Structured Models

"Populační ekologie živočichů"

Stano Pekár

Matrix model

- 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
- fertility and mortality is constant in time

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

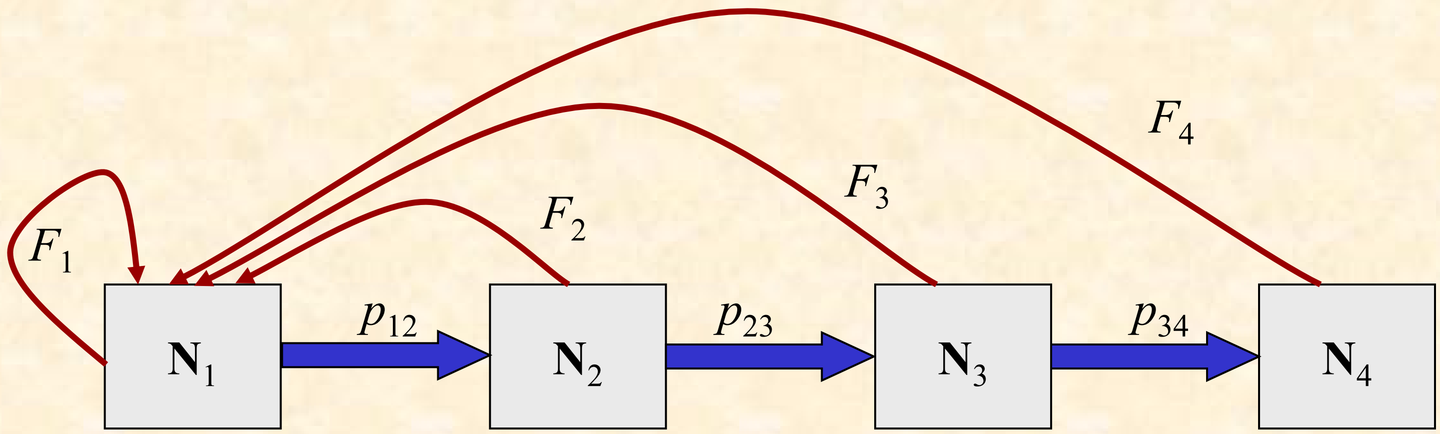
G_x .. probability of persistence in the same size/stage

F_x .. age/stage specific fertility (average no. of offspring per female),

$$F_x < m_{x+1}$$

p_x .. age/stage specific survival

Age-structured



- class 0 is omitted
- individuals cannot persist in an age class
- 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

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

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

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

- 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

- calculation of fertilities/fecundities (F) and survivals (p) depend on census and reproduction type

- <u>discrete pulses post-reproductive census</u>: census of offspring shortly after birth (class 0)

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

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

includes p of reproductive stages

- <u>discrete pulses pre-reproductive census</u>: census of offspring born last year (class 1), class 0 is omitted

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

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

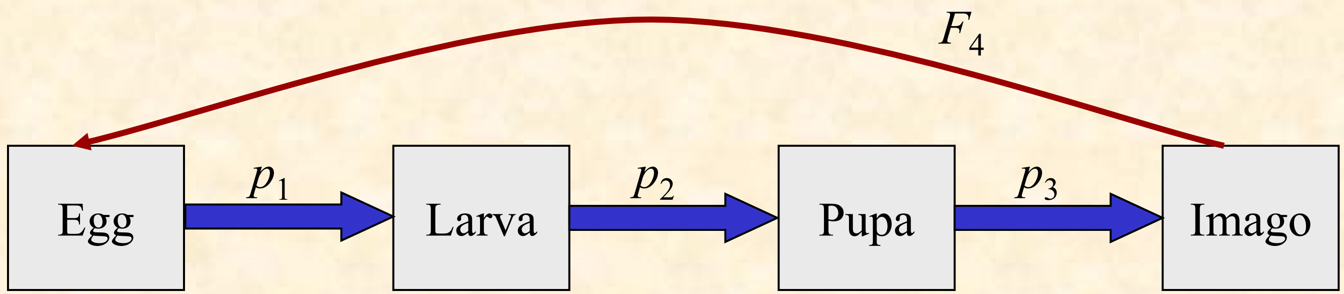
includes p of the youngest stage

- <u>continuous reproduction</u>: each class is composed of early and older age class

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

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

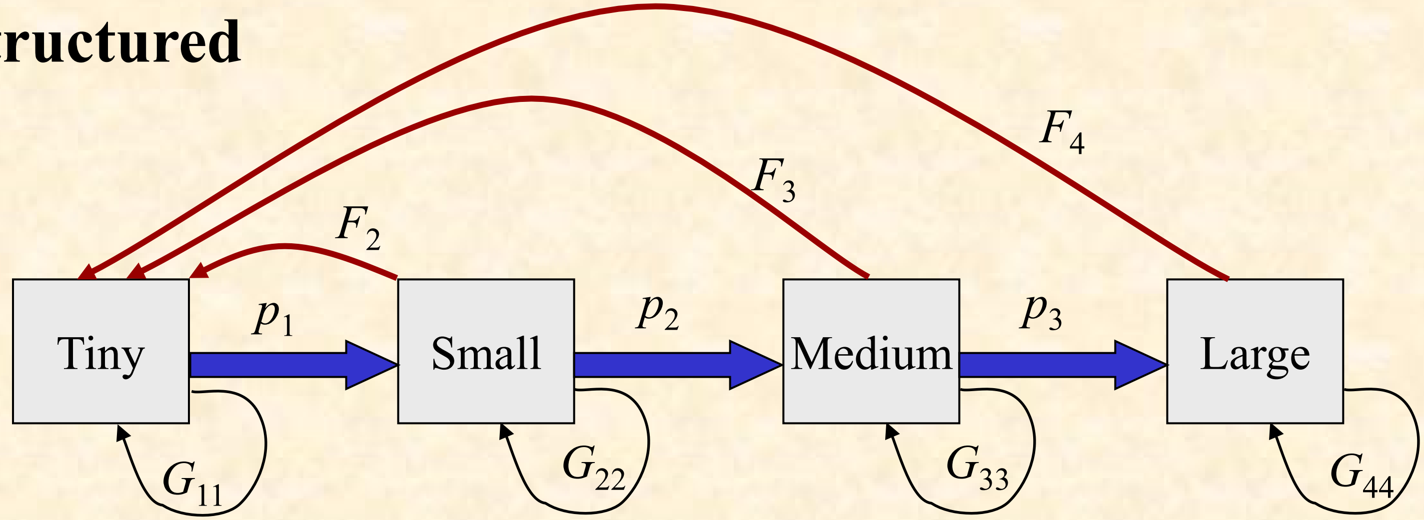
Stage-structured



- in species where parameters are function of developmental stage
- when inter-moult intervals vary in duration
- may contain persistence
- 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)
- parameters are a function of size
- $F_1 = 0$
- above diagonal elements can include *p* of shrinkage

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

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 (λ)

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

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

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

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

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

$\lambda_1 = 2.41$

$\lambda_2 = -0.41$

Density-independent model

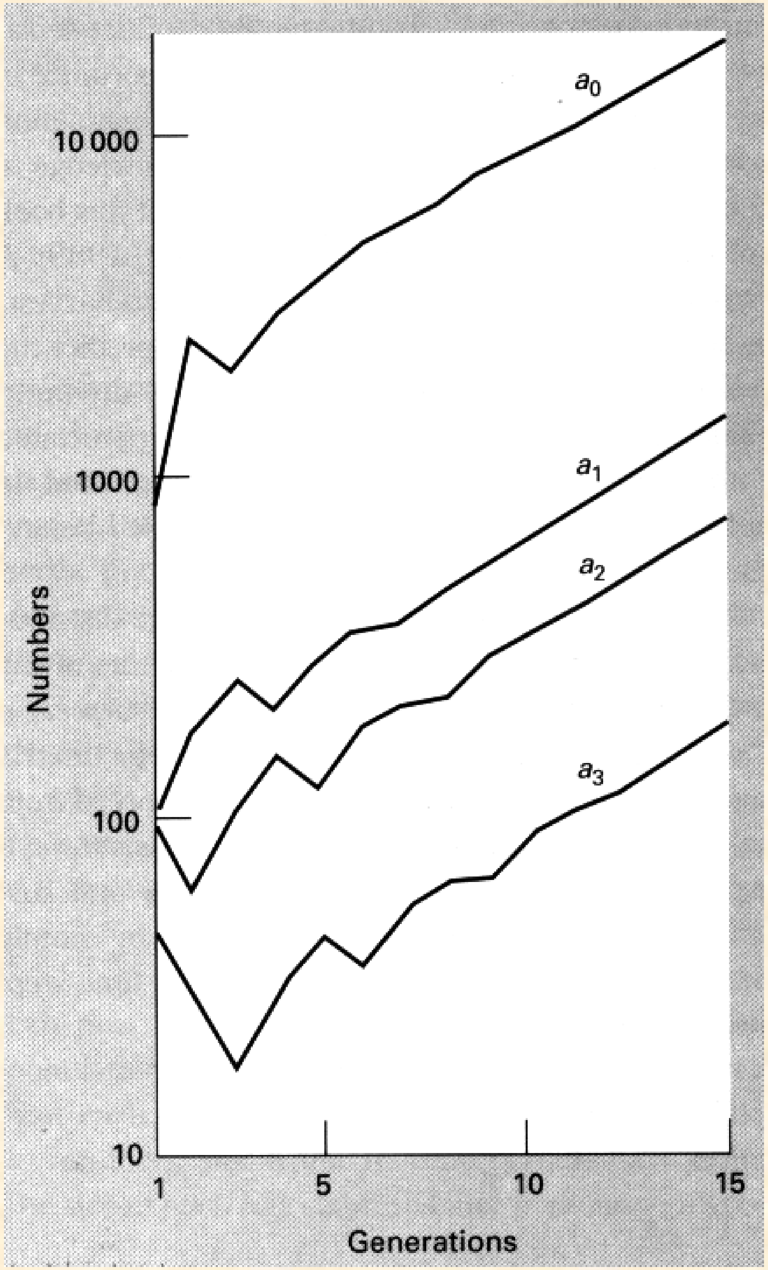
$$N_2 = AN_1$$

$$N_3 = AN_2$$

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

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

- parameters are constant over time and independent of population density
- follows constant exponential growth after reaching stable age distribution (following initial damped oscillations)



Net reproductive rate (R_0)

- average total number of offspring produced by a female in her lifetime
- equals to finite growth rate

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

Average generation time (T)

- average age of females when they give birth
- not valid for populations with generation overlap

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

Expectation of life

- age specific expectation of life – average age that is expected for particular age class
- o .. oldest age

$$e_x = \frac{T_x}{l_x}$$ where $$T_x = \sum_{x}^{o} L_x$$ $$L_x = \frac{l_x + l_{x+1}}{2}$$

Growth rates

- <u>Discrete time/generations</u>

- estimate of λ (finite growth rate) from the life table:

$$\boxed{\mathbf{A}\tilde{\mathbf{N}}_t = \lambda\tilde{\mathbf{N}}_t}$$

where $\tilde{\mathbf{N}}_t$ is vector at stable age distribution

λ is dominant positive eigenvalue of $\mathbf{A}$

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

- or $\lambda \approx \dfrac{R_0}{T}$

- <u>Continuous time</u>

- r can be estimated from λ $\boxed{r = \ln(\lambda)}$
- by approximation

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

or by Euler-Lotka method
- valid only for population with SCD

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

Stable Class distribution (SCD)

- relative abundance of different life history age/stage/size categories

▸ population approaches stable age distribution:

$N_0 : N_1 : N_2 : N_3 :....: N_s$ is stable

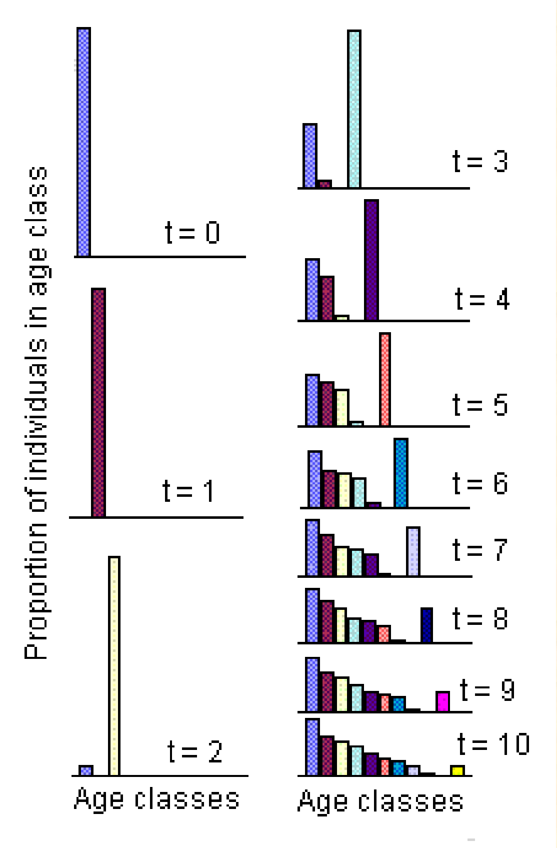
- once population reached SCD it grows exponentially

▸ $\mathbf{w}_1$ .. right eigenvector (vector of the dominant eigenvalue)

- provides stable age distribution
- scale $\mathbf{w}_1$ by sum of individuals

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

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



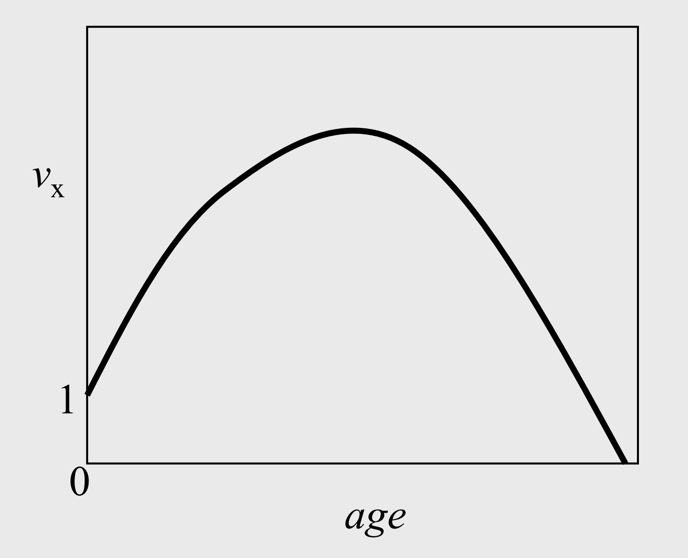
Reproductive value (v_x)

- measures relative reproductive potential and identifies age class that contributes most to the population growth (Fisher 1930)
- such class is under highest selection force
- sum of all expected offspring produced in age x and further
- when population increases then early offspring contribute more to v_x than older ones
- is a function of fertility and survival
- $\mathbf{v}_1$ .. left eigenvector (vector of the dominant eigenvalue of transposed **A**)

$$\mathbf{v}_1 \mathbf{A}' = \lambda_1 \mathbf{v}_1$$

- $\mathbf{v}_1$ is proportional to the reproductive value and scaled to the first category (class 1 = 1)

$$\boxed{v_x = \frac{v_{1x}}{v_{11}}} \qquad x \neq 1$$



Sensitivity (s)

- identifies which process (p, F, G) has largest effect on the population increase (λ_1)
- measures absolute change

- examines change in λ_1 given small change in processes (a_{ij})
- sensitivity is larger for survival of early, and for fertility of older classes
- not used for postreproductive census with class 0

$$\boxed{s_{ij} = \frac{v_{ij} w'_{ij}}{\langle \mathbf{v}, \mathbf{w} \rangle}}$$

← sum of pairwise products

Elasticity (e)

- weighted measure of sensitivity

- measures relative contribution to the population increase
- impossible transitions = 0

$$\boxed{e_{ij} = \frac{a_{ij}}{\lambda_1} s_{ij}}$$

Conservation biology (Management)

- to adopt means for population promotion (threatened) or control (pests) or sustainable yield
- in populations with short generation time and higher natality population decline stabilisation will take some delay

Conservation/control procedure

1. Construction of a life table
2. Estimation of the intrinsic rates
3. Sensitivity analysis - helps to decide where conservation /control efforts should be focused - on parameters with high elasticities
4. Development and application of management plan
5. Prediction of future