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 $\qquad$ P .. density of predators

r .. intrinsic rate of prey population $\qquad$ m .. predator mortality rate

a .. predation rate $\qquad$ b .. reproduction rate of predators

▸ in the absence of predator, prey grows exponentially →

$$\frac{\mathrm{d}H}{\mathrm{d}t} = rH$$

▸ in the absence of prey, predator dies exponentially →

$$\frac{\mathrm{d}P}{\mathrm{d}t} = -mP$$

▸ predation rate is linear function of the number of prey .. aHP

▸ each prey contributes identically to the growth of predator .. bHP

$$\frac{\mathrm{d}H}{\mathrm{d}t} = rH - aHP$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = bHP - mP$$

Analysis of the model

Zero isoclines:

▸ for prey population:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = 0 \qquad 0 = rH - aHP$$

$$\boxed{P = \frac{r}{a}}$$
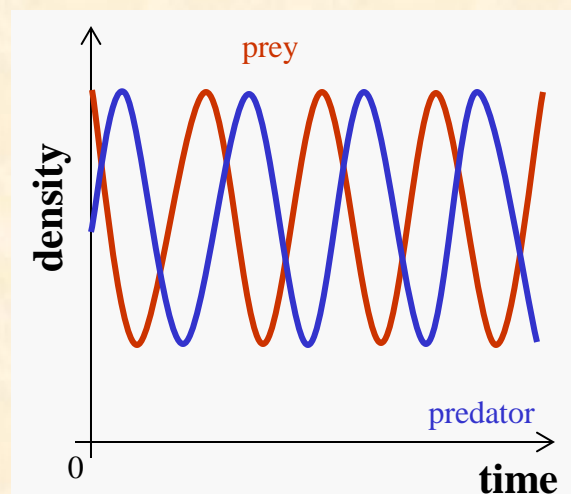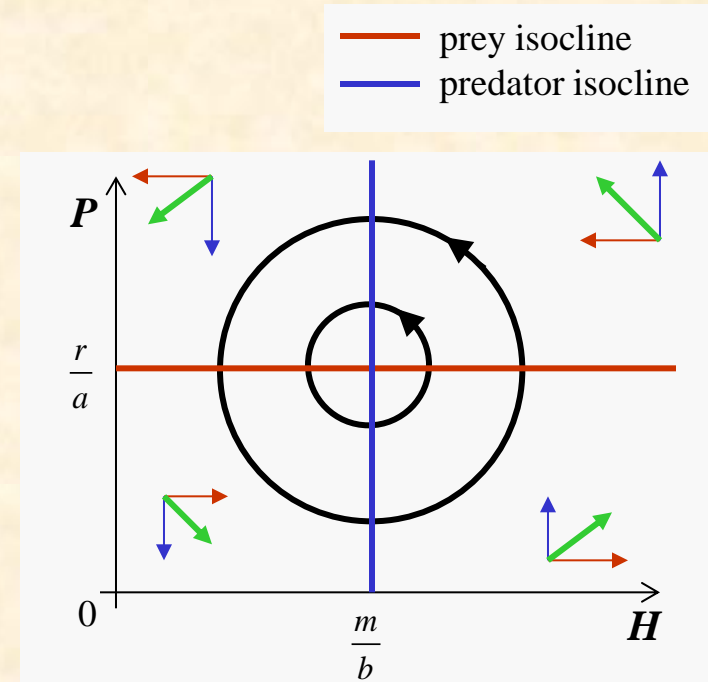
▸ for predator population:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = 0 \qquad 0 = bHP - mP$$

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

▸ do not converge, has no asymptotic stability (trajectories are closed lines)
→ **neutral stability**

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

— prey isocline
— predator isocline

Addition of density-dependence

▸ in the absence of the predator prey population reaches carrying capacity K

$$\frac{\mathrm{d}H}{\mathrm{d}t} = rH\left(1 - \frac{H}{K}\right) - aHP$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = bHP - mP$$

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

$$\frac{\mathrm{d}H}{\mathrm{d}t} = 3H\left(1 - \frac{H}{10}\right) - 0.1HP$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = 0.3HP - 2P$$

<u>Zero isoclines:</u>

▶ for <u>prey</u> population: $\dfrac{\mathrm{d}H}{\mathrm{d}t} = 0$ $0 = 3H\left(1 - \dfrac{H}{10}\right) - 0.1HP$

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

$$\boxed{P = 30 - 3H}$$
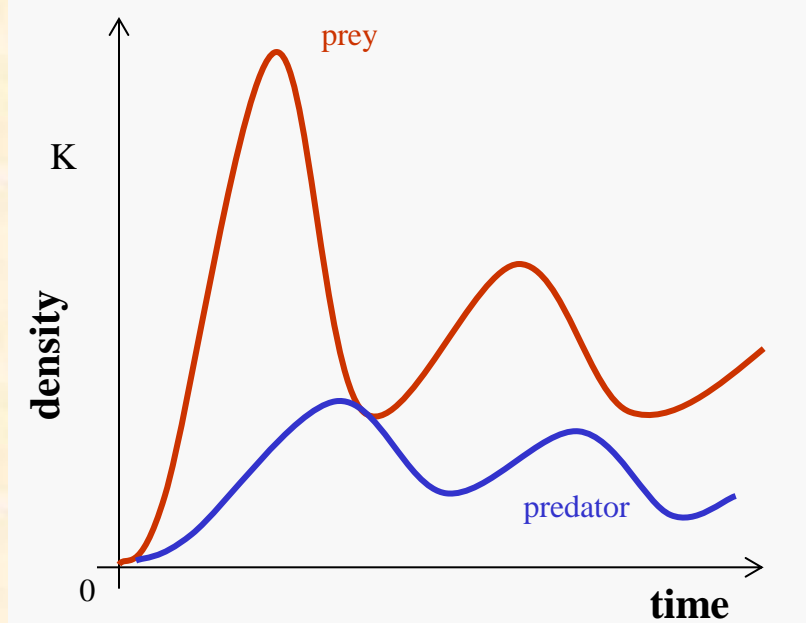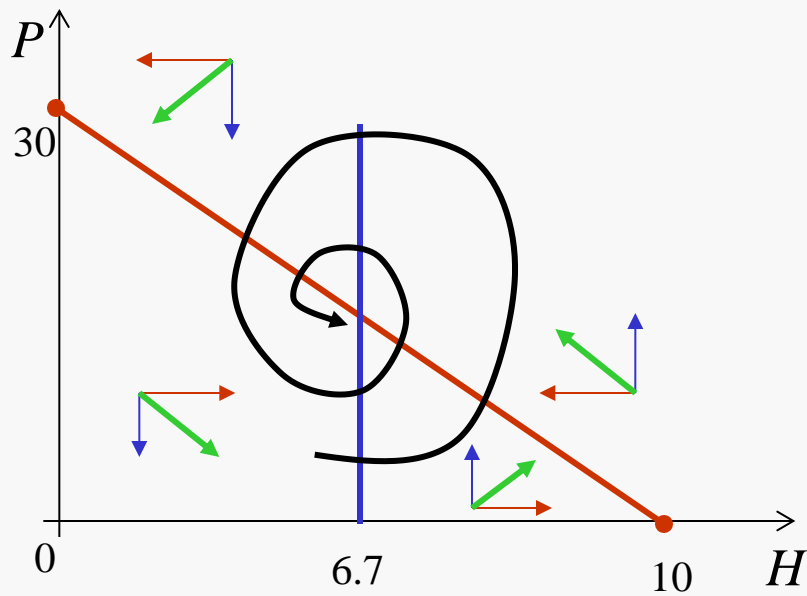
▶ for <u>predator</u> population: $\dfrac{\mathrm{d}P}{\mathrm{d}t} = 0$ $0.3HP - 2P = 0$

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

$$\boxed{H = 6.667}$$

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

$$\frac{\mathrm{d}H}{\mathrm{d}t} = r_H H\left(1 - \frac{H}{K}\right) - \frac{aHP}{1 + aHT_h} \qquad \frac{dP}{\mathrm{d}t} = bHP - mP$$

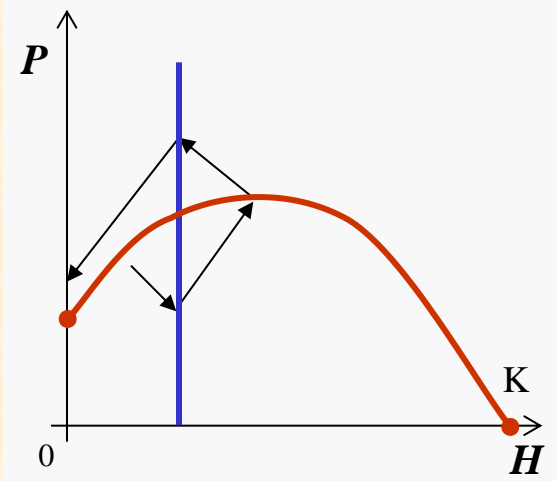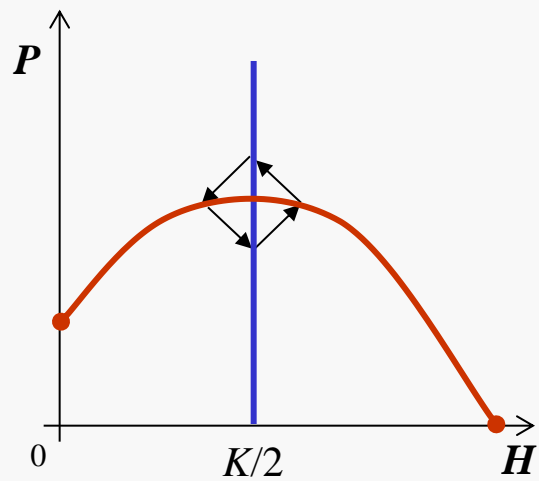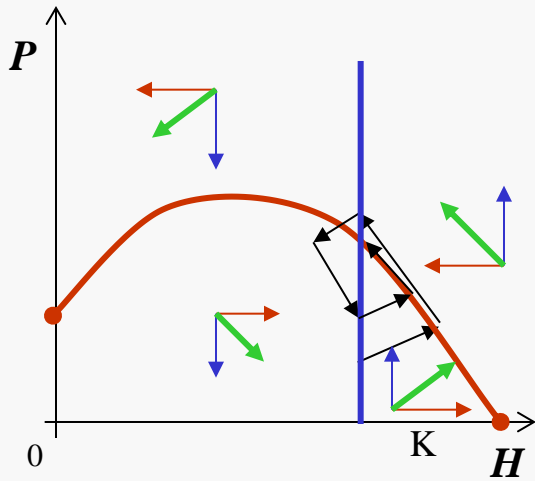▸ for parameters: $r_H = 3$, $a = 0.1$, $T_h = 2$, $K = 10$

$$\frac{\mathrm{d}H}{\mathrm{d}t} = 0 \qquad 0 = 3H\left(1 - \frac{H}{10}\right) - \frac{0.1HP}{1 + 0.1H2} \qquad\qquad H = \frac{m}{b}$$

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

► predator exploits prey close to *K*
- isocline: *H* = 9

► predator exploits prey close to *K*/2
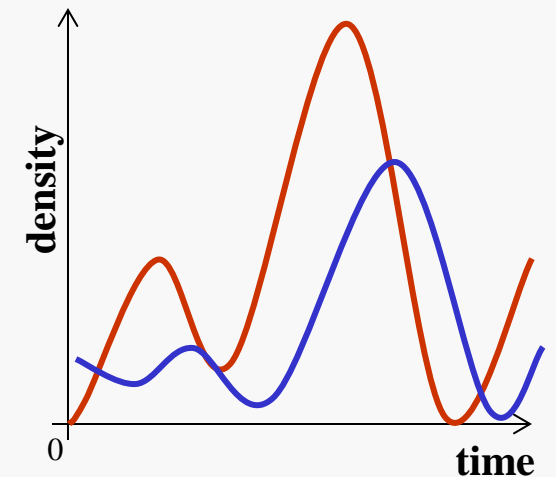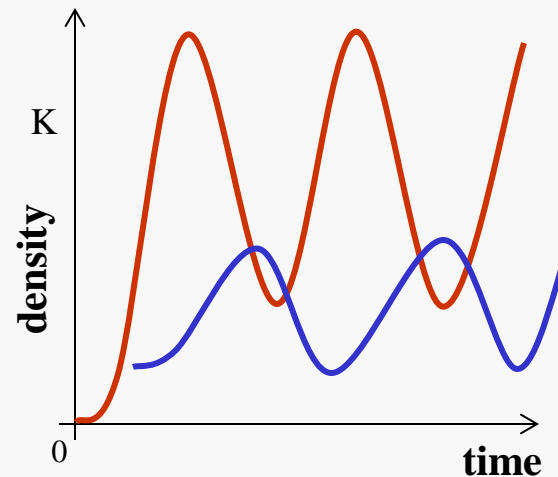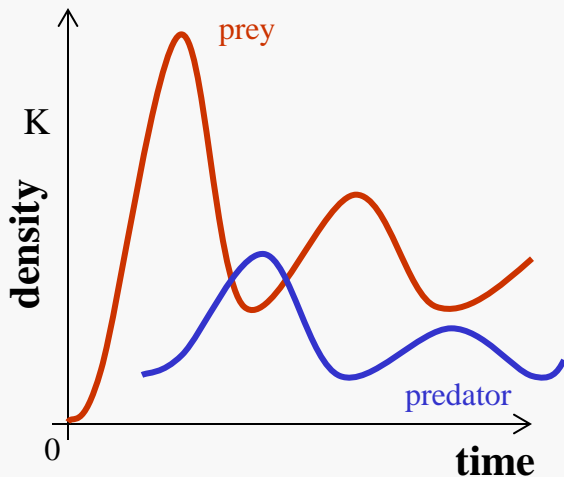- isocline: *H* = 5

► predator exploits prey at low density
- isocline: *H* = 2

Damped oscillations

Sustained oscillations

Extinction

Rosenzweig & MacArthur (1963)

Addition of predator's carrying capacity

▸ logistic model with carrying capacity proportional to H
▸ k .. parameter of carrying capacity of the predator
▸ $r_P = bH - m$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = bHP - mP$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = r_P P \left(1 - \frac{P}{kH} \right) \qquad \frac{\mathrm{d}H}{\mathrm{d}t} = r_H H \left(1 - \frac{H}{K} \right) - \frac{aHP}{1 + aHT_h}$$

▸ for parameters: $r_P = 2$, $k = 0.2$
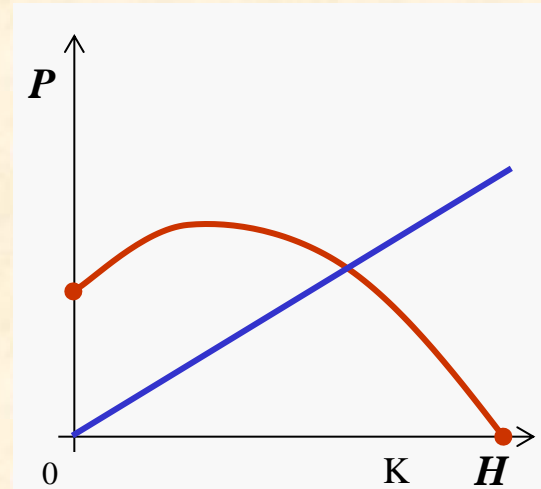
$$\frac{\mathrm{d}P}{\mathrm{d}t} = 0 \qquad 0 = 2P \left(1 - \frac{P}{0.2H} \right)$$

predator isocline: $\boxed{H = 5P}$
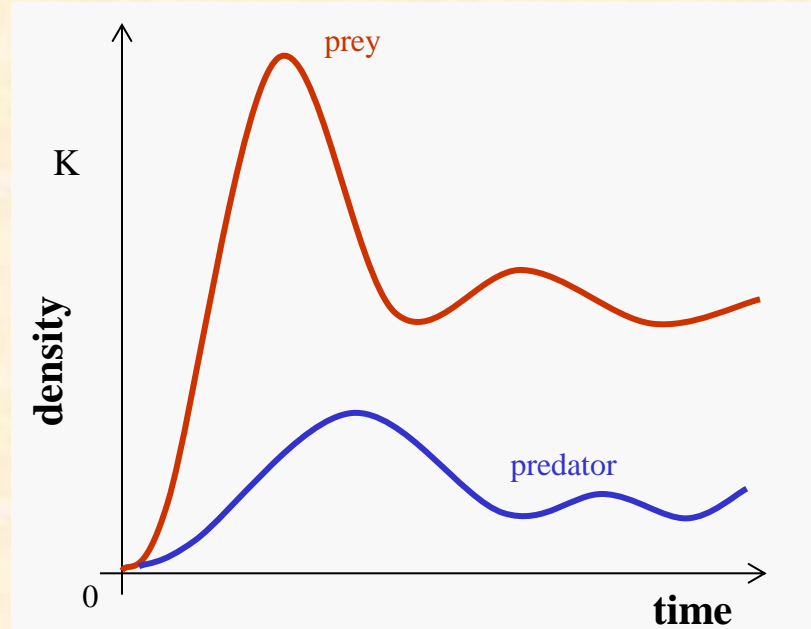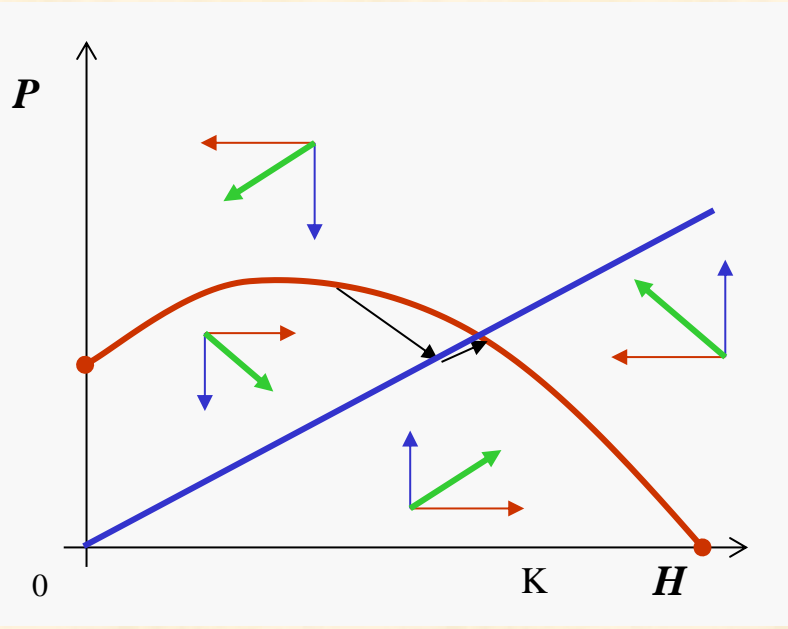
prey isocline: $\boxed{P = 30 + 6H - 0.6H^2}$

▸ 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

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

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

P_t = number of parasitoids

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

Incorporation of random search

▸ parasitoid searches randomly
▸ encounters (x) are random (Poisson distribution)

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

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

E_t = total number of encounters
a = searching efficiency

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

▸ proportion of encounters (1 or more times): $p = (1 - p_0)$
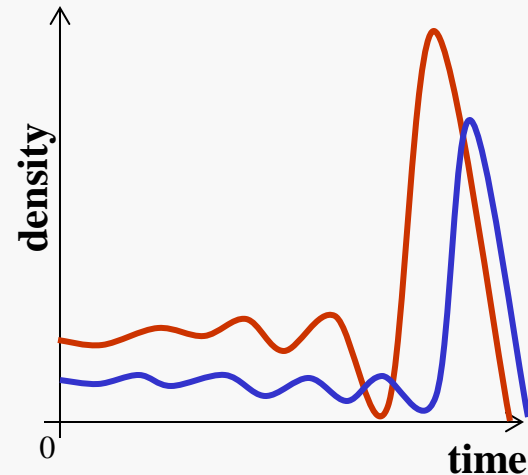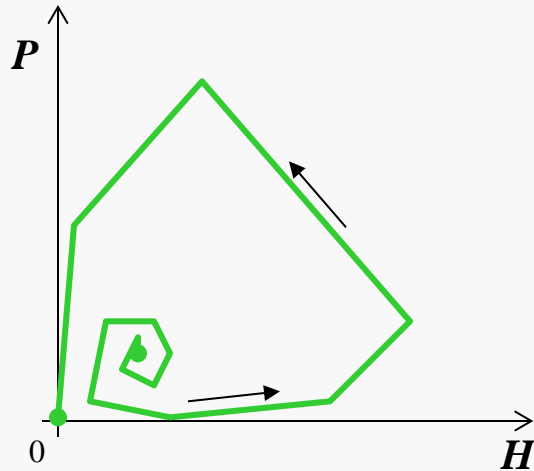
$$p = (1 - e^{-aP_t})$$

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

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

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

$$\Longrightarrow$$

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

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

▸ 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

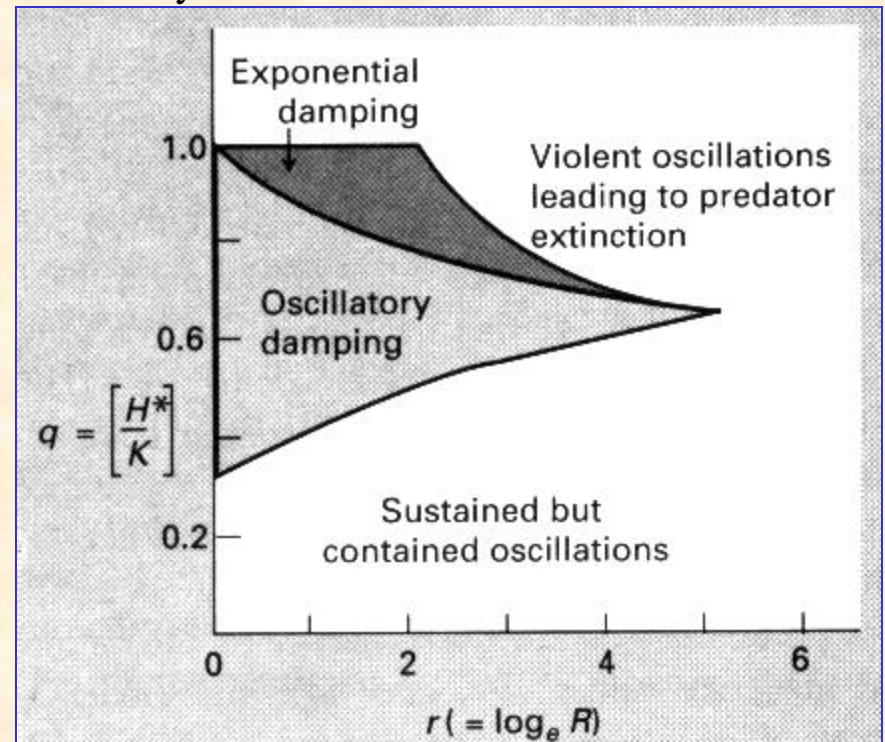▸ exponential growth of hosts is replaced by logistic equation

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

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

Stability boundaries

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

H^*.. new host carrying capacity

▸ depends on parasitoids' efficiency
- when a is low then $q \to 1$
- when a is high then $q \to 0$

▸ density-dependence have stabilising effect for moderate r and q
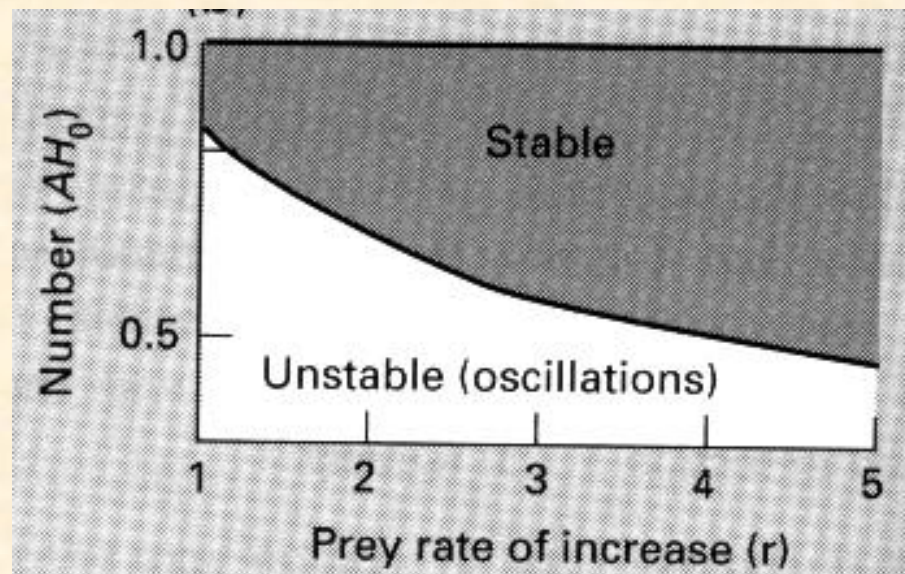

Beddington et al. (1975)

Addition of the refuge

▸ if hosts are distributed non-randomly in the space

Fixed number in refuge: H_0 hosts are always protected

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

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

▸ have strong stabilising effect even for large r

Hassell & May (1973)

Addition of aggregated distribution

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

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

where k = degree of aggregation

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

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

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

Stability boundaries:
a) $\boldsymbol{k}=\infty$, b) $\boldsymbol{k}=2$, c) $\boldsymbol{k}=1$, d) $\boldsymbol{k}=0$

(a) Exponential damping — Violent oscillations — Oscillatory damping — Sustained but contained oscillations
(b) (c) (d)
q
Prey rate of increase (r)

Hassell (1978)