

# Intraspecific Interactions

*“Populační ekologie živočichů“*

Stano Pekár

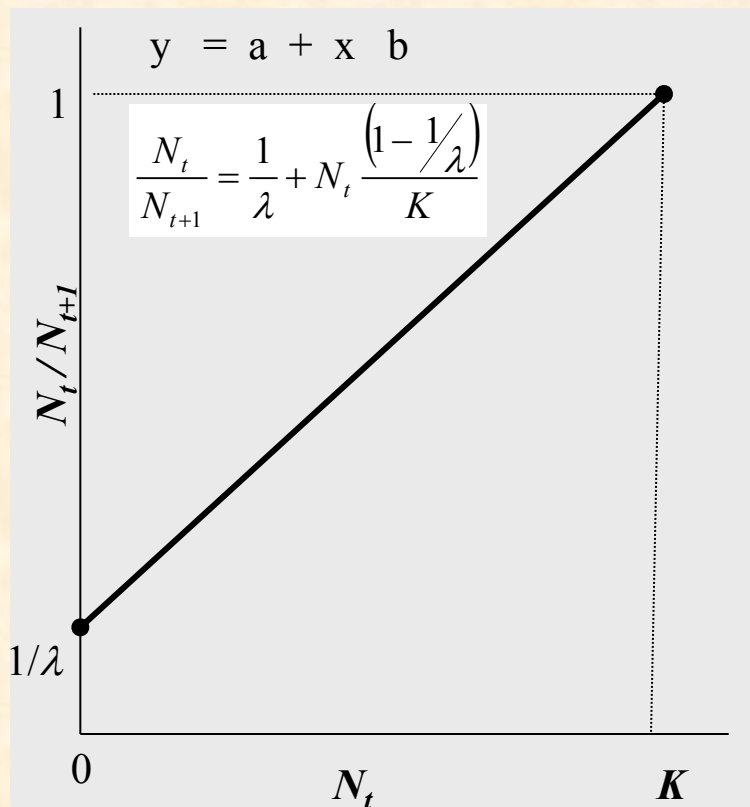
# Density-dependent growth

- ▶ includes all mechanisms of population growth that change with density
  - population structure is ignored
  - extrinsic effects are negligible
  - response of  $\lambda$  and  $r$  to  $N$  is immediate
  
- ▶  $\lambda$  and  $r$  decrease with population density either because natality decreases or mortality increases or both
  - negative feedback of the 1st order
  
- ▶  $K$  .. carrying capacity
  - upper limit of population growth where  $\lambda = 1$  or  $r = 0$
  - is a constant

# Discrete (difference) model

- there is linear dependence of  $\lambda$  on  $N$

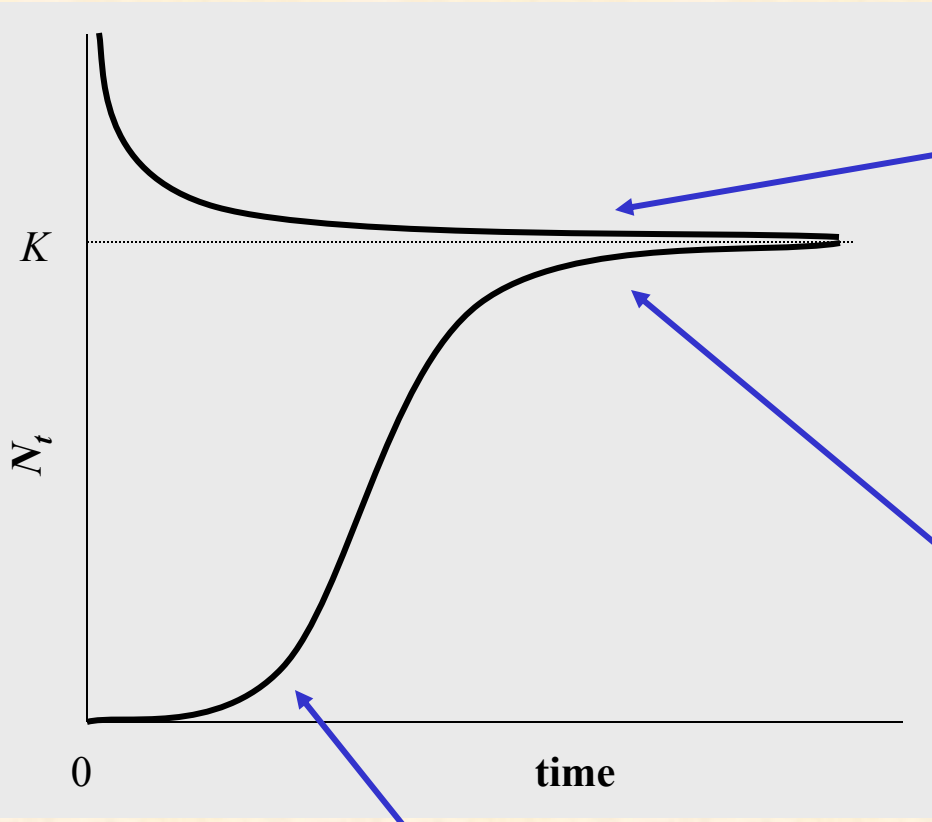
$$N_{t+1} = N_t \lambda \quad \frac{N_t}{N_{t+1}} = \frac{1}{\lambda}$$



$$N_{t+1} = \frac{N_t \lambda}{1 + \frac{(\lambda - 1)N_t}{K}}$$

if  $a = \frac{\lambda - 1}{K}$  then

$$N_{t+1} = \frac{N_t \lambda}{1 + a N_t}$$



when  $N_t > K$  then

$$\frac{\lambda}{1 + aN_t} < 1$$

- population returns to  $K$

when  $N_t \rightarrow K$  then

$$\frac{\lambda}{1 + aN_t} \approx 1$$

- density-dependent control
- S-shaped (sigmoid) growth

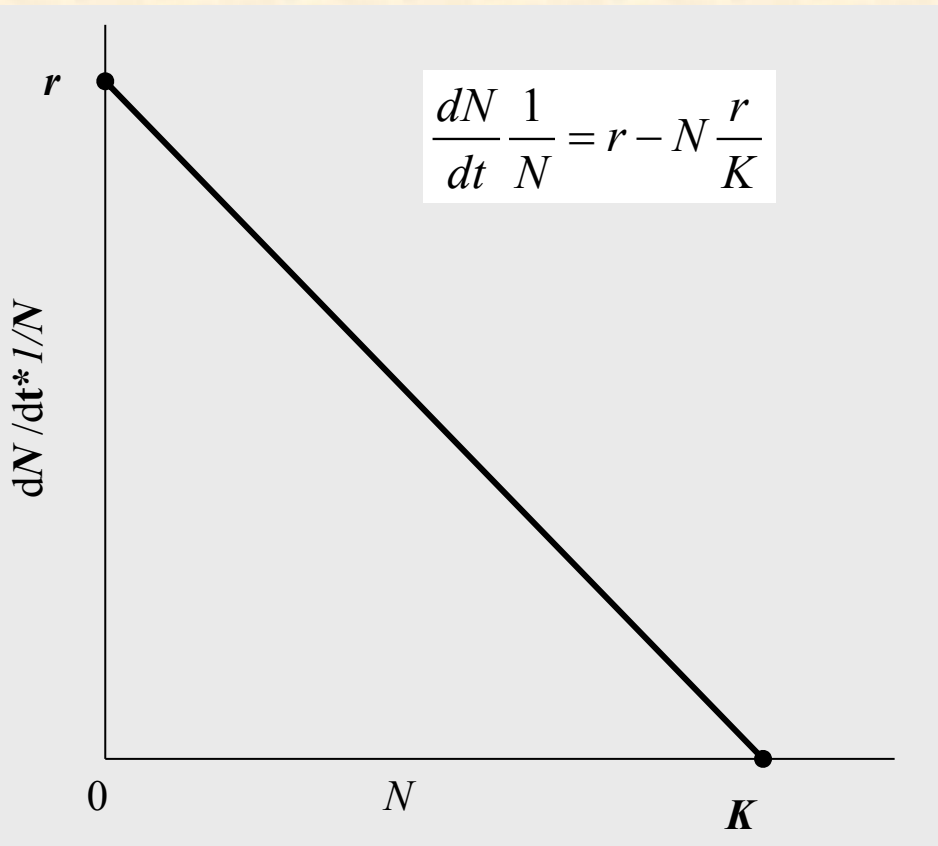
when  $N_t \rightarrow 0$  then

$$\frac{\lambda}{1 + aN_t} \approx \lambda$$

- no competition
- exponential growth

# Continuous (differential) model

- ▶ logistic growth
- ▶ first used by Verhulst (1838) to describe growth of human population
- there is linear dependence of  $r$  on  $N$



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

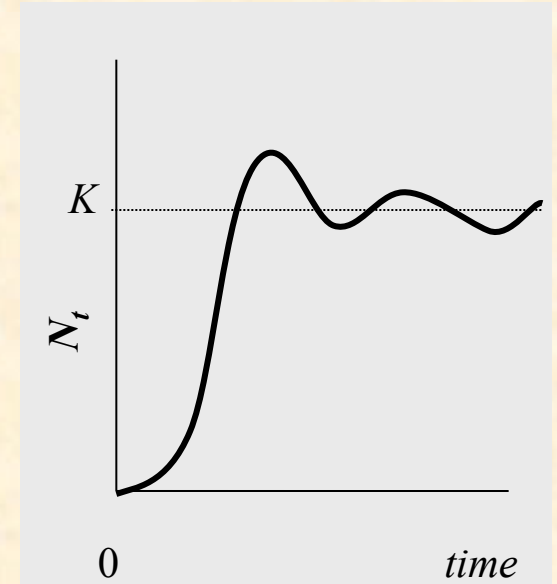
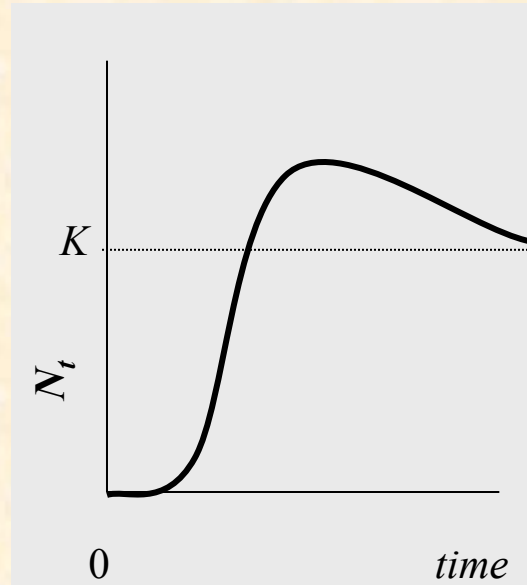
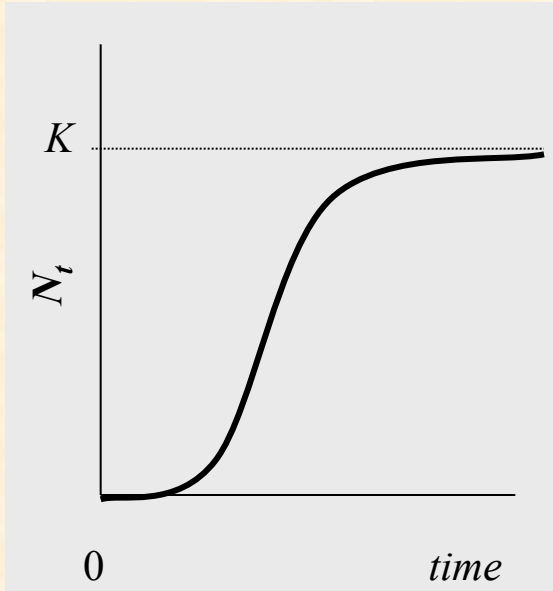
- when  $N \rightarrow K$  then  $r \rightarrow 0$

$$\frac{dN}{dt} = Nr \left( 1 - \frac{N}{K} \right)$$

Solution of the differential equation

$$N_t = \frac{KN_0}{(K - N_0)e^{-rt} + N_0}$$

# Density-dependence types



## Exact compensation

- immediate response
- returns to  $K$
- contest competition

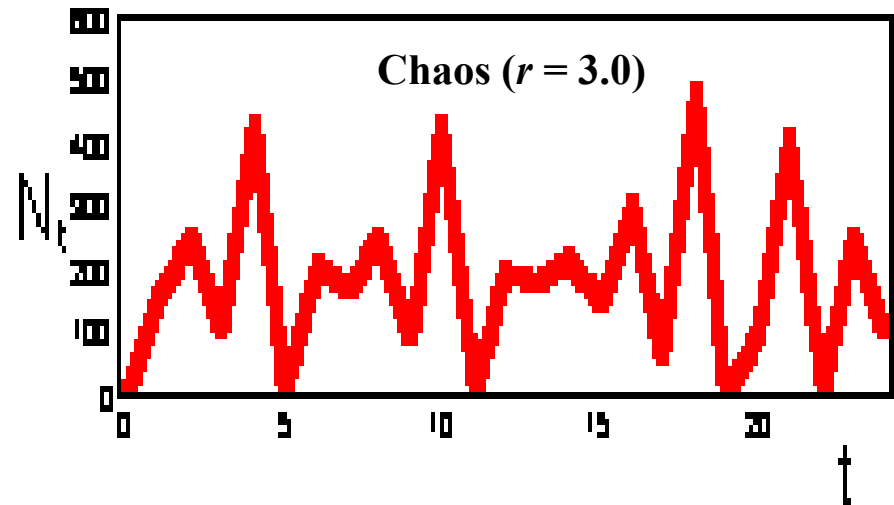
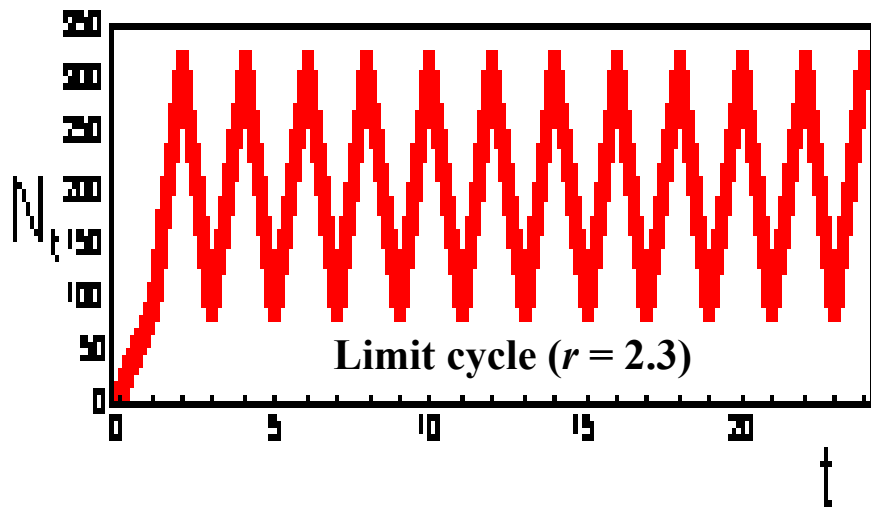
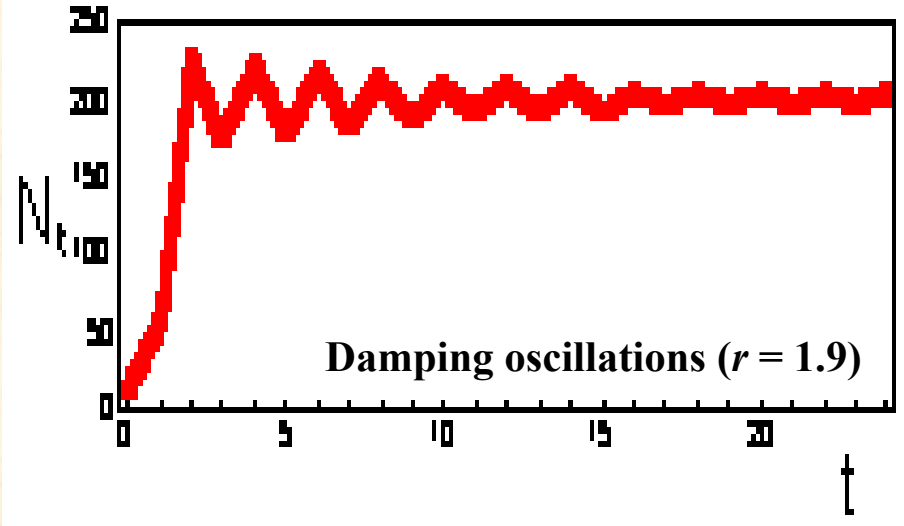
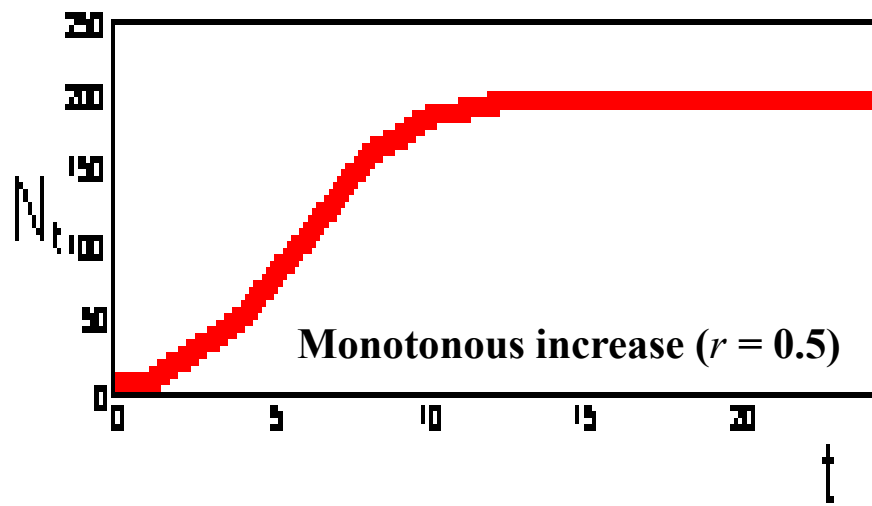
## Under-compensation

- returns slowly to  $K$
- weak DD

## Over-compensation

- strong DD
- exploitation competition
- cause oscillations

# Examination of the logistic model



# Model equilibria

1.  $N = 0$  .. unstable equilibrium
2.  $N = K$  .. stable equilibrium .. if  $0 < r < 2$ 
  - ▶ “Monotonous increase” and “Damping oscillations” has a stable equilibrium
  - ▶ “Limit cycle” and “Chaos” has no equilibrium

$r < 2$  .. stable equilibrium

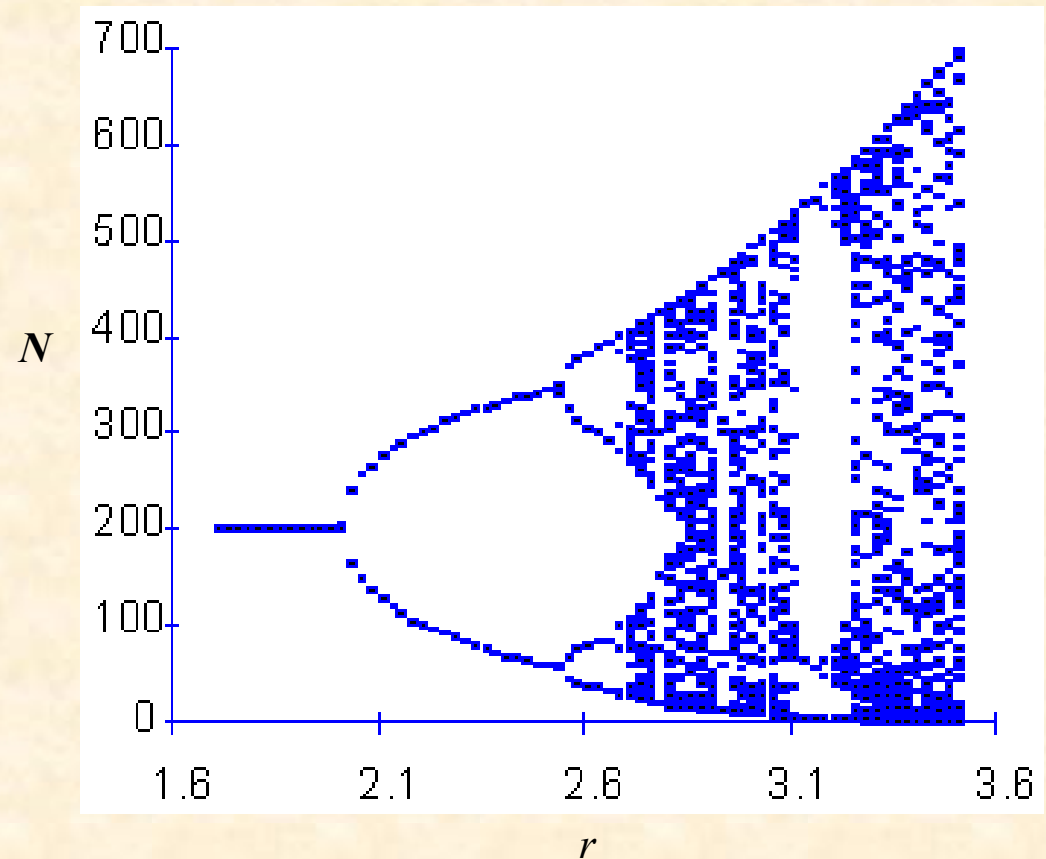
$r = 2$  .. 2-point limit cycle

$r = 2.5$  .. 4-point limit cycle

$r = 2.692$  .. chaos

▶ chaos can be produced by deterministic process

▶ density-dependence is stabilising only when  $r$  is rather low





# Observed population dynamics

a) yeast (logistic curve)

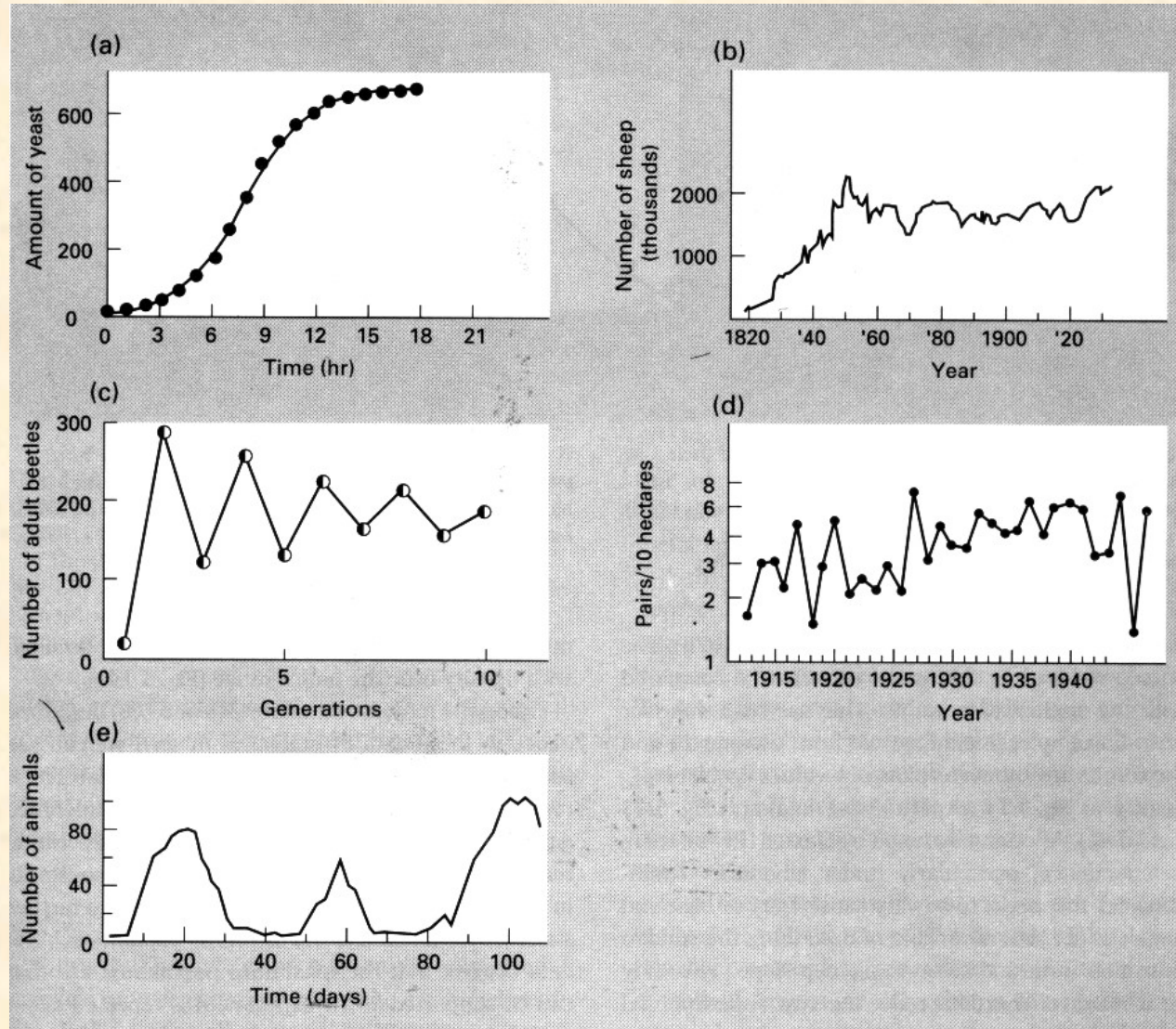
b) sheep (logistic curve with oscillations)

c) *Callosobruchus* (damping oscillations)

d) *Parus* (chaos)

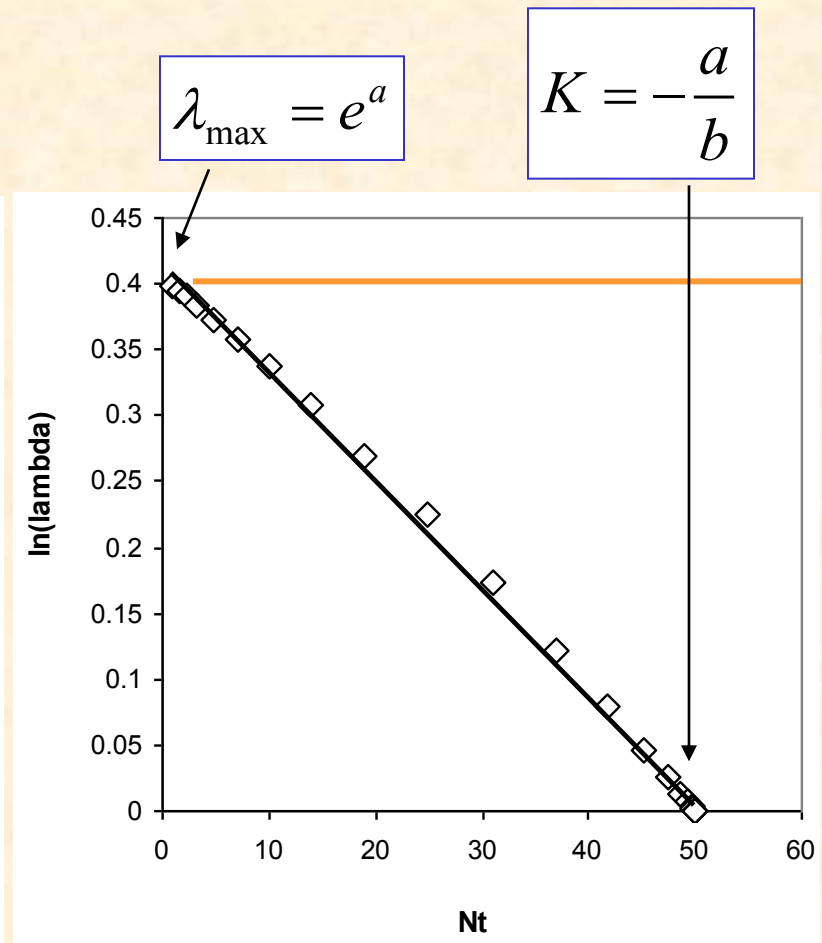
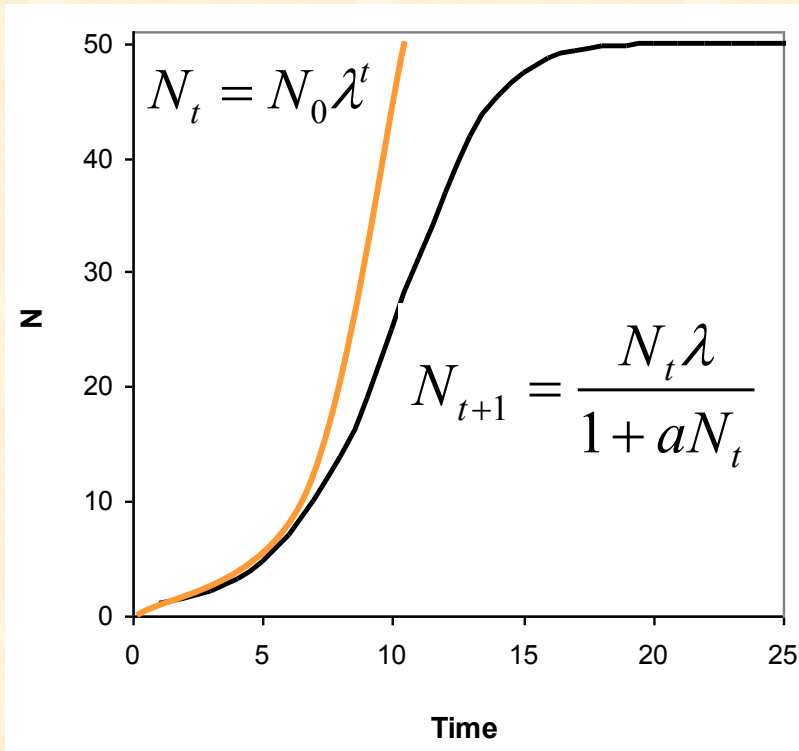
e) *Daphnia*

► of 28 insect species in one species chaos was identified, one other showed limit cycles, all other were in stable equilibrium



# Evidence of DD

- ▶ in case of density-independence  $\lambda$  is constant – independent of  $N$
- ▶ in case of DD  $\lambda$  is changing with  $N$ :  $\ln(\lambda) = a - bN_t$
- ▶ plot  $\ln(\lambda)$  against  $N_t$
- ▶ estimate  $\lambda$  and  $K$



# General logistic model

- ▶ rate may not be linearly dependent on  $N_t$
- ▶ Hassell (1975) proposed general model for DD
- $r$  is not linearly dependent on  $N$

$$N_{t+1} = \frac{N_t \lambda}{(1 + aN_t)^\theta}$$

$$\frac{dN}{dt} = rN \left( 1 - \left( \frac{N}{K} \right)^\theta \right)$$

where  $\theta$ .. the strength of competition

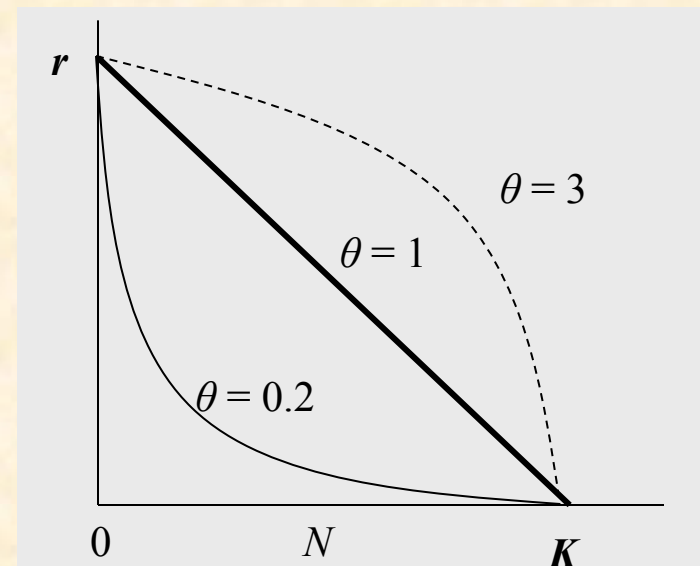
$\theta < 1$  .. strong DD at low densities

-  $N$  will be over  $K$

$\theta > 1$  .. strong DD near to  $K$

-  $N$  will be less than  $K$

- in most animals ...  $\theta < 1$



# Models with time-lags

- ▶ species response to resource change is not immediate (as in case of hunger) but delayed due to maternal effect, seasonal effect, predator pressure
- ▶ appropriate for species with long generation time where reproductive rate is dependent on the past (previous generations)
- ▶ time lag ( $d$  or  $\tau$ ) .. negative feedback of the 2nd order

discrete model

$$N_{t+1} = \frac{N_t \lambda}{1 + aN_{t-d}}$$

continuous model

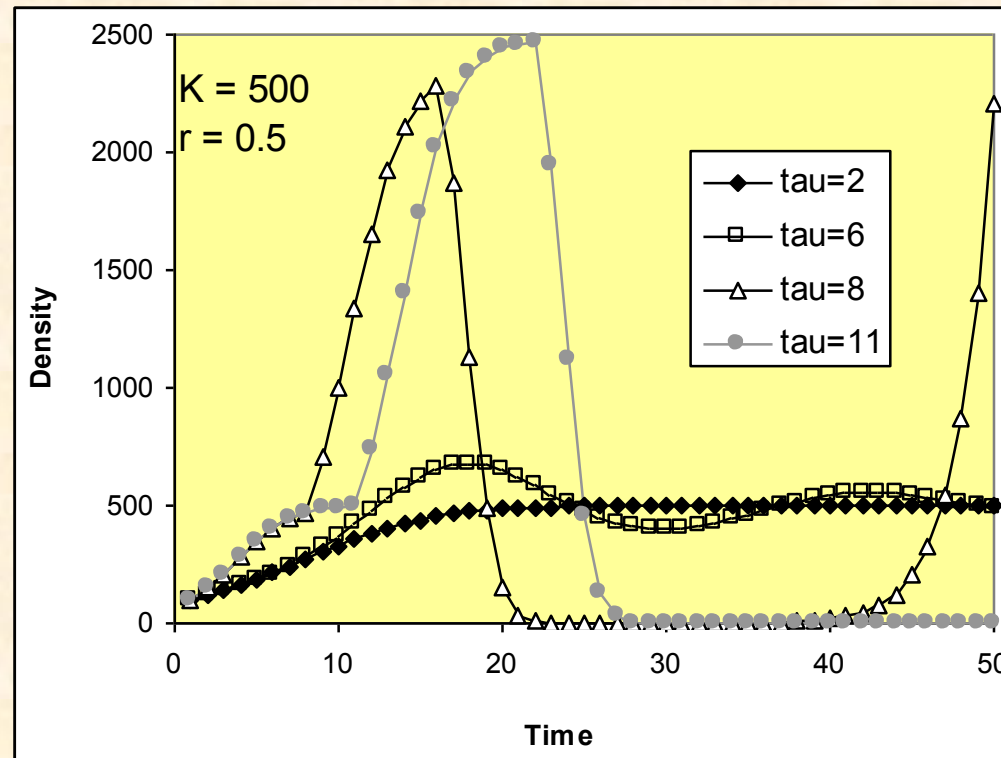
$$\frac{dN}{dt} = N_t r \left( 1 - \frac{N_{t-\tau}}{K} \right)$$

- ▶ many populations of mammals cycle with 3-4 year periods
- ▶ time-lag provokes fluctuations of certain amplitude at certain periods
- ▶ period of the cycle in continuous model is always  $4\tau$

## Solution of the continuous model:

$$N_{t+1} = N_t e^{r \left(1 - \frac{N_{t-\tau}}{K}\right)}$$

- $r \tau < 1 \rightarrow$  monotonous increase
- $r \tau < 3 \rightarrow$  damping fluctuations
- $r \tau < 4 \rightarrow$  limit cycle fluctuations
- $r \tau > 5 \rightarrow$  extinction



# Harvesting

## ► Maximum Sustainable Harvest (MSH)

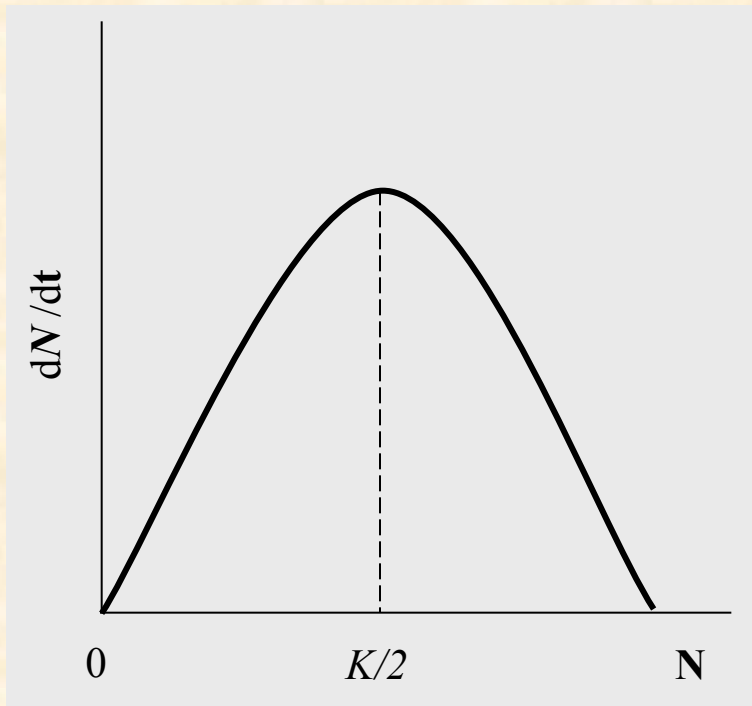
- to harvest as much as possible with the least negative effect on  $N$
- ignore population structure
- ignore stochasticity

$$\frac{dN}{dt} = Nr \left( 1 - \frac{N}{K} \right) = 0$$

local maximum:  $N^* = \frac{K}{2}$

Amount of MSH ( $V_{\max}$ ):  
at  $K/2$ :

$$\text{MSH} = \frac{rK}{4}$$



► Robinson & Redford (1991)

- Maximum Sustainable Yield (MSY)

$$\text{MSY} = a \left( \frac{\lambda K - K}{2} \right)$$

where  $a = 0.6$  for longevity  $< 5$   
 $a = 0.4$  for longevity  $= (5,10)$   
 $a = 0.2$  for longevity  $> 10$

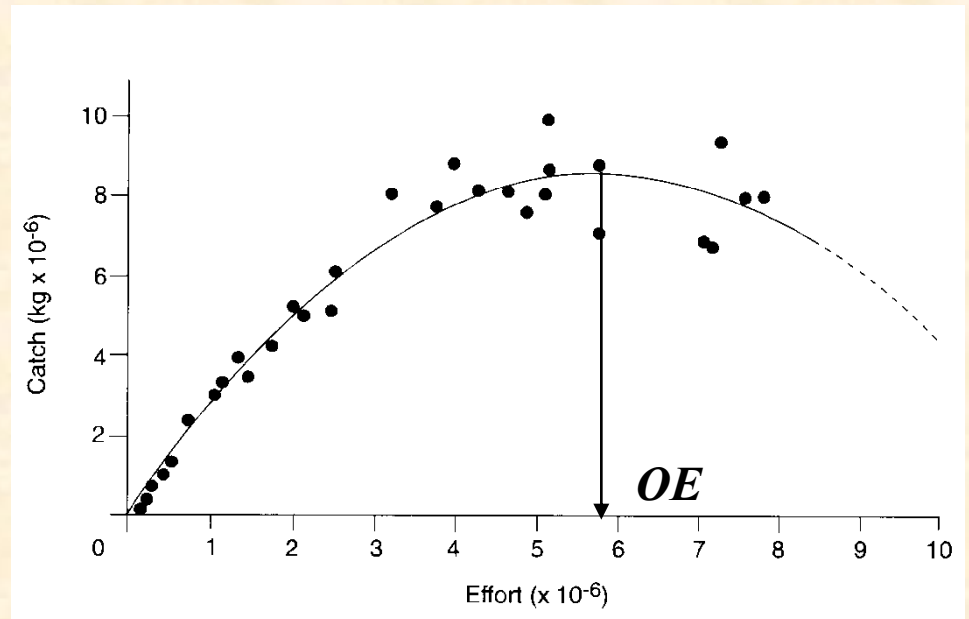
► Surplus production (catch-effort) models

- when  $r$ ,  $\lambda$  and  $K$  are not known  
- effort and catch over several years is known

- Schaefer quadratic model

$$\text{catch} = \alpha + \beta E + \gamma E^2$$

- local maximum of the function identifies optimal effort ( $OE$ )



# Allee effect

▶ individuals in a population may cooperate in hunting, breeding – positive effect on population increase

▶ Allee (1931) – discovered inverse DD

- genetic inbreeding – decrease in fertility

- demographic stochasticity – biased sex ratio

- small groups – cooperation in foraging, defence, mating, thermoregulation

▶  $K_2$  .. extinction threshold,

- unstable equilibrium

▶ population increase is slow

at low density but fast at higher density

$$\frac{dN}{dt} = Nr \left( 1 - \frac{N}{K_1} \right) \left( \frac{N}{K_2} - 1 \right)$$

