# Predator-prey models, limit cycles, Hopf bifurcation

vincent.jansen@rhul.ac.uk

# Outline

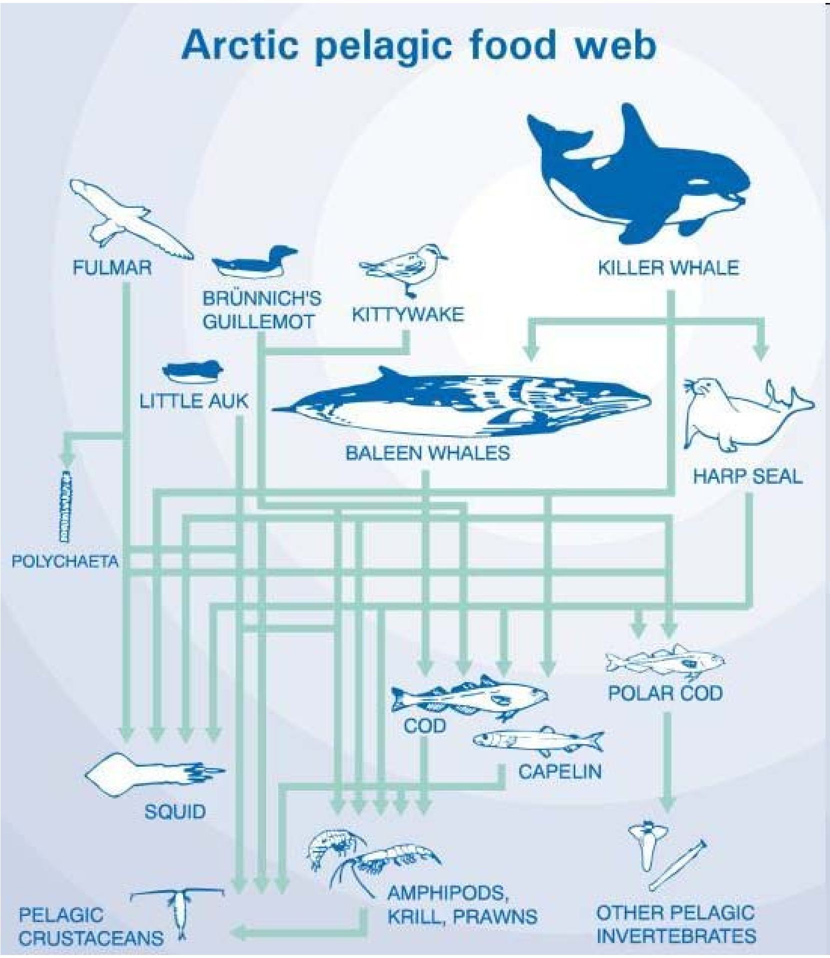
- Trophic interactions
- D’Ancona’s observation & Volterra predator-prey model
- The Rosenzweig-MacArthur model
- Stable limit cycles, the paradox of enrichment
- Parasitism, the Nicholson Bailey model
- Spatial interactions

# Trophic interactions

- Trophic interactions capture all interactions where one species uses another species to feed and reproduce on.
- This includes predation, herbivory and parasitism.

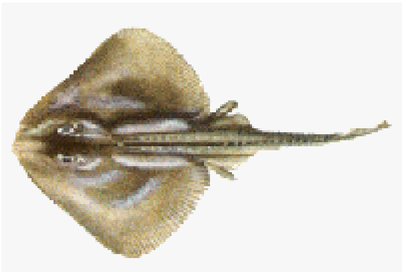
# Trophic interactions

- Trophic interactions are conspicuous
- They are fairly easy to detect and quantify (gut contents)
  - They are therefore probably over-represented in ecological studies compared to competitive interactions
  - Food web theory is almost exclusively dedicated to trophic interactions, competition in food webs is rarely measured

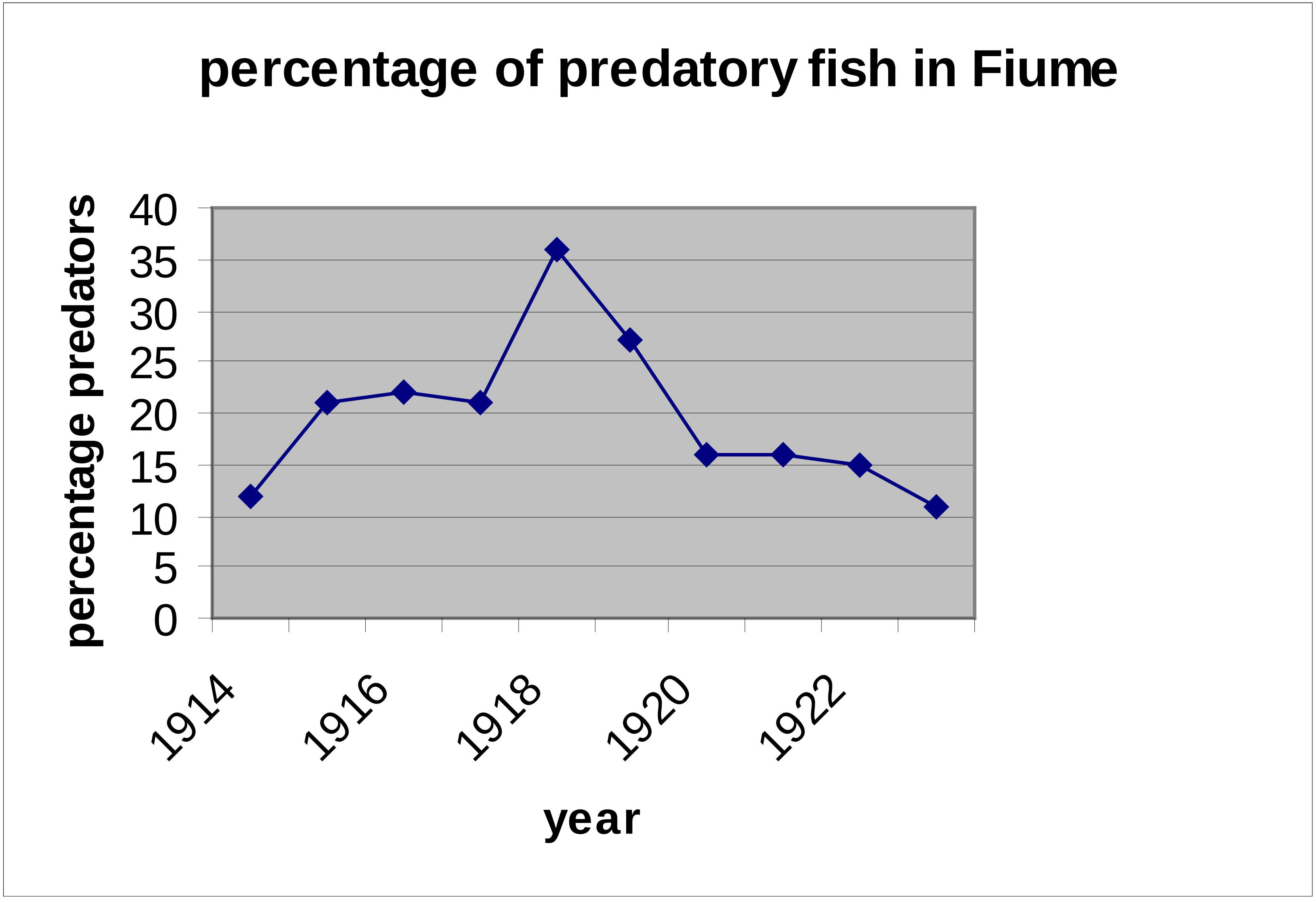


# D’Ancona’s observation

- D’Ancona studied data of the Adriatic fisheries
- During the first world war (1914-1918) the fishery effort in the Adriatic had been much reduced


# Fiume (Riyeka) fishmarket


percentage of predatory fish in Fiume
percentage predators
40
35
30
25
20
15
10
5
0
1914
1916
1918
1920
1922
year

# D’Ancona’s observation

- He noticed that the proportion of predatory fish (sharks, skates, rays etc.) had increased.
- Fishermen concentrate on prey fish.
- Why the increase?

# D'Ancona's observation

- This is puzzling as fishermen prefer to catch prey fish.
- Humberto D'Ancona, who studied the fisheries data, asked his fiancee's father how this could be explained.
- The father was Vito Volterra, a theoretical physicist.

Vito Volterra
(1860-1940)

# Lotka-Volterra predator-prey model

- Volterra produced a model (Alfred Lotka produced a similar model at about the same time)
- The model is similar in structure to the L-V competition model. In the competition model both species suffer from each others presence (--) in this model the prey suffers, the predator benefits (-+)

# Predators and their prey

Volterra's assumed:

- Without predators the prey population grows unbounded, no density dependence
- Without prey the predator population disappears
- The number of prey caught only depends on encounter probabilities

# Lotka-Volterra predator-prey model

- We will use a slightly different notation (following Gotelli)
  - $V$: density of the prey (victim) population
  - $P$: density of the predator population
- In the absence of the predator the prey grows exponentially

$$\frac{dV}{dt} = rV$$

# Lotka-Volterra predator-prey model

- Functional response: the per predator effect of predation on the prey's growth rate
- $\alpha$ is the capture efficiency, assumed to be constant
- The functional response is $\alpha V$
- The prey's growth rate is:

$$\frac{dV}{dt} = rV - \alpha VP \quad = (r - \alpha P)V$$

# Lotka-Volterra predator-prey model

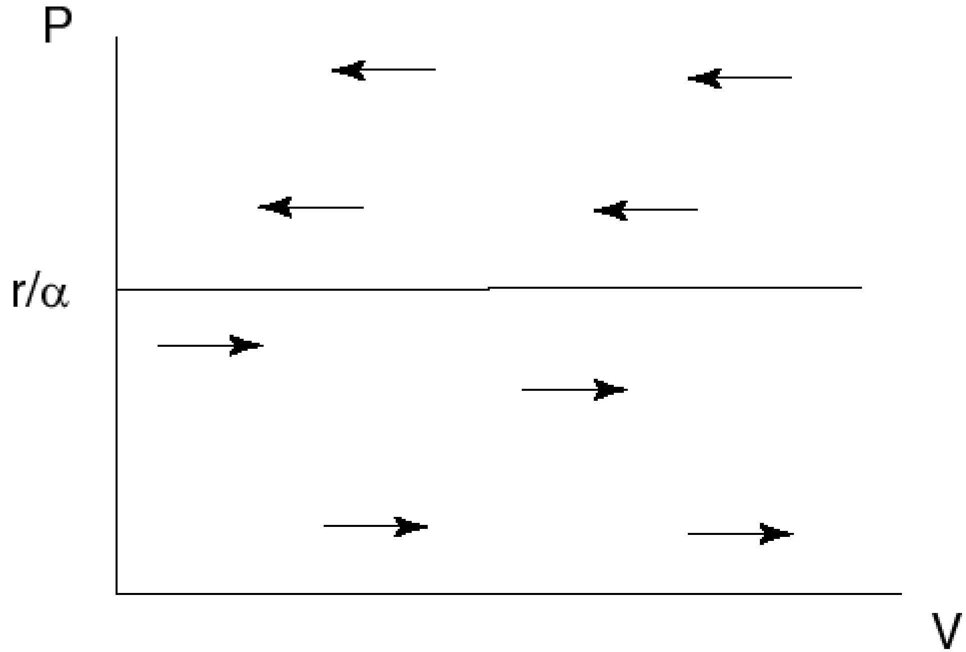
- The per capita prey growth rate is

$$(r - \alpha P)$$

- The per capita prey growth rate is independent of prey density
- If the predator density is low, the prey population increases, if it is high it decreases

# Lotka-Volterra predator-prey model

- Prey dynamics if predator density is constant



# Lotka-Volterra predator-prey model

- In the absence of the prey the predator population will decrease
- The predator's death rate is $q$
- In the absence of prey, the predator population changes as:

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

# Lotka-Volterra predator-prey model

- $\beta$ is the amount of energy gained per unit of time. (If $e$ is the conversion efficiency, $\beta = e\alpha$)
- The numerical response is $\beta V$
- The predator's growth rate is

$$\frac{dP}{dt} = \beta VP - qP \quad = (\beta V - q)P$$

# Lotka-Volterra predator-prey model

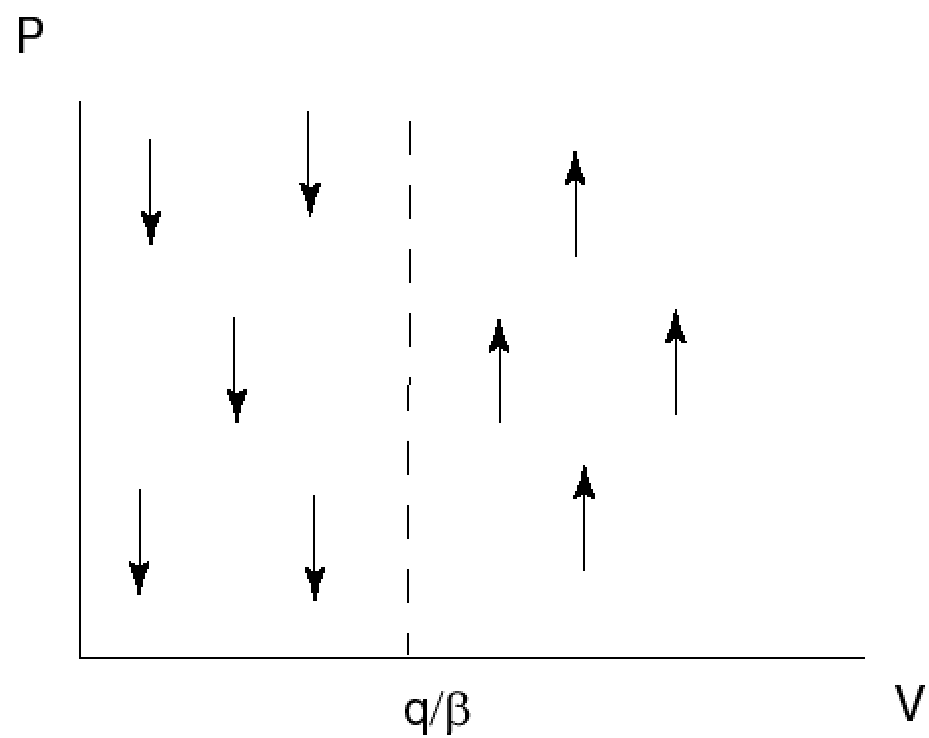
- The per capita predator growth rate is

$$(\beta V - q)$$

- The per capita predator growth rate is independent of predator density
- If the prey density is low, the predator population decreases, if it is high it increases

# Lotka-Volterra predator-prey model

- Predator dynamics if prey density is constant



# Lotka-Volterra predator-prey model

- The densities of predator and prey change simultaneously
- This is described by a system of 2 differential equations:

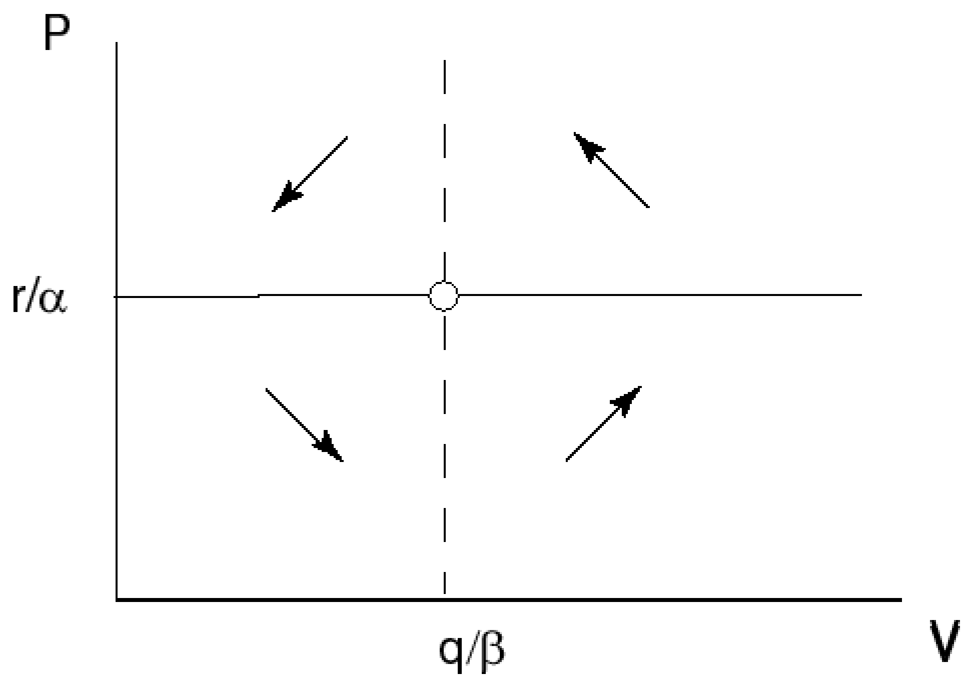
$$\frac{dV}{dt} = V(r - \alpha P)$$

$$\frac{dP}{dt} = P(\beta V - q)$$

- This model is known as the Lotka-Volterra predator-prey model

# Lotka-Volterra predator-prey model

- Combined isoclines



# Lotka-Volterra predator-prey model

- The prey equilibrium density is given by $q/\beta$: only depends on the parameters relating to the *predator*.
- The predator equilibrium density is given by $r/\alpha$ only depends on the parameters relating to the *prey*.

# Lotka-Volterra predator-prey model with fishery effort

- If we assume that fish is caught with rate f, the model reads:

$$\frac{dV}{dt} = (r - f)V - \alpha VP$$

$$\frac{dP}{dt} = \beta VP - (q + f)P$$

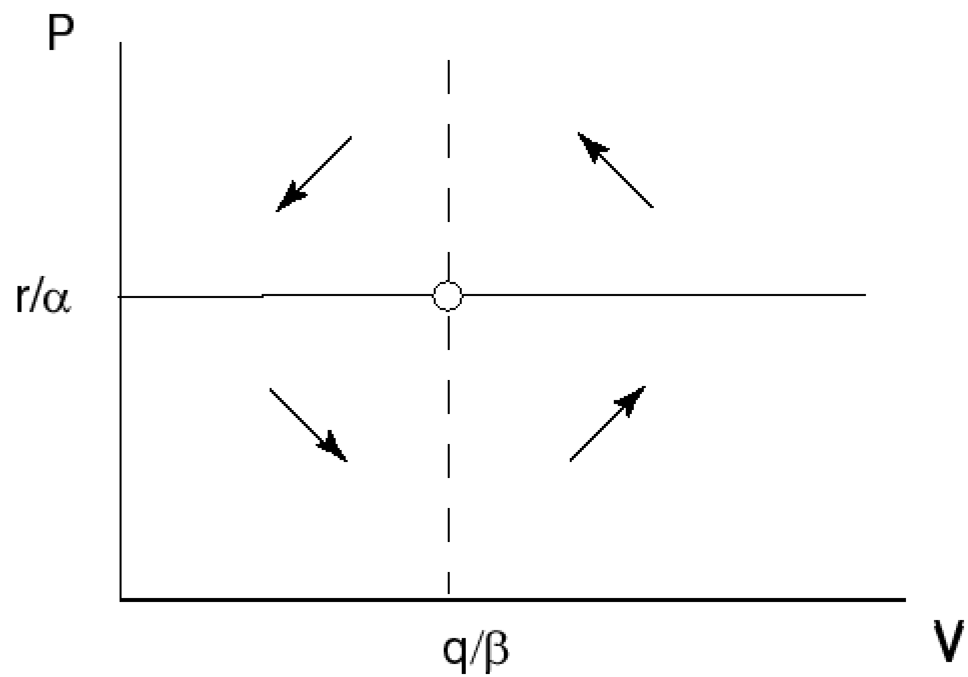
- The prey equibrium is now $V^{*}=(q+f)/\beta$
- The predator equilibrium is now $P^{*}=(r-f)/\alpha$

# Lotka-Volterra predator-prey model

- A reduced fishing effort (directed at prey and predatory fish) will have two effects: it <u>increases</u> the predator’s equilibrium density and <u>decreases</u> the prey’s equilibrium density
- This can explain D’Ancona’s observation why relatively more predator fish was caught after a reduced fishing effort

# Lotka-Volterra predator-prey model, dynamics

- Combined isoclines

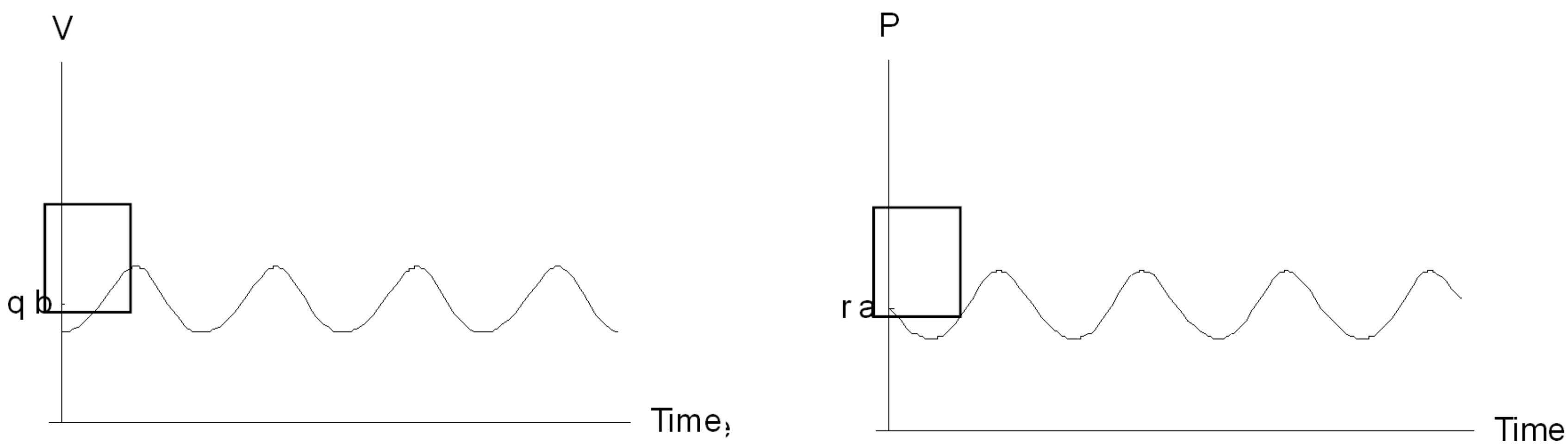


# XPP

- **The Lotka-Volterra predator-prey model**

# Lotka-Volterra predator-prey model

- Solution over time

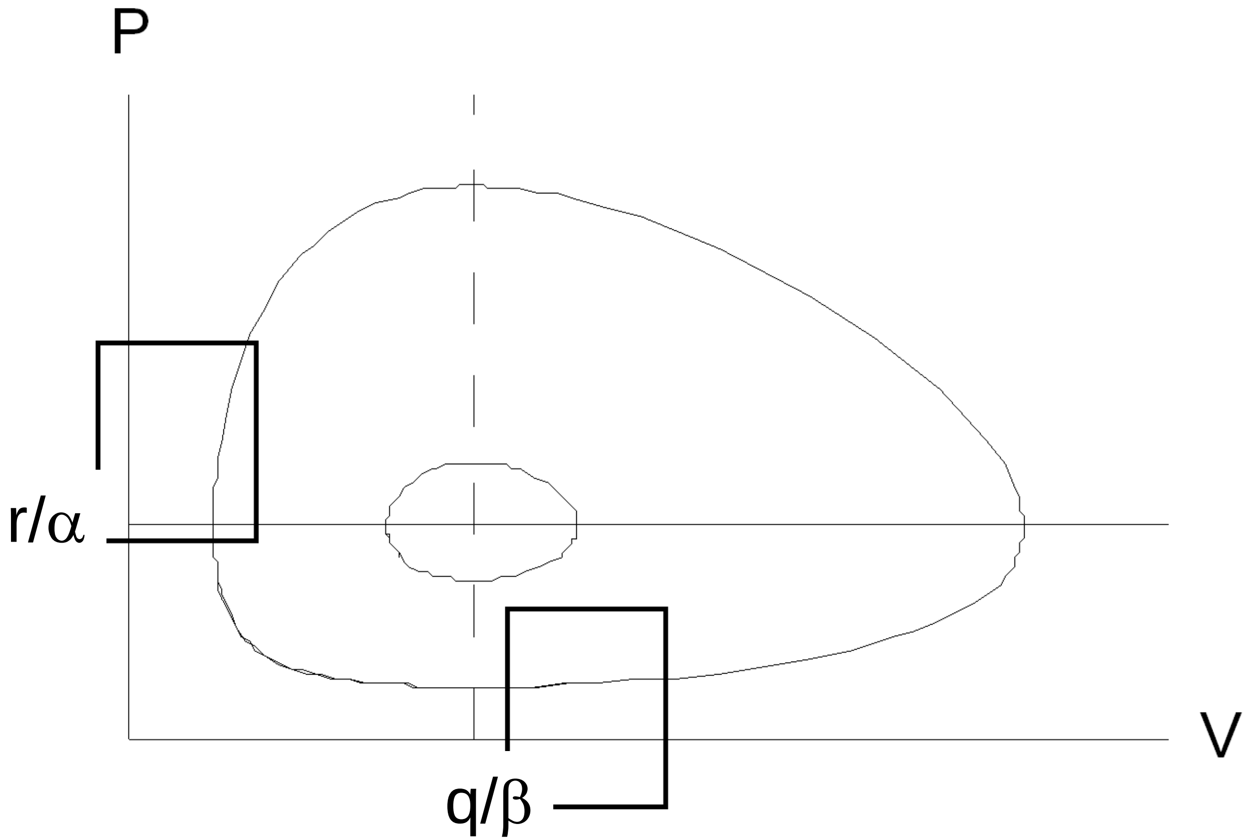



The solutions oscillate over time, the amplitude depends on the initial condition much like the motion of a pendulum

[redacted]

# Lotka-Volterra predator-prey model

- Solution as an orbit in a phase plot



# Stability

- To find the stability we use the distance from the equilibrium $x=V-V^*$ and $y=P-P^*$ linearise the system, to find

$$\begin{pmatrix} \dfrac{dx}{dt} \\ \dfrac{dP}{dt} \end{pmatrix} = \begin{pmatrix} r-\alpha P^* & -\alpha V^* \\ P^*\beta & \beta V^* - q \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

pplyapnv.ode

# Stability

- The model has a constant of motion:

$$H = \beta V - q \ln V + \alpha P - r \ln P$$

- Over one cycle, the value of H is constant.
- If the starting point moves away from one cycle, after on revolution you are back to where you started, you remain the same distance from the other cycle
- The cycles are therefore all neutrally stable.

# Lotka-Volterra predator-prey model

- Assumptions of the model
- No delays
- No (age, spatial) structure
- No prey density dependence
- Constant prey capture rate
- No stochastic effects

# Lotka-Volterra predator-prey model

- Because the model is degenerate it is very sensitive to a change in the assumptions, slightly changing the assumptions will make (real part of ) the eigenvalues +ive or -ive
- For this reason it is said that the L-V predator-prey model is not robust

# Density dependent prey growth

- We can easily add a density dependent prey growth by assuming that the prey will grow according to the logistic model
- The prey growth rate is then given by

$$r(k - V) - \alpha P$$

# Density dependent prey growth

- The model changes to

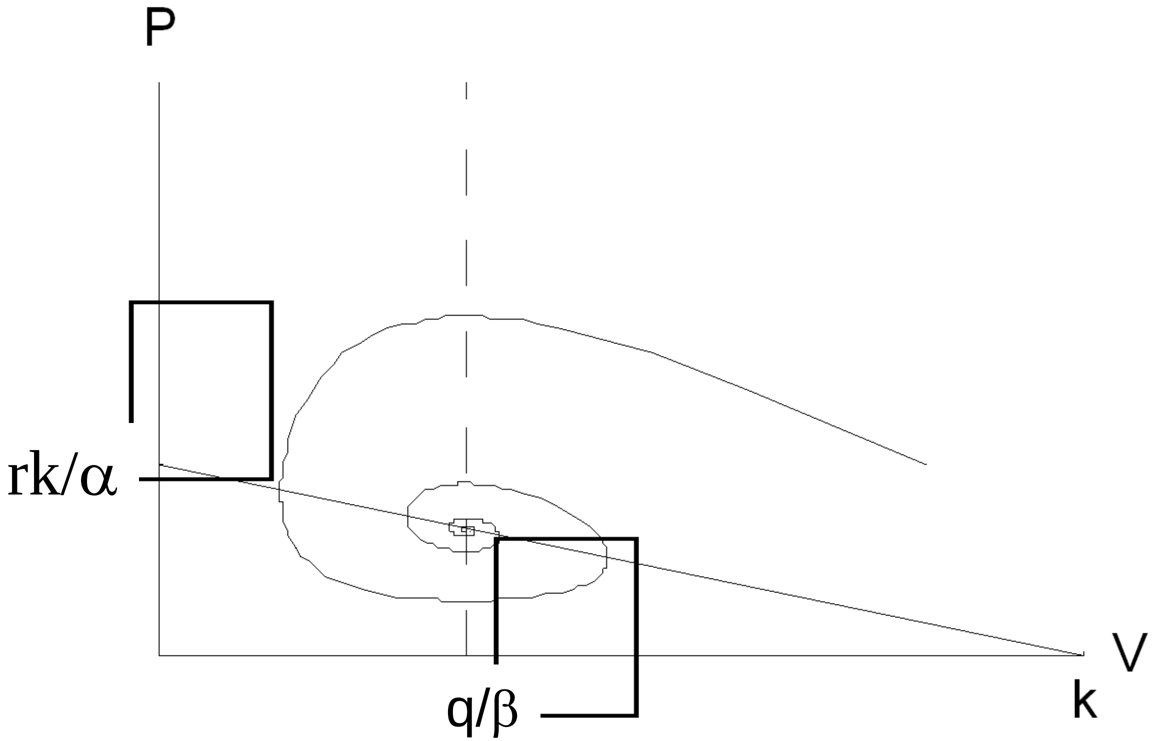
$$\frac{dV}{dt} = V(r(k - V) - \alpha P)$$

$$\frac{dP}{dt} = P(\beta V - q)$$

- Xpp
- **Draw the bifurcation diagram in k for the Lotka-Volterra model with prey density dependence**

# Density dependent prey growth

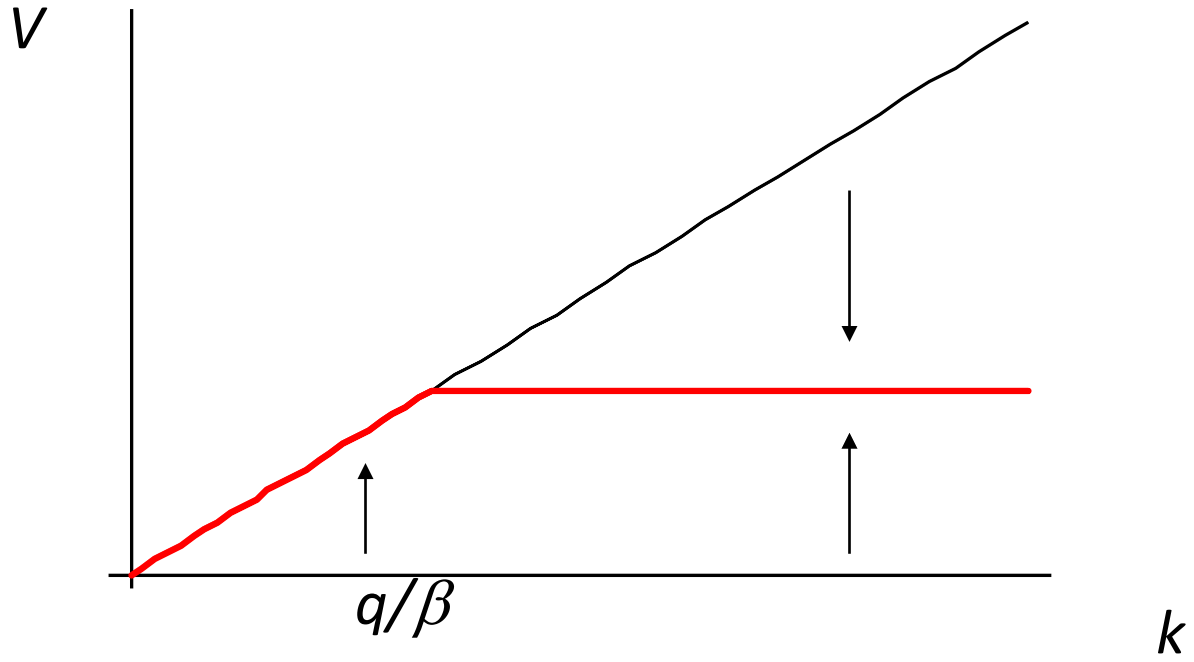
- Solutions




- Density dependent prey growth acts stabilising

# Density dependent prey growth

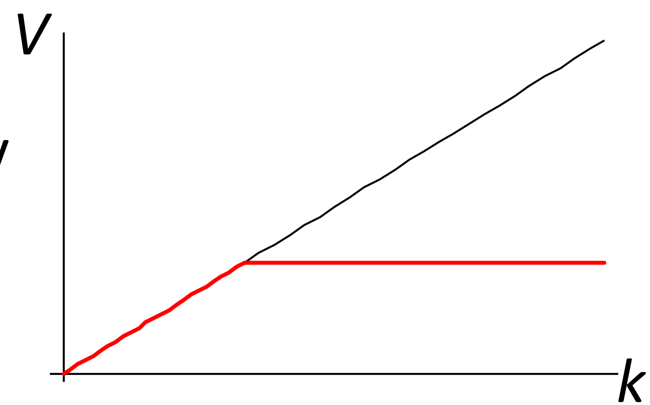
- Bifurcation diagram in k



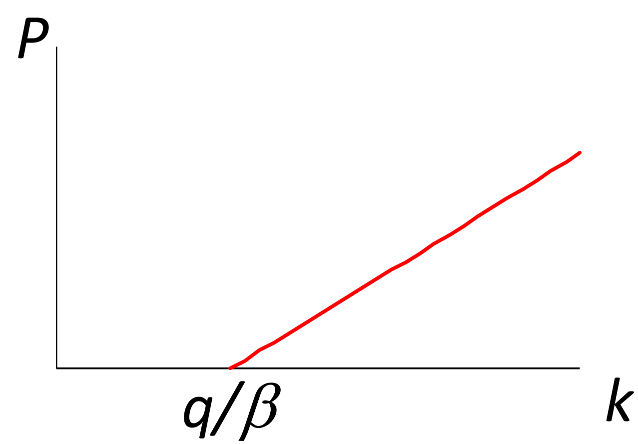
# Density dependent prey growth

- Bifurcation diagram in k

Prey density




Predator density



# Holling (II) functional response

- So far we assumed that the functional response (the per predator effect of predation on the prey's growth rate) is proportional to the amount of prey
- This amounts to saying that the nr of prey eaten will always go up with the number of prey

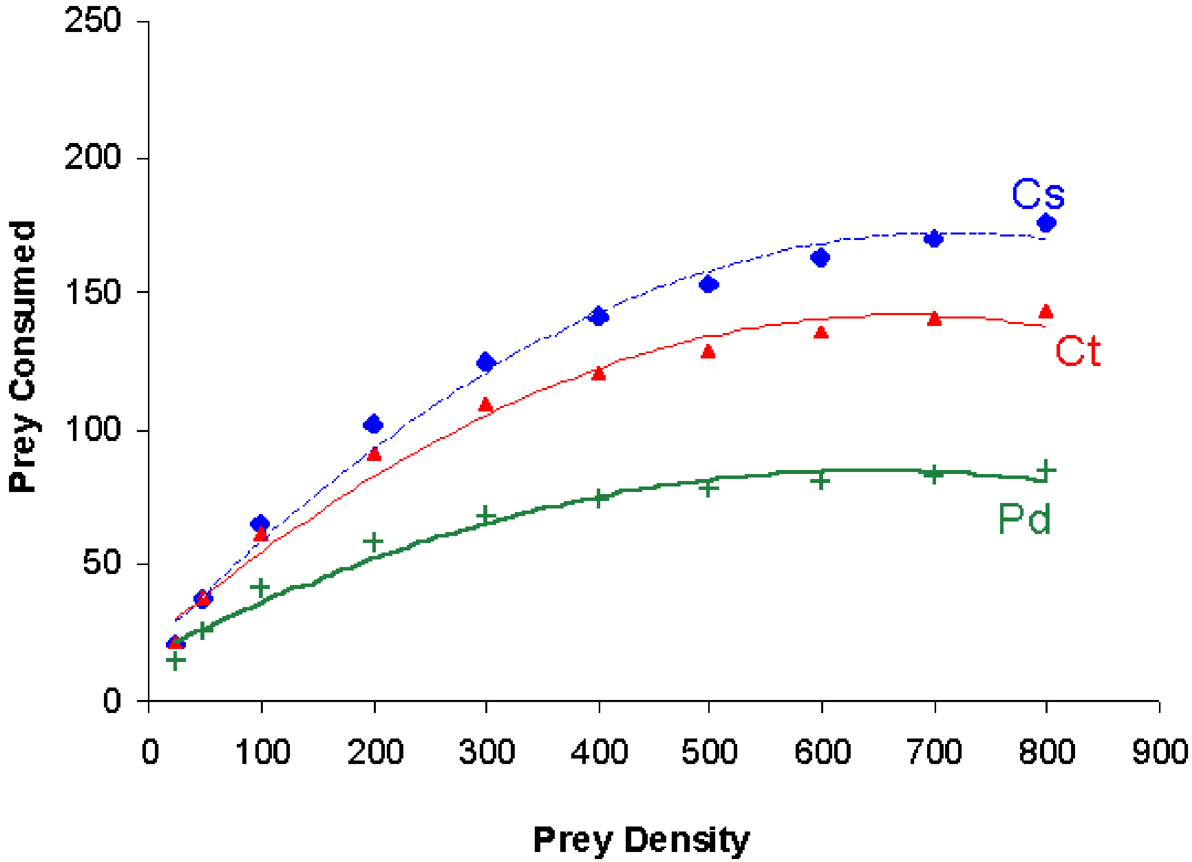
# Holling (II) functional response

- Often this is not the case because predators need time to ‘handle’ their prey
- Handling includes the time needed for hunting, eating and digesting
- Even if prey is abundant this will limit the number of prey eaten per predator per unit of time

# Holling (II) functional response

The he

nu




The number of aphids (*M. persicae*) consumed in 24 hrs by 3 different ladybird species (*C. sexmaculatus*, *C. transversalis* and *P. dissecta*) as a function of aphid density. From Pervez and Omkar, J.Insect Science 5:5 (2005)

# Holling (II) functional response

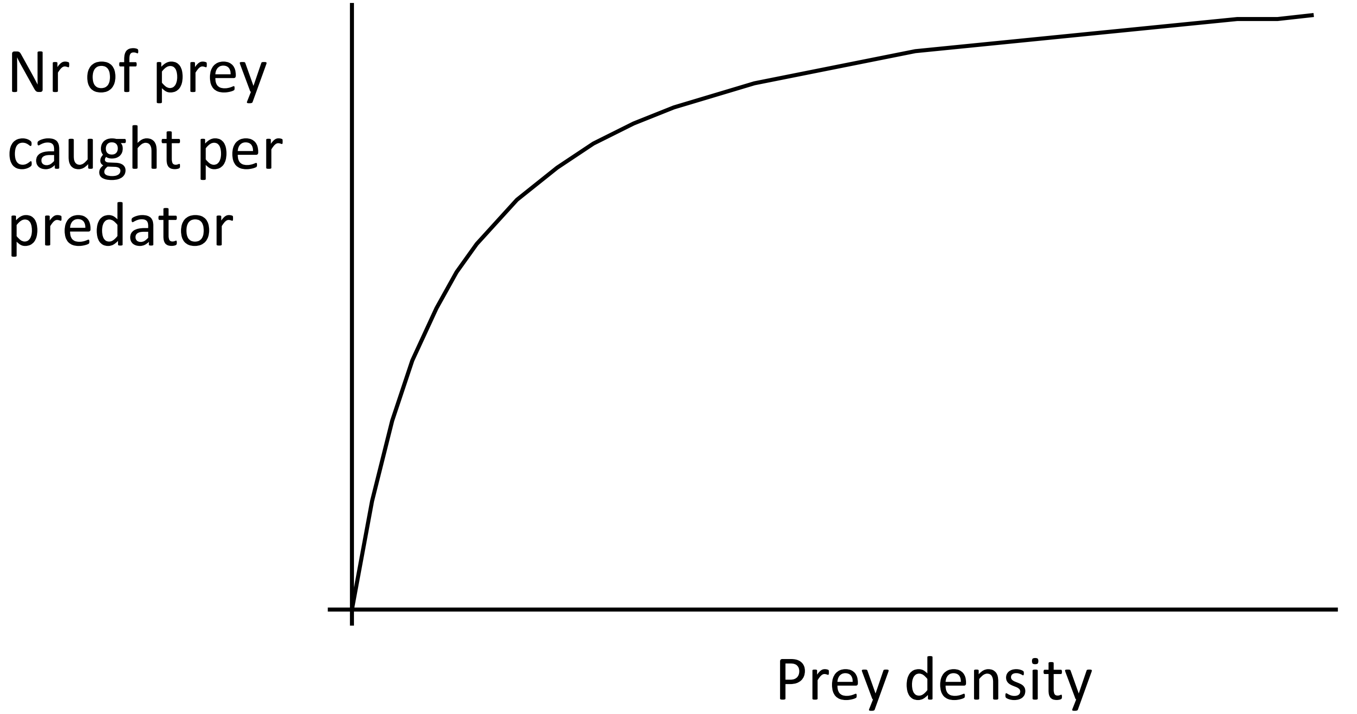
- The Holling (II) functional response assumes the predator on average has a constant time to handle prey
- The functional response then takes the form

$$\left(\frac{1}{\alpha V}+h\right)^{-1}=\frac{\alpha V}{1+\alpha V h}$$

- The handling time is $h$
- Note that if $h=0$ this reduces to $\alpha V$, which is what we had before

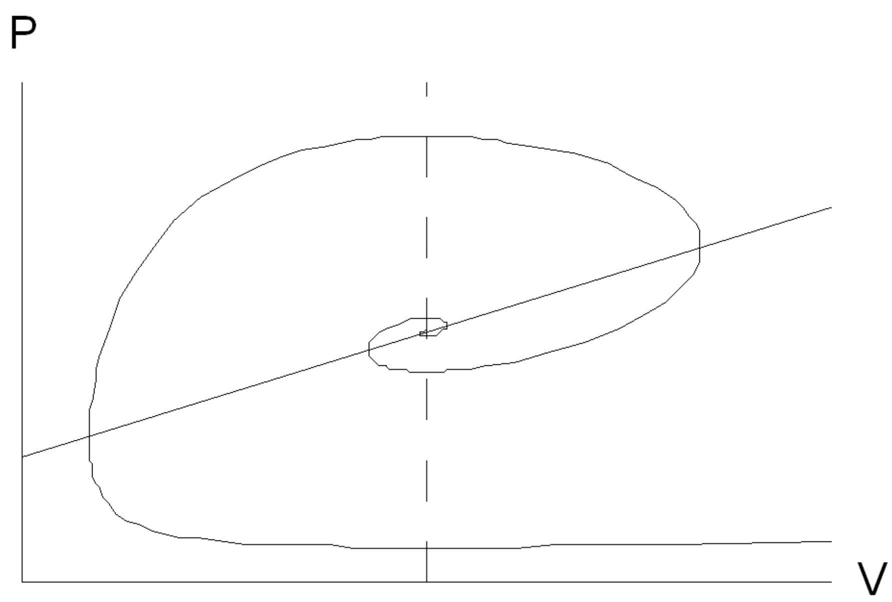
# Holling (II) functional response

The number of prey caught depends on the number of prey present



# Holling (II) functional response

If we include this in the model, solutions look like this




A limit on the number of prey eaten per unit of time acts destabilising

# The Rosenzweig-McArthur model

- The model with a prey carrying capacity and the type II functional response is known as the Rosenzweig-McArthur model:

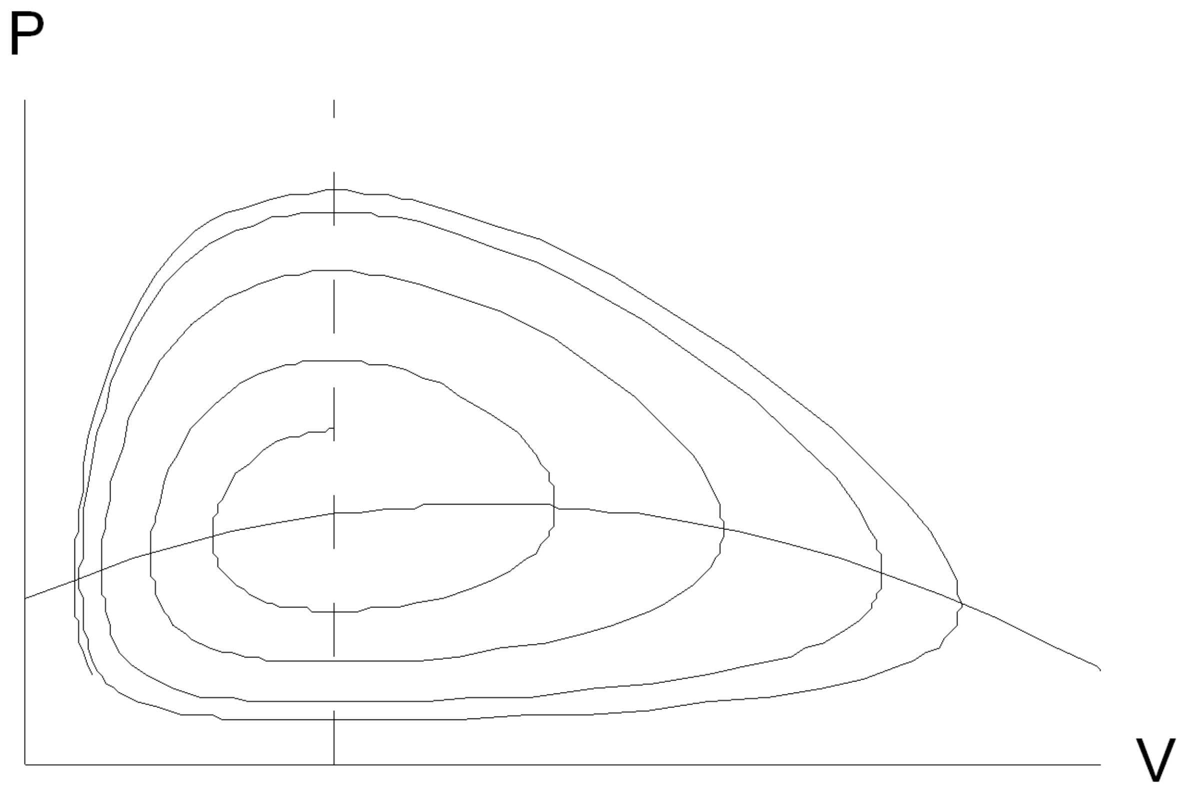
$$\frac{dV}{dt} = V(r(k-V) - \frac{\alpha P}{1+\alpha hV})$$

$$\frac{dP}{dt} = P(\frac{\beta V}{1+\alpha hV} - q)$$

# Stable limit cycle

- If prey density dependence and a Holling type II functional response is combined it can lead to sustained oscillations
- These oscillations are independent of the initial conditions
- This is called a stable limit cycle

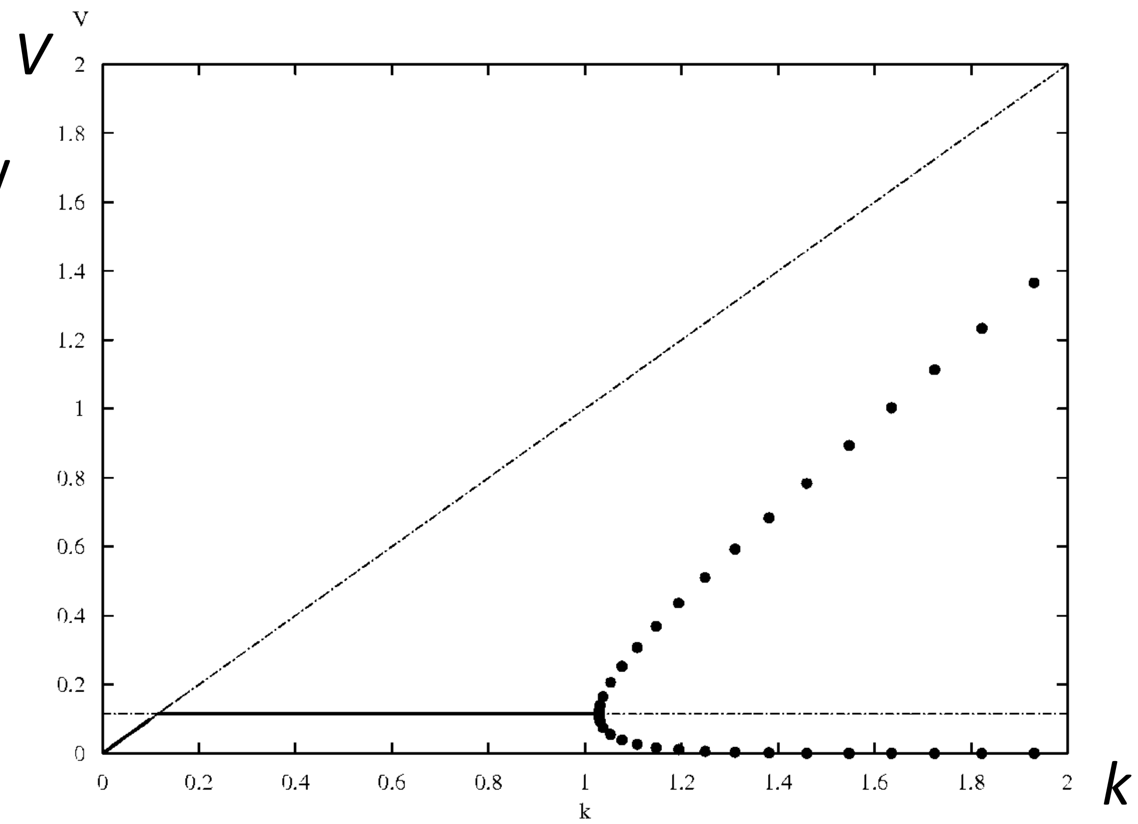
# Stable limit cycle



- Exercise here
- **Investigate the dynamics of the Rosenzweig-McArthur model.**

# The Hopf bifurcation

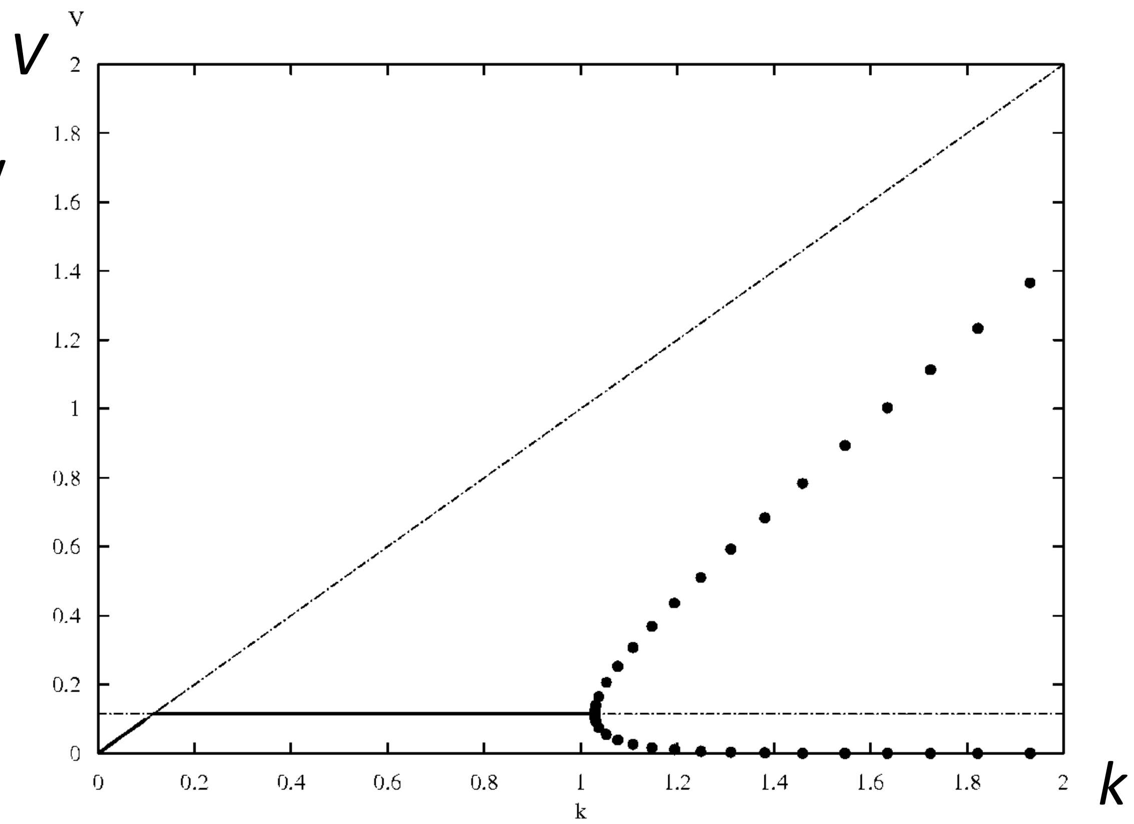
Prey density




In a Hopf bifurcation, the real part of a pair of complex eigenvalues becomes positive. It results in a limit cycle.

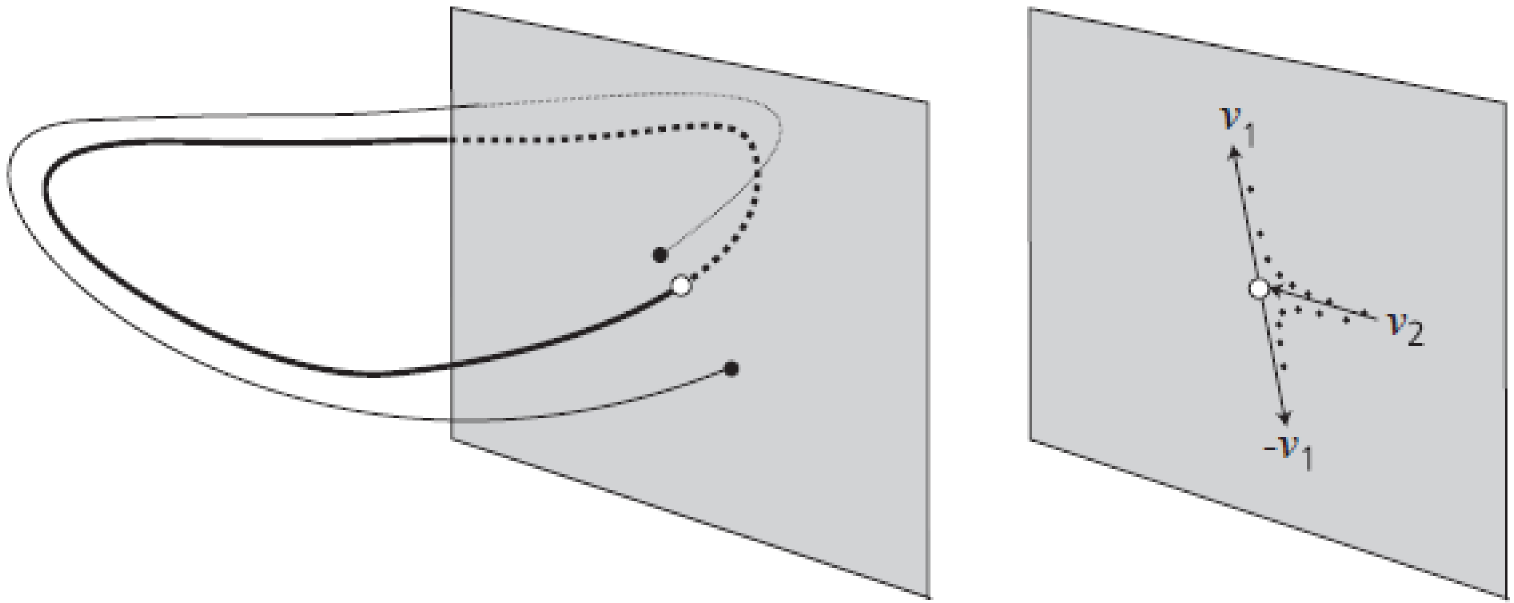
# The paradox of enrichment

Prey density




The paradox of enrichment: the better the environment for the prey, the worse they do.

# How do they do that?




The Poincaré map is the next intersection of an orbit with a cross section to the periodic solution, the Poincaré section (left). The periodic orbit is a fixed point of the Poincaré map; it is unstable if nearby orbits move away from it (right). $v_1$ and $v_2$ are respectively the unstable and stable eigenvectors of the linearized Poincaré map $B(T)$.

# Predators and their prey

- Some predator and prey population show this cyclic behaviour

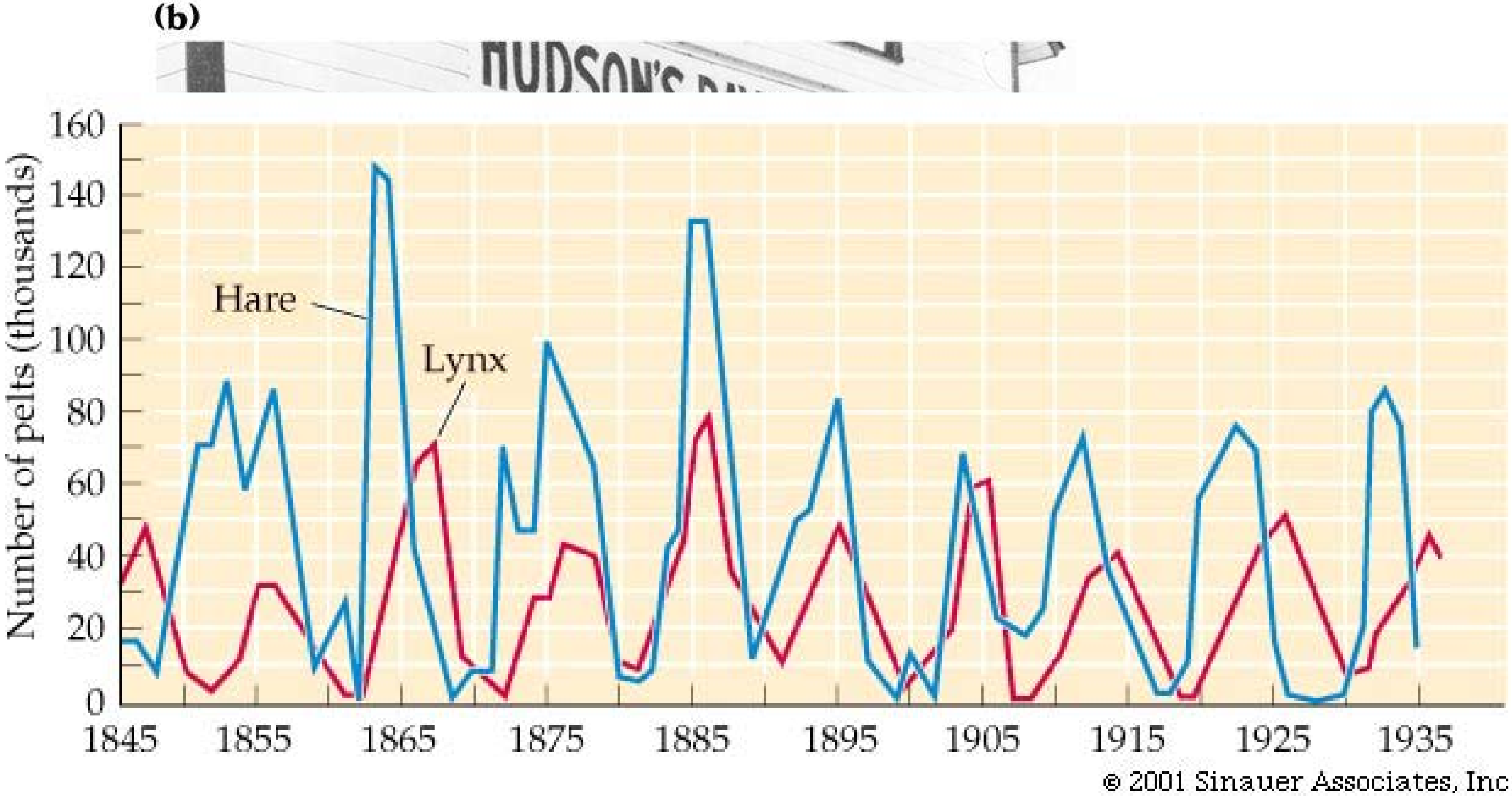
Lynx and

Snowshoe hare

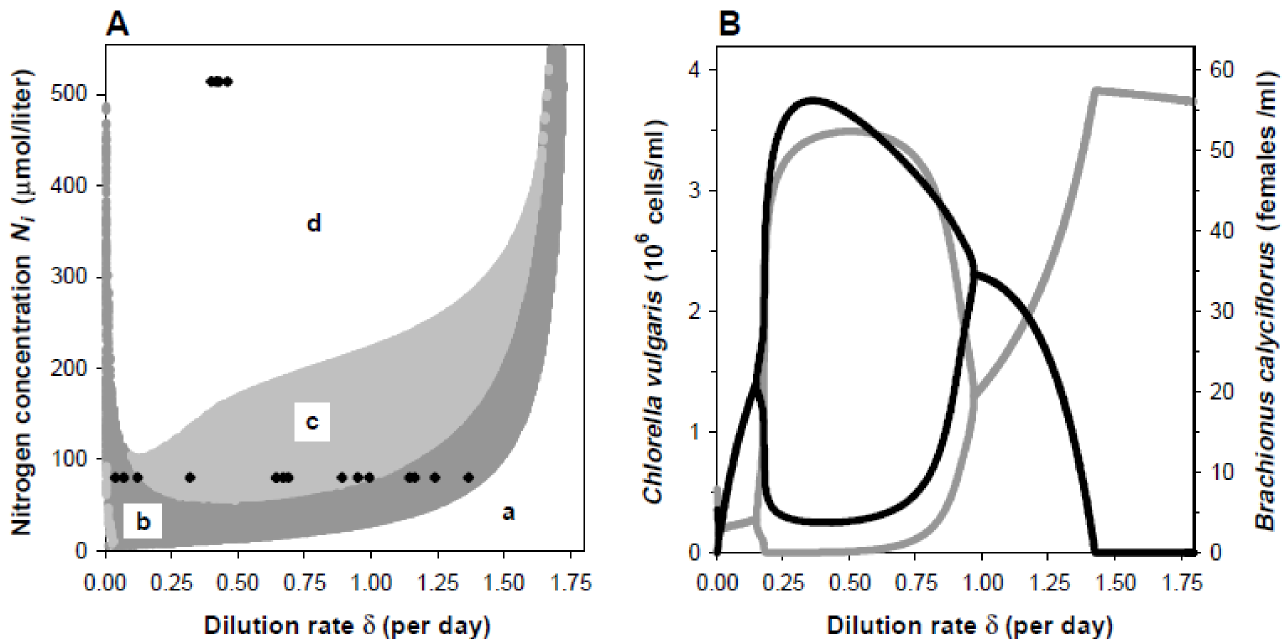

The Hudson's Bay Company traded in pelts, and kept immaculate records

# Predators and their prey

- Nr of hare and lynx pelts traded through the Hudson's Bay Company

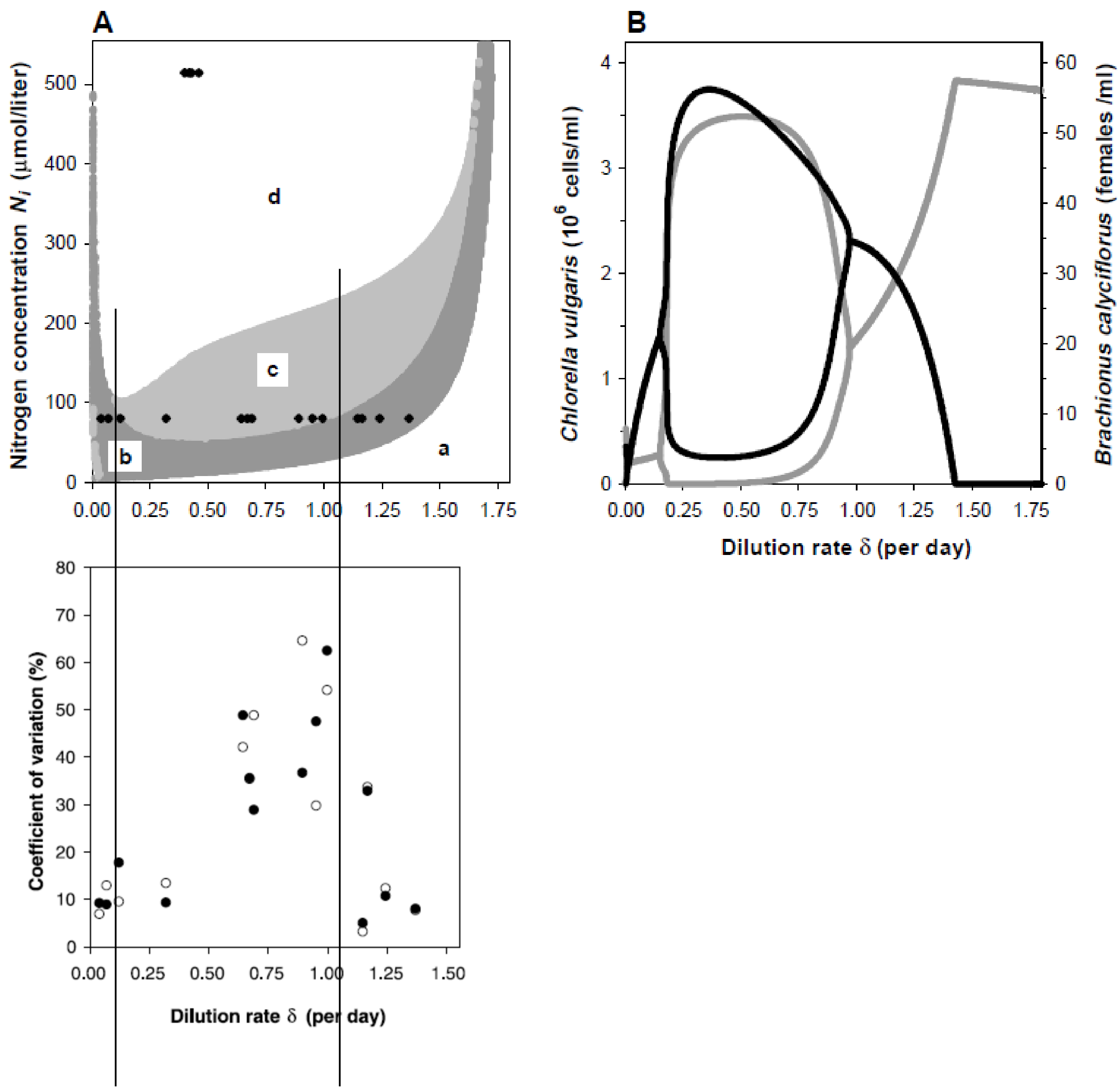


# Experimental demonstration




Mathematical model predicting the dynamics of a rotifer feeding on algae.

Fussman et al. Science (2000).



A
Nitrogen concentration $N_i$ (µmol/liter)
0
100
200
300
400
500
0.00
0.25
0.50
0.75
1.00
1.25
1.50
1.75
a
b
c
d
B
Chlorella vulgaris ($10^6$ cells/ml)
Brachionus calyciflorus (females /ml)
0
1
2
3
4
10
20
30
40
50
60
Dilution rate δ (per day)
Coefficient of variation (%)
70
80
Dilution rate δ (per day)

t,

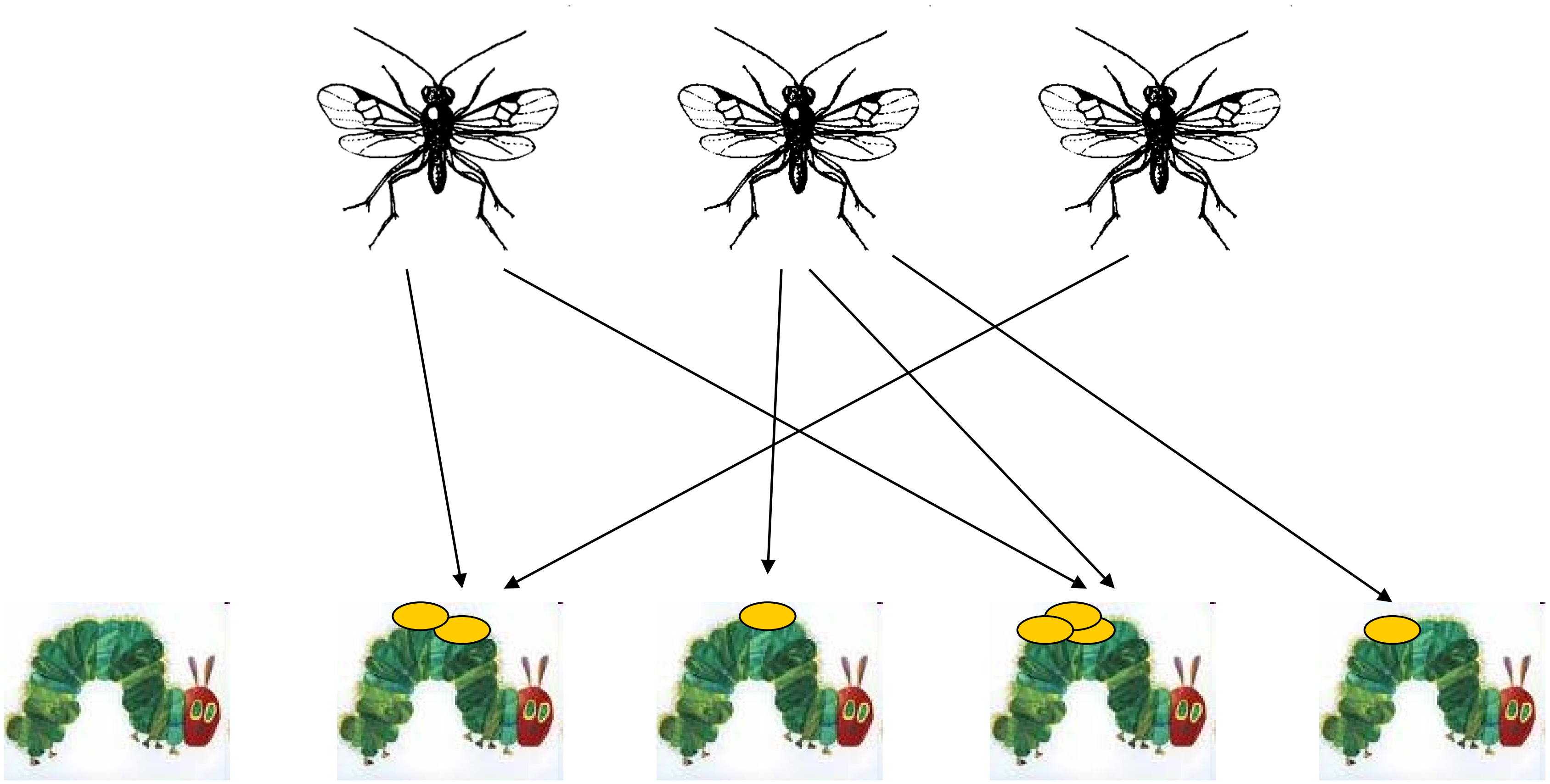
g

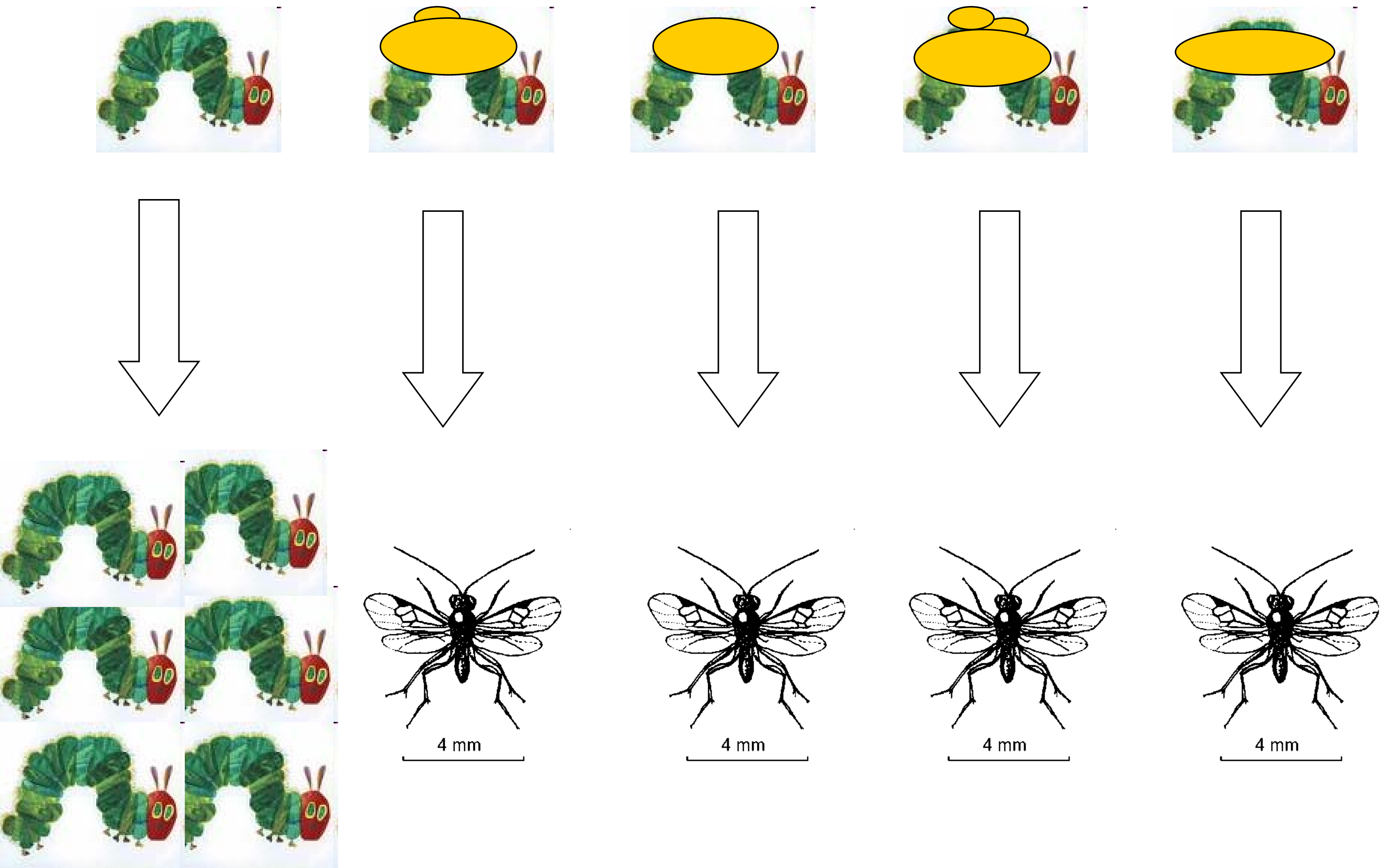
# Parasitism

- Nicholson and Bailey (1935) developed a simple model for host-parasitoid interactions
- Hosts are discovered by parasitoids. The more parasitoids there are, the larger the probability to be discovered.

# Parasitism

- All hosts that are parasitised give rise to one new parasitoid
- Nr of new parasitoids: nr of hosts times probability of being parasitised
- All hosts that are not parasitised lay $\lambda$ eggs and give rise to $\lambda$ new hosts

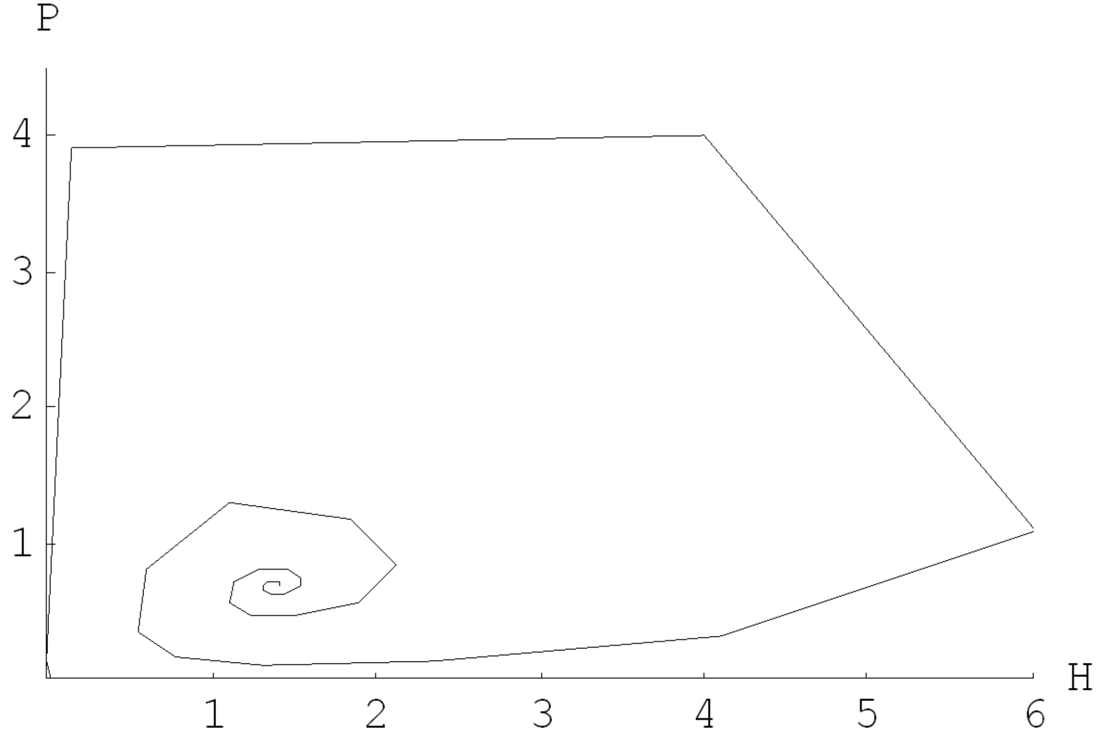



4 mm
4 mm
4 mm
4 mm

# Parasitism

- The Nicholson Bailey model reads:

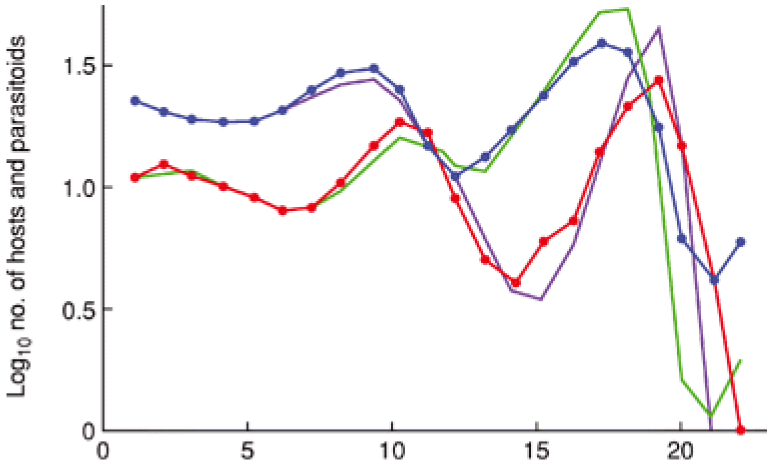
$$P_{t+1}=H_t(1-e^{-aPt})$$



# Parasitism

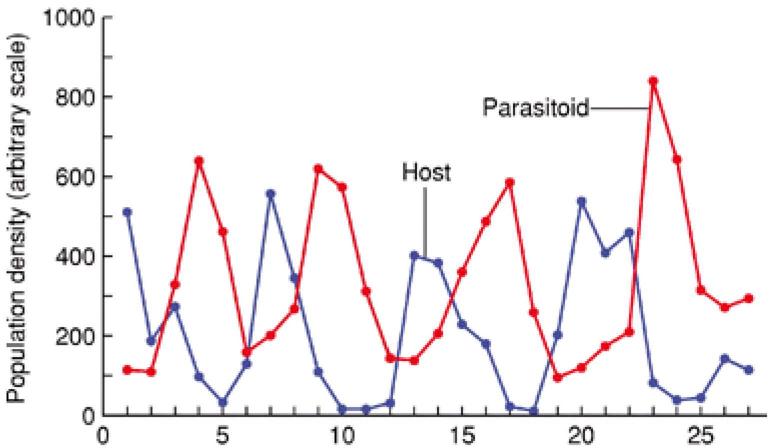
- Delays destabilise the host-parasitoid (and predator-prey) interaction
- The model can be adapted to produce cyclic dynamics

# Parasitism



(a)

The population dynamics of a parasitoid and host population kept in a lab, compared to the Nicholson-Bailey model



(b)

Stable oscillations of parasitoid and host

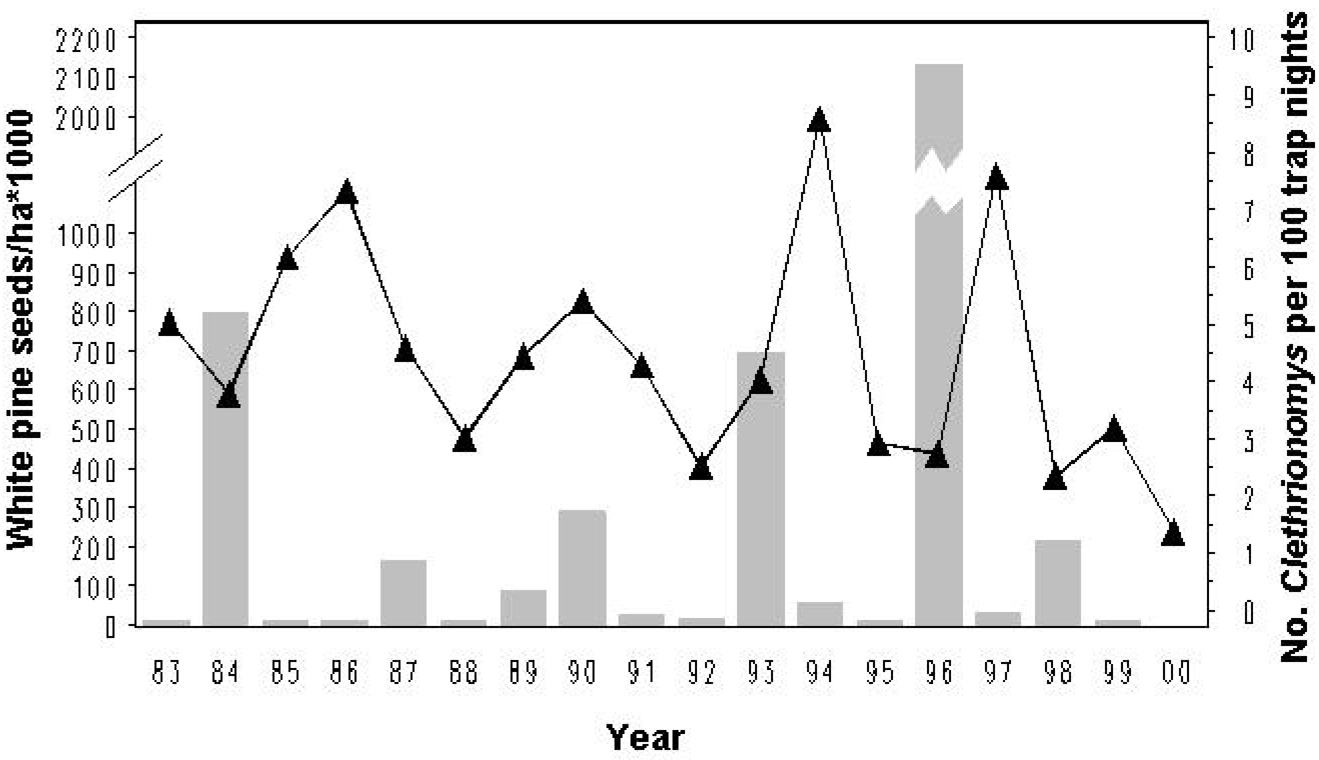
# Spatial interactions

- Most predator-prey models are prone to produce cyclic dynamics with large oscillations that suggest that these populations are likely suffer to extinction

# Spatial interactions

- A number of natural predator-prey systems that show sustained oscillations have been found
- Some examples: the hare-lynx cycle, grouse cycles, the cyclic dynamics of rodents in Scandinavia, moose-wolves on Isle Royal, several insect populations, etc.

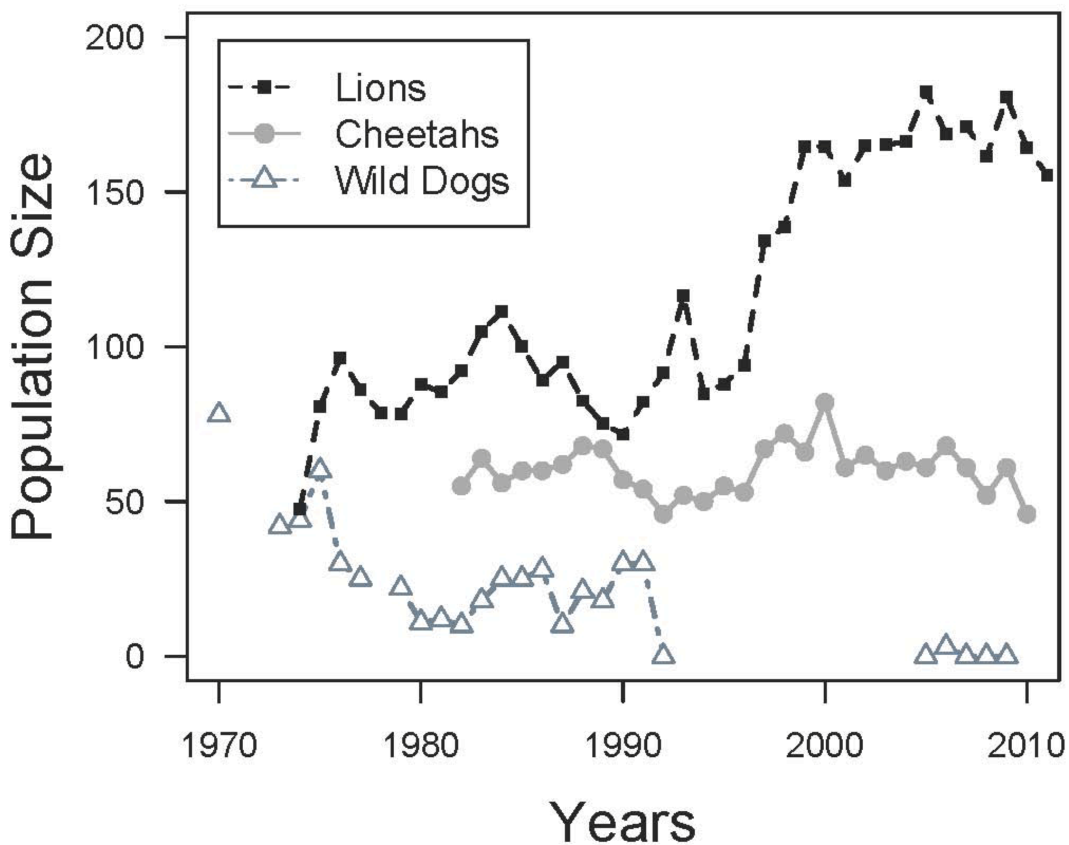
# Red backed voles in Holt forest



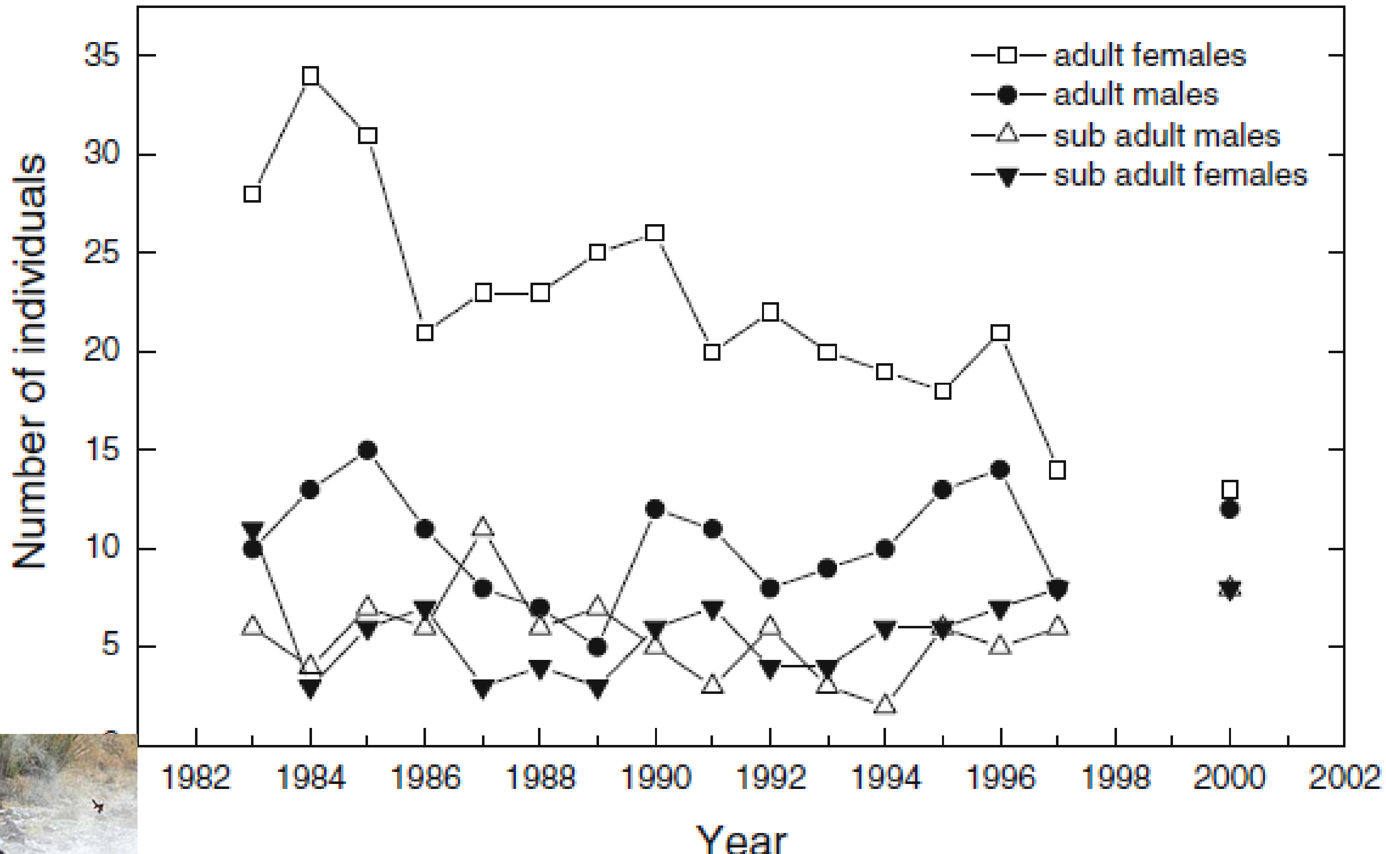

# Predators and their prey

- Most predator and prey populations do **not** show such fluctuations in the wild

# Predators in the Serengeti




# Lions in Etosha (SA)




Trinkel, Naturwissenschaften 2013

# Predators and their prey

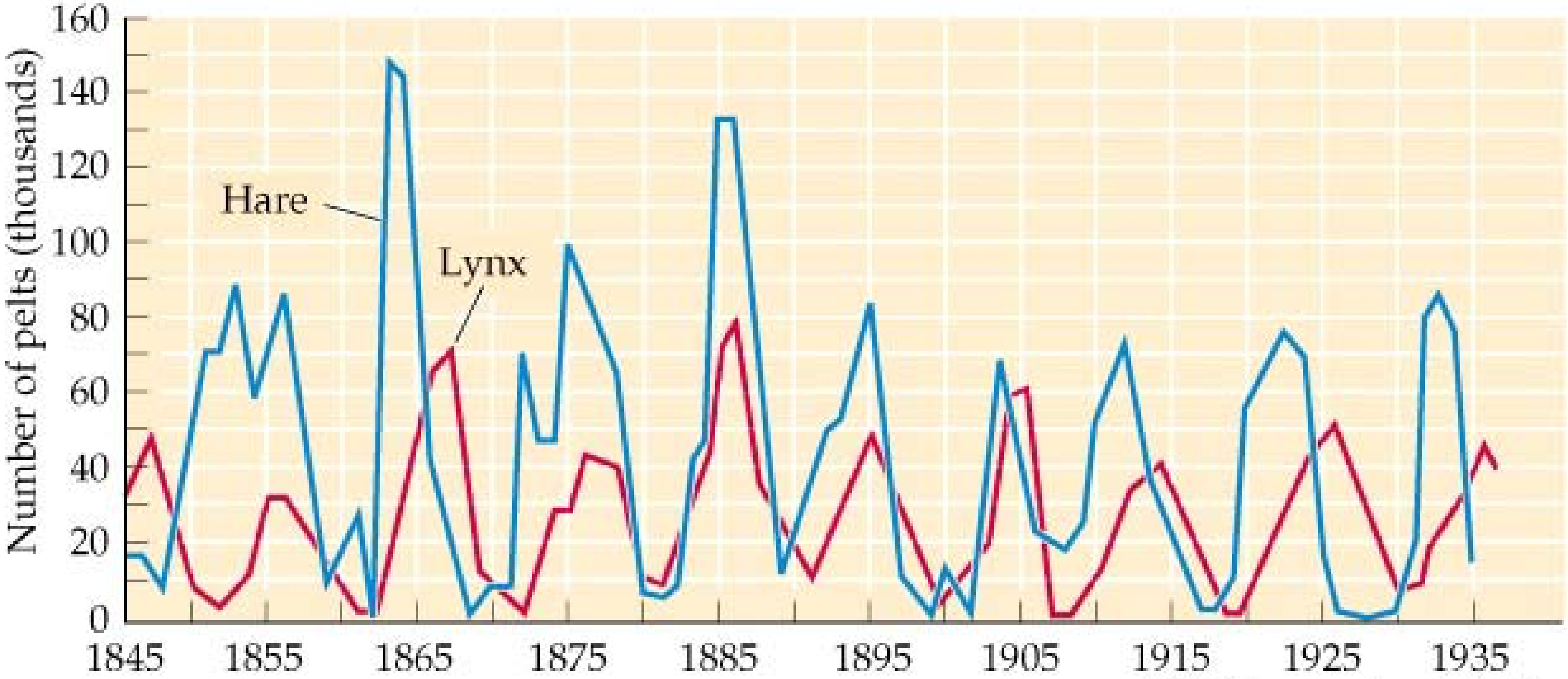
- Most predator and prey populations do **not** show such fluctuations in the wild
- In the lab populations many populations do show strong fluctuations and are difficult to keep alive

# Spatial interactions

- Why the discrepancy?
- Nicholson and Bailey (1934) conjectured, after observing that populations do not persist in their model that populations can locally go extinct, but that other ones will start elsewhere
- Can spatial interactions lead to persistence?

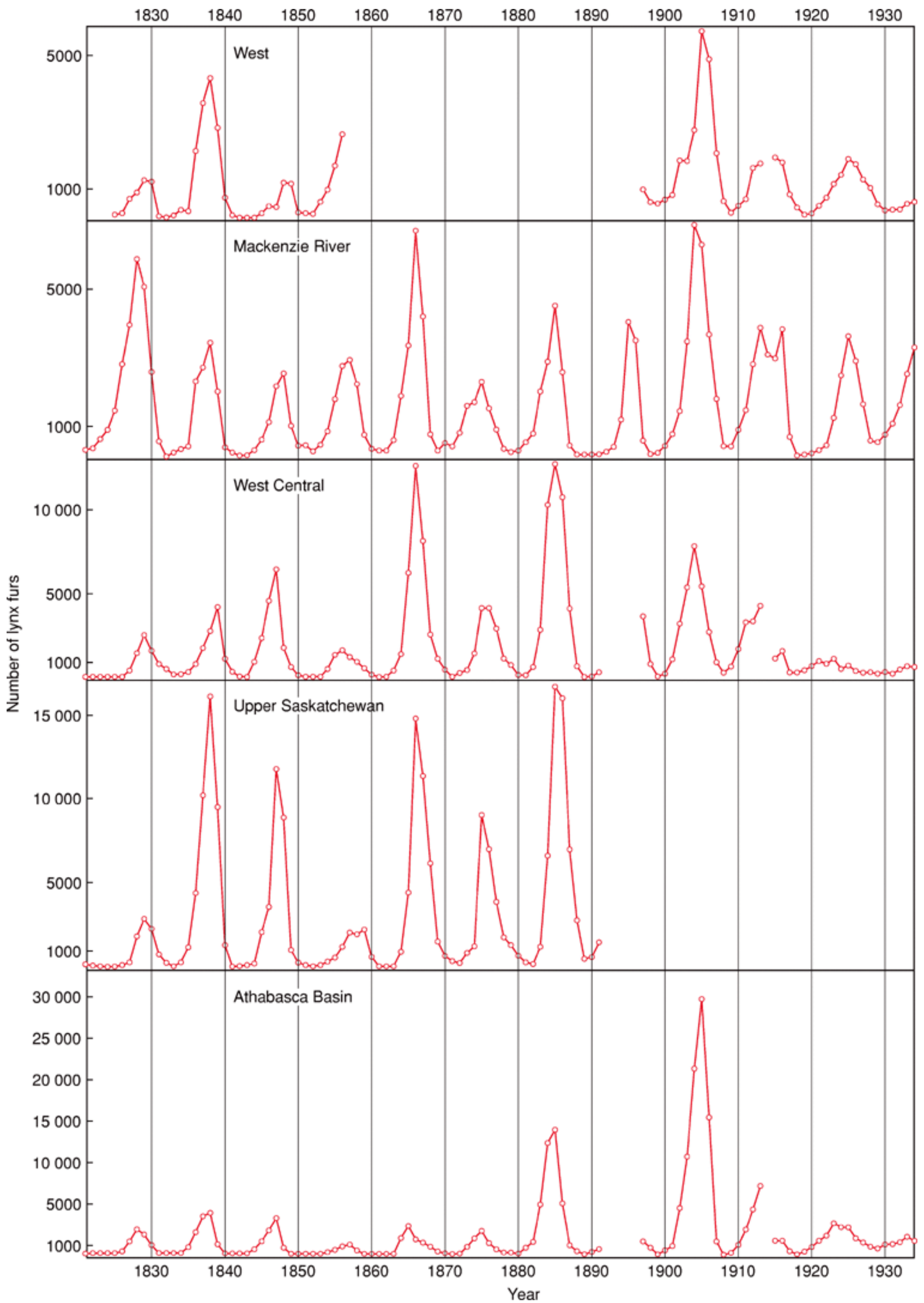
# Stable limit cycle

- *A closer look at the hare-lynx cycle*



# Spatial interactions

Cycles in the number of lynx fur returns of the Hudson's Bay Company, from 1821 to 1934, grouped into five regions. Note the different scales




From: M. Gillman: Population Dynamics: Introduction. DOI: 10.1038/npg.els.0003164. Original source: Elton and M. Nicholson, 1942

# Spatial interactions

- Huffaker's mites

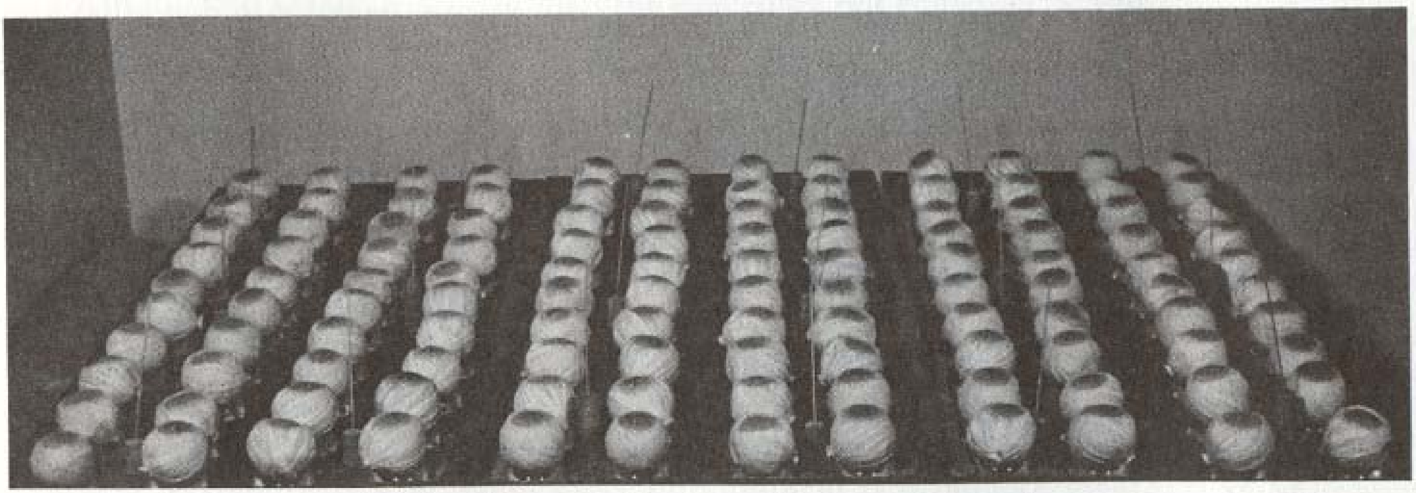
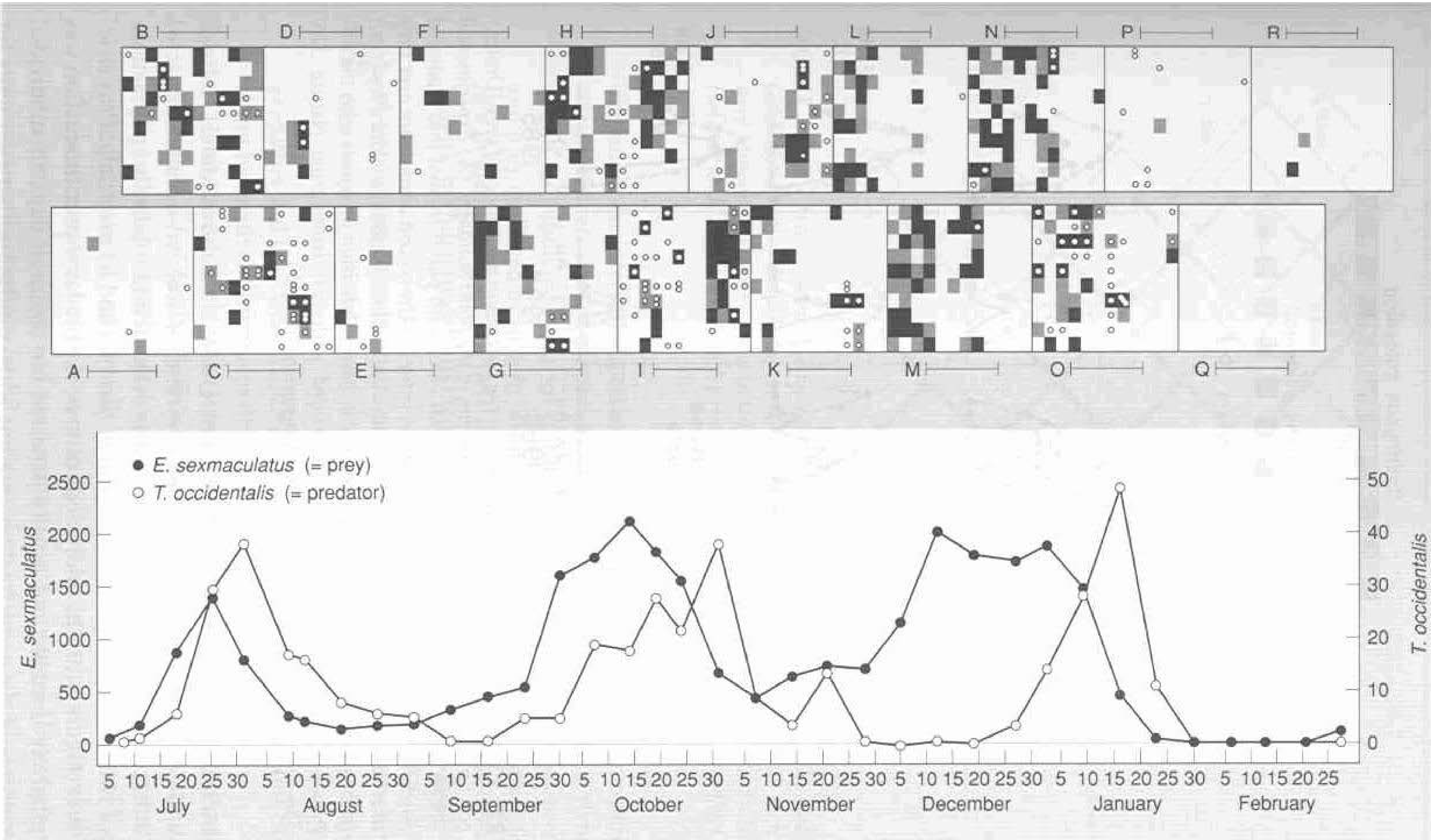


**FIGURE 5–18.** Universe of 120 oranges used in studies of predator–prey interaction (prey: *Eotetranychus sexmaculatus;* predator: *Typhlodromus occidentalis*). Each orange has $\frac{1}{20}$ of its area exposed. Partial barriers of Vaseline form a complex maze of impediments between the oranges. Wooden dowels allow prey to disperse by climbing on a dowel, dropping on a silken strand, and being carried by an air current into a different area. (From Huffaker, 1958. Photograph by F. E. Skinner.)

# Spatial interactions

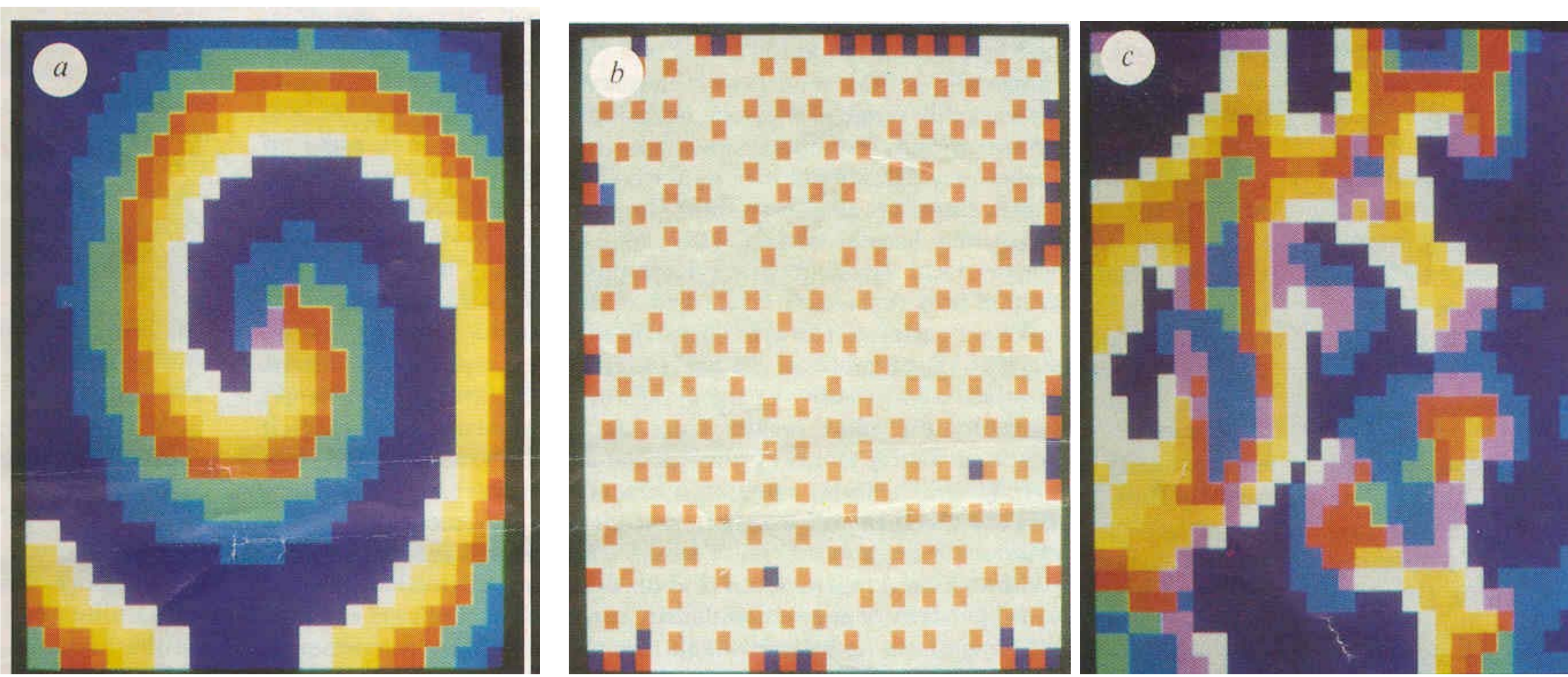


# Spatial interactions

- Hassell, Comins and May (1991) made a model in which they assumed that the local interactions were given by the Nicholson-Bailey model, but hosts and parasitoids could disperse to neighbouring sites

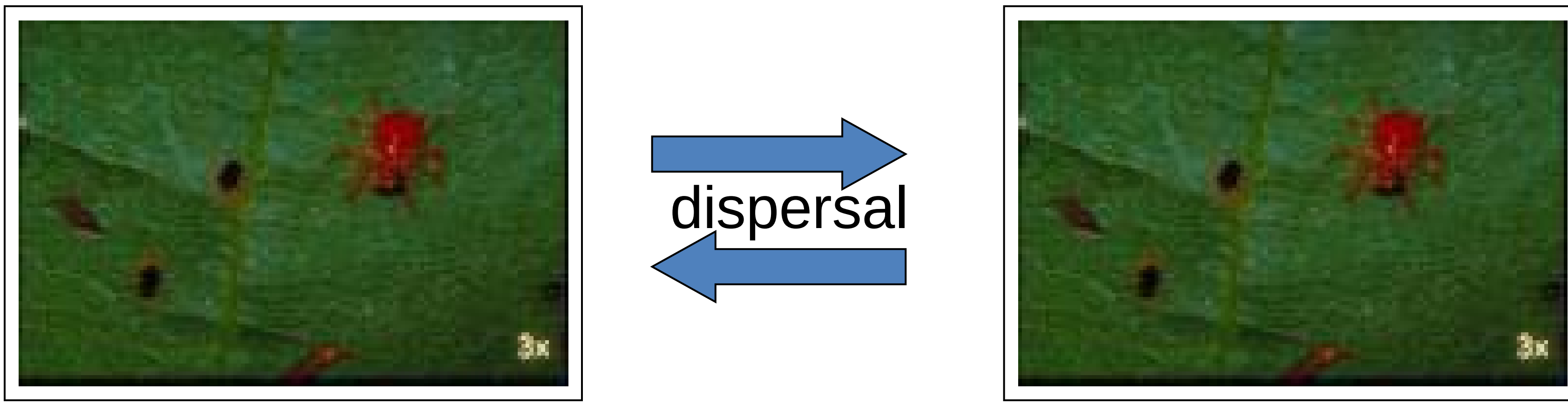
# Spatial interactions

- Hassell, Comins and May’s simulation results. Different colours represent different densities



# Spatial interactions

- A similar pattern can occur in coupled predator-prey models




Space 1 Space 2

- The model equations are very much like two coupled pendulums

# Spatial interactions

- A similar pattern can occur in coupled predator-prey models

$$\frac{dV_2}{dt} = V_2(r(k - V_2) - \frac{\alpha V_2 P_2}{1 + \alpha h V_2})$$
$$\frac{dP_2}{dt} = P_2(\frac{\beta V_2}{1 + \alpha h V_2} - q) + d(P_1 - P_2)$$

dispersal

$P_1$

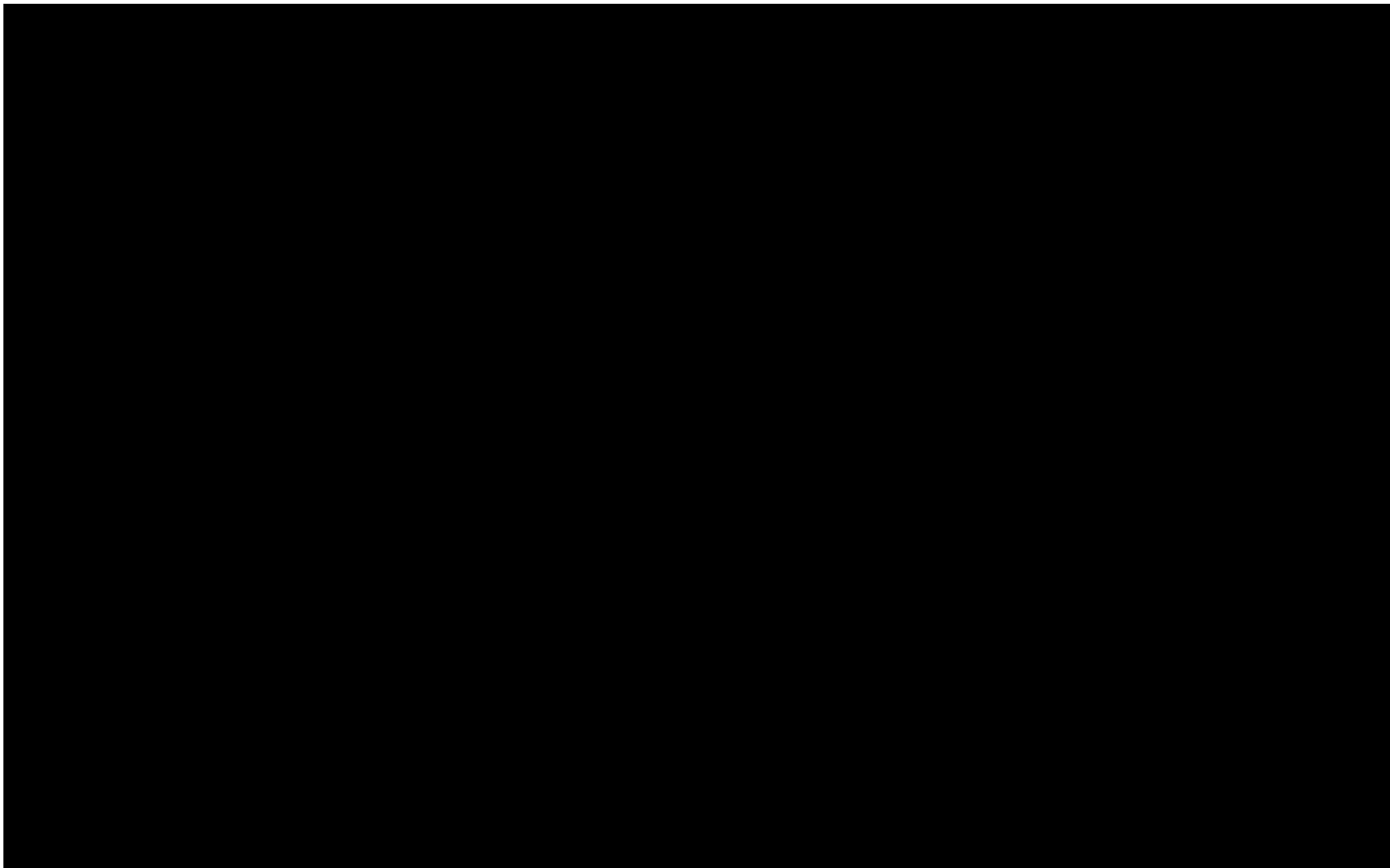
$$\frac{dV_1}{dt} = V_1(r(k - V_1) - \frac{\alpha V_1 P_1}{1 + \alpha h V_1})$$
$$\frac{dP_1}{dt} = P_1(\frac{\beta V_1}{1 + \alpha h V_1} - q) + d(P_2 - P_1)$$

Space 1

Space 2

- The model equations are very much like two coupled pendulums

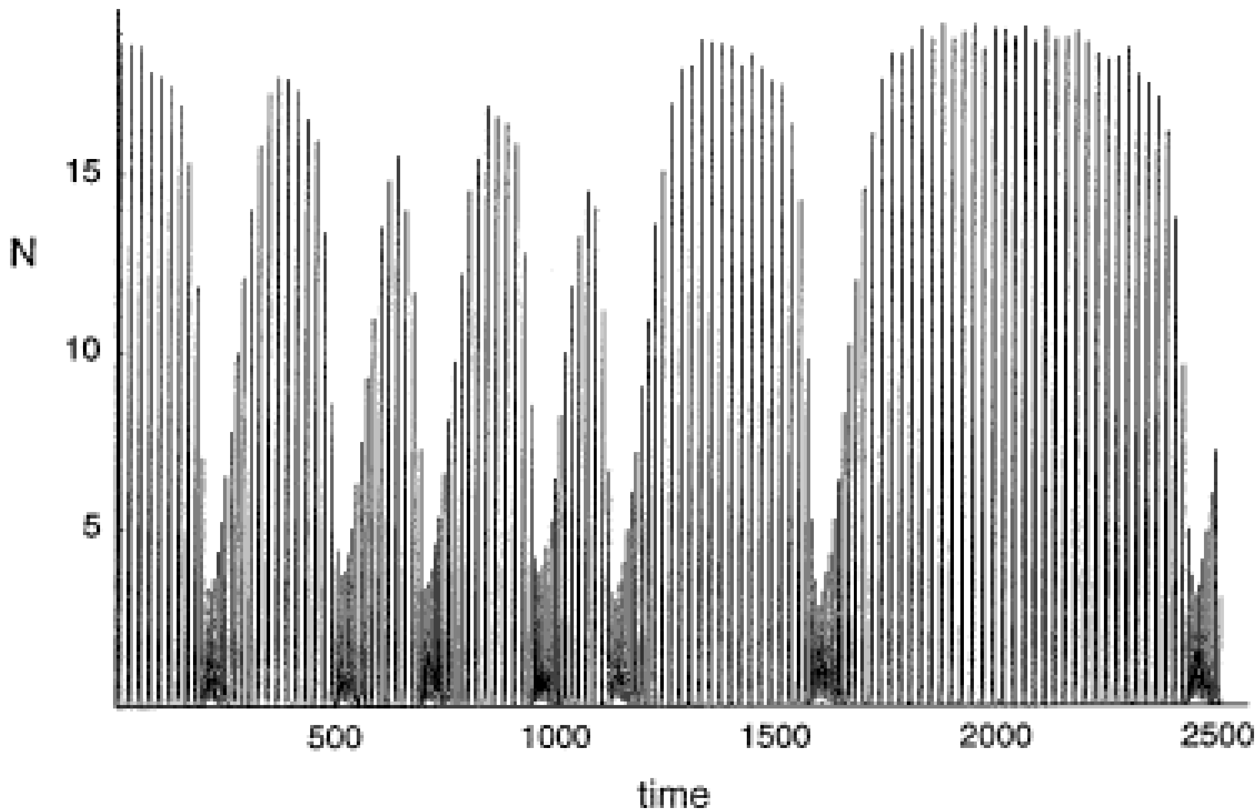
# Video 2 coupled pendulums here



# Exercise

**The effect of space on the dynamics of a predator-prey model.**

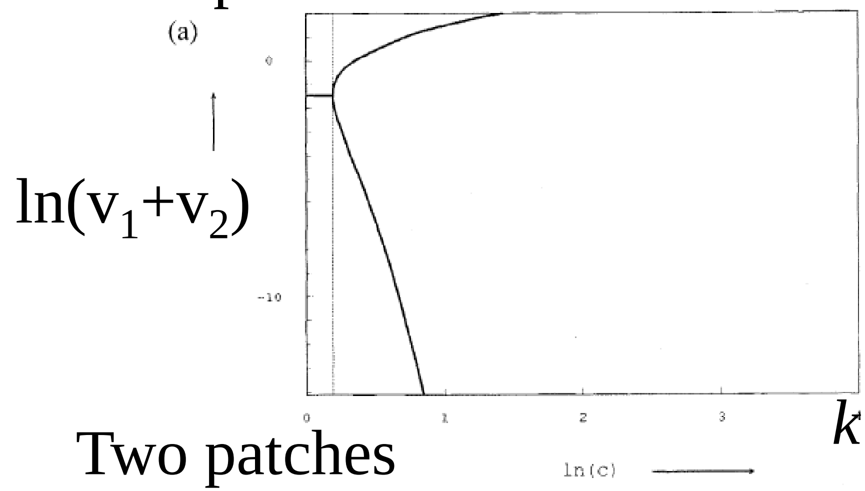
# Spatial interactions



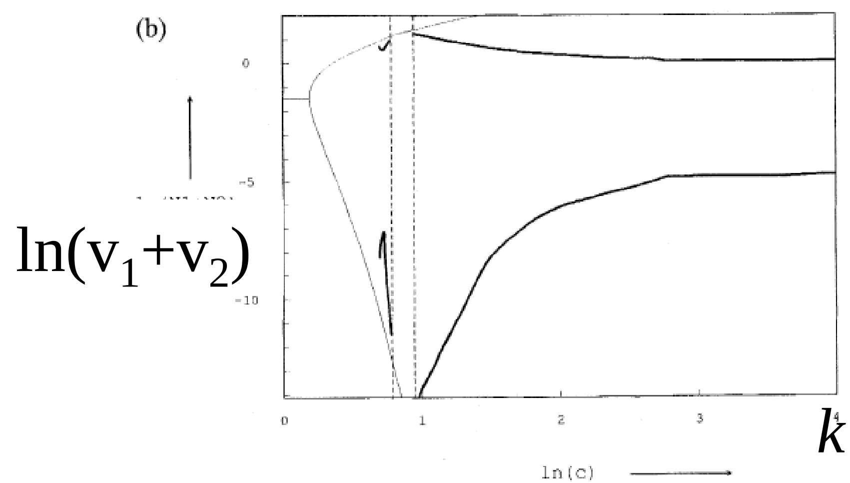
# Spatial interactions

- This offers a solution to the paradox of enrichment

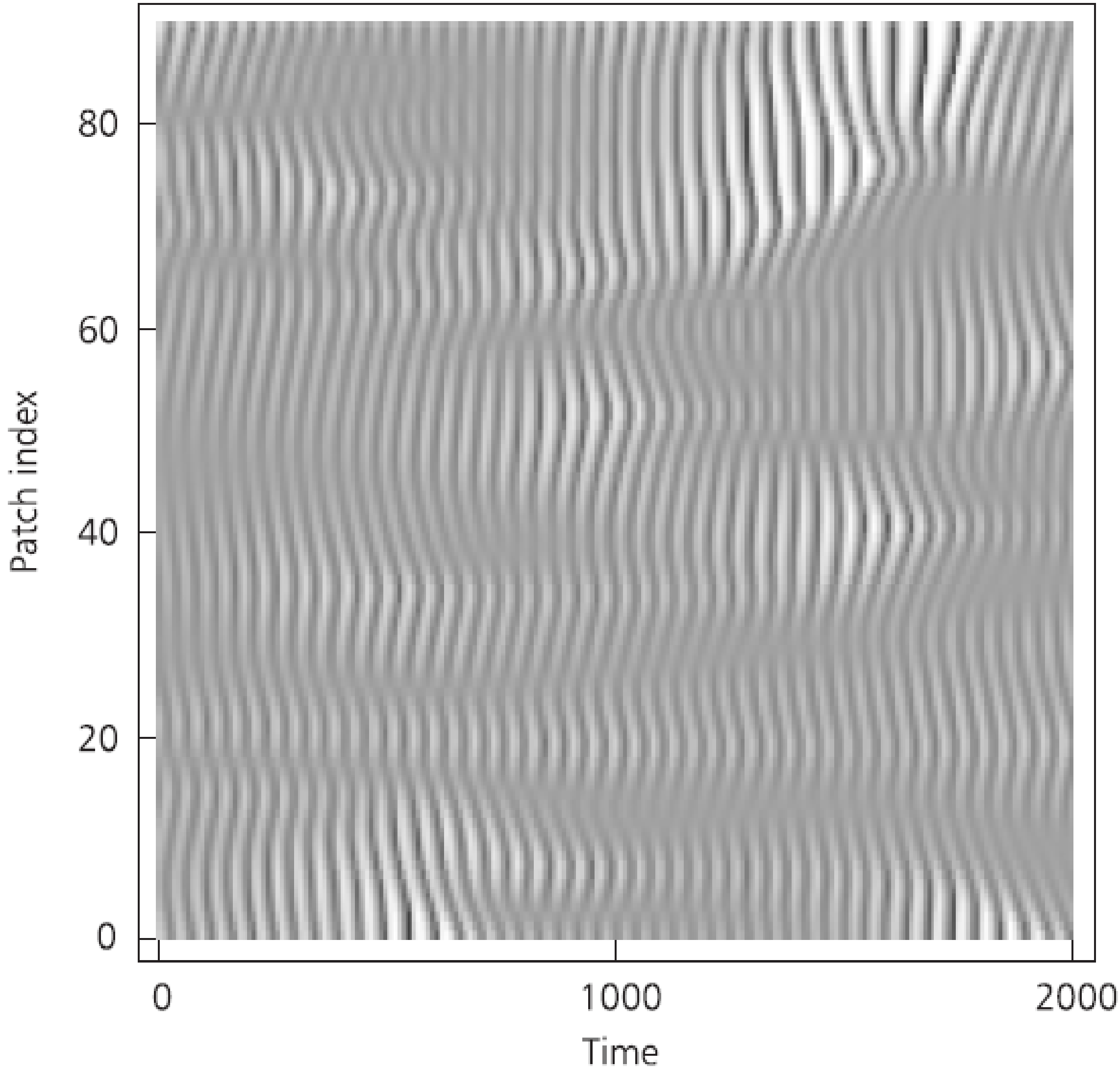
One patch




Two patches

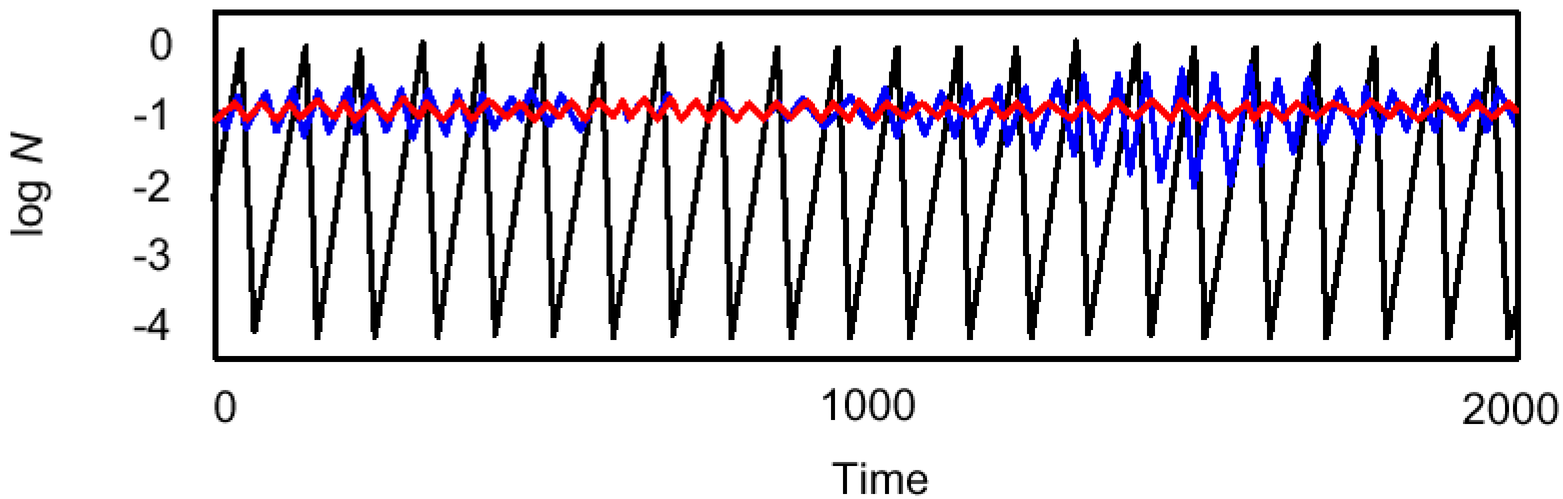


# With many patches:



# Predators and prey in space

- The isolated, coupled and mean dynamics:



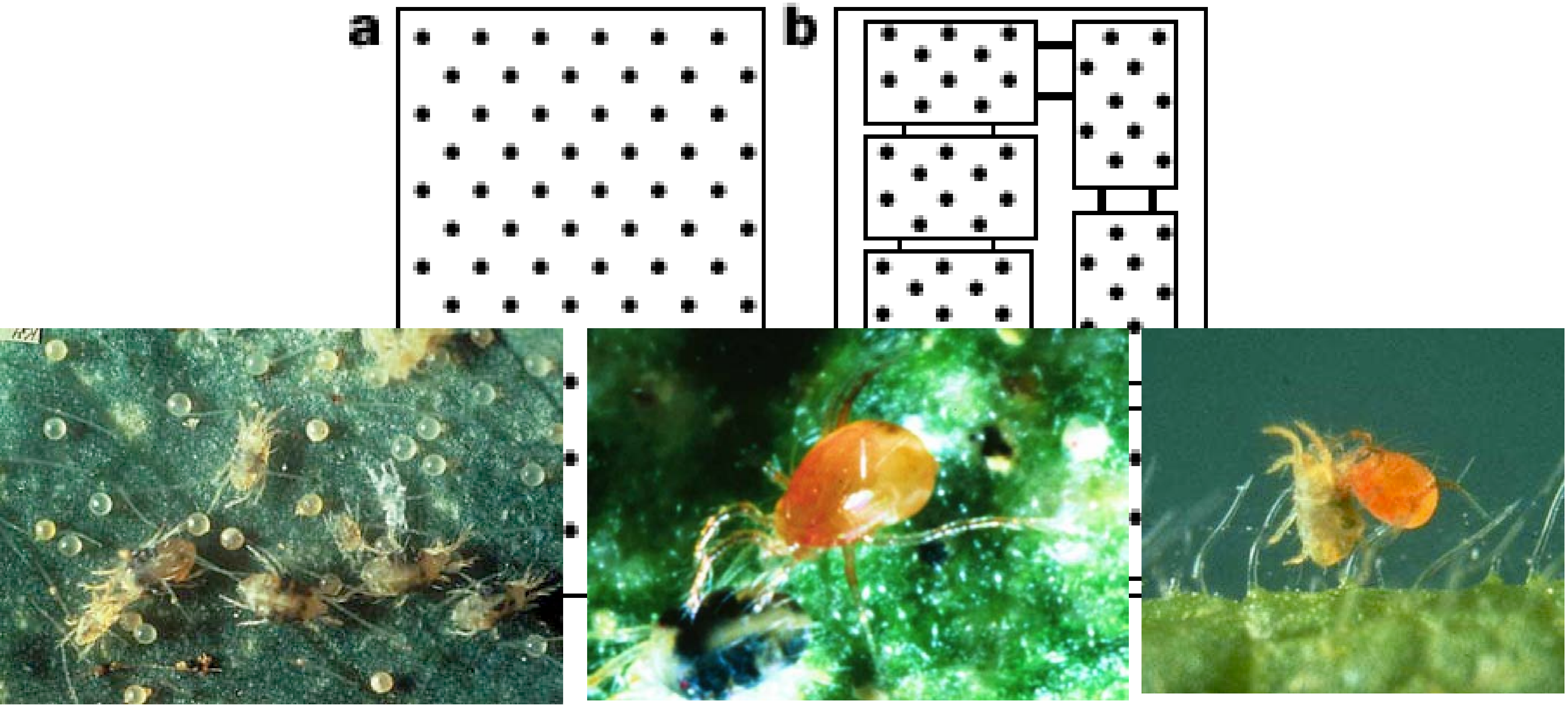

In a spatial system predator and prey populations do not oscillate as much and are less likely to become extinct

# Spatial interactions

- This suggests that spatial interactions can make the host parasitoid (predator-prey) system to persist
- But does it really work?

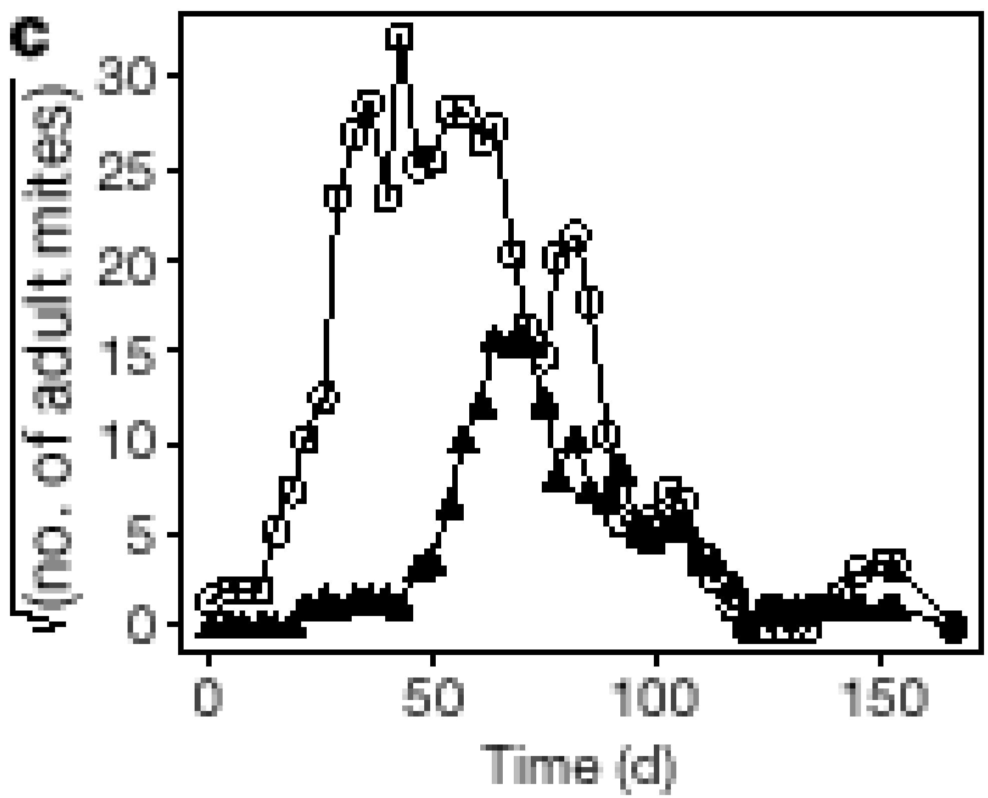
# Spatial interactions

- Description of Janssen's experiment



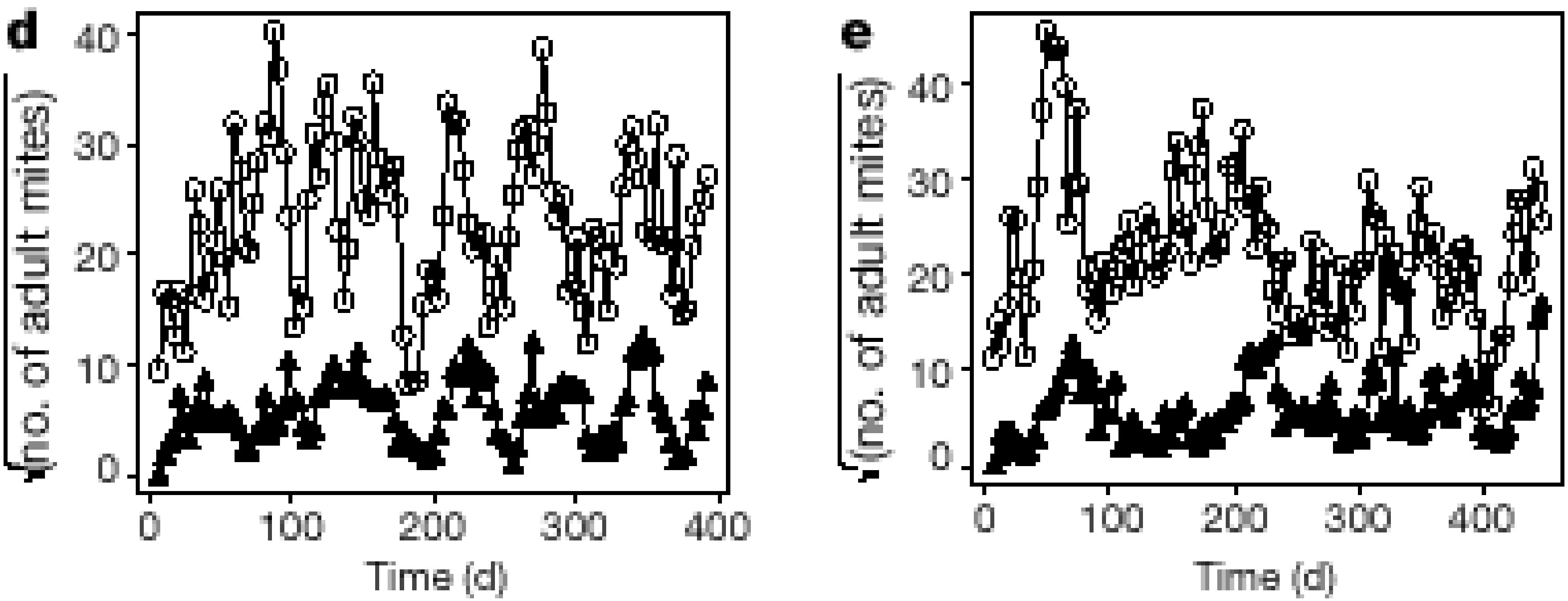
# Spatial interactions

- Result in the single island system



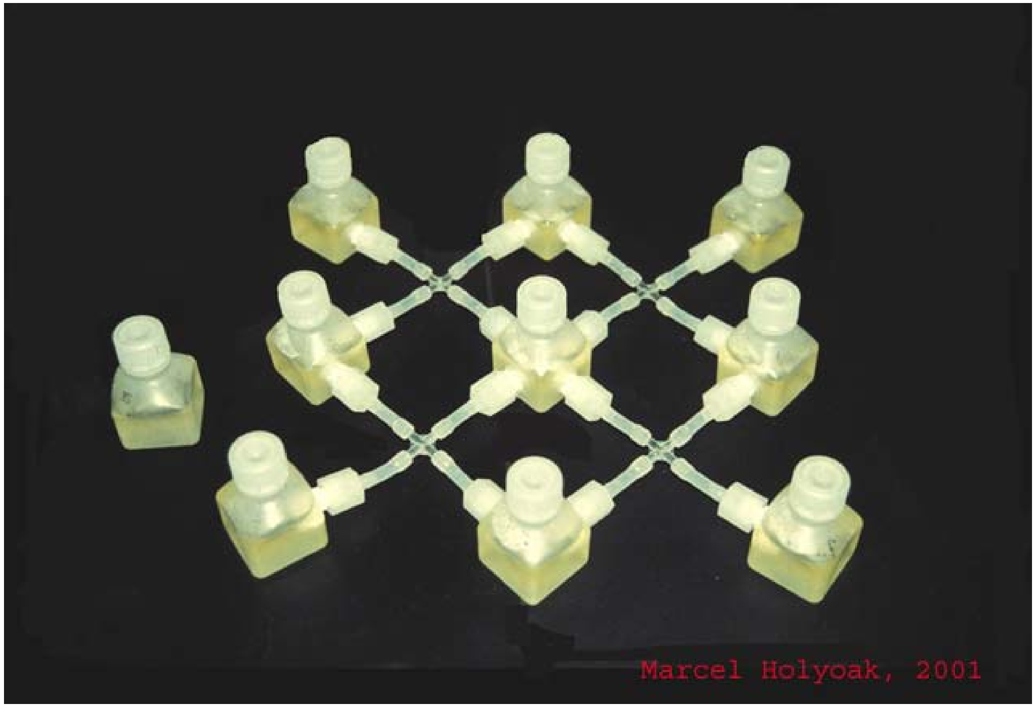
# Spatial interactions

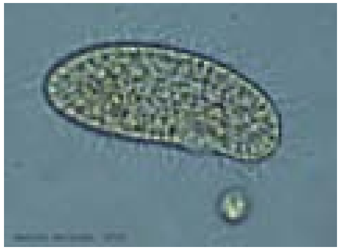
- Result in the coupled islands system



# Spatial interactions

- Another example:



Prey: *Colpidium striatum*

Predator: *Didinium nastutum*

- In the array predator and prey populations persist for much longer than in a single jar (Holyoak and Lawler)

# Learning outcomes

- Understand the logic underlying the Lotka-Volterra predator model and its limitations
- Appreciate the effects of prey density dependence, functional responses, time delays and spatial structure