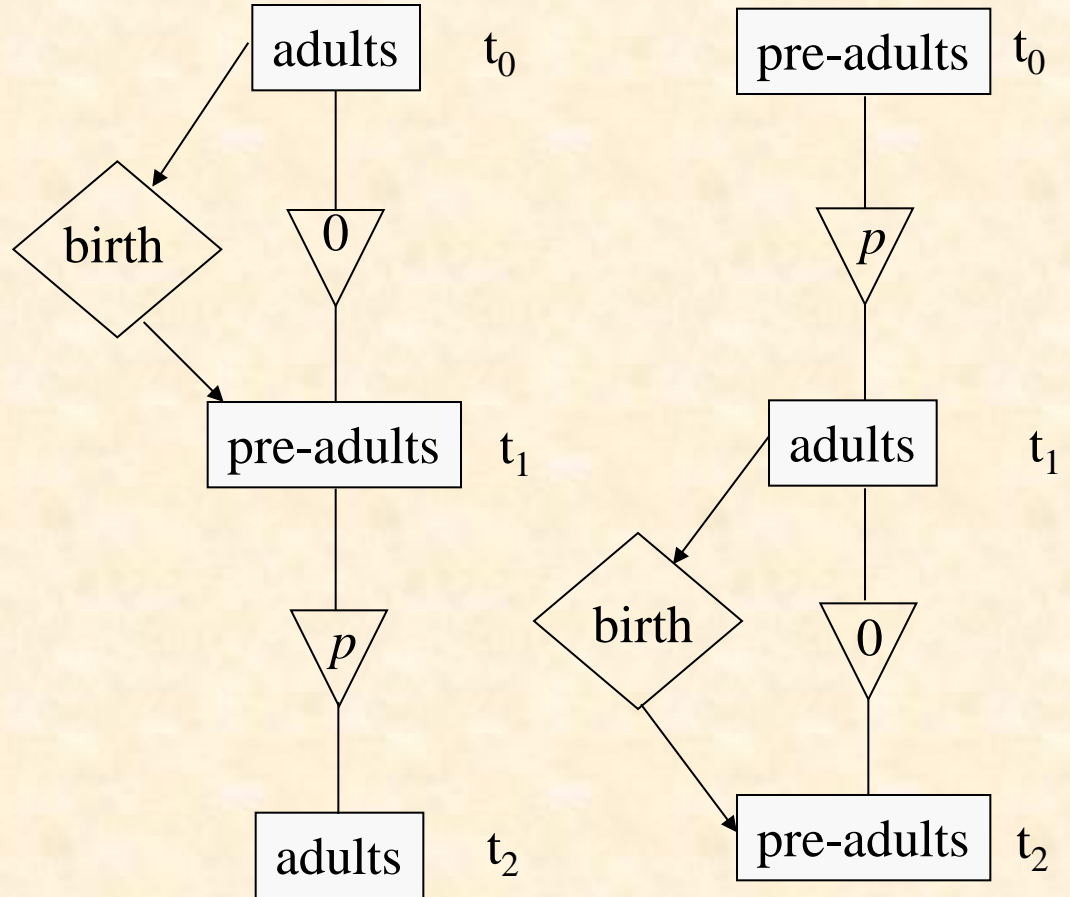
- ▶ main focus on births and deaths
- ▶ immigration & emigration is ignored
- ▶ no adult survive
- ▶ one (not overlapping) generation per year
- ▶ egg pods over-winter
- ▶ despite high fecundity they just replace themselves

## Annual species

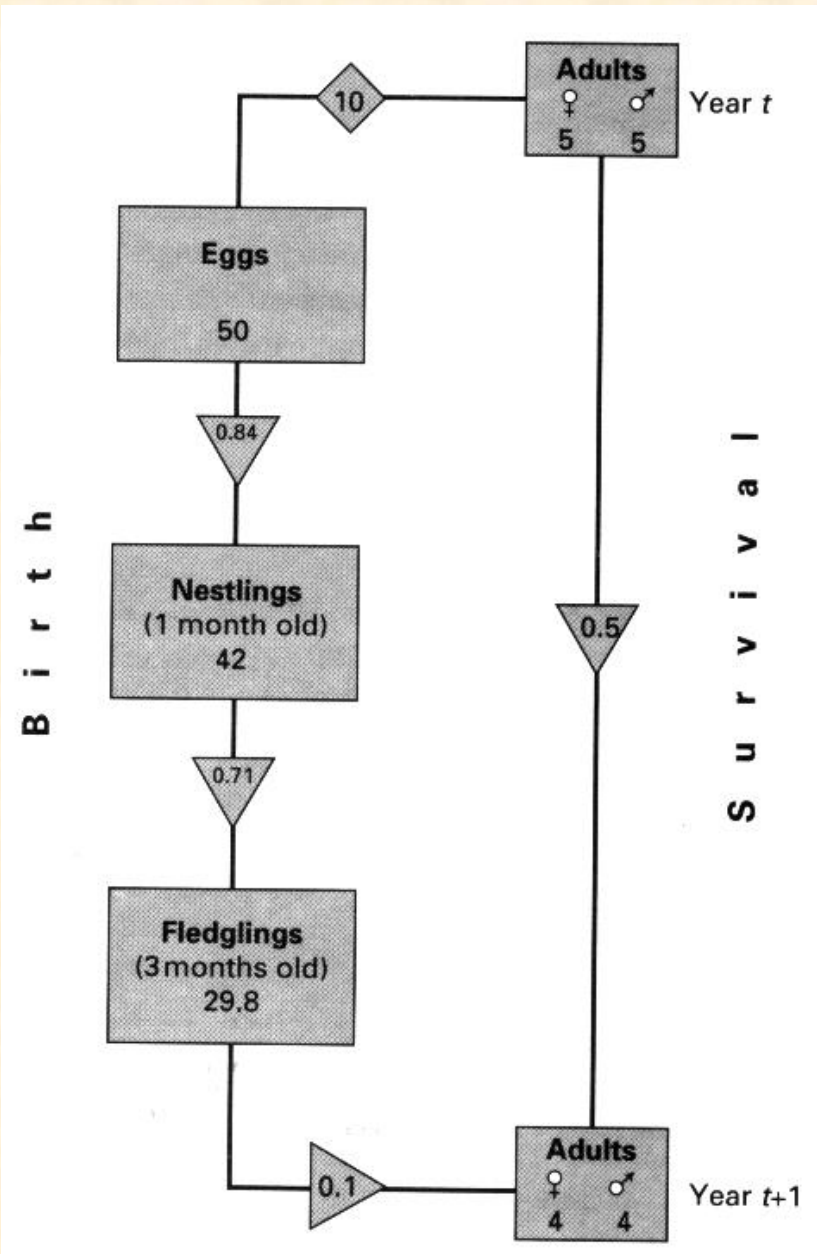


- ▶ breed at discrete periods
- ▶ no overlapping generations

## Biennial species



- ▶ breed at discrete periods
- ▶ adult generation may overlap



# 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*

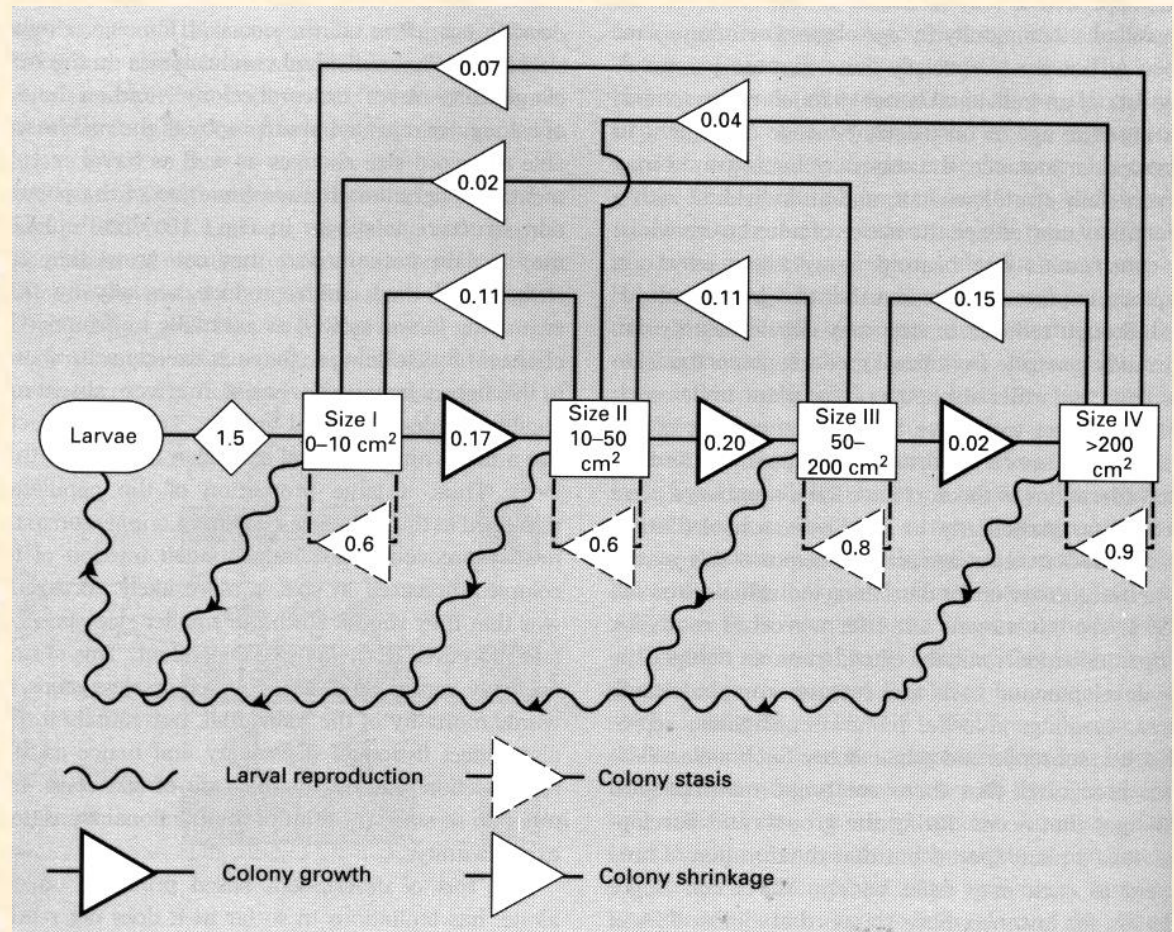
# Age-size-stage life-table

▶ 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

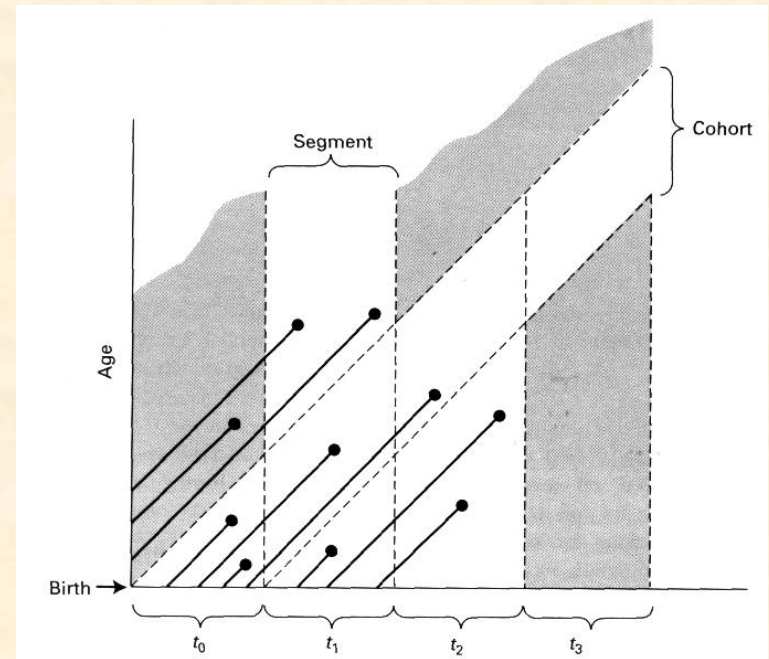
- ▶ examination of a population during one segment (time interval)

- 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*

$S_x$  .. 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

<b>x</b>	<b>S<sub>x</sub></b>	<b>D<sub>x</sub></b>	<b>l<sub>x</sub></b>	<b>p<sub>x</sub></b>	<b>q<sub>x</sub></b>	<b>m<sub>x</sub></b>
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)

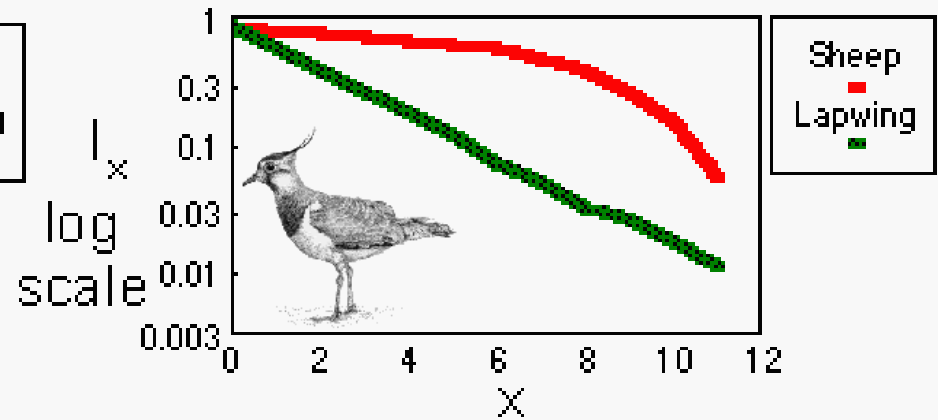
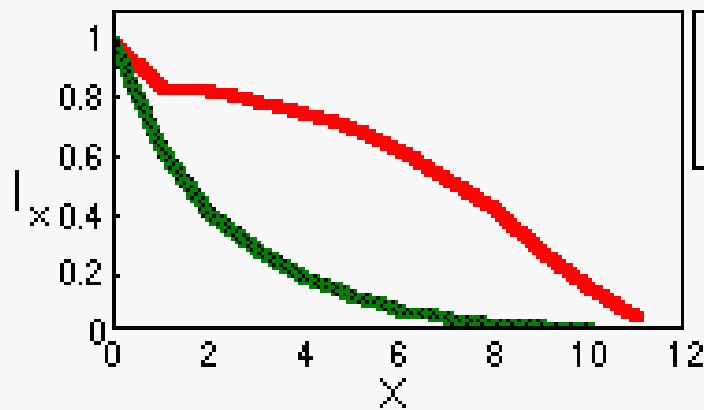
x	Sx	Dx	lx	px	qx	mx
Egg	450	68	1.000	0.849	0.151	0
Larva I	382	67	0.849	0.825	0.175	0
Larva II	315	158	0.700	0.498	0.502	0
Larva III	157	118	0.349	0.248	0.752	0
Larva IV	39	7	0.087	0.821	0.179	0
Larva V	32	9	0.071	0.719	0.281	0
Larva VI	23	1	0.051	0.957	0.043	0
Pre-pupa	22	4	0.049	0.818	0.182	0
Pupa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

*Lymantria dispar*



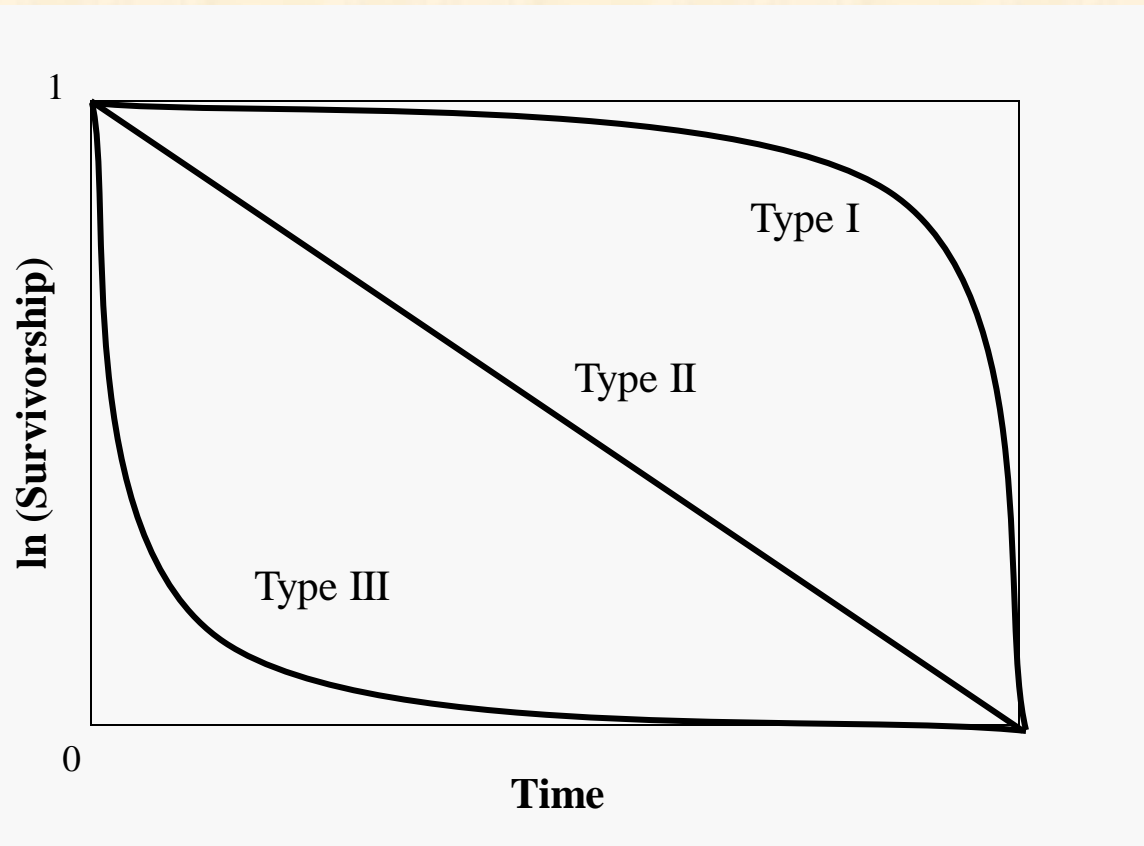
# Survivorship curves

- ▶ 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



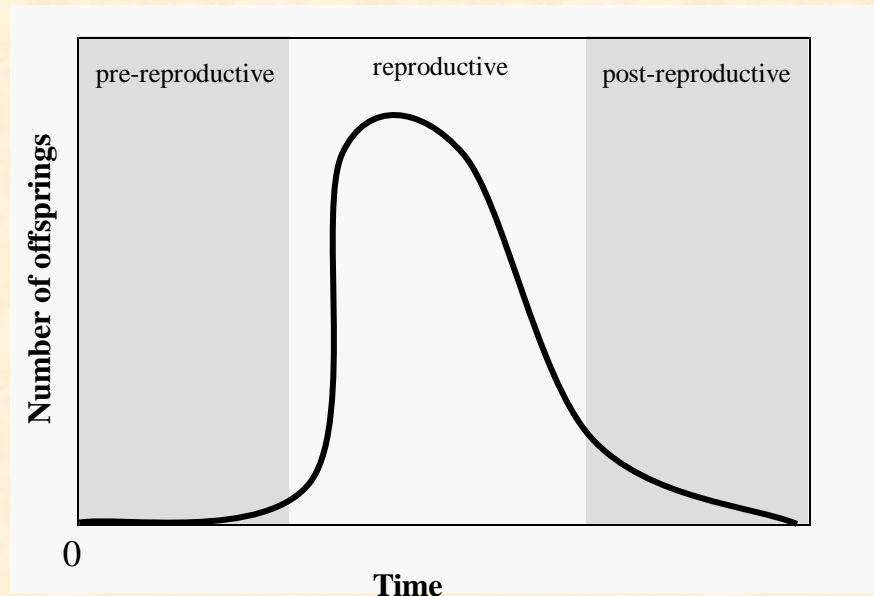
Pearls (1928) classified hypothetical age-specific mortality:

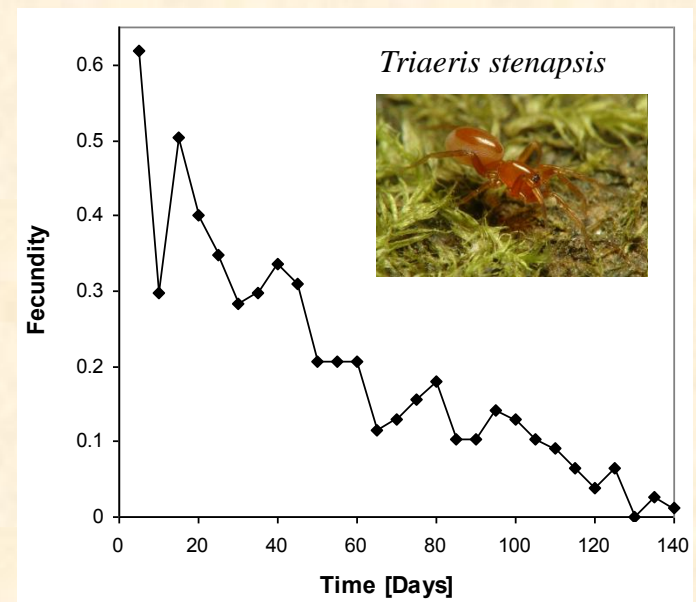
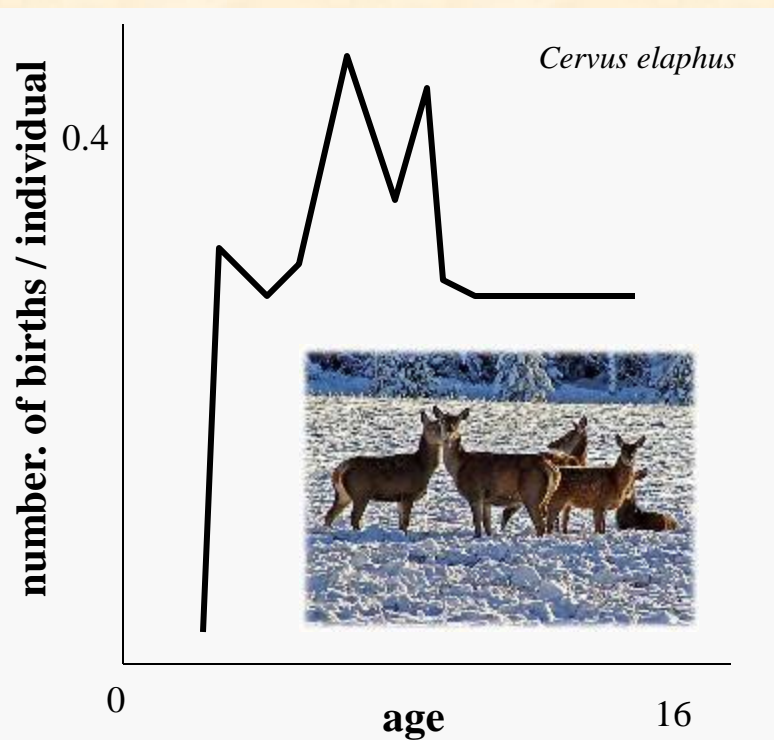
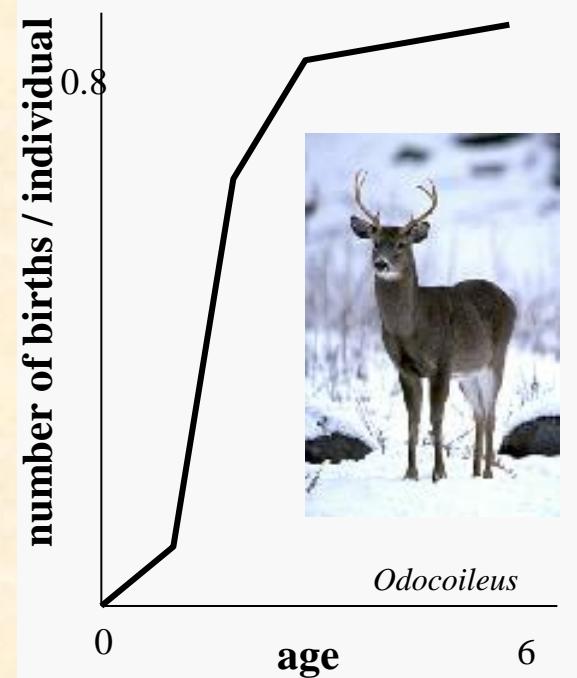
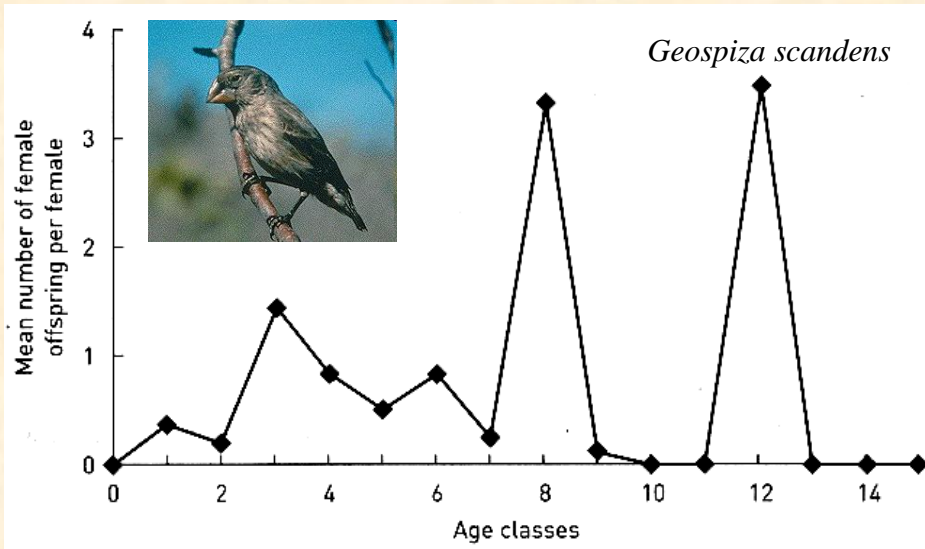
- ▶ Type I .. mortality is concentrated at the end of life span (humans)
- ▶ Type II .. mortality is constant over age (seeds, birds)
- ▶ Type III .. mortality is highest in the beginning of life (invertebrates, fish, reptiles)



# 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







# 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*

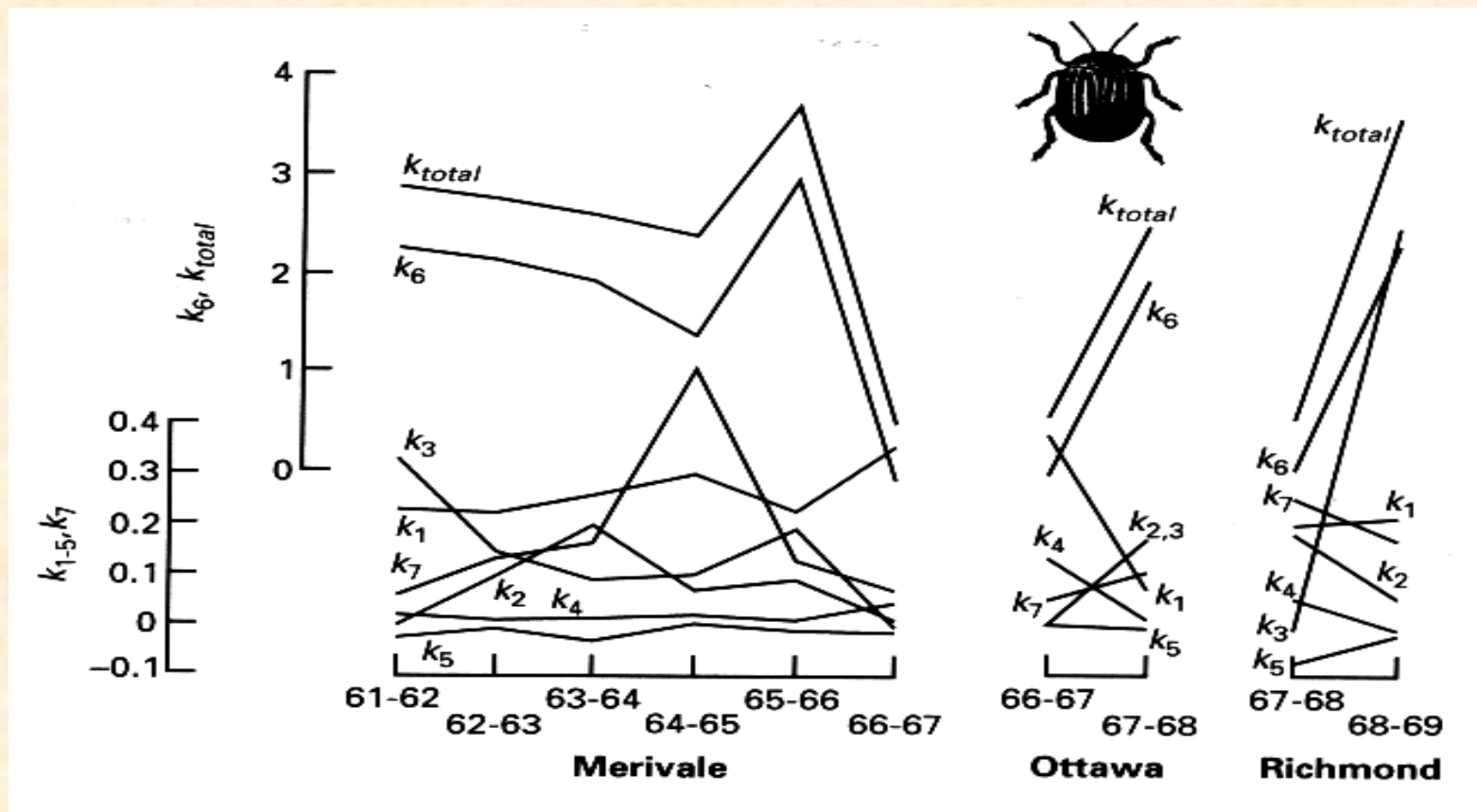
- ▶ over-wintering adults emerge in June → eggs are laid in clusters on the lower side of leaves → larvae pass through 4 instars → form pupal cells in the soil → summer adults emerge in August → begin to hibernate in September
- ▶ mortality factors overlap



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	<i>D. doryphorae</i>	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)

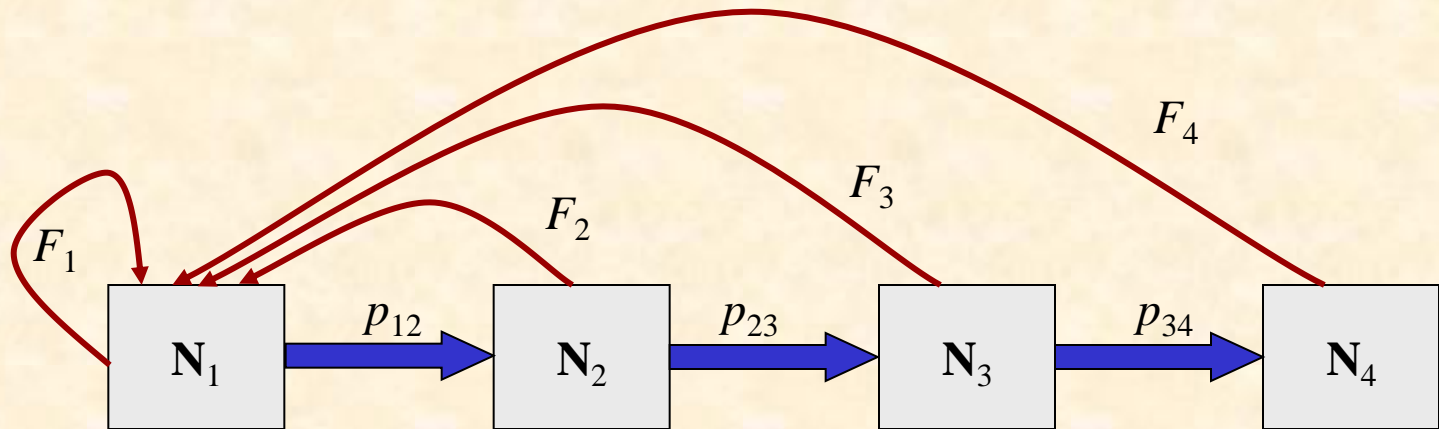
$N_{x,t}$  .. no. of organisms in age  $x$  and time  $t$

$G_x$  .. 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

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

- ▶ number of individuals in the remaining age class

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

$$\underbrace{\begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ p_{12} & 0 & 0 & 0 \\ 0 & p_{23} & 0 & 0 \\ 0 & 0 & p_{34} & 0 \end{bmatrix}}_{\text{transition matrix } \mathbf{A}} \times \underbrace{\begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \end{bmatrix}}_{\text{age distribution vectors } \mathbf{N}_t} = \begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix}$$

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

- ▶ each column in  $\mathbf{A}$  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  $p_{23}$
- ▶  $\mathbf{A}$  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

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

$$F_x = p_x m_{x+1}$$

includes  $p$  of reproductive stages

- populations with discrete pulses pre-reproductive census

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

$$F_x = p_0 m_{x+1}$$

includes  $p$  of the youngest stage

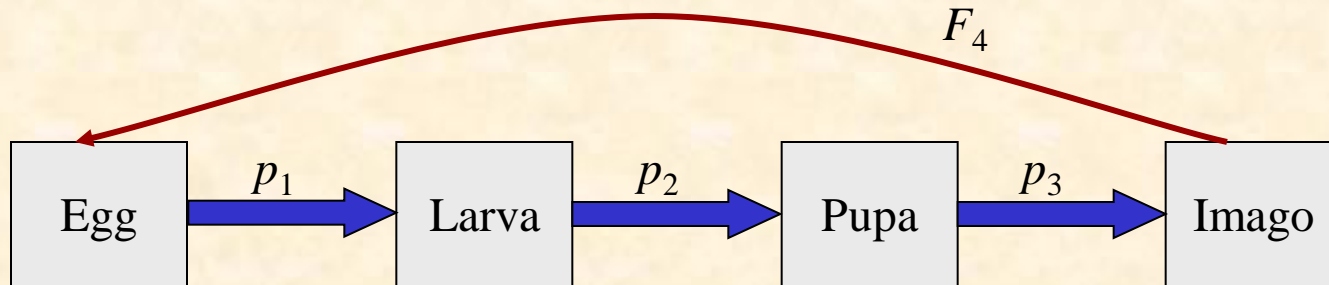
- for pre-reproductive census 0 age is omitted

- for populations with continuous reproduction

$$p_x = \left( \frac{l_x + l_{x+1}}{l_{x-1} + l_x} \right)$$

$$F_x = \frac{\sqrt{l_1} (m_x + p_x m_{x+1})}{2}$$

## Stage-structured

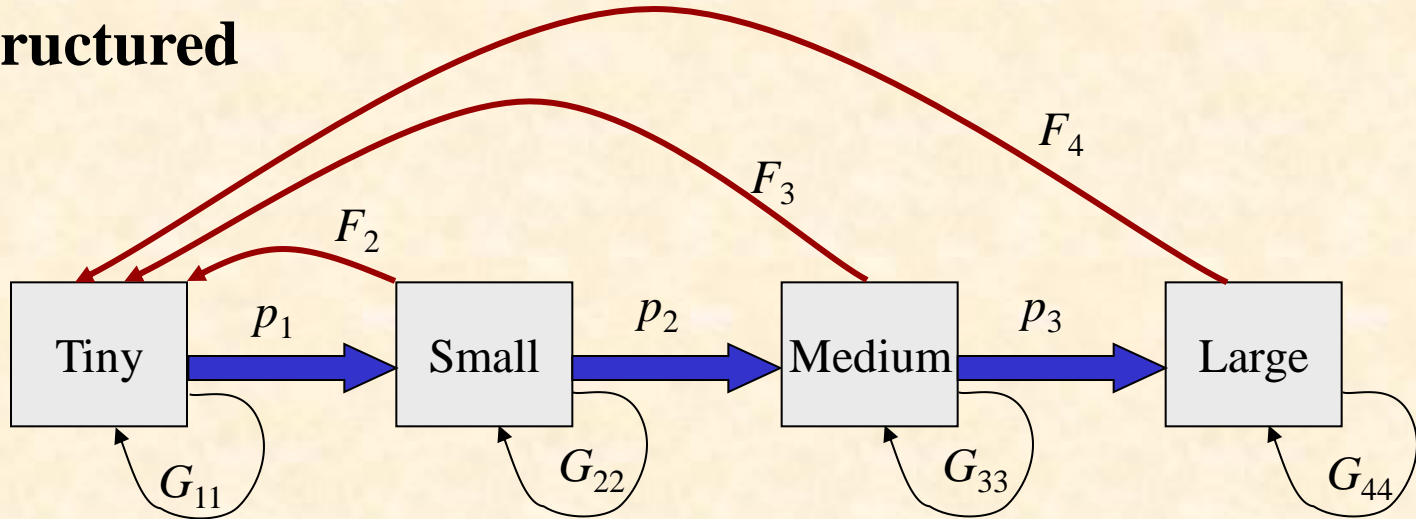


- ▶ only imagoes reproduce thus  $F_{1,2,3} = 0$
- ▶ no imago survives to another reproduction period:  $p_4 = 0$

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



# 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

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

## ▶ determinant

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

## ▶ eigenvalue ( $\lambda$ )

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

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

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

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

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

$$\lambda_1 = 2.41$$

$$\lambda_2 = -0.41$$

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

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

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

$$\mathbf{N}_t = \mathbf{A}^t\mathbf{N}_0$$

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

