

# Enemy-Victim Models

*“Populační ekologie živočichů“*

Stano Pekár

# Predator-prey system

*Acarus*



*Cheyletus*



# Predator-prey model

- ▶ continuous model of Lotka & Volterra (1925-1928) used to explain decrease in prey fish and increase in predatory fish after World War I
- ▶ assumptions
  - continuous predation (high population density)
  - populations are well mixed
  - closed populations (no immigration or emigration)
  - no stochastic events
  - predators are specialised on one prey species
  - populations are unstructured
  - reproduction immediately follows feeding

$H$  .. 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:

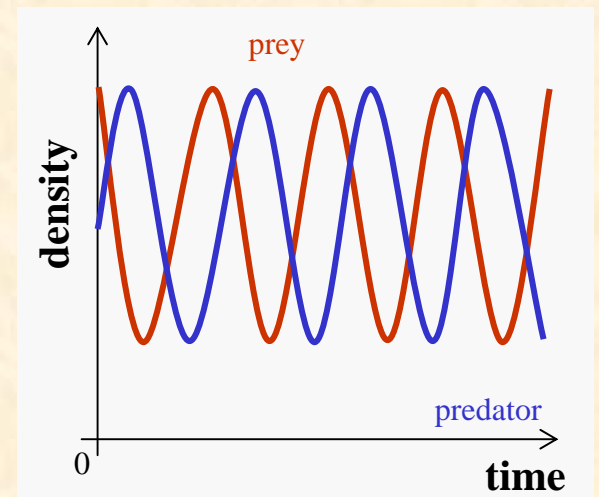
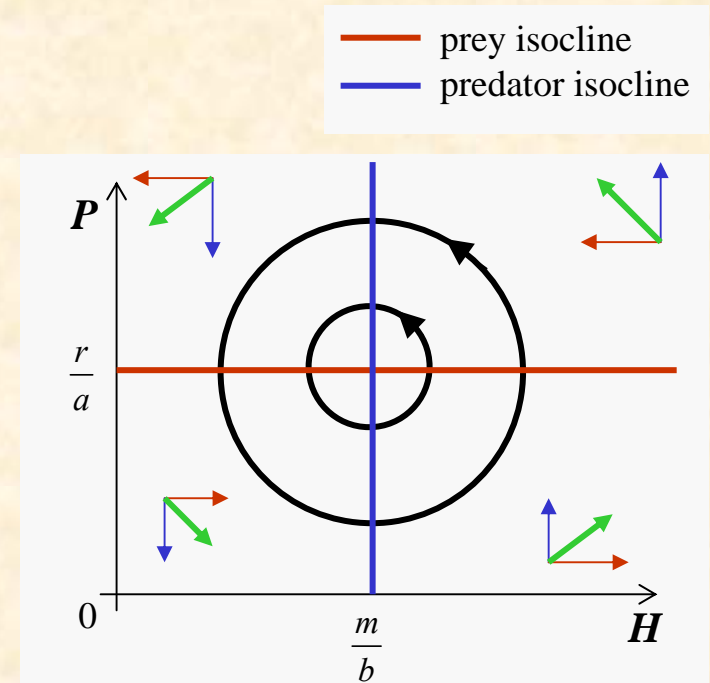
$$\frac{dP}{dt} = 0 \quad 0 = bHP - mP$$

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

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

→ **neutral stability**

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



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

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

$$P = 30 - 3H$$

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

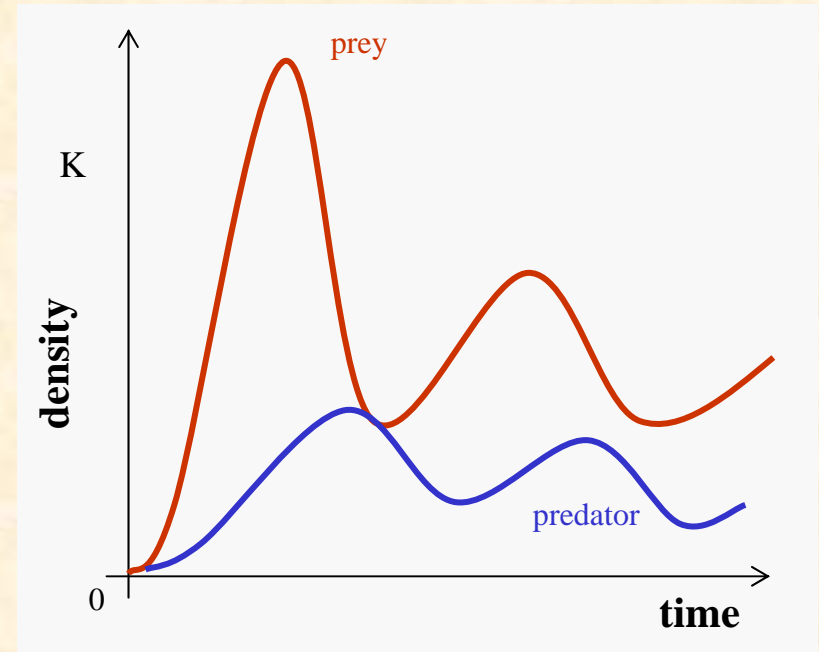
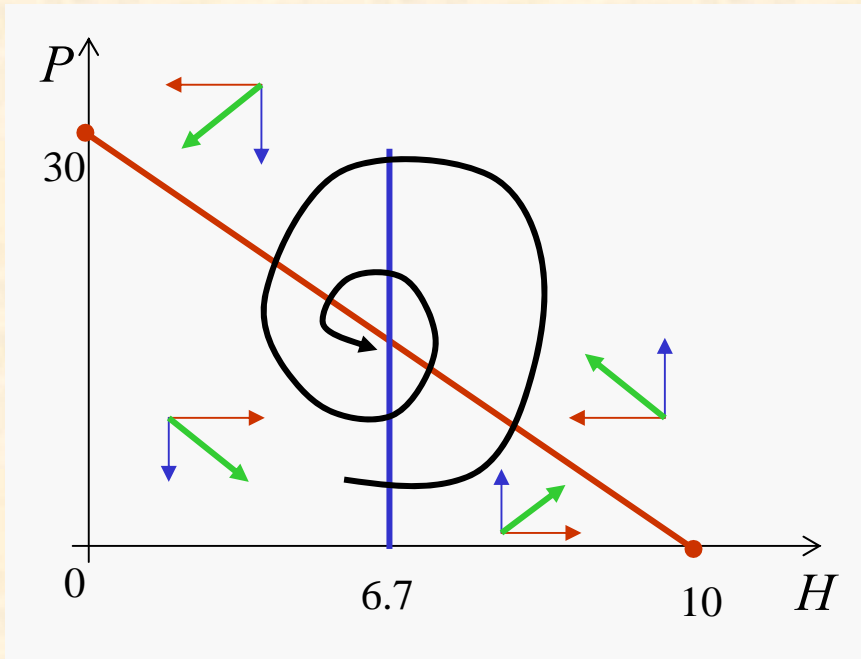
if  $P = 0$  (trivial solution)

or if  $0.3H - 2 = 0$

$$H = 6.667$$

▶ gradient of prey isocline is negative





- ▶ has single positive asymptotically stable equilibrium defined by crossing of isoclines
- ▶ converges to the stable equilibrium



# Addition of functional response of Type II

▶ 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:

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

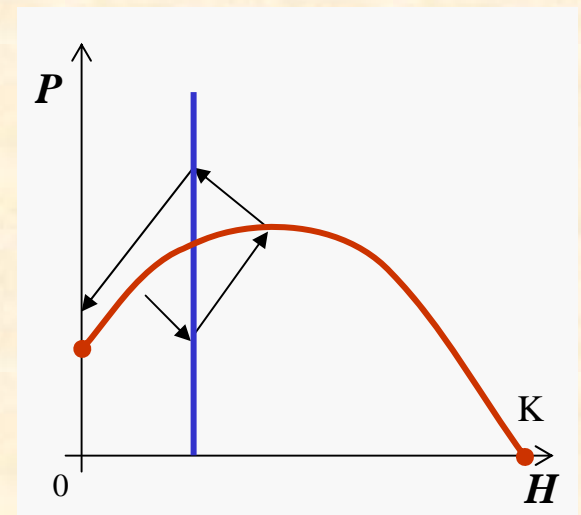
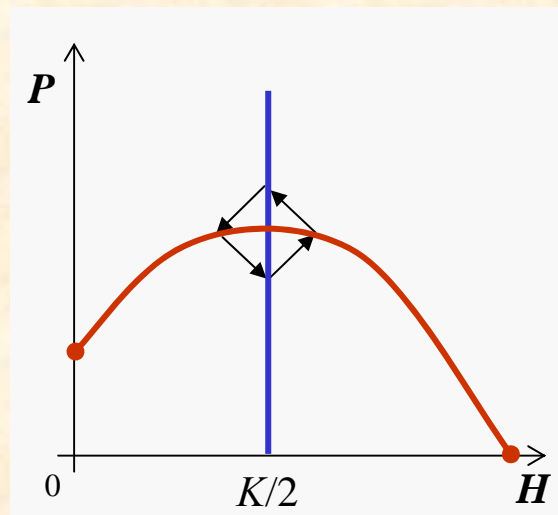
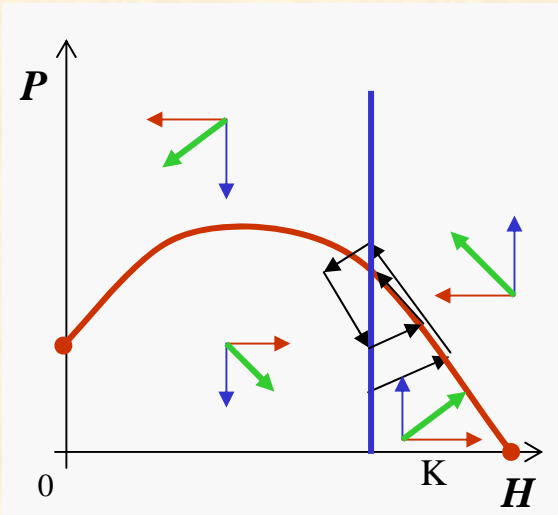
predator isocline:

$$H = \text{constant}$$

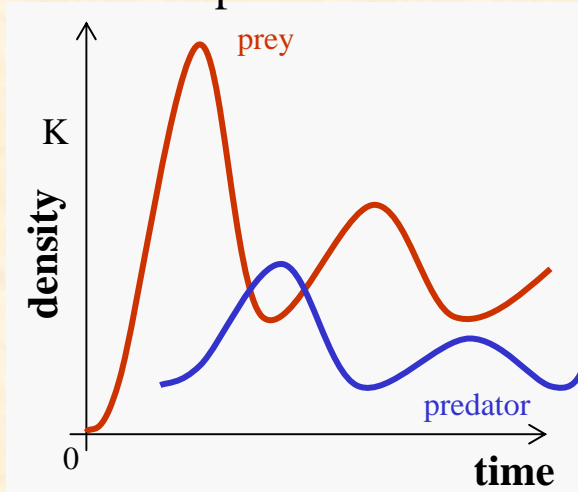
▶ predator exploits prey close to  $K$   
 - isocline:  $H = 9$

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

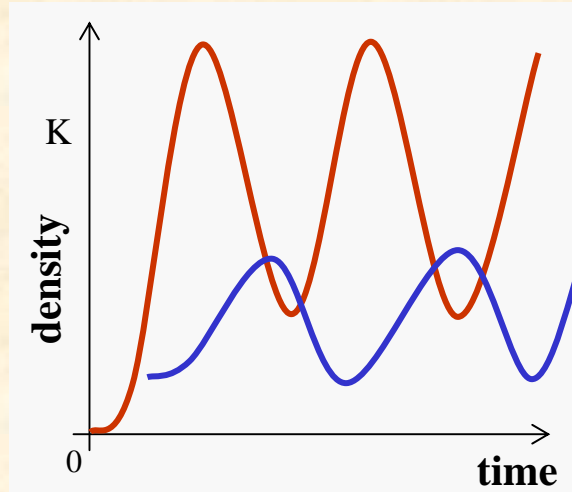
▶ predator exploits prey at low density  
 - isocline:  $H = 2$



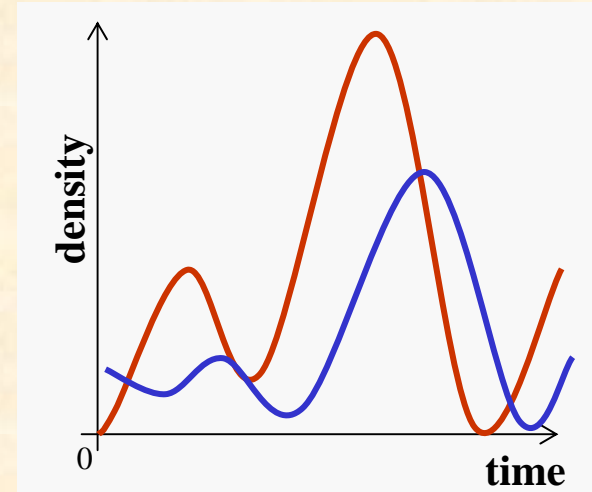
Damped oscillations



Sustained oscillations



Extinction



# Addition 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:  $r_P = 2, k = 0.2$

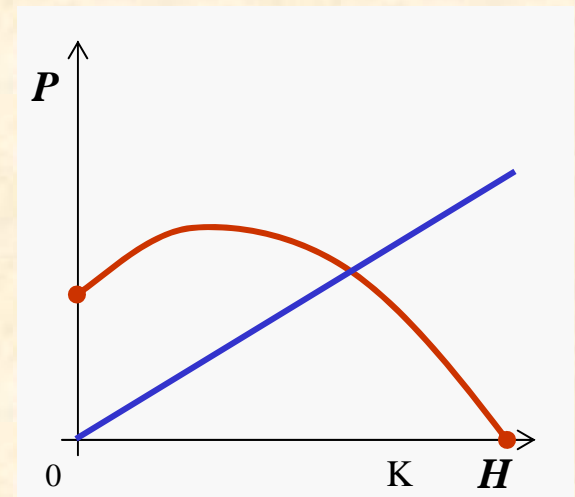
$$\frac{dP}{dt} = 0 \quad 0 = 2P \left( 1 - \frac{P}{0.2H} \right)$$

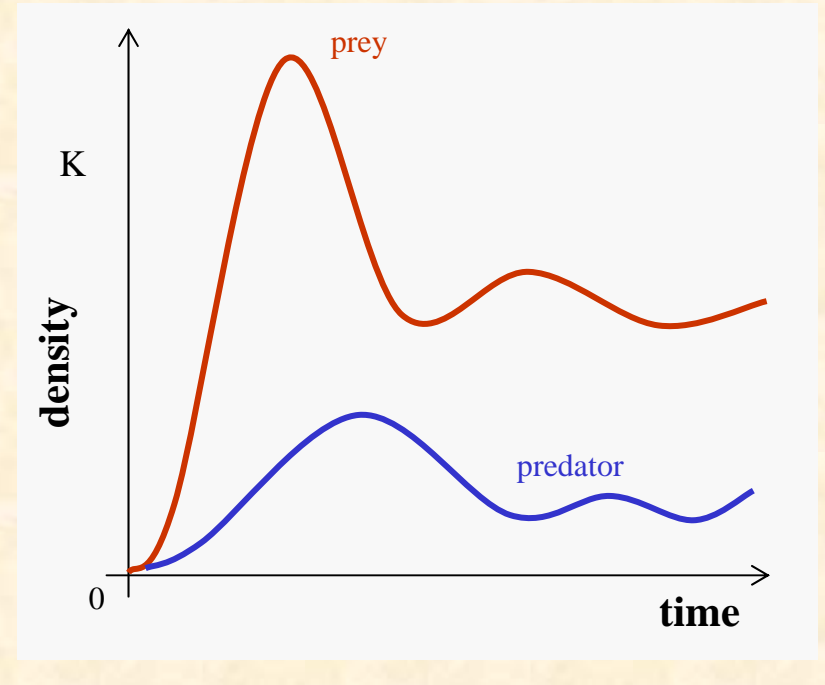
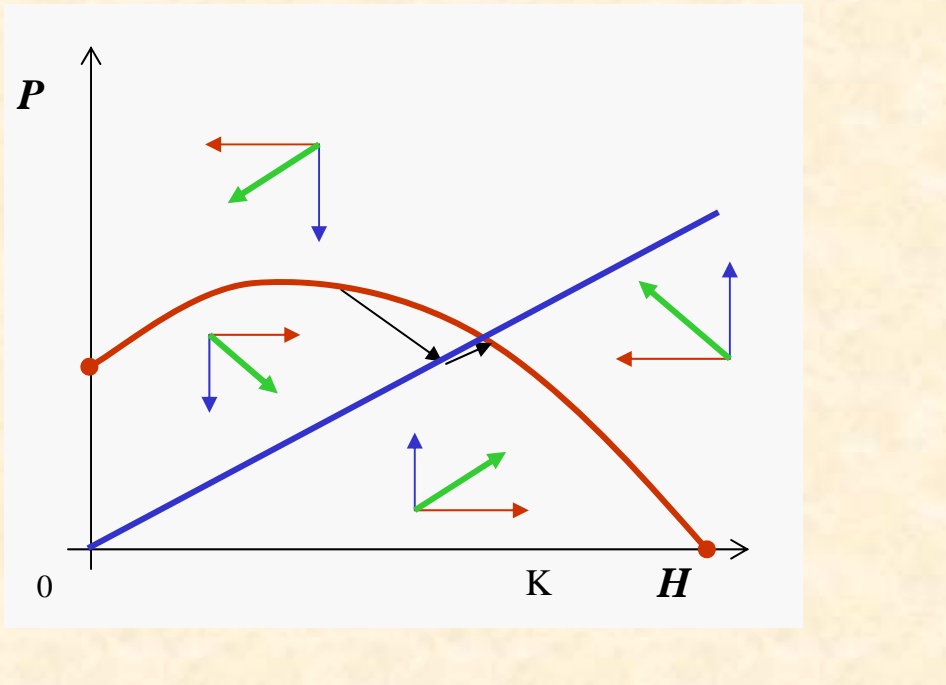
predator isocline:

$$H = 5P$$

prey isocline:

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





► quick approach to stable equilibrium

# Host-parasitoid system

*Zatypota*



*Theridion*



# Host-parasitoid model

- ▶ discrete model of Nicholson & Bailey (1935)
- discrete generations
- 1, ..., several, or less than 1 host
- random host search and functional response Type III
- lay eggs in aggregation

$H_t$  = number of hosts in time  $t$

$H_a$  = number of attacked hosts

$\lambda$  = finite rate of increase of the host

$P_t$  = number of parasitoids

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

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

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

# Incorporation of random search

- ▶ parasitoid searches randomly
- ▶ 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,  $\mu$  .. mean number of encounters

$E_t$  = total number of encounters

$a$  = searching efficiency (proportion of hosts encountered)

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

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

$$p = (1 - e^{-a P_t})$$

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

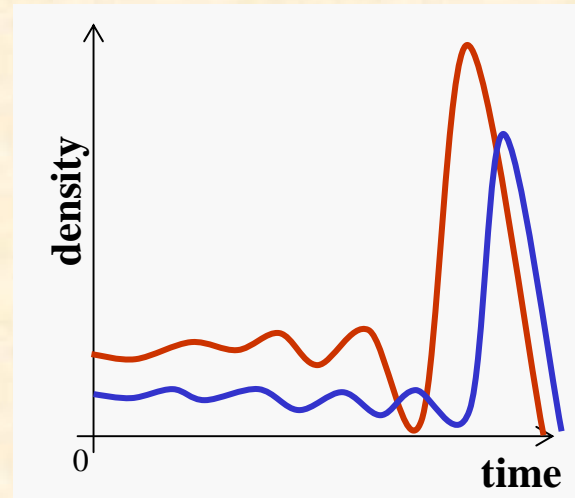
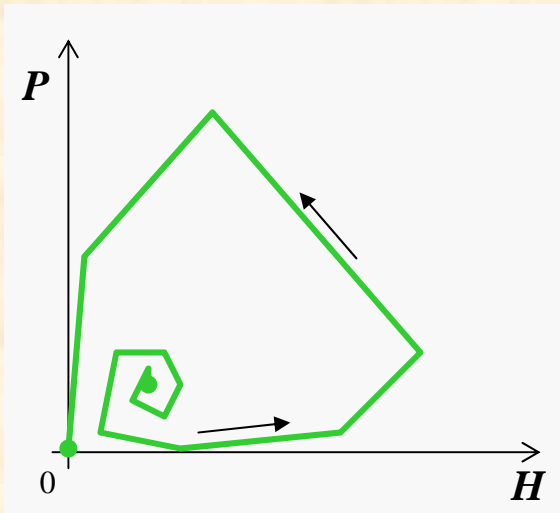
$$H_{t+1} = \lambda(H_t - H_a)$$

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



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

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





# Addition of density-dependence

- ▶ exponential growth of hosts is replaced by logistic equation

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

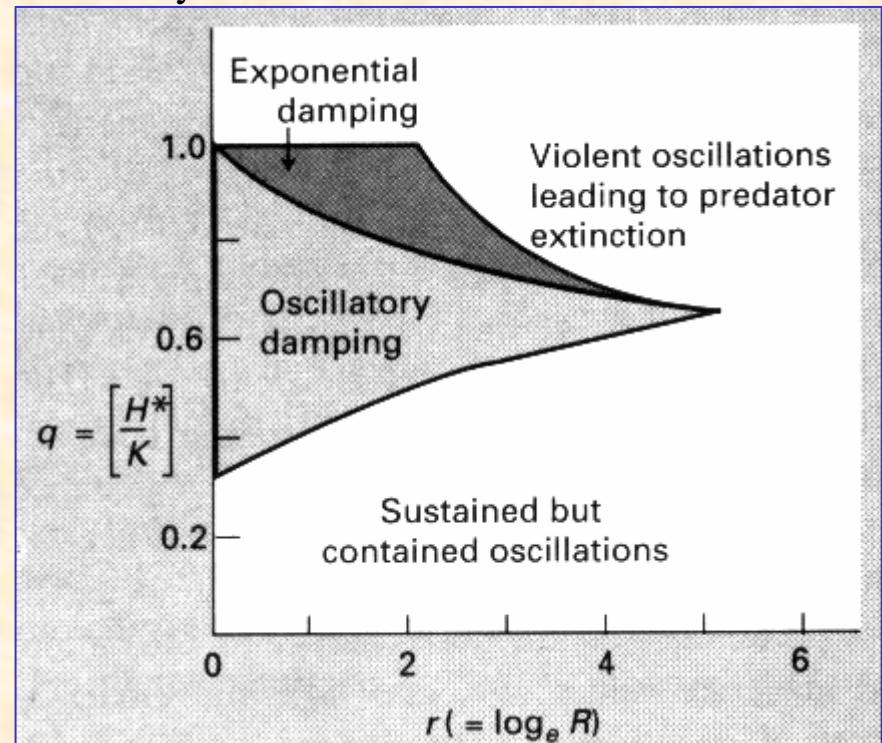
$$P_{t+1} = H_t \left(1 - e^{-aP_t}\right)$$

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

$H^*$ .. 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



# Addition of the refuge

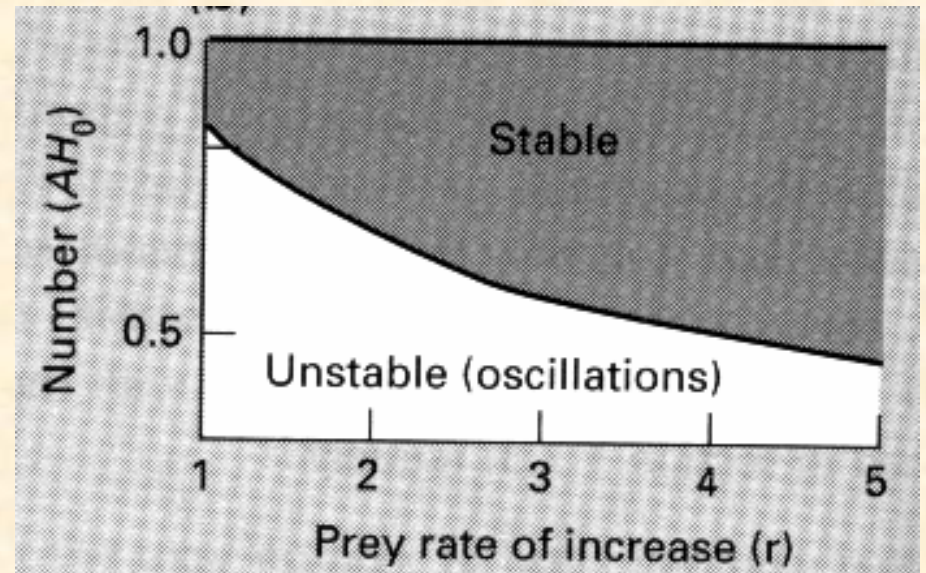
- ▶ if hosts are distributed non-randomly in the space

Fixed number in 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  $r$



# Addition 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  $k = \text{degree of aggregation}$

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

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

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

Stability boundaries:

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

