

Enemy-Victim Models

“Populační ekologie živočichů“

Stano Pekár

Predator-prey model

- ▶ continuous model of Lotka & Volterra (1925-1928)

H .. density of prey

r .. intrinsic rate of prey population

a .. predation rate

P .. density of predators

m .. predator mortality rate

b .. reproduction rate of predators

- ▶ in the absence of predator, prey grows exponentially \rightarrow

$$\frac{dH}{dt} = rH$$

- ▶ in the absence of prey, predator dies exponentially \rightarrow

$$\frac{dP}{dt} = -mP$$

- ▶ predation rate is linear function of the number of prey .. aHP

- ▶ each prey contributes identically to the growth of predator .. bHP

$$\frac{dH}{dt} = rH - aHP$$

$$\frac{dP}{dt} = bHP - mP$$

Analysis of the model

Zero isoclines:

- ▶ for prey population:

$$\frac{dH}{dt} = 0 \quad 0 = rH - aHP$$

$$P = \frac{r}{a}$$

- ▶ for predator population:

$$\frac{dP}{dt} = 0 \quad 0 = bHP - mP$$

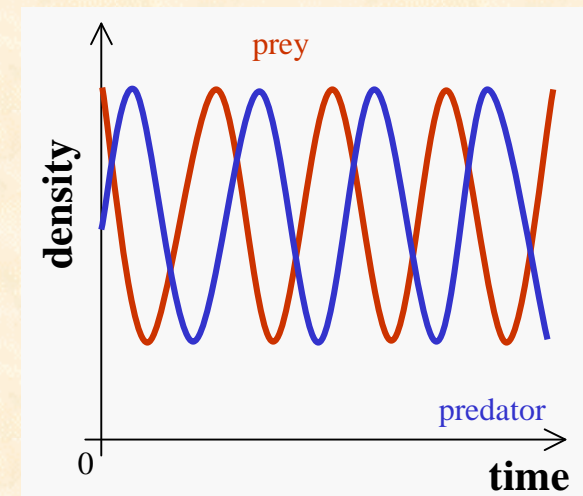
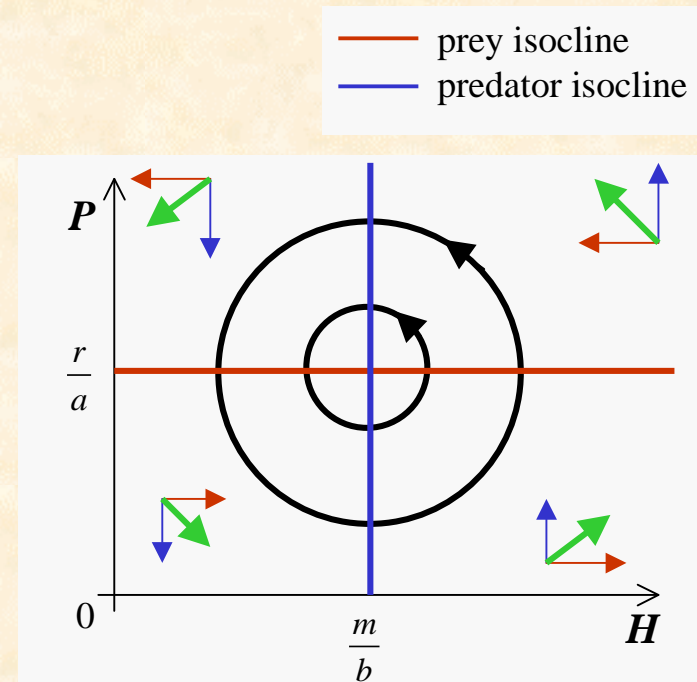
$$H = \frac{m}{b}$$

- ▶ prey population would grow to infinity
→ **neutral stability**

- ▶ do not converge, has no asymptotic stability (trajectories are closed lines)

- ▶ unstable system, amplitude of the cycles is determined by initial numbers

- ▶ POOR model



Incorporation of density-dependence

- ▶ in the absence of the predator prey population reaches carrying capacity K

$$\frac{dH}{dt} = rH \left(1 - \frac{H}{K} \right) - aHP$$

$$\frac{dP}{dt} = bHP - mP$$

- ▶ for given parameter values: $r = 3$, $m = 2$, $a = 0.1$, $b = 0.3$, $K = 10$

$$\frac{dH}{dt} = 3H \left(1 - \frac{H}{10} \right) - 0.1HP$$

$$\frac{dP}{dt} = 0.3HP - 2P$$

Zero isoclines:

▶ for prey population: $\frac{dH}{dt} = 0$ $0 = 3H\left(1 - \frac{H}{10}\right) - 0.1HP$

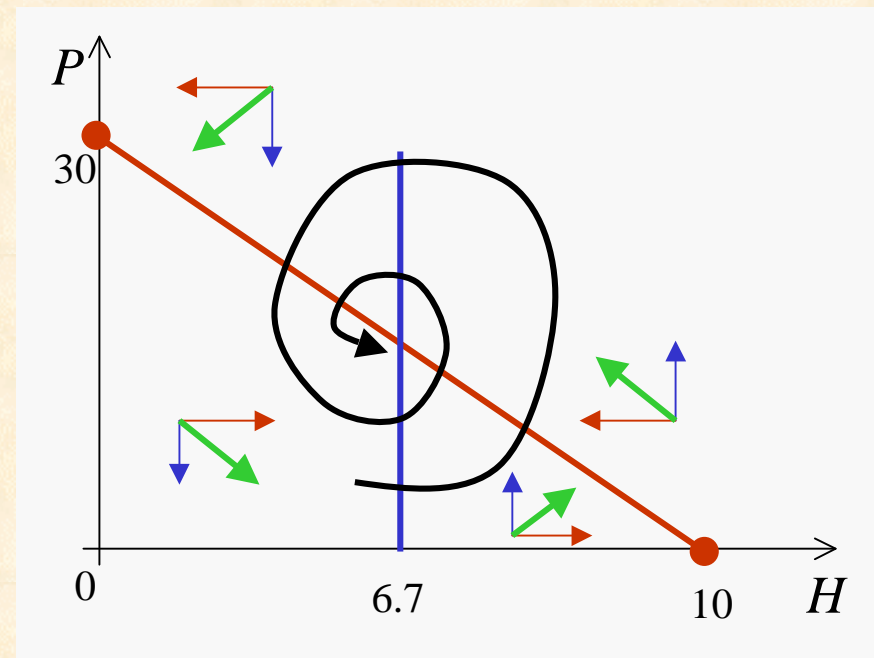
if $H = 0$ (trivial solution) or if $0 = 3\left(1 - \frac{H}{10}\right) - 0.1P$ $P = 30 - 3H$

▶ for predator population: $\frac{dP}{dt} = 0$ $0.3HP - 2P = 0$

if $P = 0$ (trivial solution)
or if $0.3H - 2 = 0$

$$H = 6.667$$

▶ if gradient of prey isocline
is negative .. approached stable
equilibrium



Incorporation of functional response

► functional response Type II:

$$H_a = \frac{aHT}{1 + aHT_h}$$

► rate of consumption by all predators:

$$\frac{H_a P}{T} = \frac{aHP}{1 + aHT_h}$$

$$\frac{dH}{dt} = r_H H \left(1 - \frac{H}{K} \right) - \frac{aHP}{1 + aHT_h} \quad \frac{dP}{dt} = bHP - mP$$

► for parameters: $r_H = 3$, $a = 0.1$, $T_h = 2$, $K = 10$

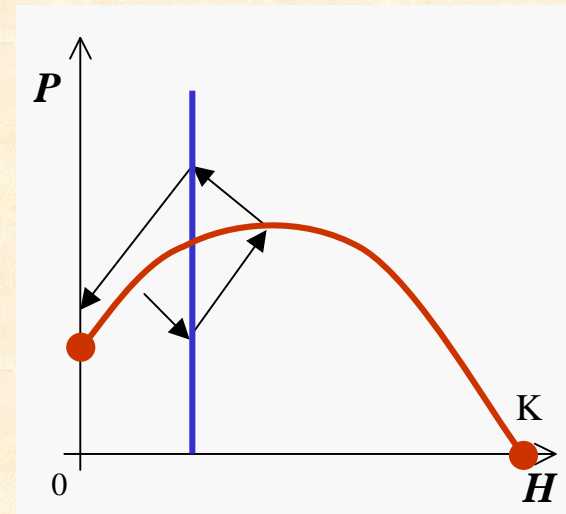
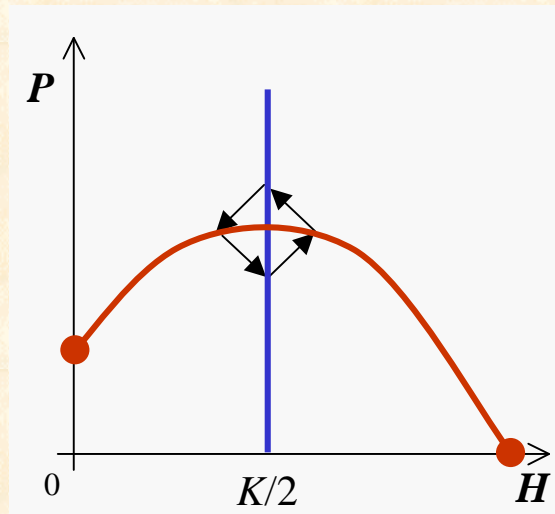
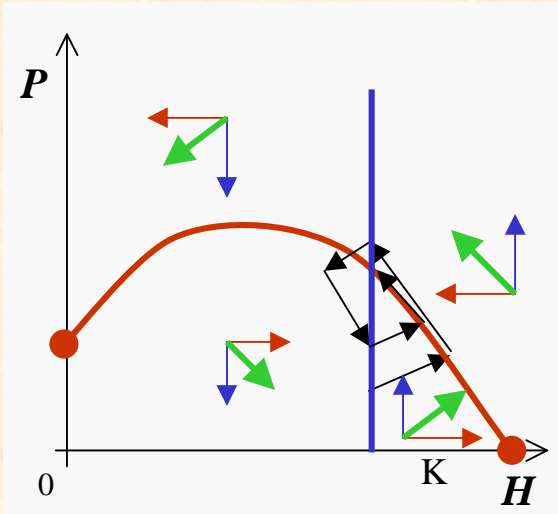
$$\frac{dH}{dt} = 0 \quad 0 = 3H \left(1 - \frac{H}{10} \right) - \frac{0.1HP}{1 + 0.1H2}$$

prey isocline: $P = 30 + 6H - 0.6H^2$

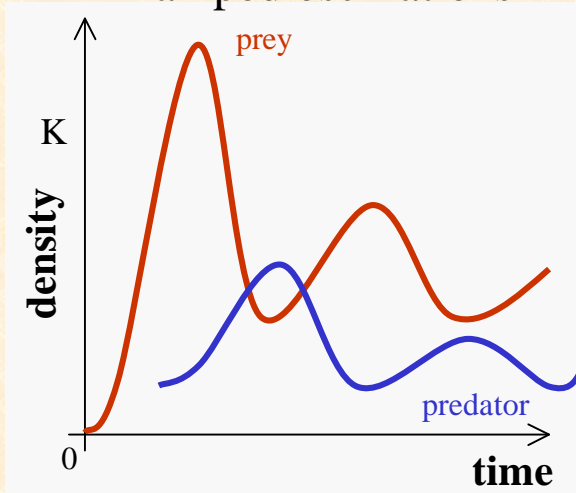
▶ predator exploits prey close to K
 - isocline: $H = 9$

▶ predator exploits prey close to $K/2$
 - isocline: $H = 5$

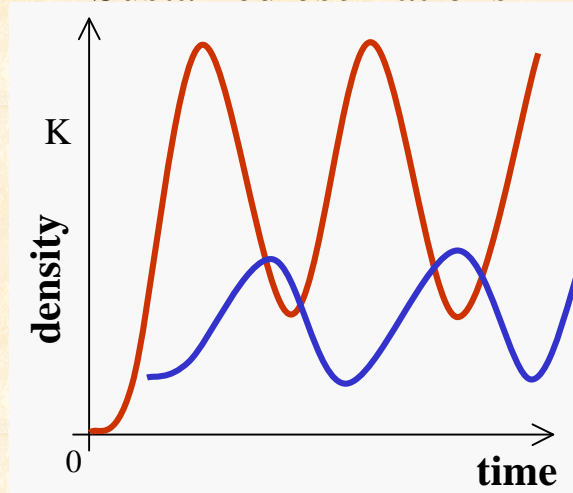
▶ predator exploits prey at low density
 - isocline: $H = 2$



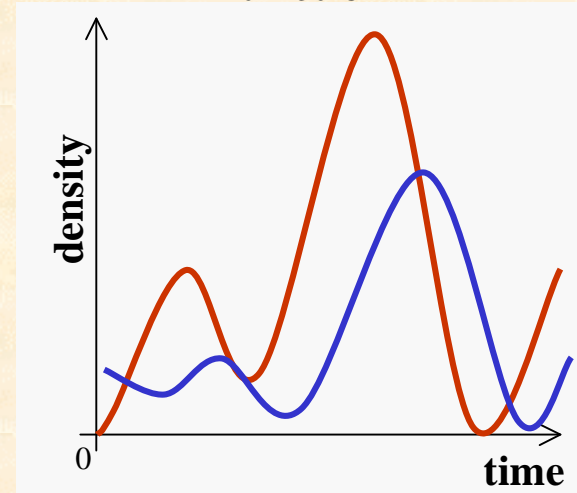
Damped oscillations



Sustained oscillations



Extinction



Incorporation of predator's carrying capacity

- ▶ logistic model with carrying capacity proportional to H
- ▶ k .. carrying capacity of the predator
- ▶ $r_p = bH - m$

$$\frac{dP}{dt} = bHP - mP$$

$$\frac{dP}{dt} = r_p P \left(1 - \frac{P}{kH} \right) \quad \frac{dH}{dt} = r_H H \left(1 - \frac{H}{K} \right) - \frac{aHP}{1 + aHT_h}$$

- ▶ for parameters: $r_p = 2, k = 0.2$

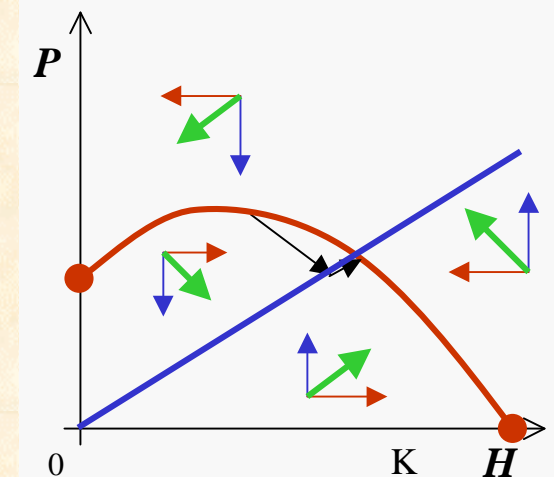
$$\frac{dP}{dt} = 0 \quad 0 = 2P \left(1 - \frac{P}{0.2H} \right)$$

predator isocline:

$$H = 5P$$

prey isocline:

$$P = 30 + 6H - 0.6H^2$$



Host-parasitoid model

- ▶ discrete model of Nicholson & Bailey (1935)

H_t = number of hosts in time t

H_a = number of attacked hosts

λ = finite rate of increase of the host

P_t = number of parasitoids

c = conversion rate, no. of parasitoids for 1 host (=1)

$$H_{t+1} = \lambda(H_t - H_a)$$

$$P_{t+1} = cH_a = H_a$$

Incorporation of random search

- ▶ parasitoid searches randomly, has unlimited ability to lay eggs
- ▶ encounters (x) are random (Poisson distribution)

$$p_x = \frac{\mu^x e^{-\mu}}{x!} \quad x = 0, 1, 2, \dots \quad p_0 = e^{-\mu}$$

p_0 = proportion of not encountered, μ .. mean number of encounters

E_t = total number of encounters

a = searching efficiency (proportion of hosts encountered)

$$E_t = a H_t P_t \quad \mu = \frac{E_t}{H_t} = aP_t \quad p_0 = e^{-aP_t}$$

- ▶ proportion of encounters (1 or more times): $p = (1 - p_0)$

$$p = (1 - e^{-aP_t})$$

$$H_a = H_t (1 - e^{-aP_t})$$

$$H_{t+1} = \lambda(H_t - H_a)$$

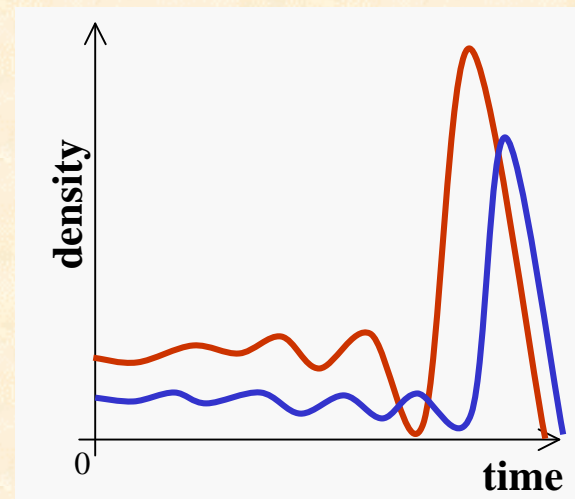
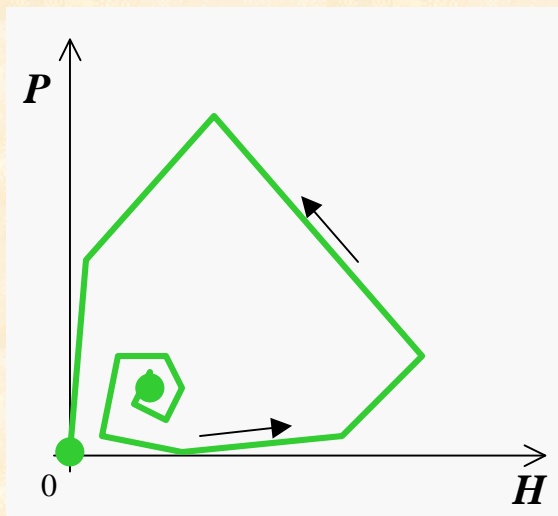
$$P_{t+1} = H_a$$



$$H_{t+1} = \lambda H_t e^{-aP_t}$$

$$P_{t+1} = H_t (1 - e^{-aP_t})$$

- ▶ highly unstable model for all parameter values:
 - equilibrium is possible but the slightest disturbance leads to divergent oscillations (extinction of parasitoid)



Incorporation of density-dependence

- ▶ exponential growth of hosts is replaced by logistic equation

$$H_{t+1} = \lambda H_t e^{\left(1 - \frac{H_t}{K}\right) - aP_t}$$

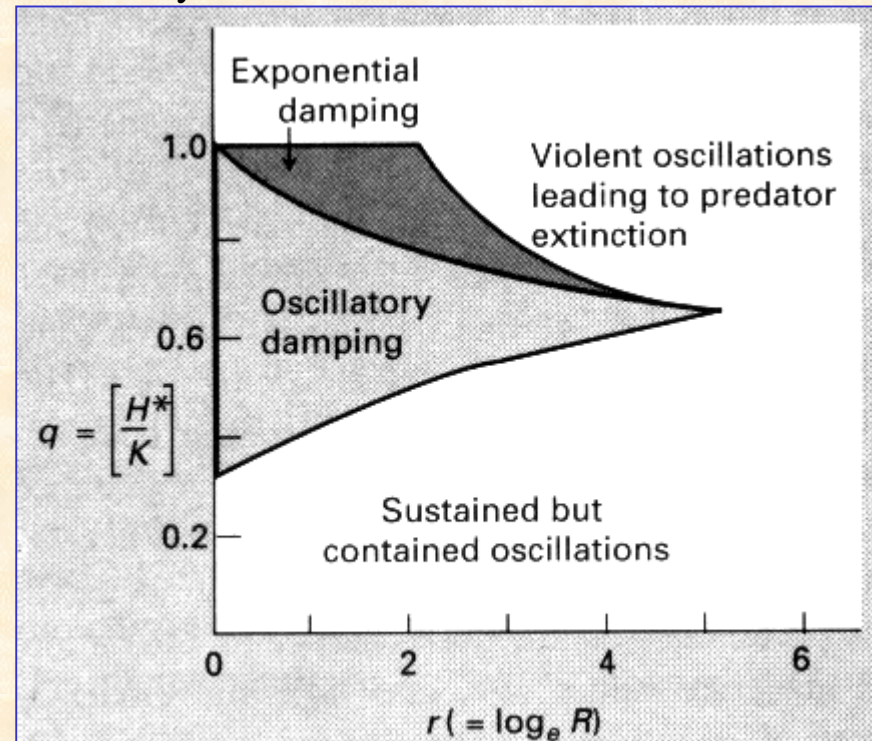
$$P_{t+1} = H_t \left(1 - e^{-aP_t}\right)$$

$$q = \frac{H^*}{K}$$

H^* .. new host carrying capacity

- ▶ depends on parasitoids' efficiency
 - when a is low then $q \rightarrow 1$
 - when a is high then $q \rightarrow 0$
- ▶ density-dependence have stabilising effect for moderate r and q

Stability boundaries



Incorporation of the refuge

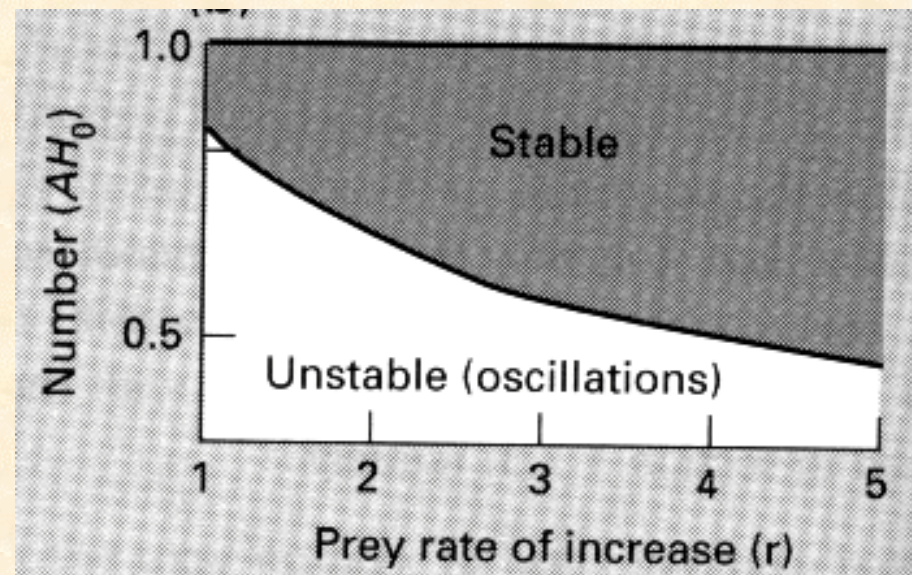
- ▶ if hosts are distributed non-randomly in the space

Fixed number refuge: H_0 hosts are always protected

$$H_{t+1} = \lambda H_0 + \lambda(H_t - H_0)e^{-aP_t}$$

$$P_{t+1} = (H_t - H_0)(1 - e^{-aP_t})$$

- ▶ have strong stabilising effect even for large r



Incorporation of aggregated distribution

► distribution of encounters is not random but aggregated (negative binomial distribution)

- proportion of hosts not encountered (p_0):
$$p_0 = \left(1 + \frac{aP_t}{k}\right)^{-k}$$

where k = degree of aggregation

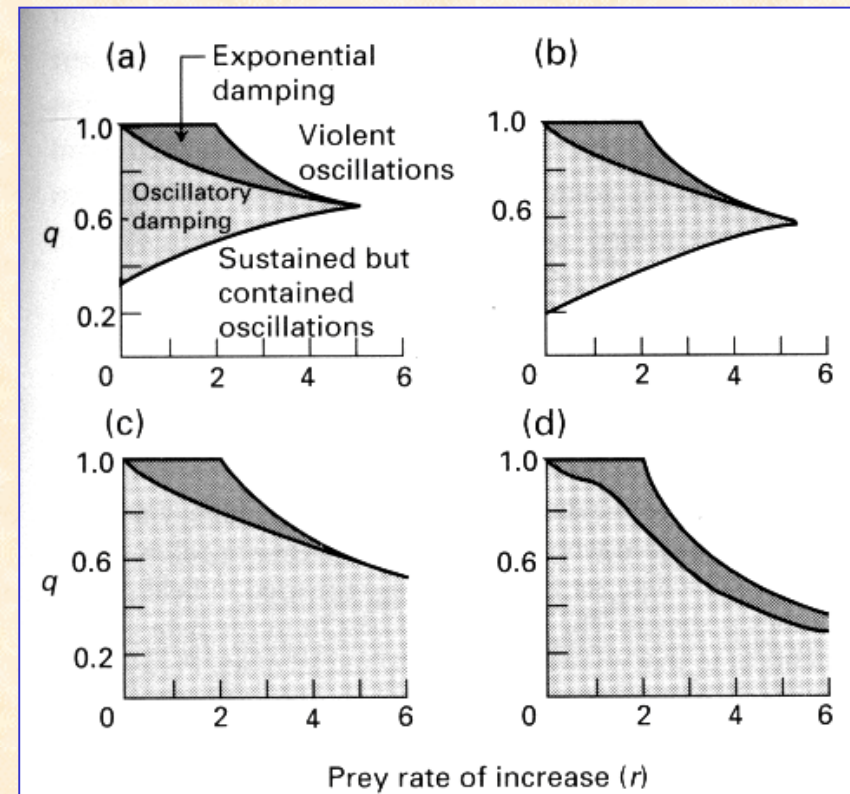
$$H_{t+1} = \lambda H_t e^{\left(1 - \frac{H_t}{K}\right) \left(1 + \frac{aP_t}{k}\right)^{-k}}$$

$$P_{t+1} = H_t \left(1 - \left(1 + \frac{aP_t}{k}\right)^{-k}\right)$$

► very stable model system if $k \leq 1$

Stability boundaries:

a) $k=\infty$, b) $k=2$, c) $k=1$, d) $k=0$



Example 16

You want to control population of mites. Before introduction of predatory mites you want to simulate the predator-prey dynamic using the following model:

$$\frac{dH}{dt} = r_H H \left(1 - \frac{H}{K} \right) - \frac{aHP}{1 + aHT_h} \quad \frac{dP}{dt} = \frac{aHP}{1 + aHT_h} - dP$$

To estimate parameters you need to run the following experiments:

1. Keep prey population without predators, record densities over a month and estimate intrinsic rate of increase (r_H) and carrying capacity (K).

You found that $r_H = 0.2$ and $K = 500$.

2. Keep predators at constant density of prey, record predator densities over a month and estimate natural predators' mortality (d). You found that $d = 0.1$.

3. Offer one predator different prey densities and estimate the functional response. You find that $a = 0.001$ and $T_h = 0.5$.

4. How long it takes for the predatory mite to control mite pests if pests has a density of 200 individuals and the predators is only 1?

```
predprey<-function(t,y,pa){
H<-y[1]
P<-y[2]
with(as.list(pa),{
dH.dt<-rH*H*(1-H/K)-a*H*P/(1+a*H*Th)
dP.dt<- a*H*P/(1+a*H*Th)-d*P
return(list(c(dH.dt,dP.dt)))})}

H<-200; P<-1
time<-seq(0,500,0.1)
pa<-c(rH=0.2,K=500,a=0.001,Th=0.5,d=0.1)
library(deSolve)
out<-data.frame(ode(c(H,P),time,predprey,pa))
matplot(time,out[,-1],type="l",lty=1:2,col=1)
legend("right",c("H","P"),lty=1:2)
```


Example 17

Aphids has increased their population density to 50 individuals/plant. You have observed that their $\lambda = 3$, $K = 800$, $T_h = 0.3$ You need to control aphids using a parasitoid. You can choose from three parasitoid species (A, B, C). The three species differ in the number of hosts they infect (c) and in their search efficiency (a):

| | A | B | C |
|----------|----------|----------|----------|
| c | 1 | 2 | 5 |
| a | 0.3 | 0.07 | 0.001 |

Use the discrete Nicholson-Bailey host-parasitoid model with functional response of the type II within POPULUS. Introduce a single parasitoid and find which of the three species will achieve the quickest control.