

Enemy-Victim Models

“Populační ekologie živočichů“

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Predator-prey system

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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:

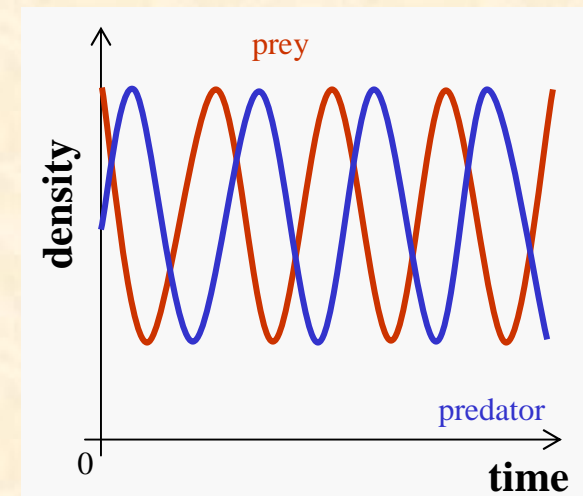
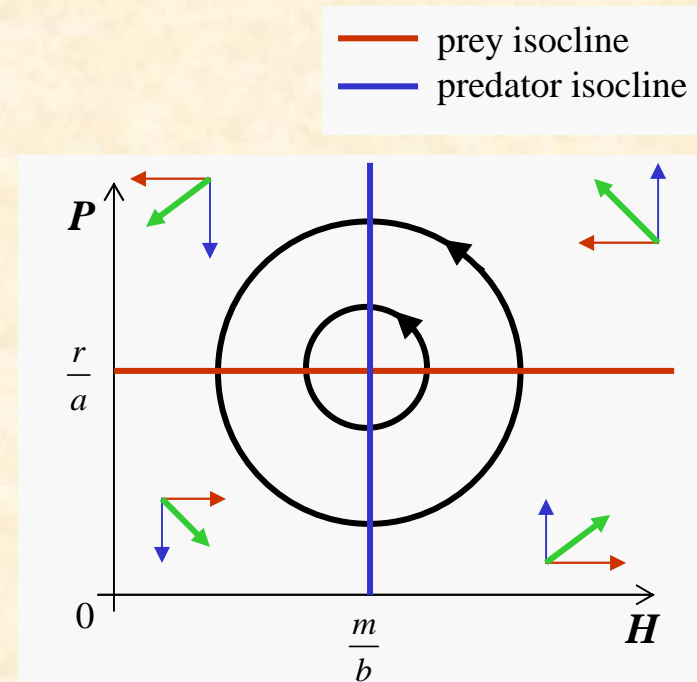
$$\frac{dP}{dt} = 0 \quad 0 = bHP - mP$$

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

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

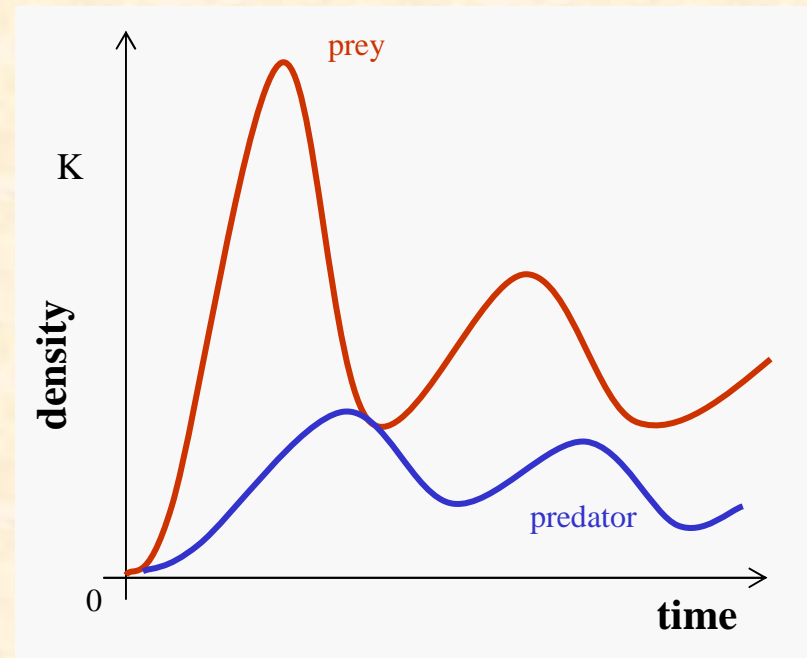
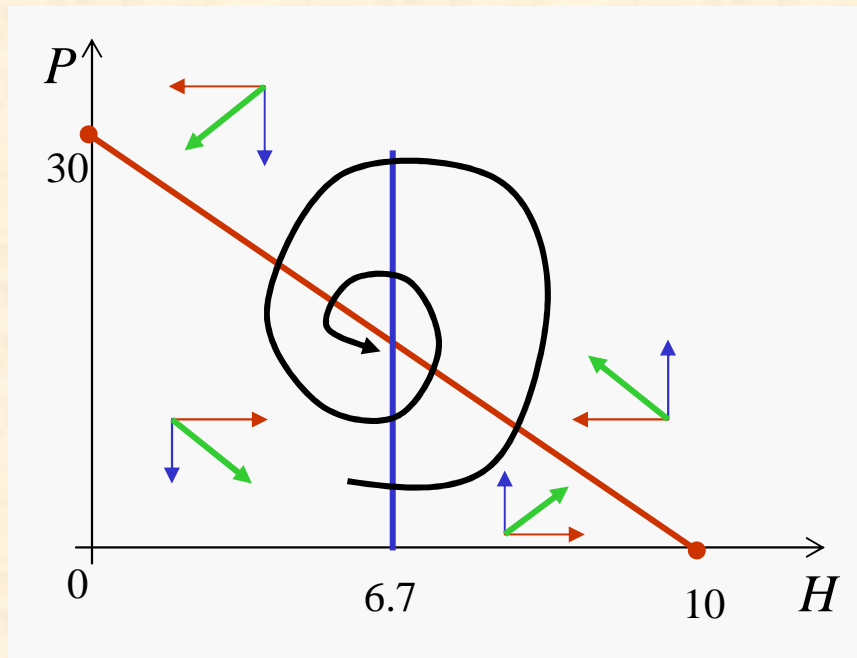
if $P = 0$ (trivial solution)

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

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

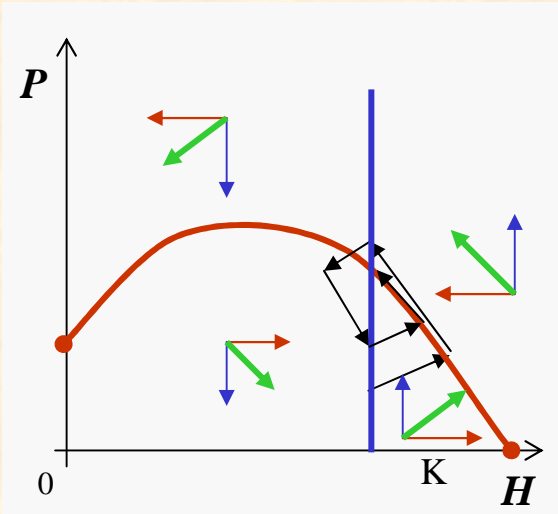
▶ for parameters: $r_H = 3, a = 0.1, T_h = 2, K = 10$

$$\frac{dH}{dt} = 0 \quad 0 = 3H \left(1 - \frac{H}{10} \right) - \frac{0.1HP}{1 + 0.1H \cdot 2} \quad H = \frac{m}{b}$$

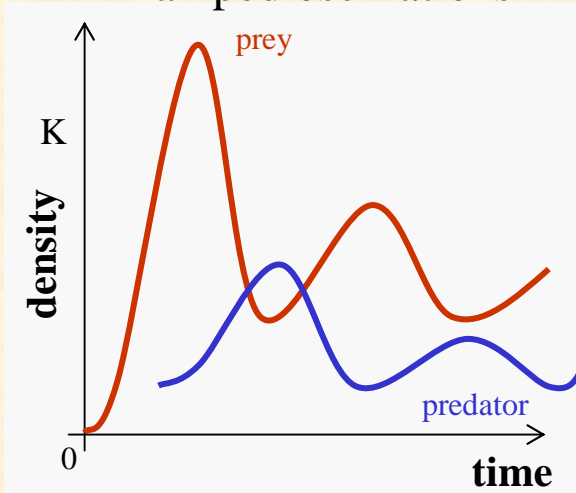
prey isocline: $P = 30 + 6H - 0.6H^2$ predator isocline: $H = \text{constant}$

▶ predator exploits prey close to K

- isocline: $H = 9$

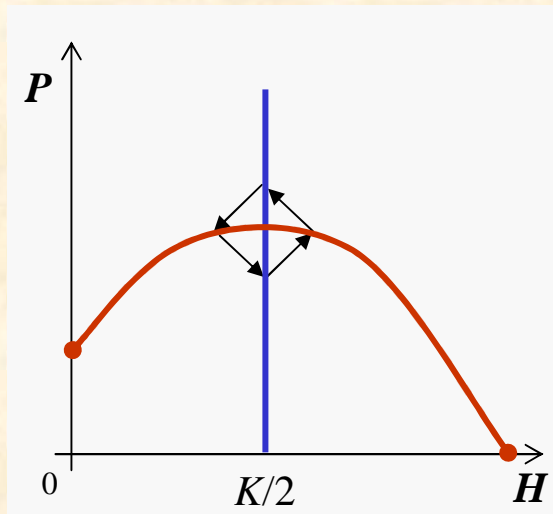


Damped oscillations

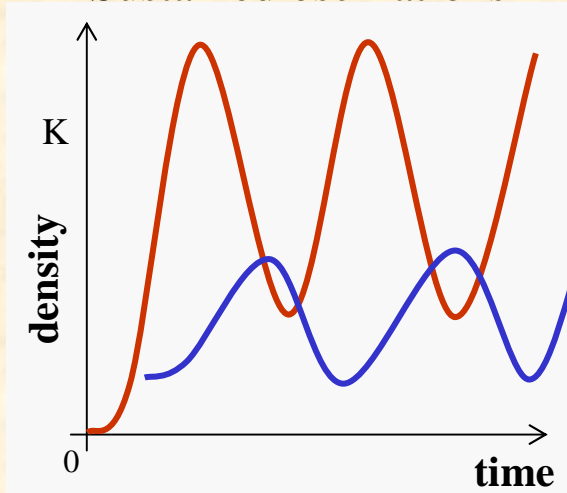


▶ predator exploits prey close to $K/2$

- isocline: $H = 5$

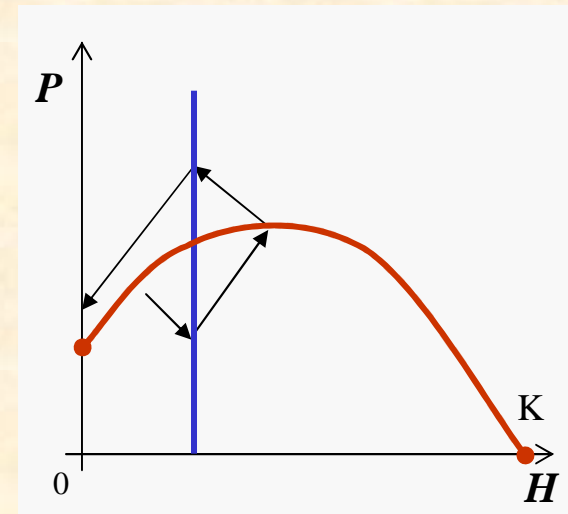


Sustained oscillations

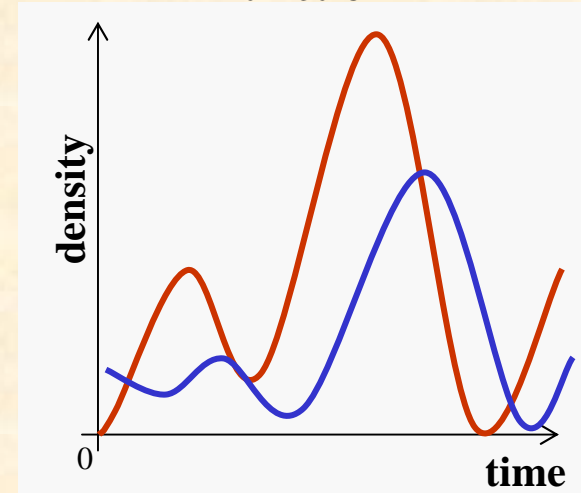


▶ predator exploits prey at low density

- isocline: $H = 2$



Extinction



Addition of predator's carrying capacity

- ▶ logistic model with carrying capacity proportional to H
- ▶ k .. parameter of 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: $r_p = 2, k = 0.2$

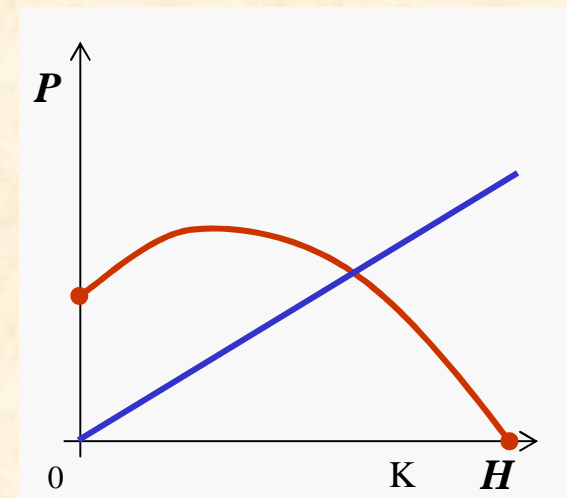
$$\frac{dP}{dt} = 0 \quad 0 = 2P \left(1 - \frac{P}{0.2H} \right)$$

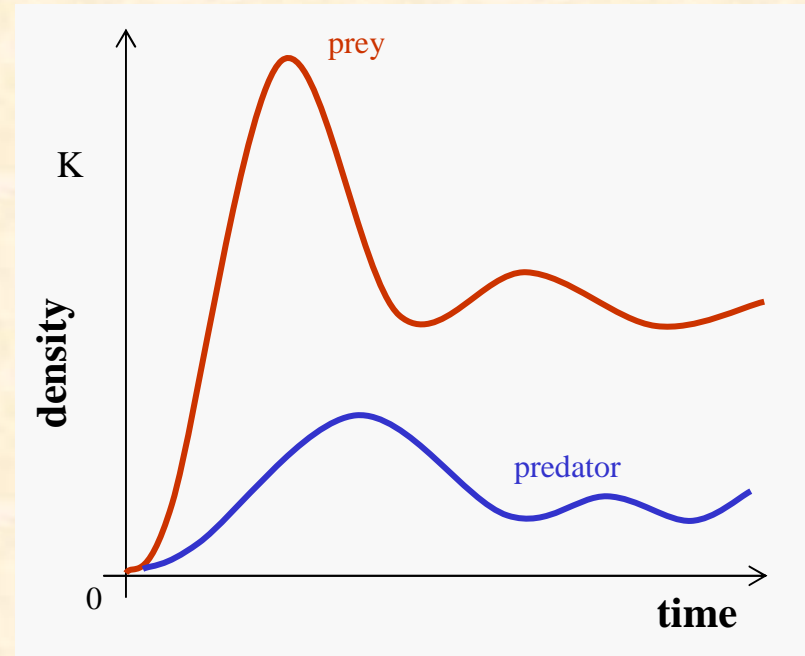
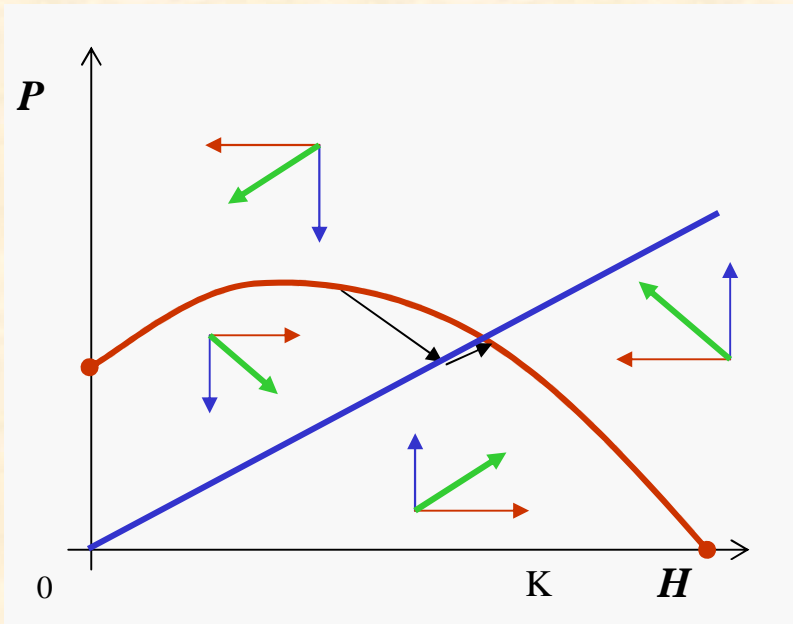
predator isocline:

$$H = 5P$$

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
- attack happens at reproduction
- 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

λ = 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, μ .. mean number of encounters

E_t = total number of encounters

a = searching efficiency

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

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

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

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

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

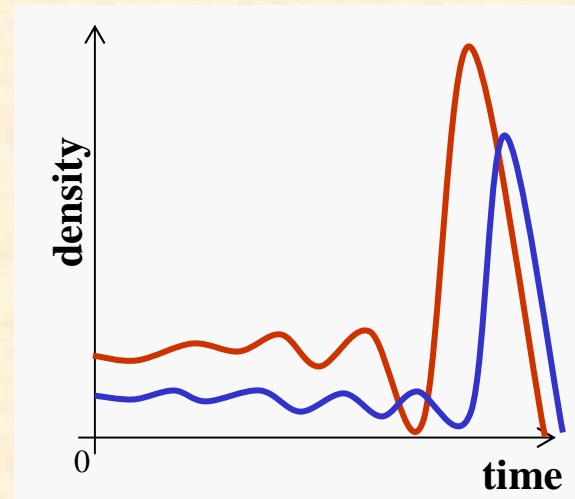
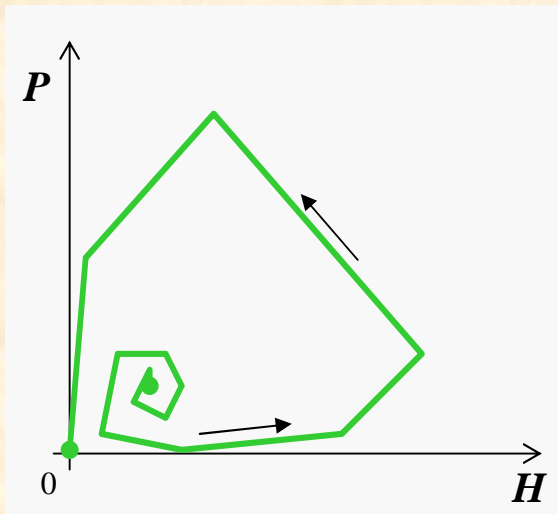
$$P_{t+1} = H_a$$



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

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

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



Addition of density-dependence

- ▶ exponential growth of hosts is replaced by logistic equation

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

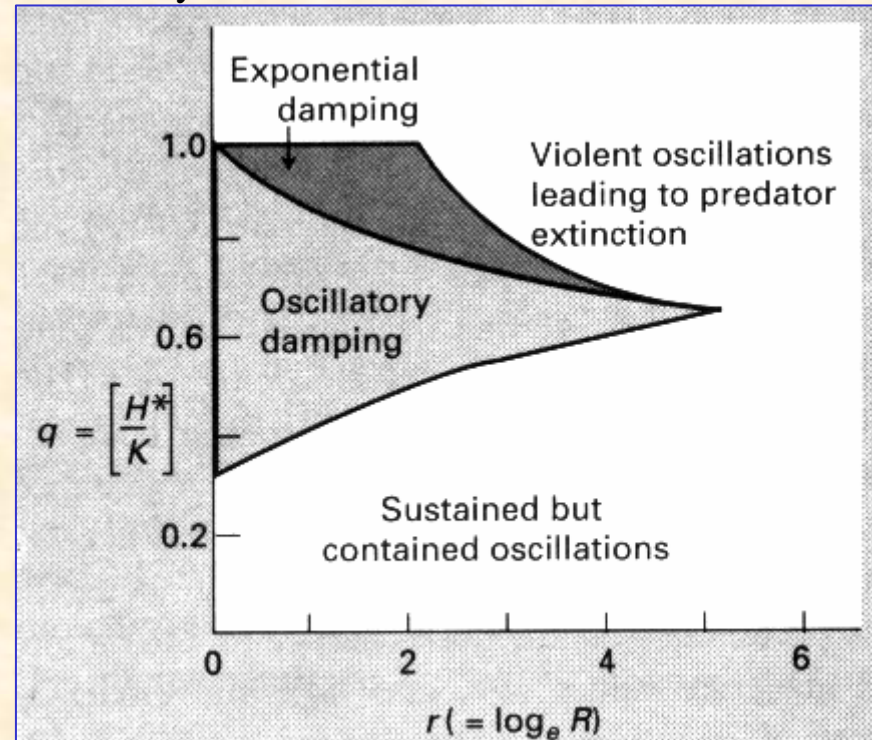
$$P_{t+1} = H_t \left(1 - e^{-aP_t}\right)$$

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

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

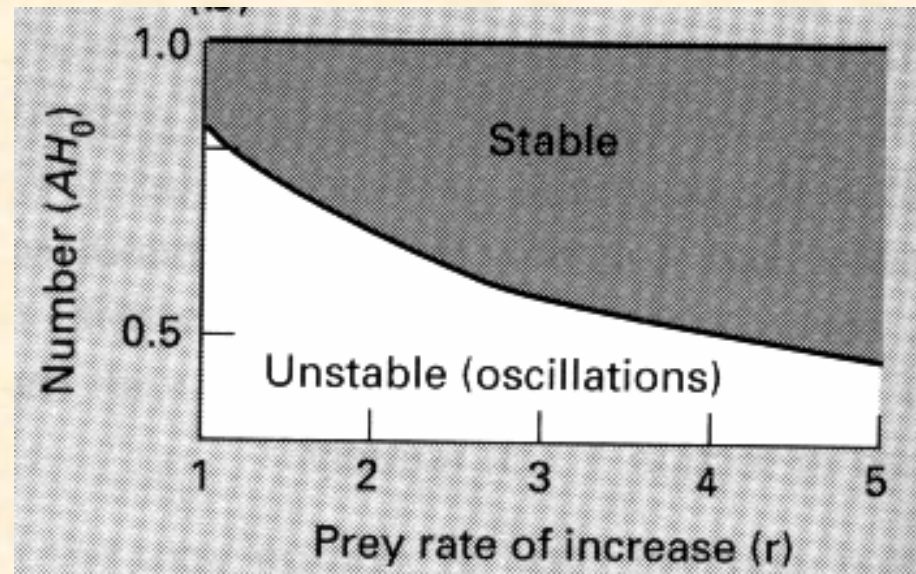
- ▶ if hosts are distributed non-randomly in the space

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 = 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) $k=0$

