

Predator-prey models, limit cycles, Hopf bifurcation

vincent.jansen@rhul.ac.uk

Outline

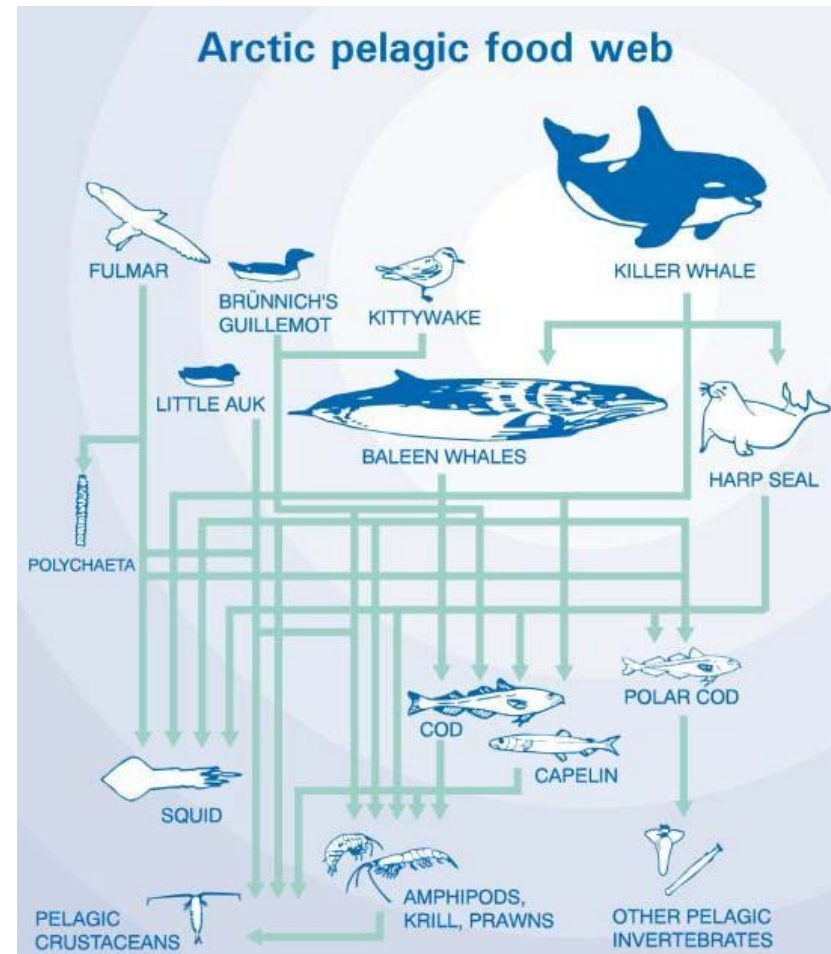
- Trophic interactions
- d'Ancona's observation & Volterra predator-prey model
- The Rosenzweig-MacArthur model
- Stable limit cycles, the paradox of enrichment
- Parasitism, the Nicholson Bailey model
- Spatial interactions

Trophic interactions

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

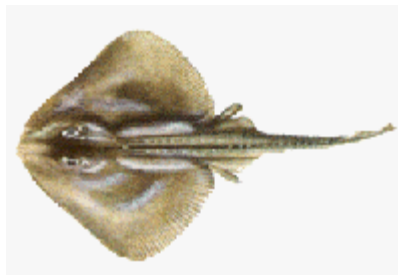
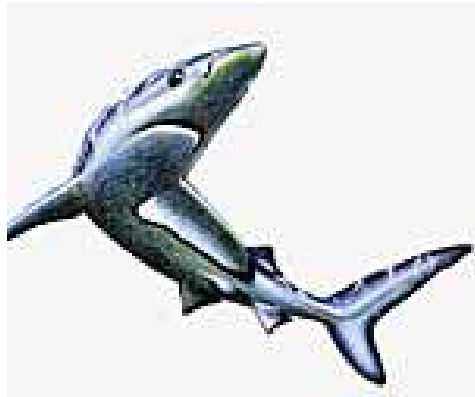
Trophic interactions

- 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

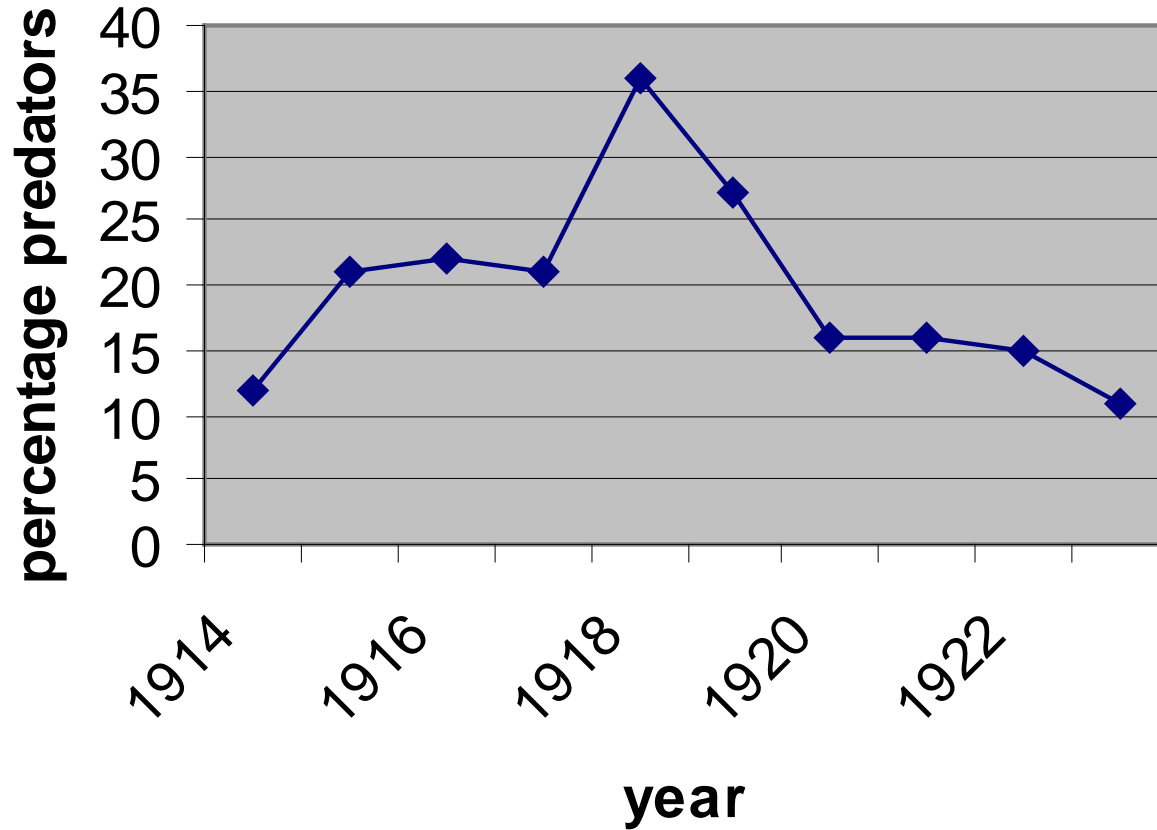


D'Ancona's observation

- 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



percentage of predatory fish in Fiume



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 fiancée'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
- α is the capture efficiency, assumed to be constant
- The functional response is αV
- The prey's growth rate is:

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

Lotka-Volterra predator-prey model

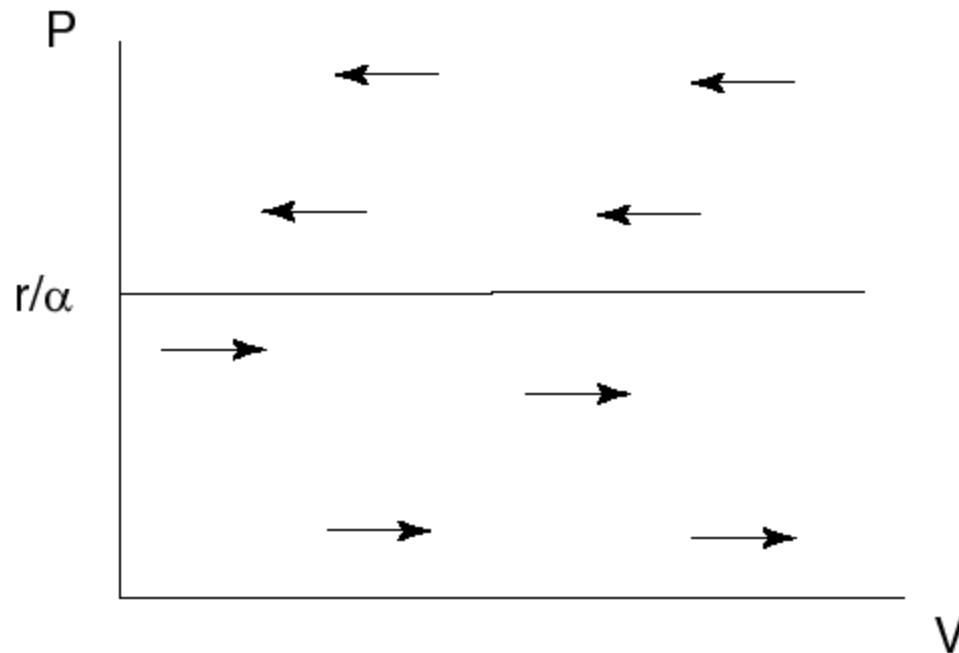
- The per capita prey growth rate is

$$(r - \alpha P)$$

- 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

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

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

Lotka-Volterra predator-prey model

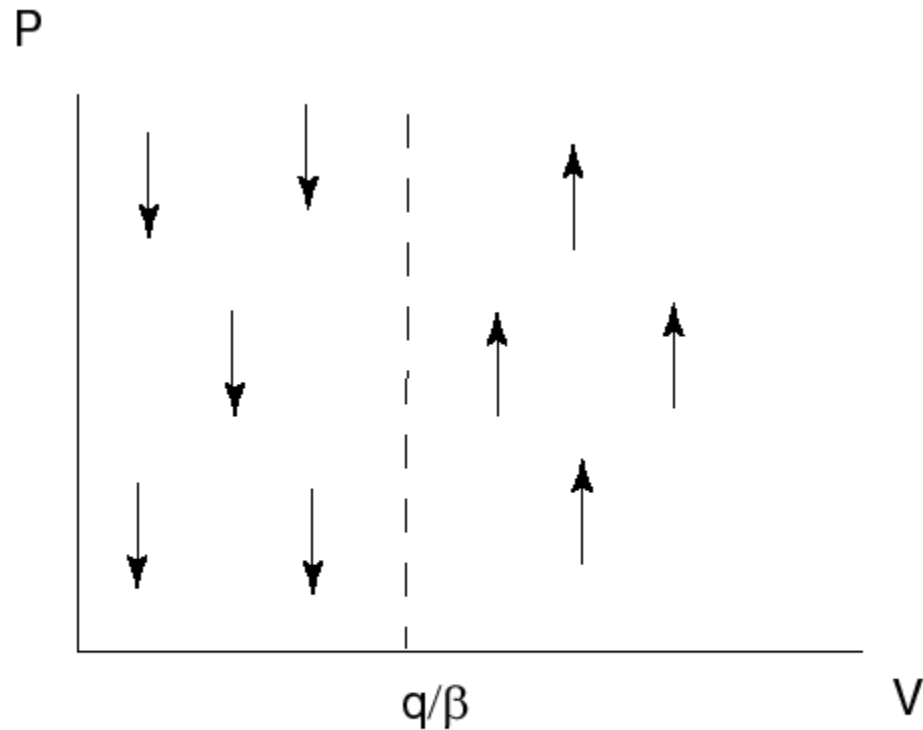
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Lotka-Volterra predator-prey model

- 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:

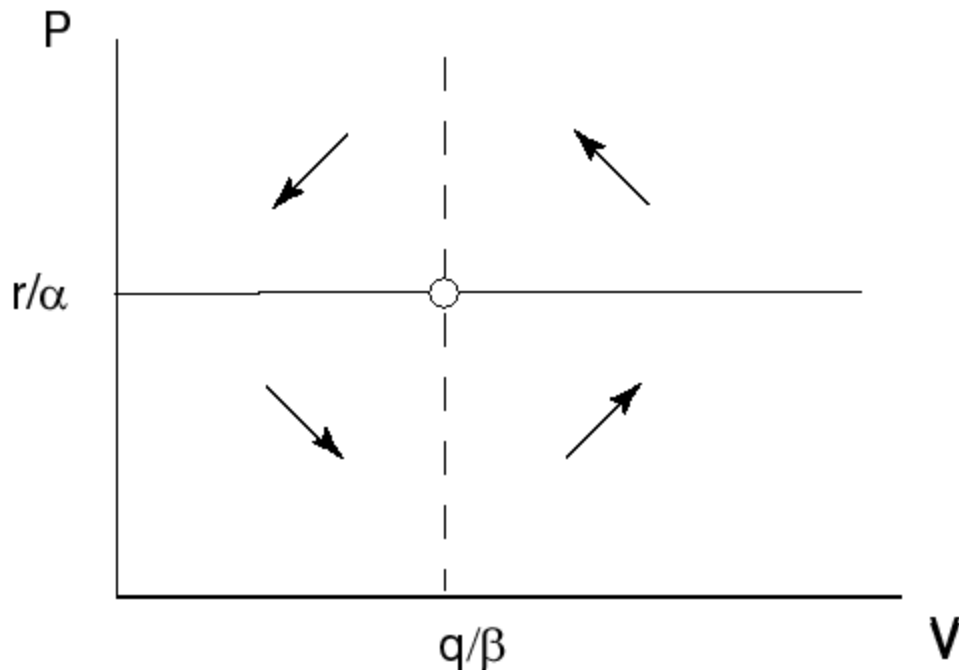
$$\frac{dV}{dt} = V(r - \alpha P)$$

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

- 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/β : only depends on the parameters relating to the *predator*.
- The predator equilibrium density is given by r/α 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:

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

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

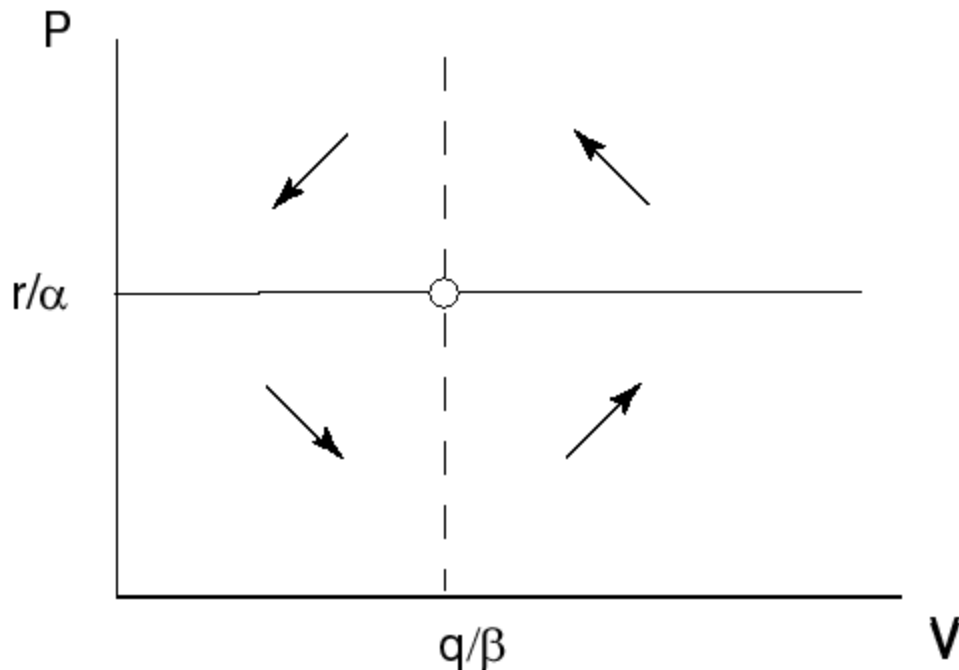
- The prey equilibrium is now $V^* = (q + f) / \beta$
- The predator equilibrium is now $P^* = (r - f) / \alpha$

Lotka-Volterra predator-prey model

- A reduced fishing effort (directed at prey and predatory fish) will have two effects: it increases the predator's equilibrium density and decreases 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

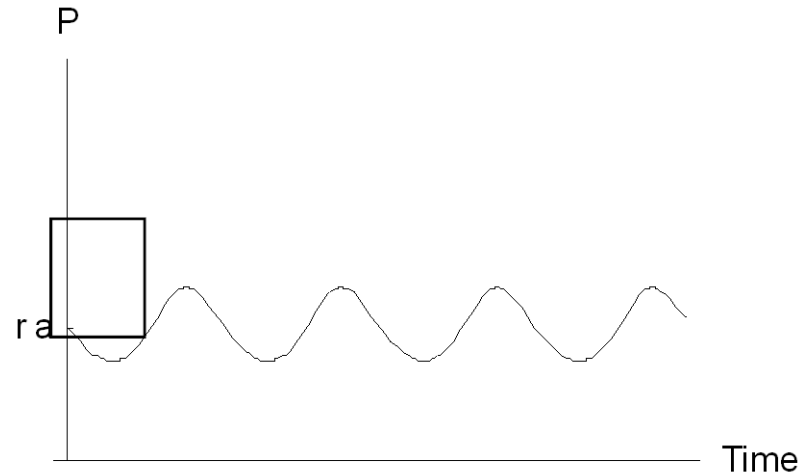
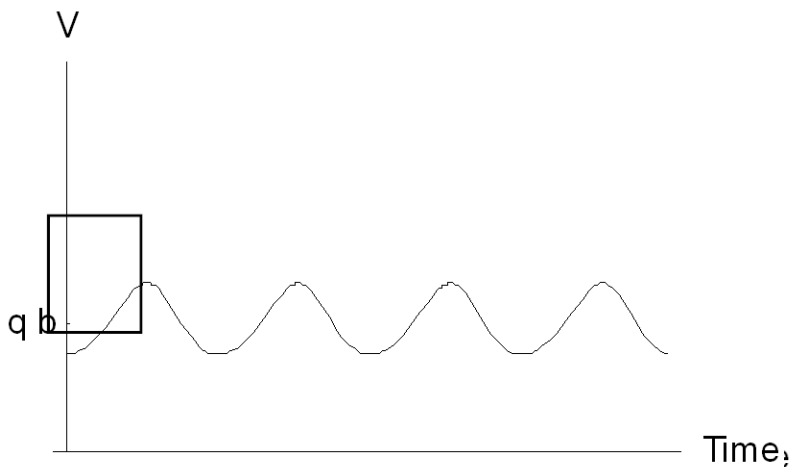


XPP

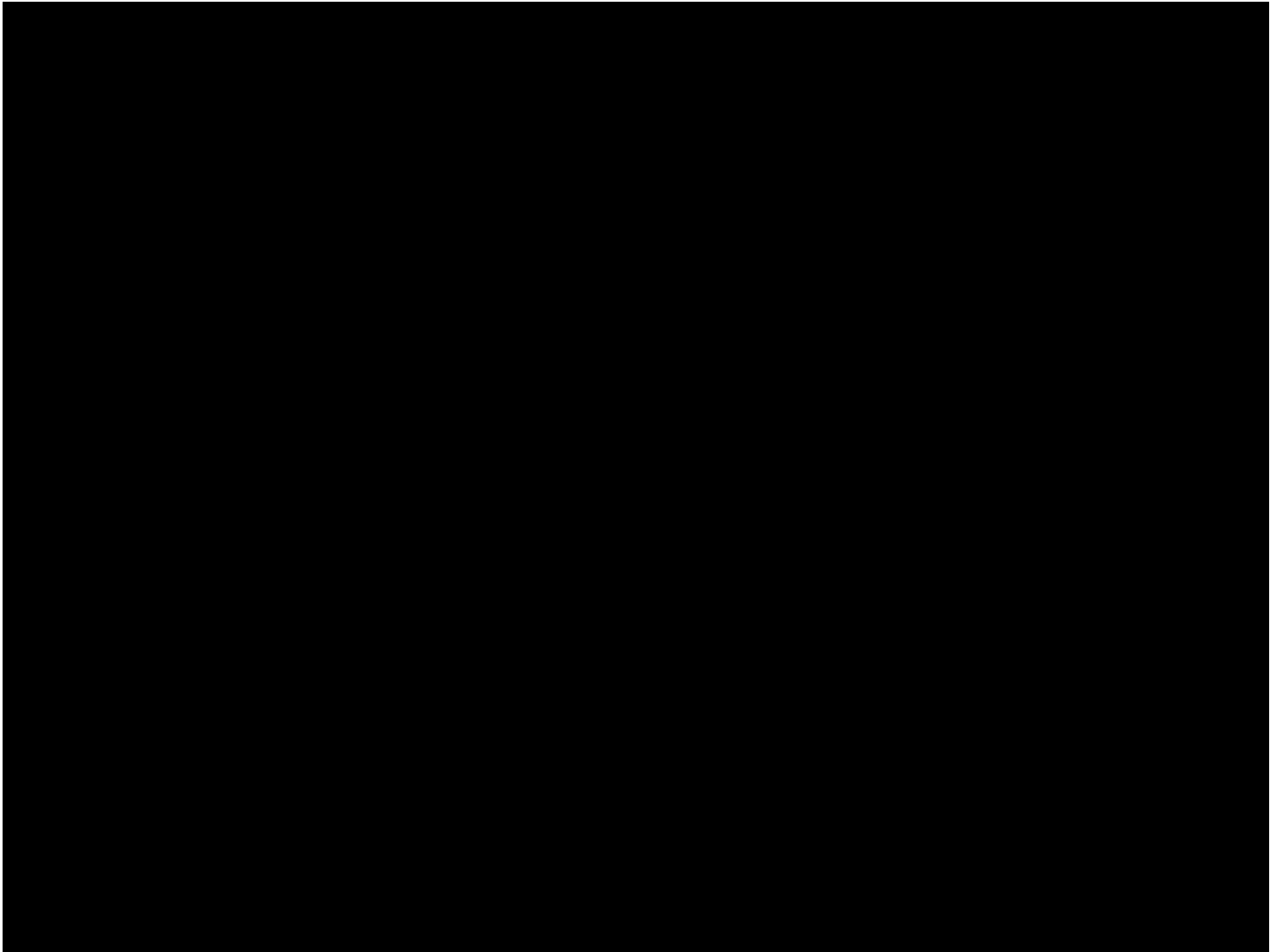
- **The Lotka-Volterra predator-prey model**

Lotka-Volterra predator-prey model

- Solution over time

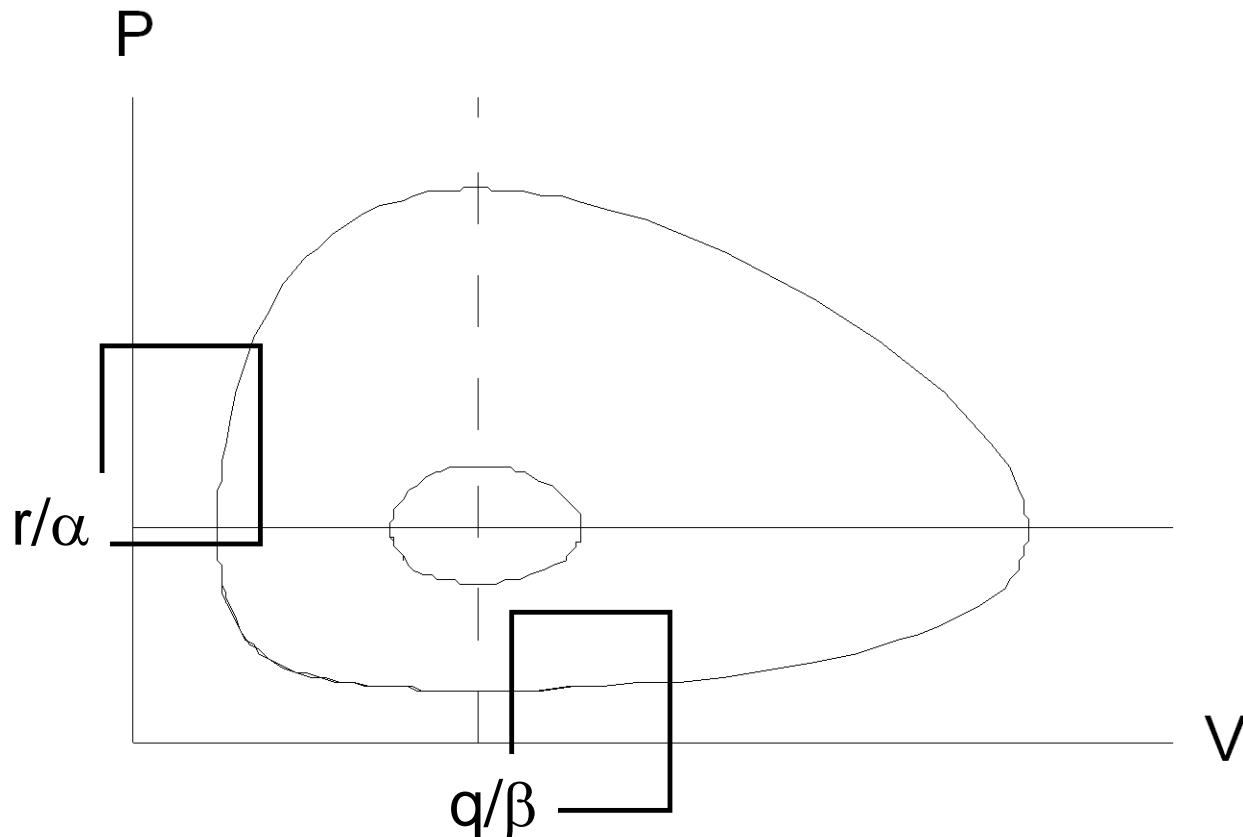


The solutions oscillate over time, the amplitude depends on the initial condition much like the motion of a pendulum



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

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



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 one 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
- 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

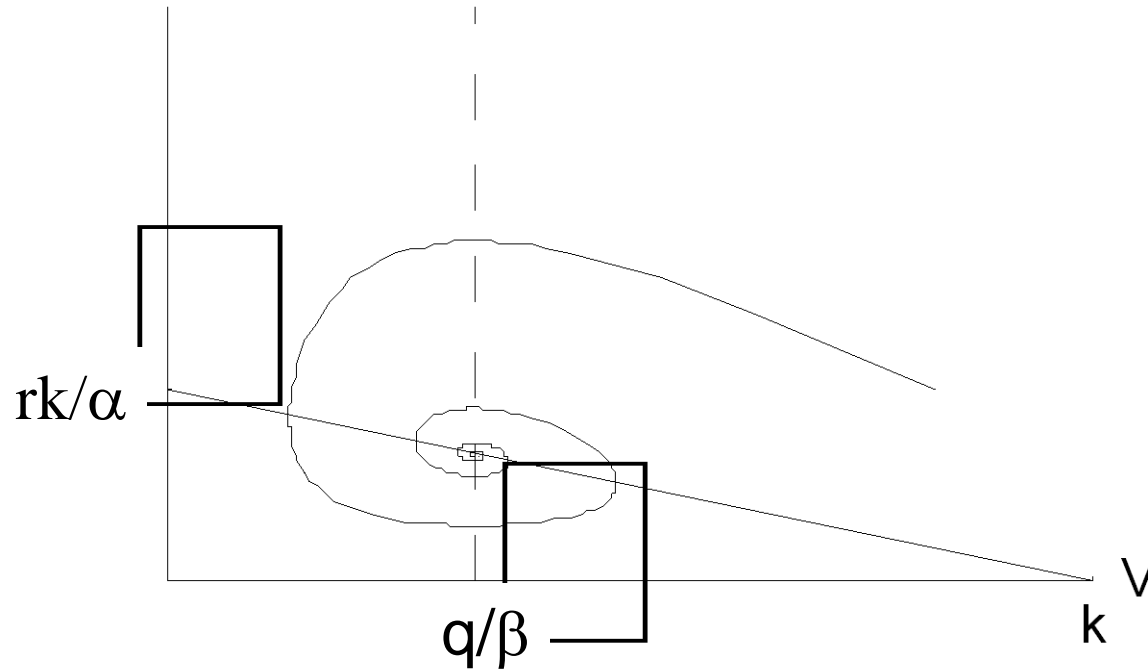
$$\frac{dV}{dt} = V(r(k - V) - \alpha P)$$

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

- X_{pp}
- **Draw the bifurcation diagram in k for the Lotka-Volterra model with prey density dependence**

Density dependent prey growth

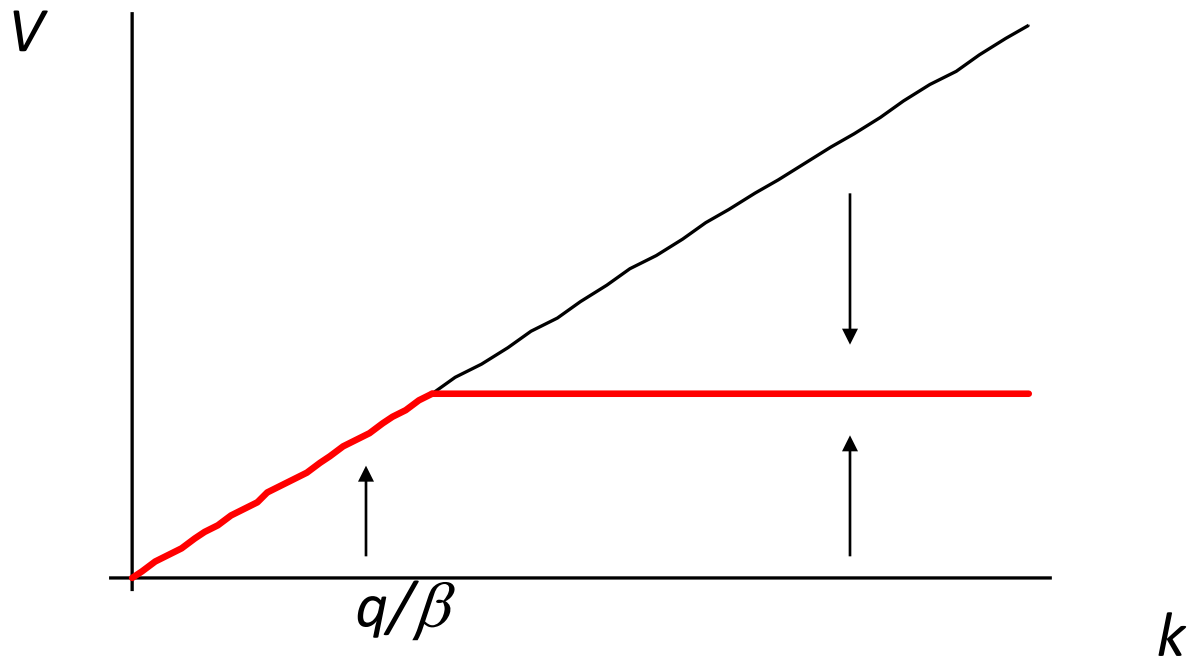
- Solutions



- Density dependent prey growth acts stabilising

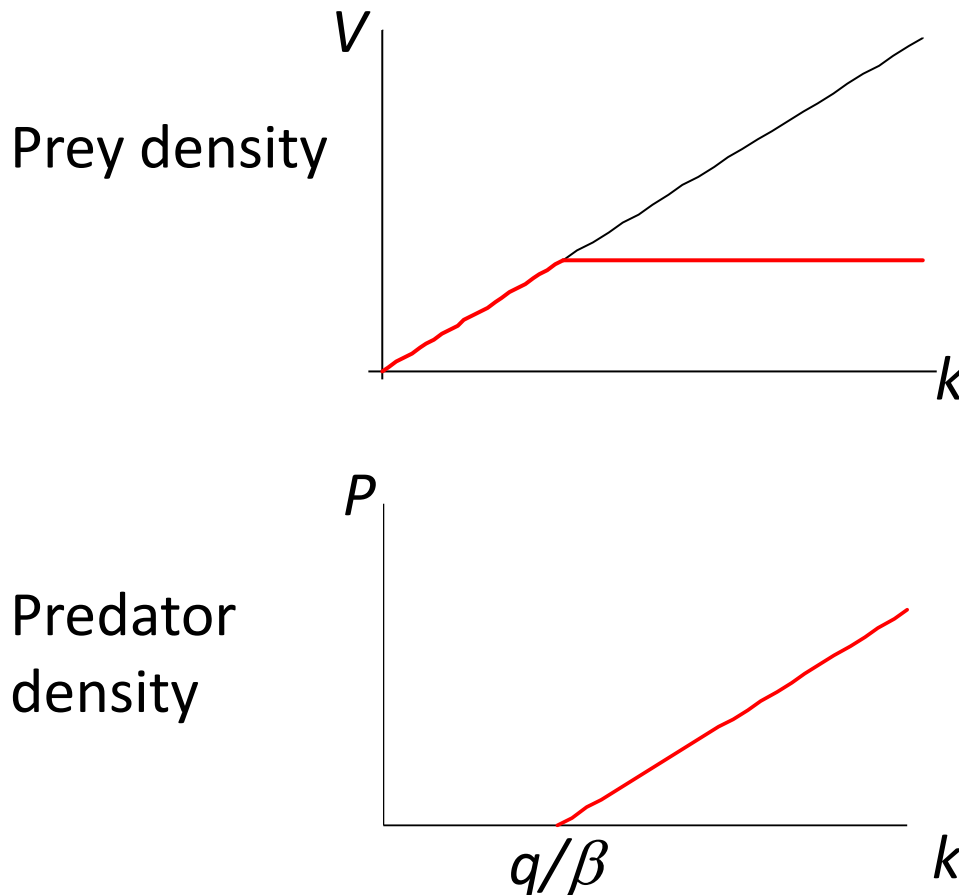
Density dependent prey growth

- Bifurcation diagram in k



Density dependent prey growth

- Bifurcation diagram in k



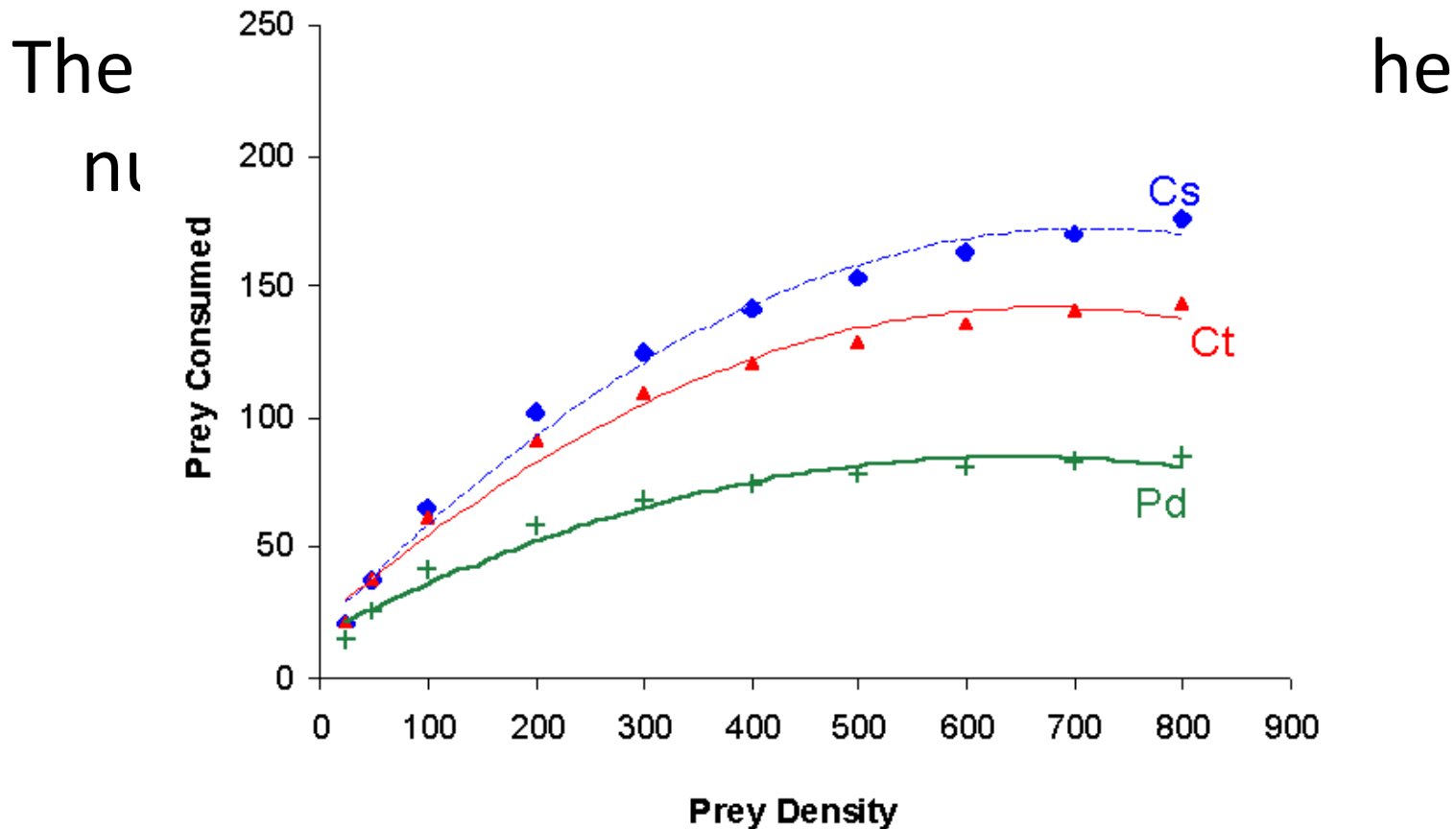
Holling (II) functional response

- 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 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

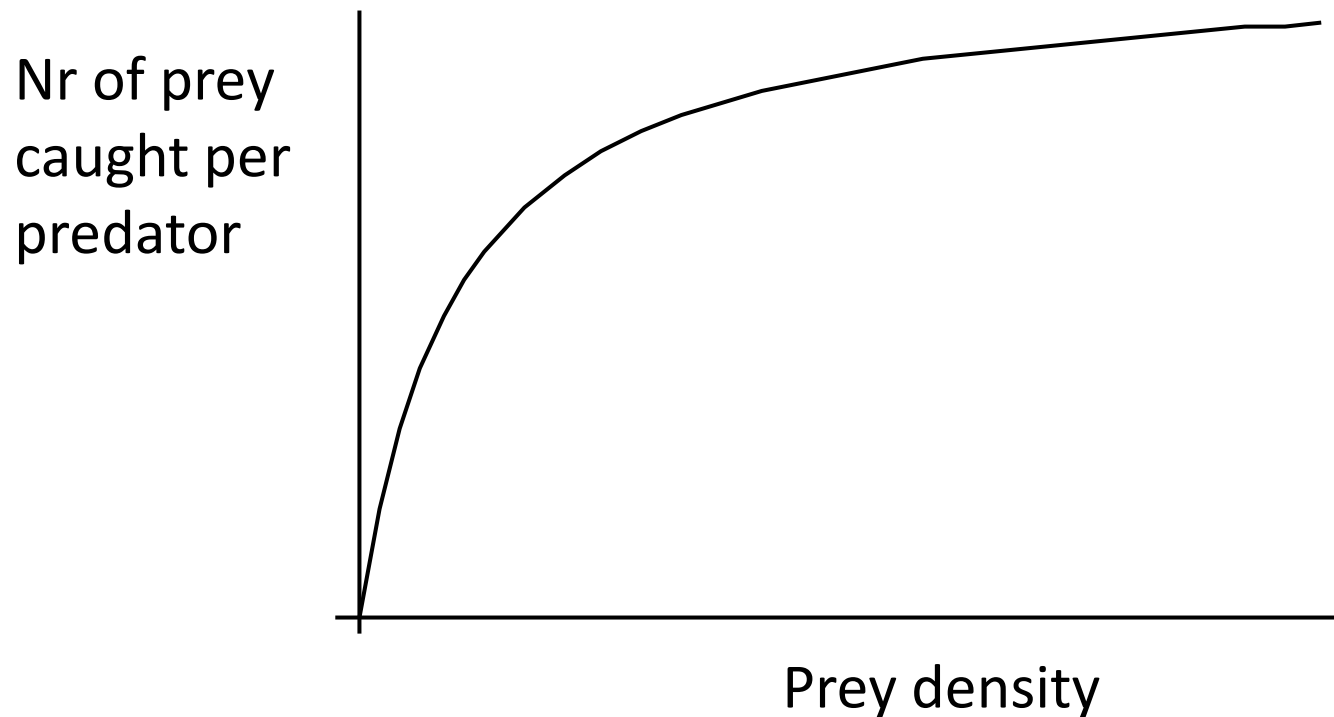
- The functional response then takes the form

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

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

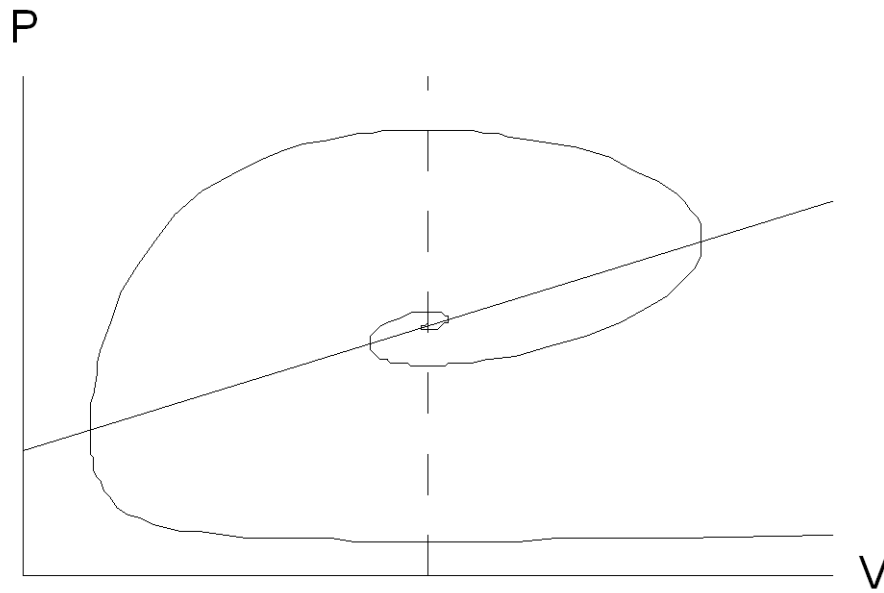
Holling (II) functional response

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:

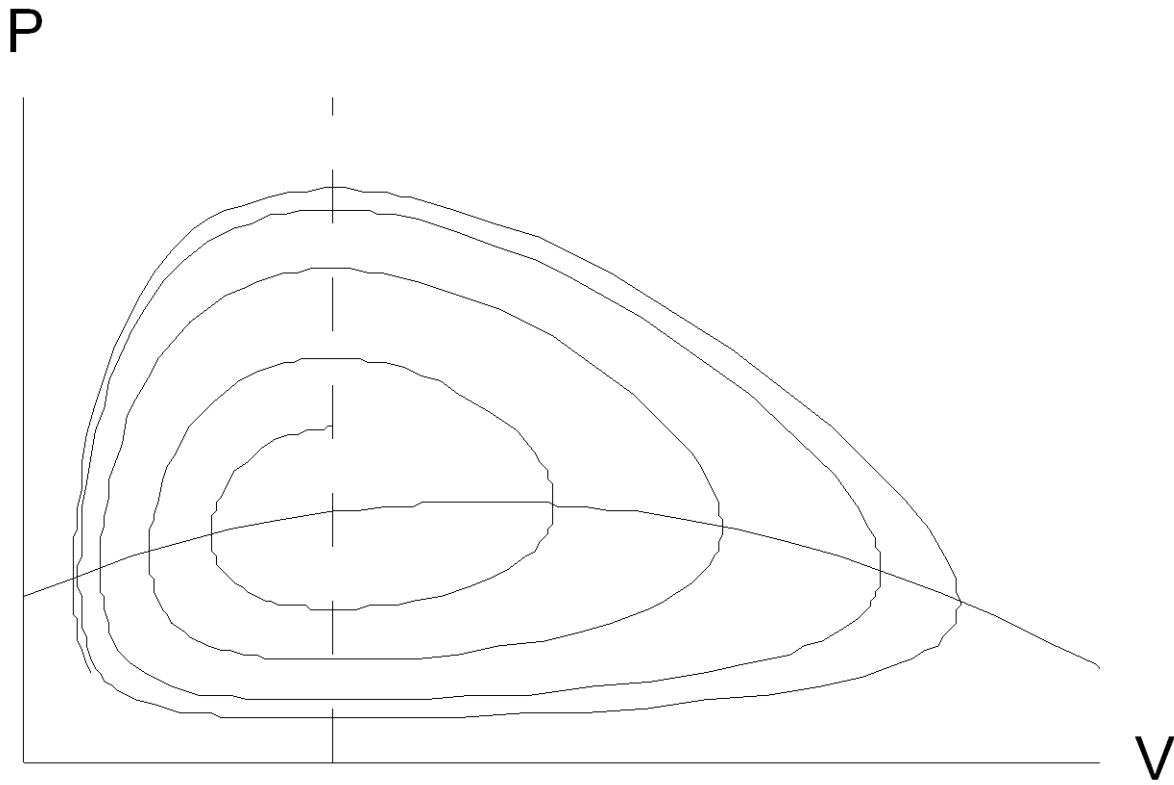
$$\frac{dV}{dt} = V \left(r(k - V) - \frac{\alpha P}{1 + \alpha h V} \right)$$

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

Stable limit cycle

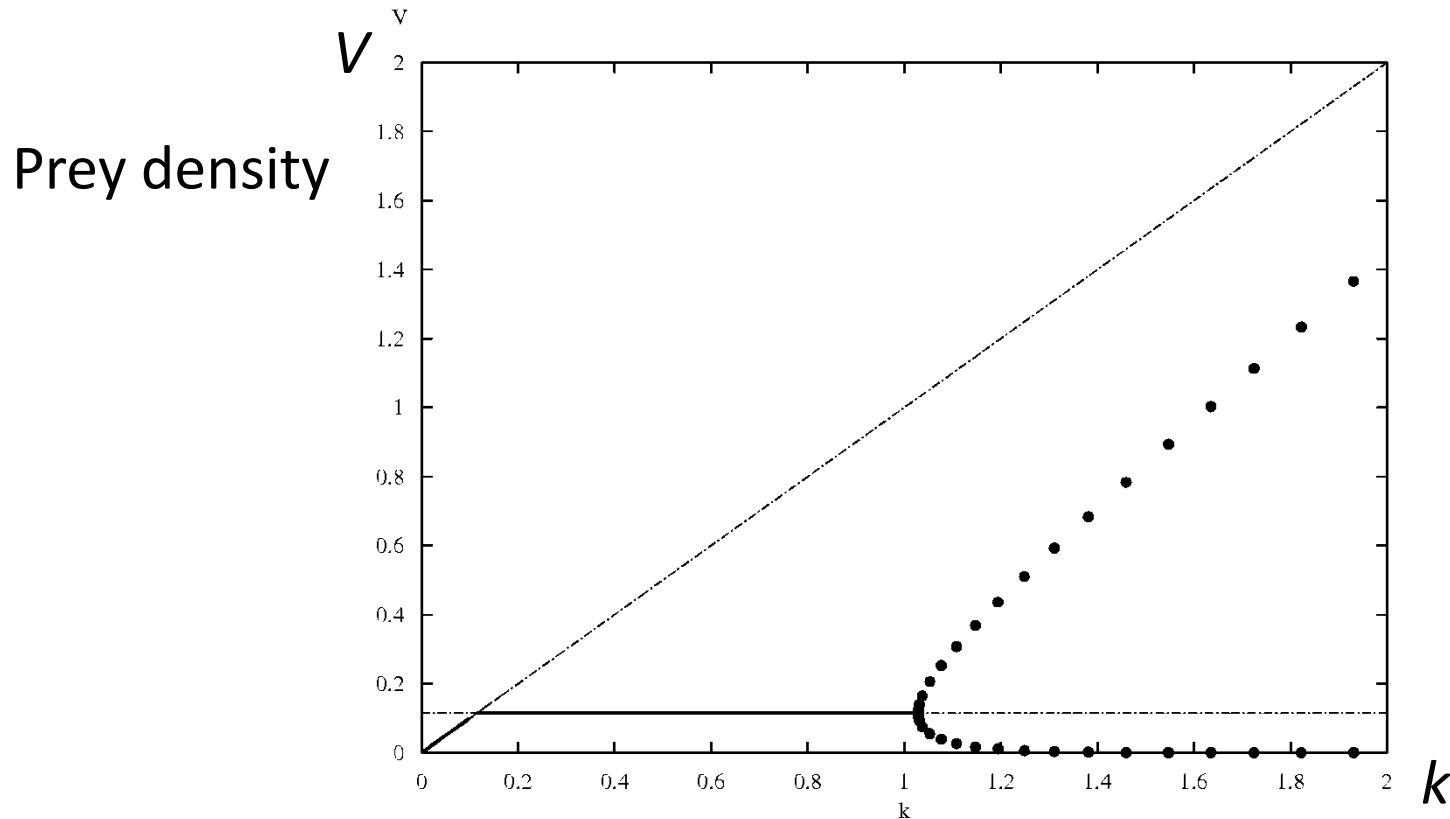
- If prey density dependence and a Holling type II functional response is combined it can lead to sustained oscillations
- These oscillations are independent of the initial conditions
- This is called a stable limit cycle

Stable limit cycle



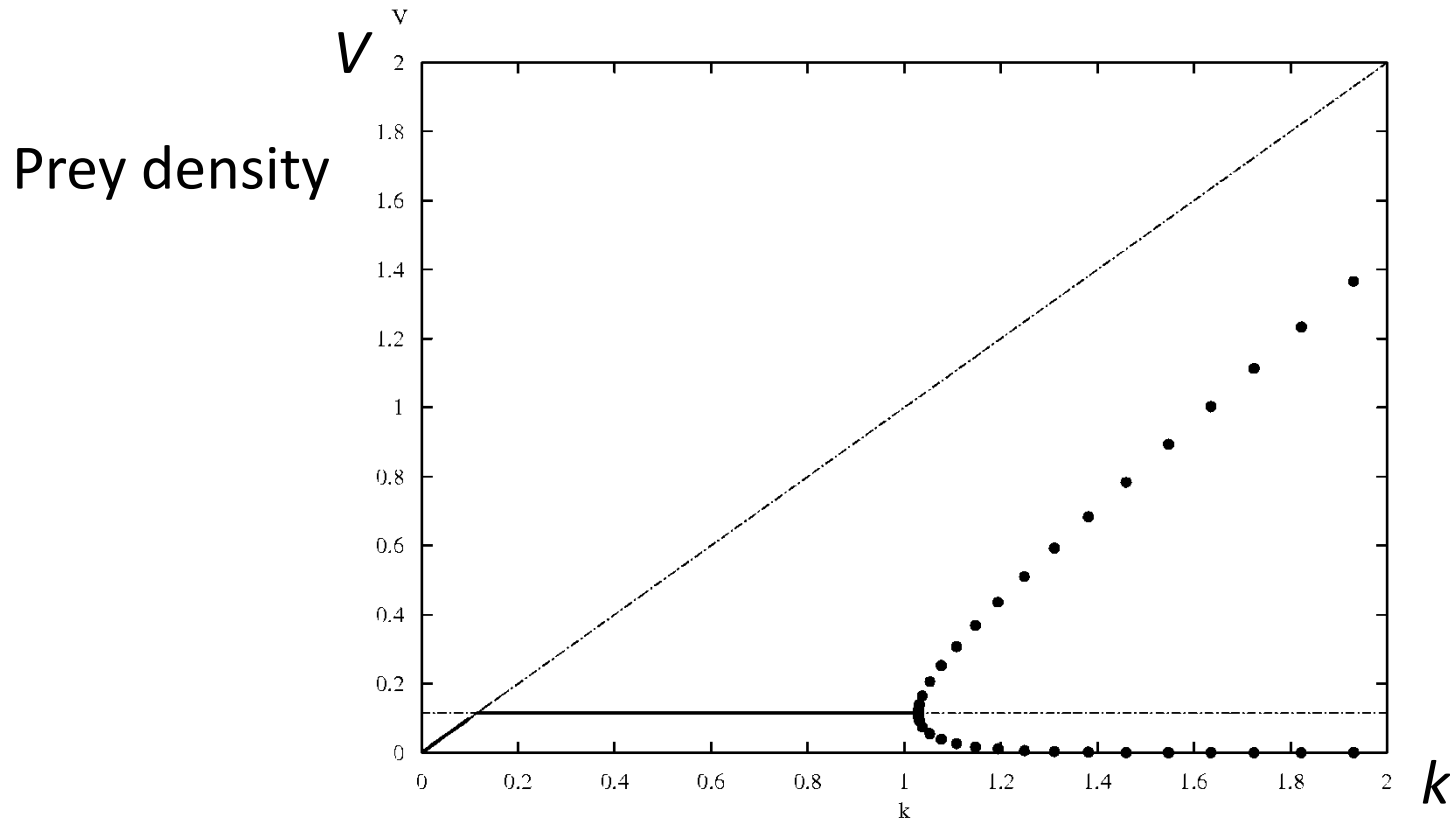
- Exercise here
- **Investigate the dynamics of the Rosenzweig-McArthur model.**

The Hopf bifurcation



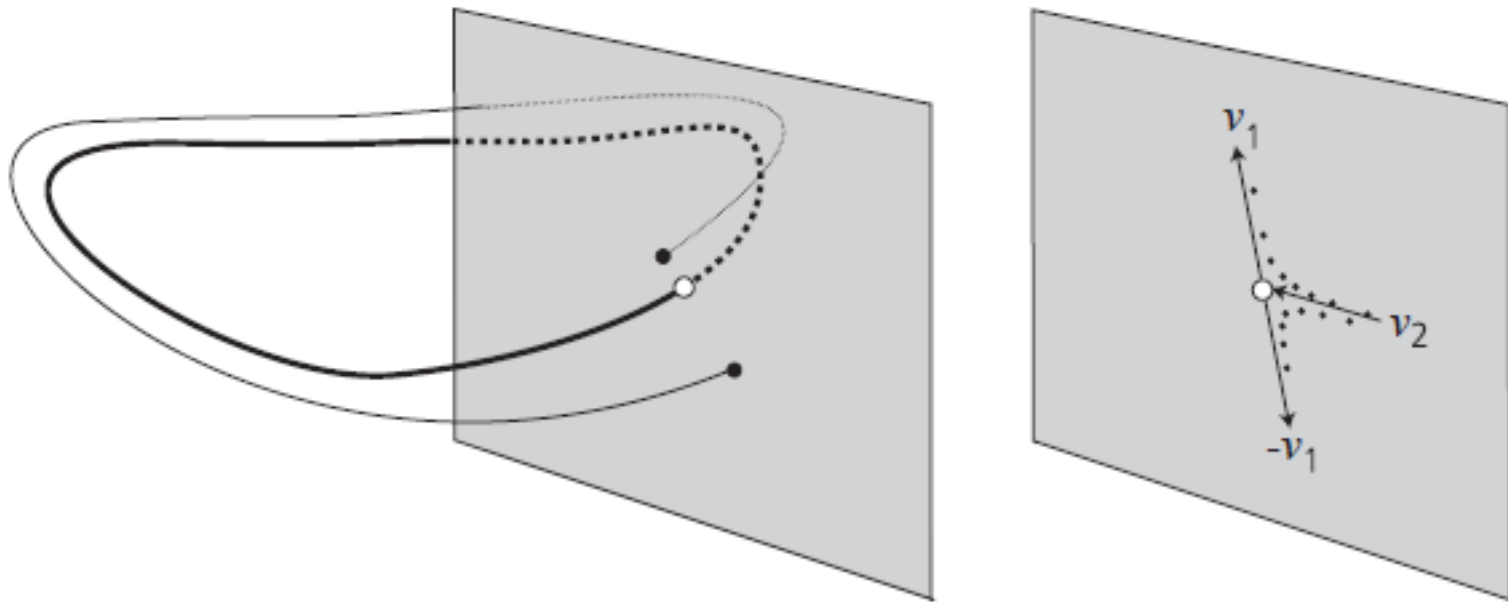
In a Hopf bifurcation, the real part of a pair of complex eigenvalues becomes positive. It results in a limit cycle.

The paradox of enrichment



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

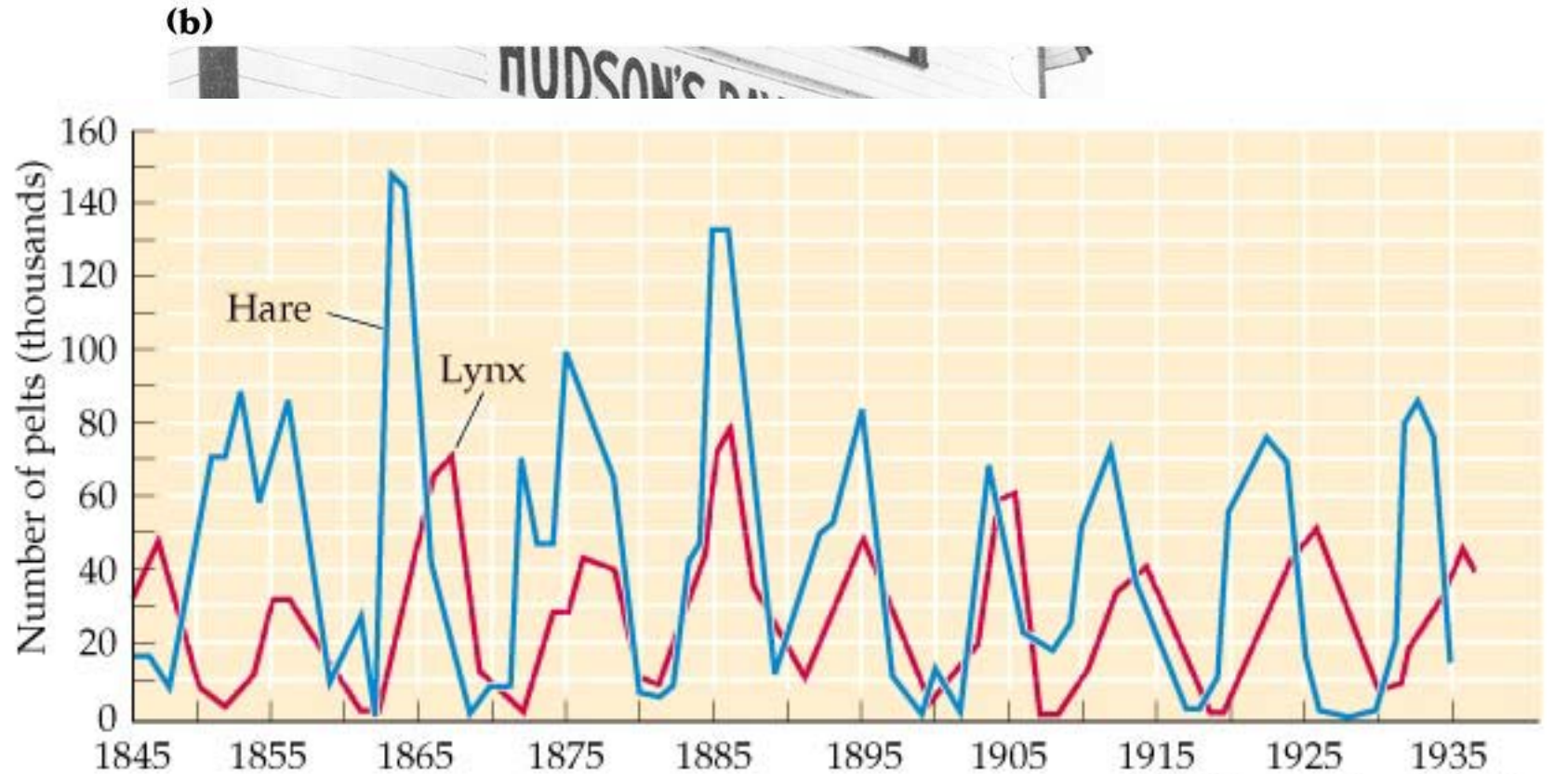




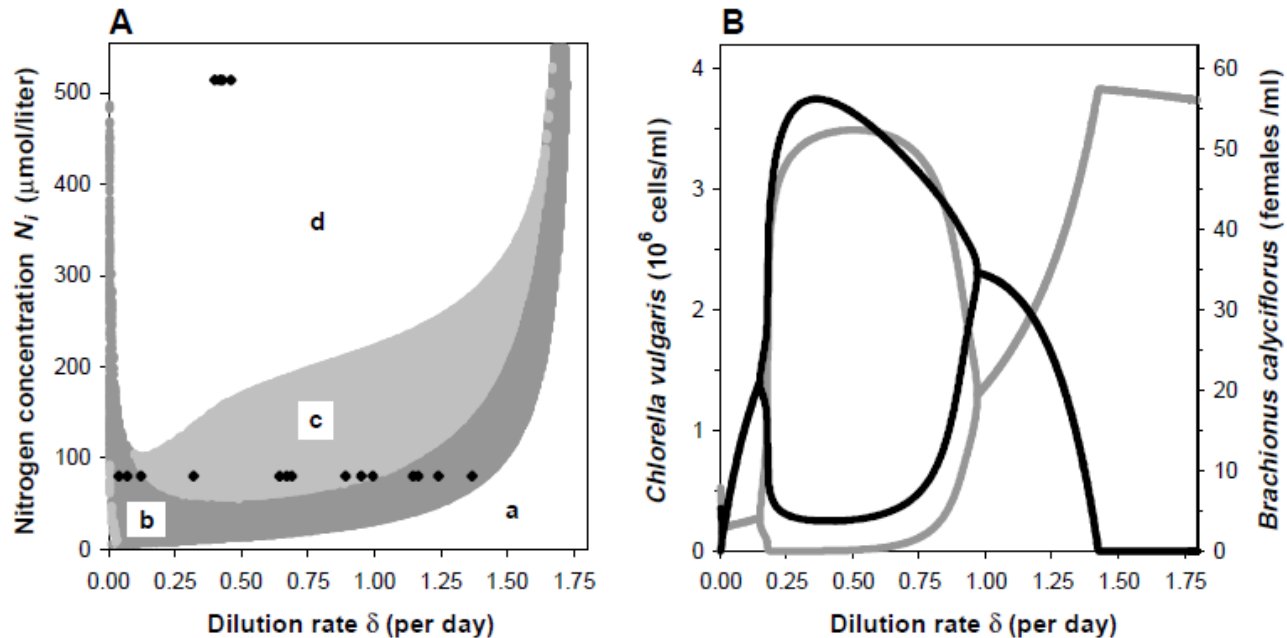
The Hudson's Bay Company traded in pelts,
and kept immaculate records

Predators and their prey

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

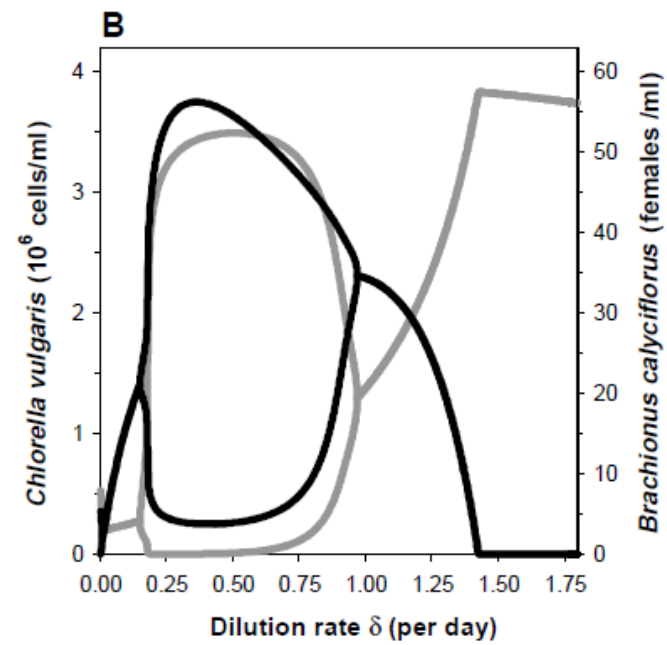
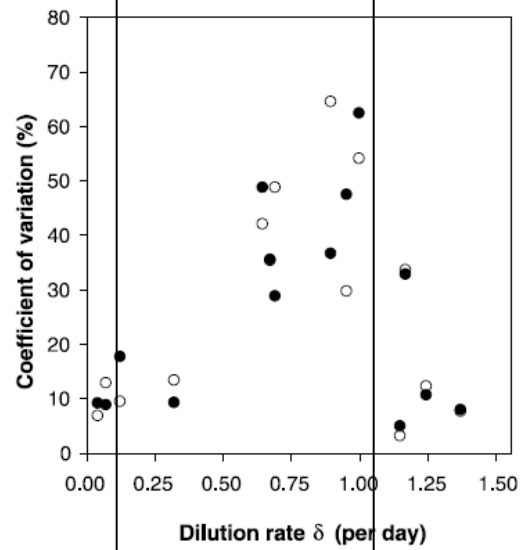
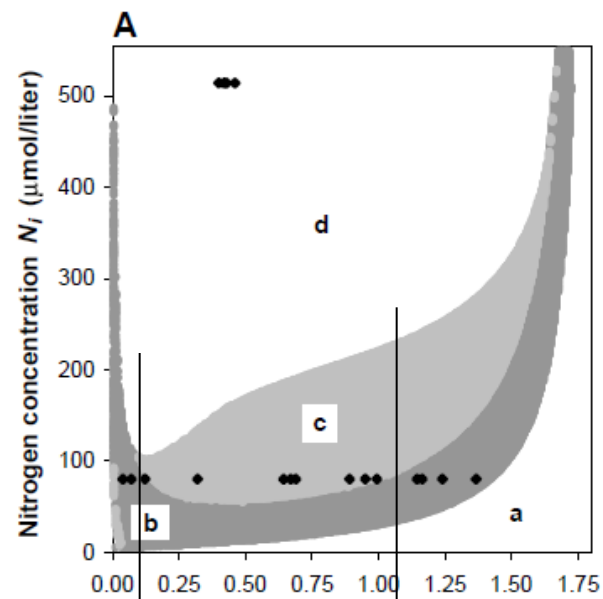


Experimental demonstration



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

Fussman et al. Science (2000).





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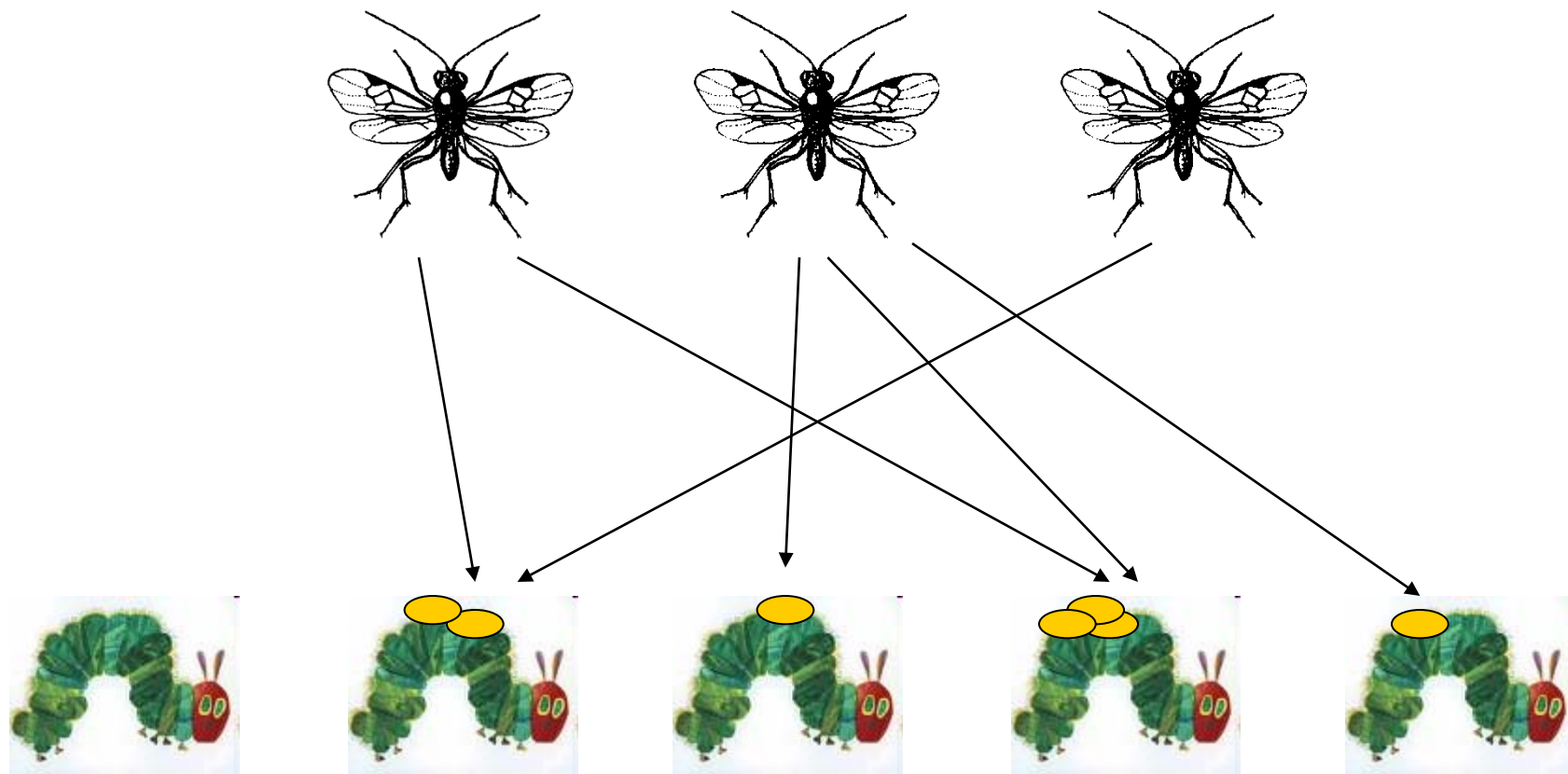
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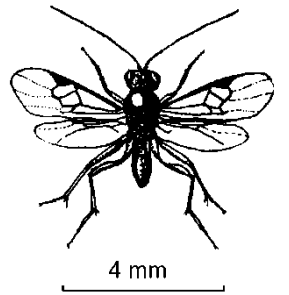
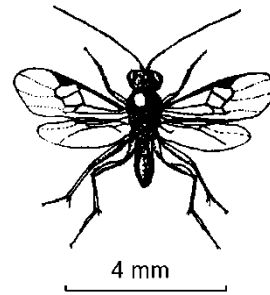
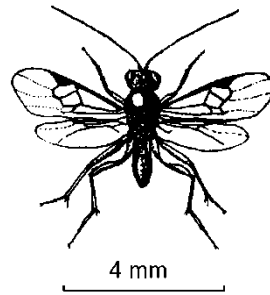
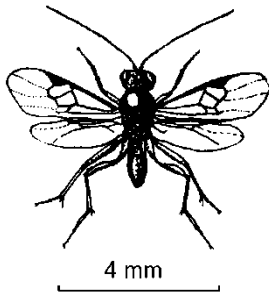
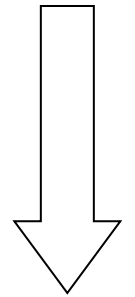
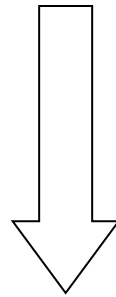
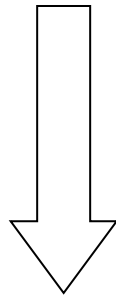
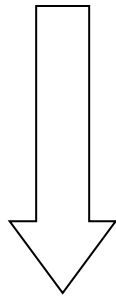
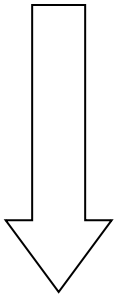
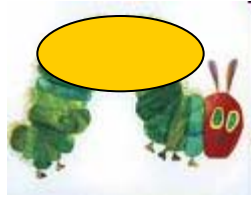
Parasitism

- 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 λ eggs and give rise to λ new hosts

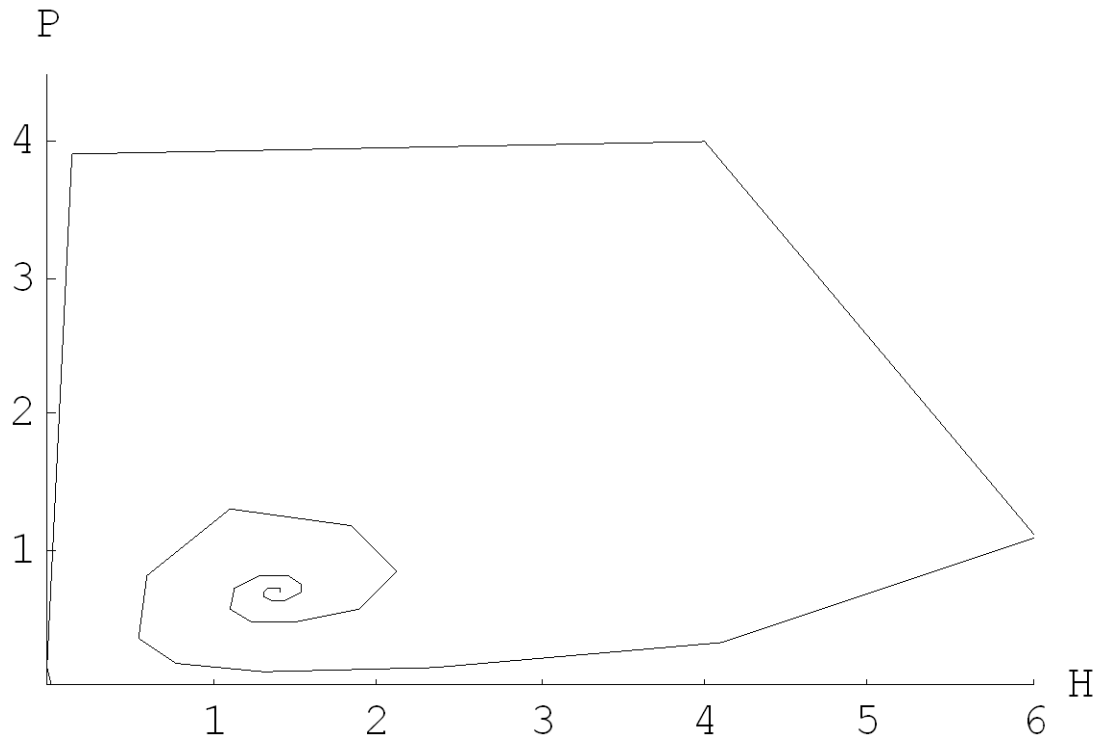




Parasitism

- The Nicholson Bailey model reads:

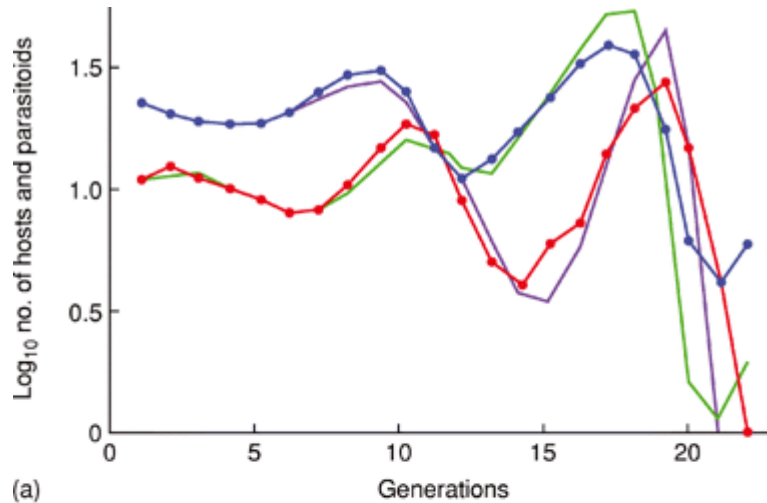
$$P_{t+1} = H_t(1 - e^{-aP_t})$$



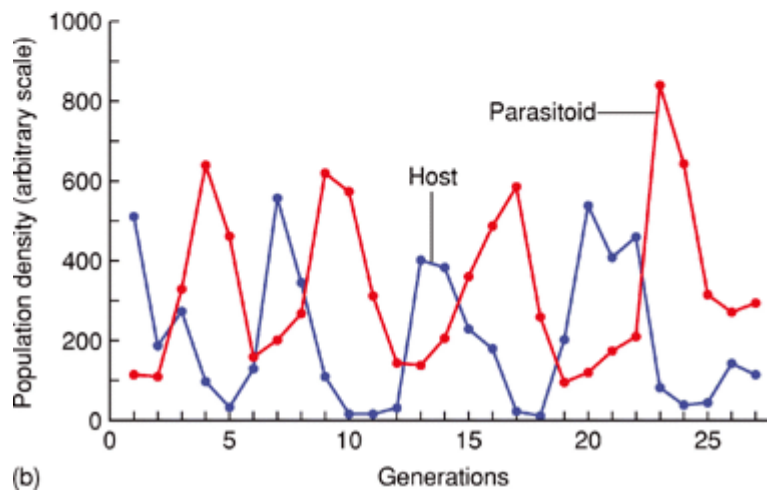
Parasitism

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

Parasitism



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



Stable oscillations of parasitoid and host

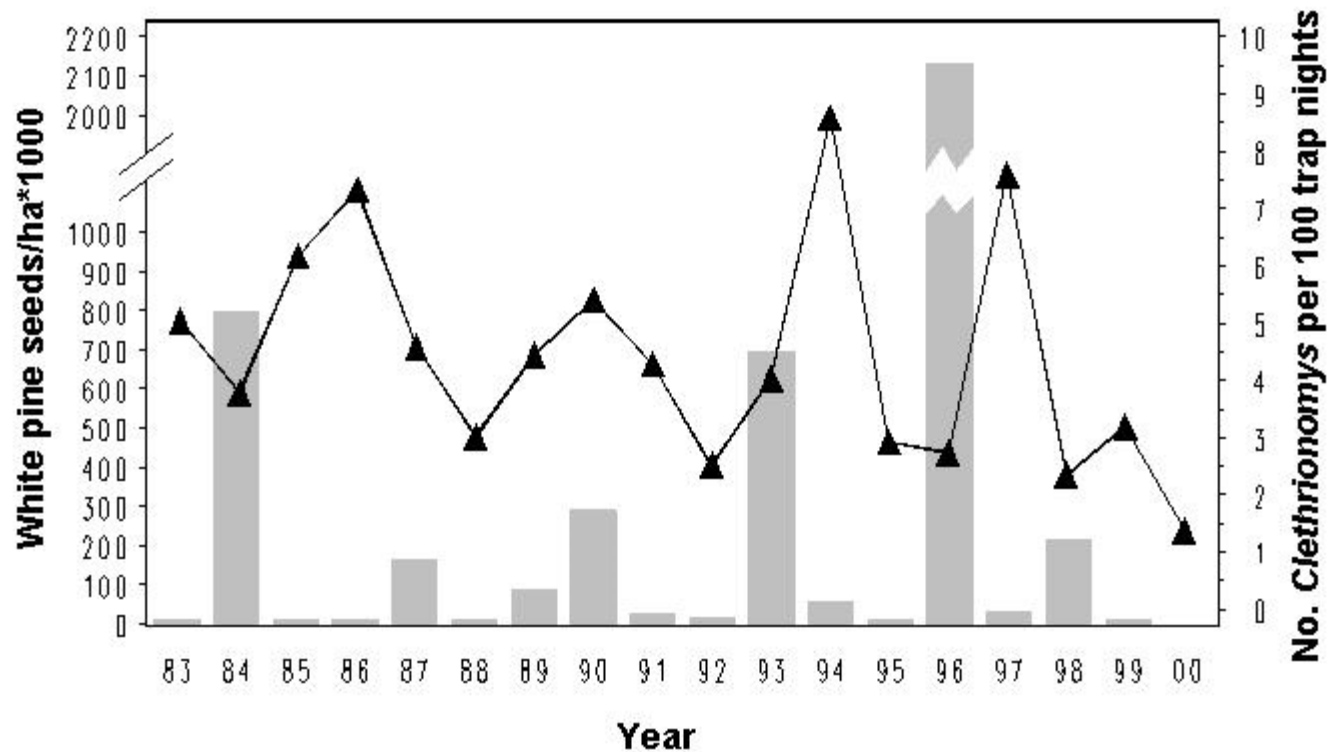
Spatial interactions

- 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.

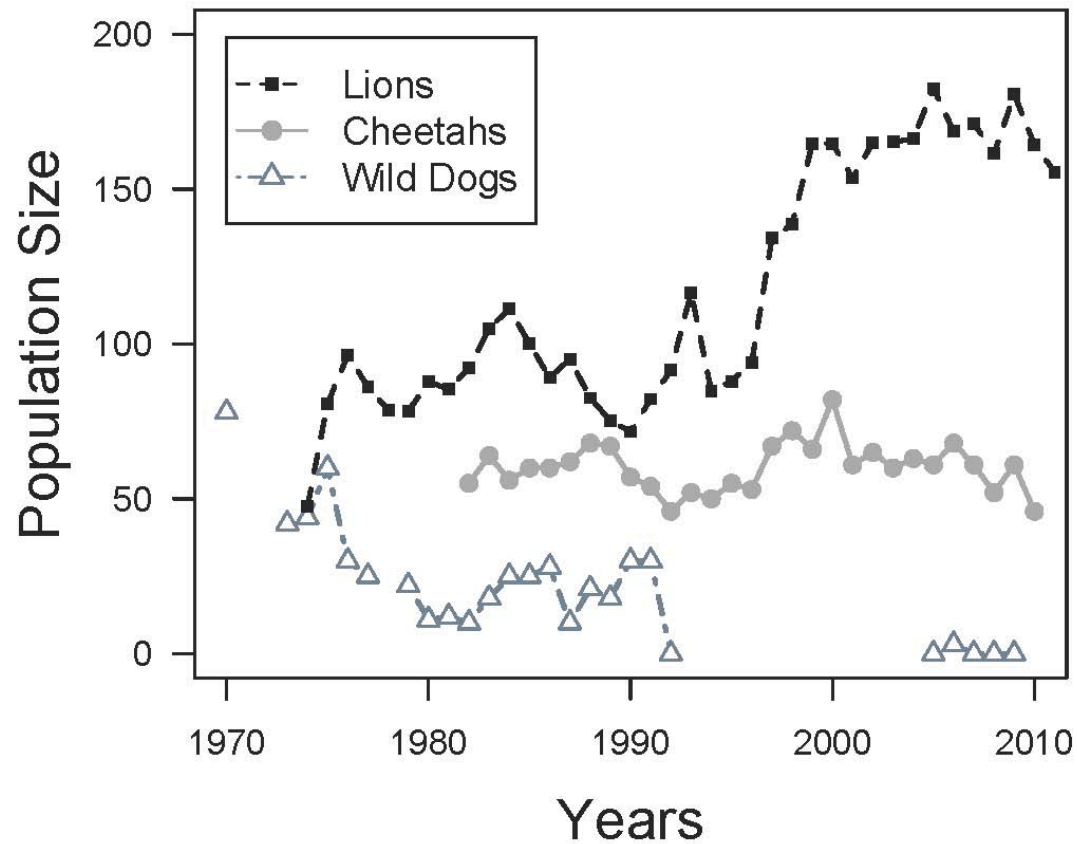
Red backed voles in Holt forest



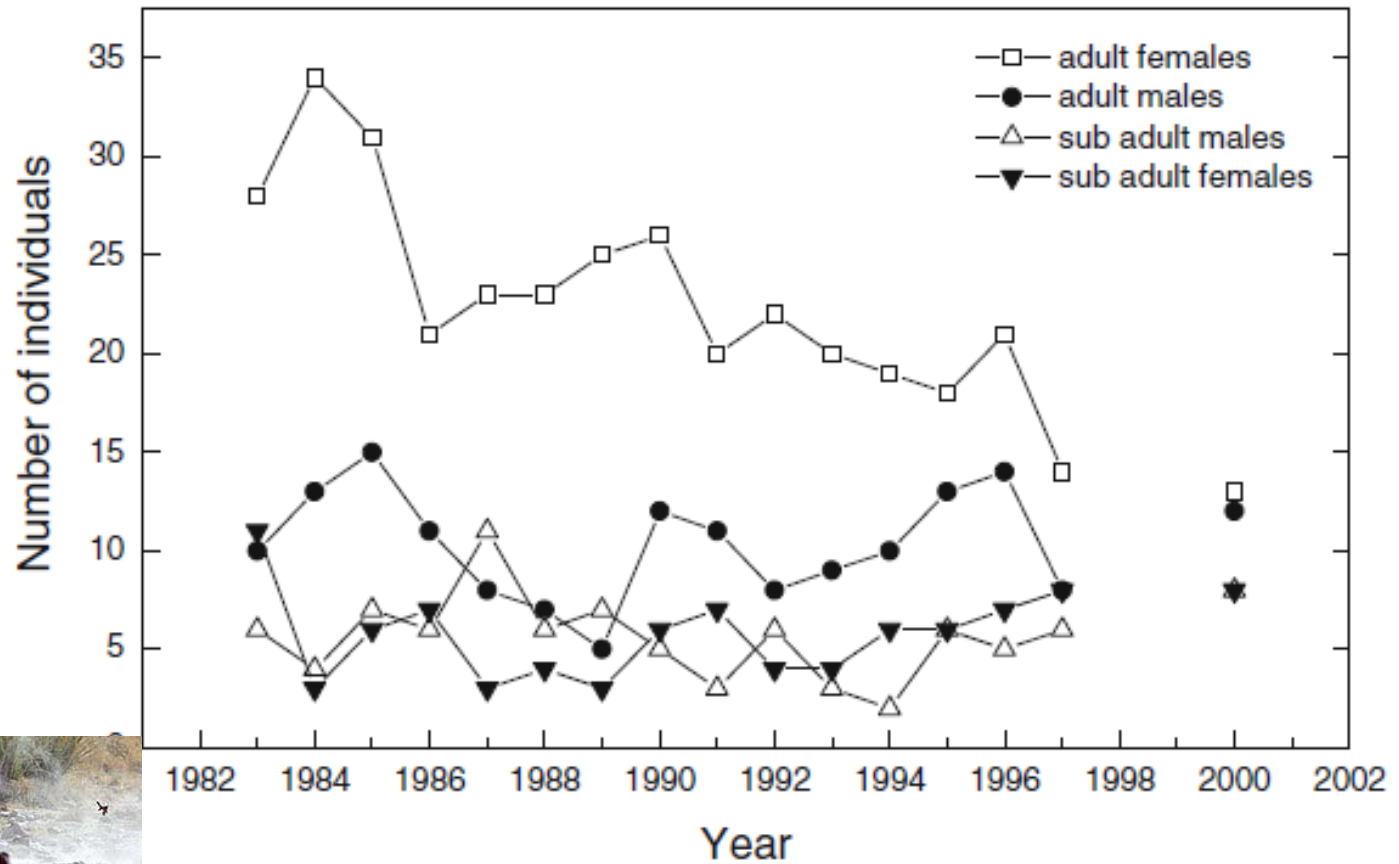
Predators and their prey

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

Predators in the Serengeti



Lions in Etosha (SA)



Predators and their prey

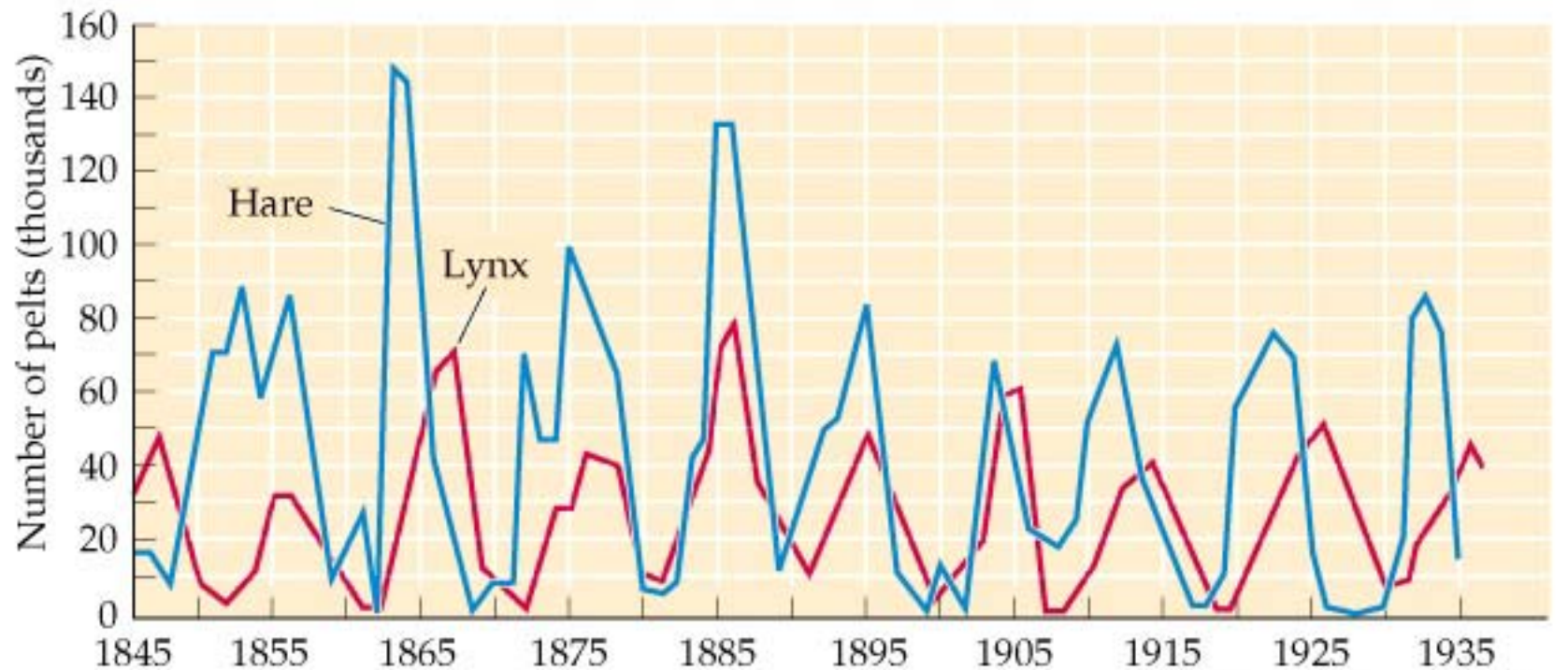
- Most predator and prey populations do **not** show such fluctuations in the wild
- In the lab populations many populations do show strong fluctuations and are difficult to keep alive

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?

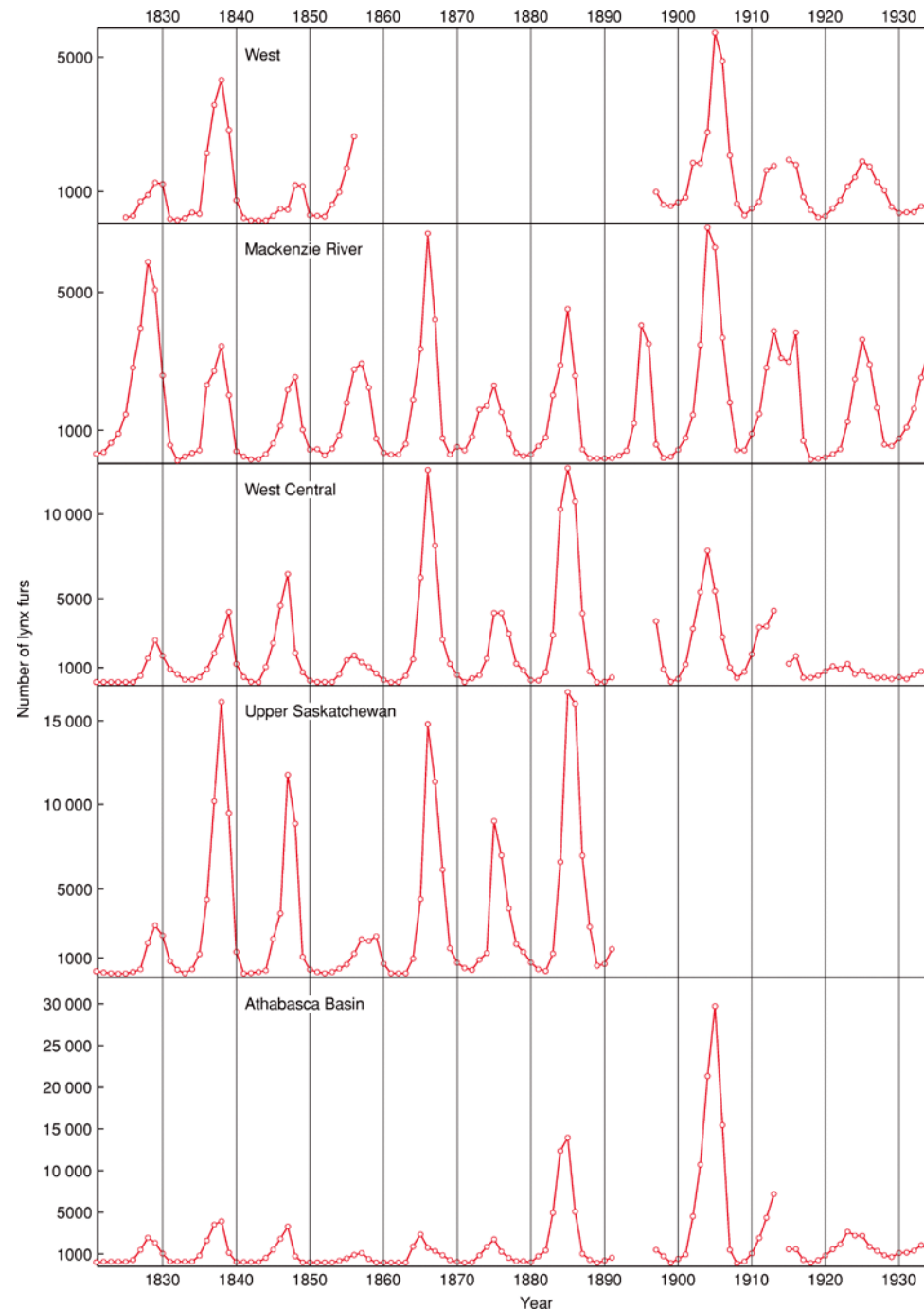
Stable limit cycle

- 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

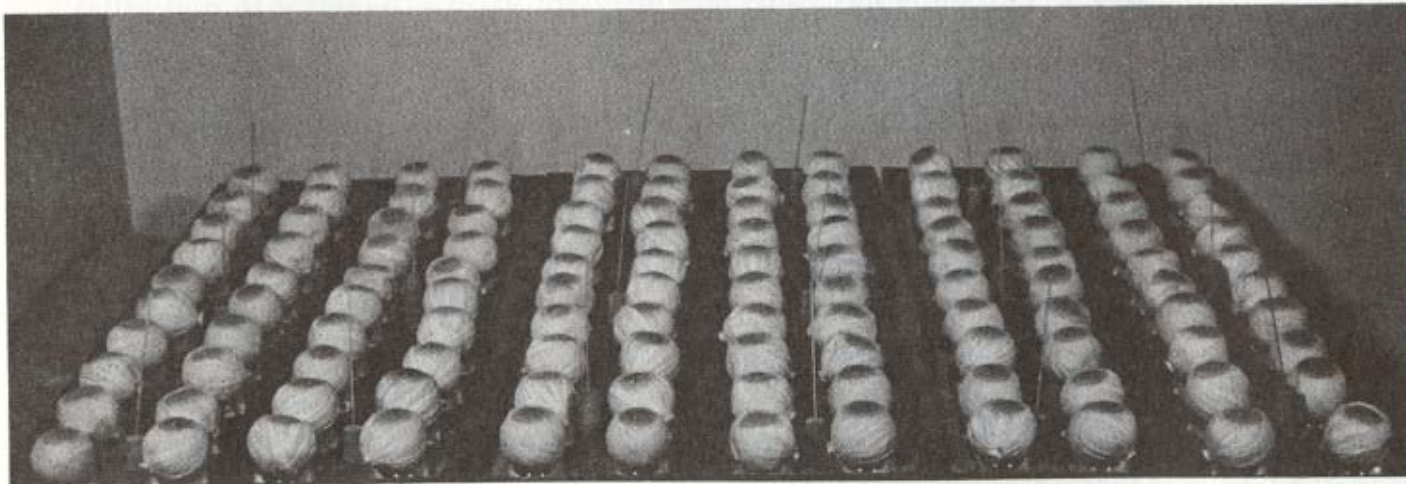
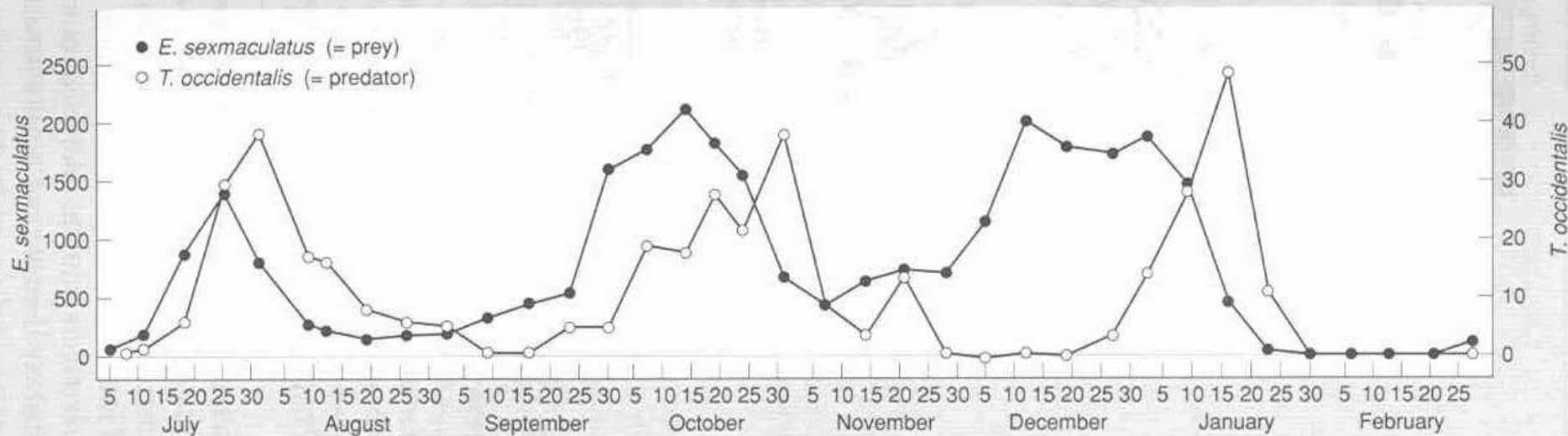
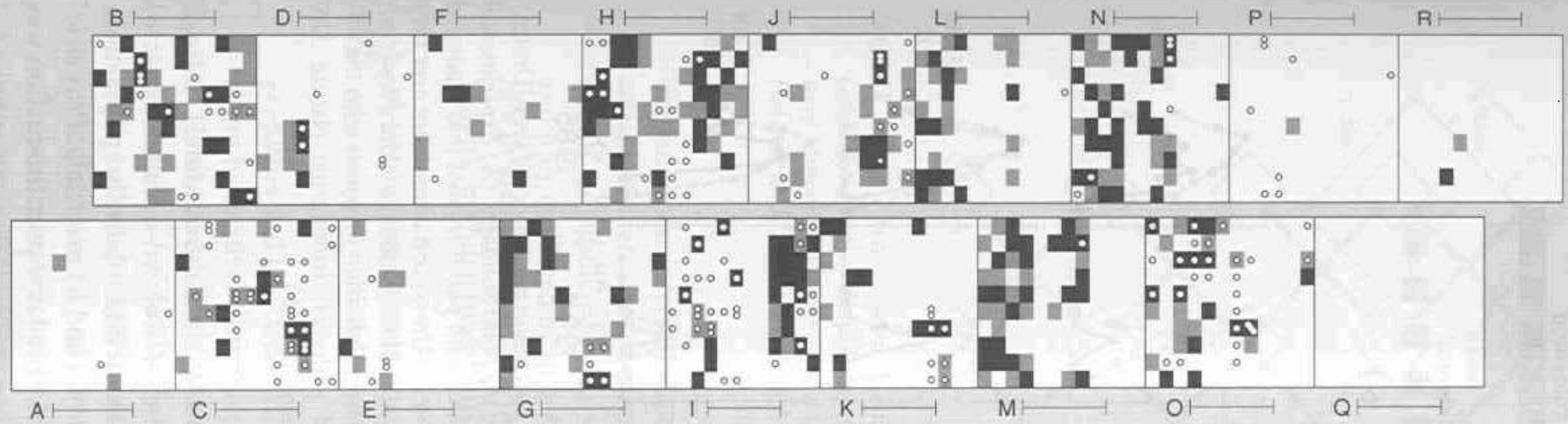


FIGURE 5-18. Universe of 120 oranges used in studies of predator-prey interaction (prey: *Eotetranychus sexmaculatus*; predator: *Typhlodromus occidentalis*). Each orange has $\frac{1}{20}$ of its area exposed. Partial barriers of Vaseline form a complex maze of impediments between the oranges. Wooden 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

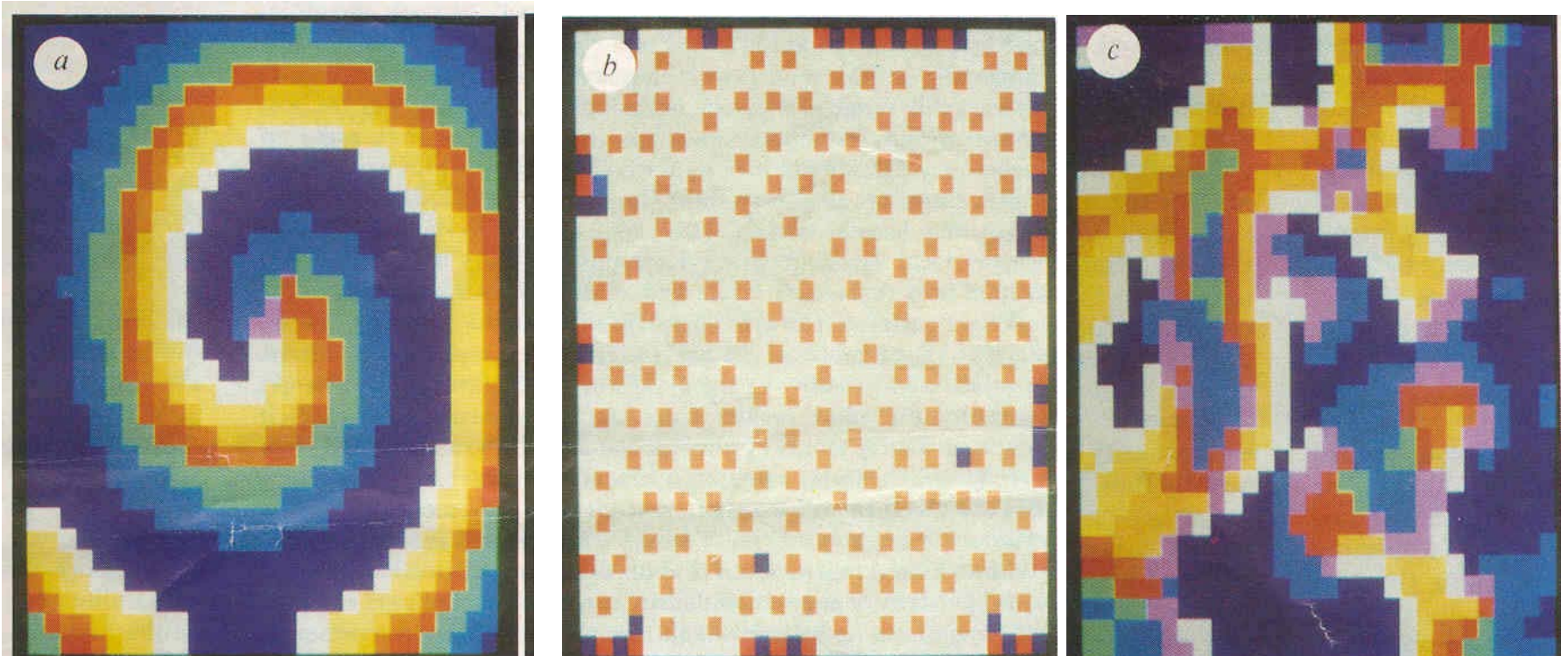


Spatial interactions

- 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

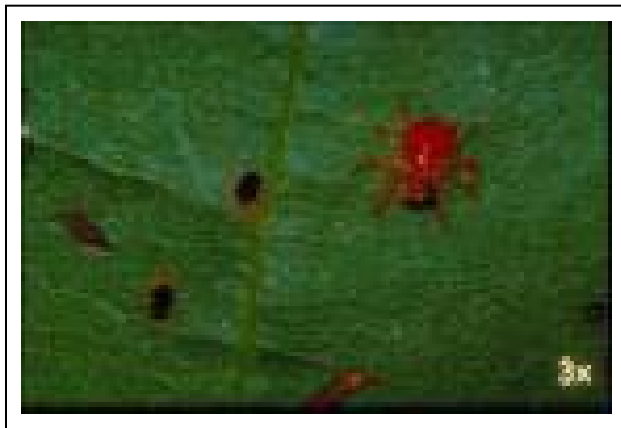
Spatial interactions

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

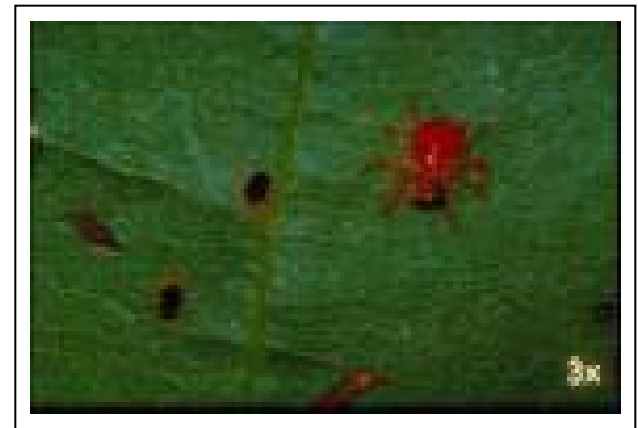
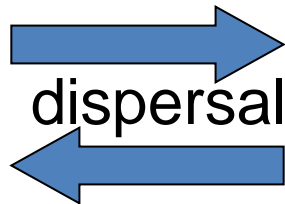


Spatial interactions

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



Space 1

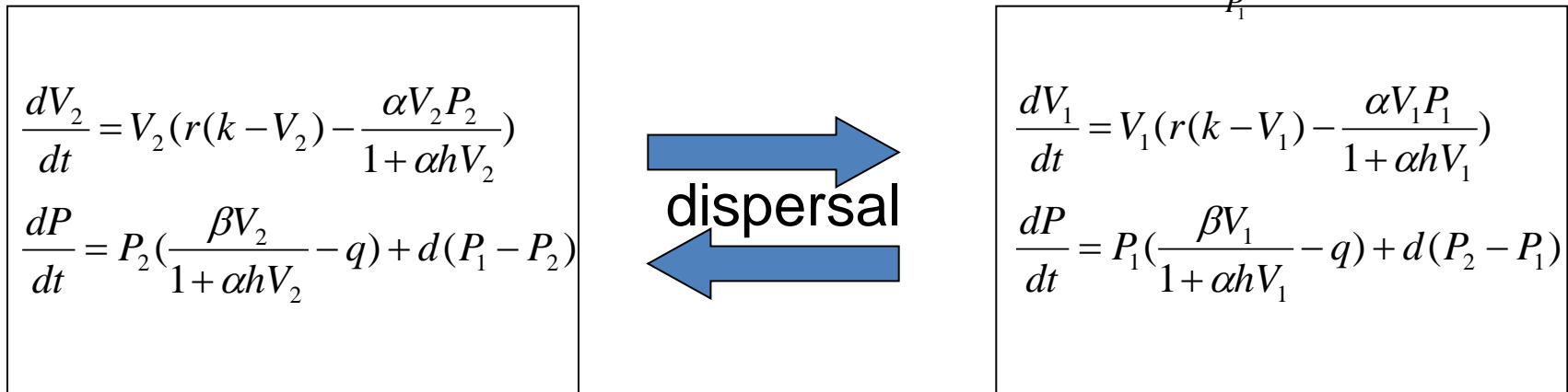


Space 2

- The model equations are very much like two coupled pendulums

Spatial interactions

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

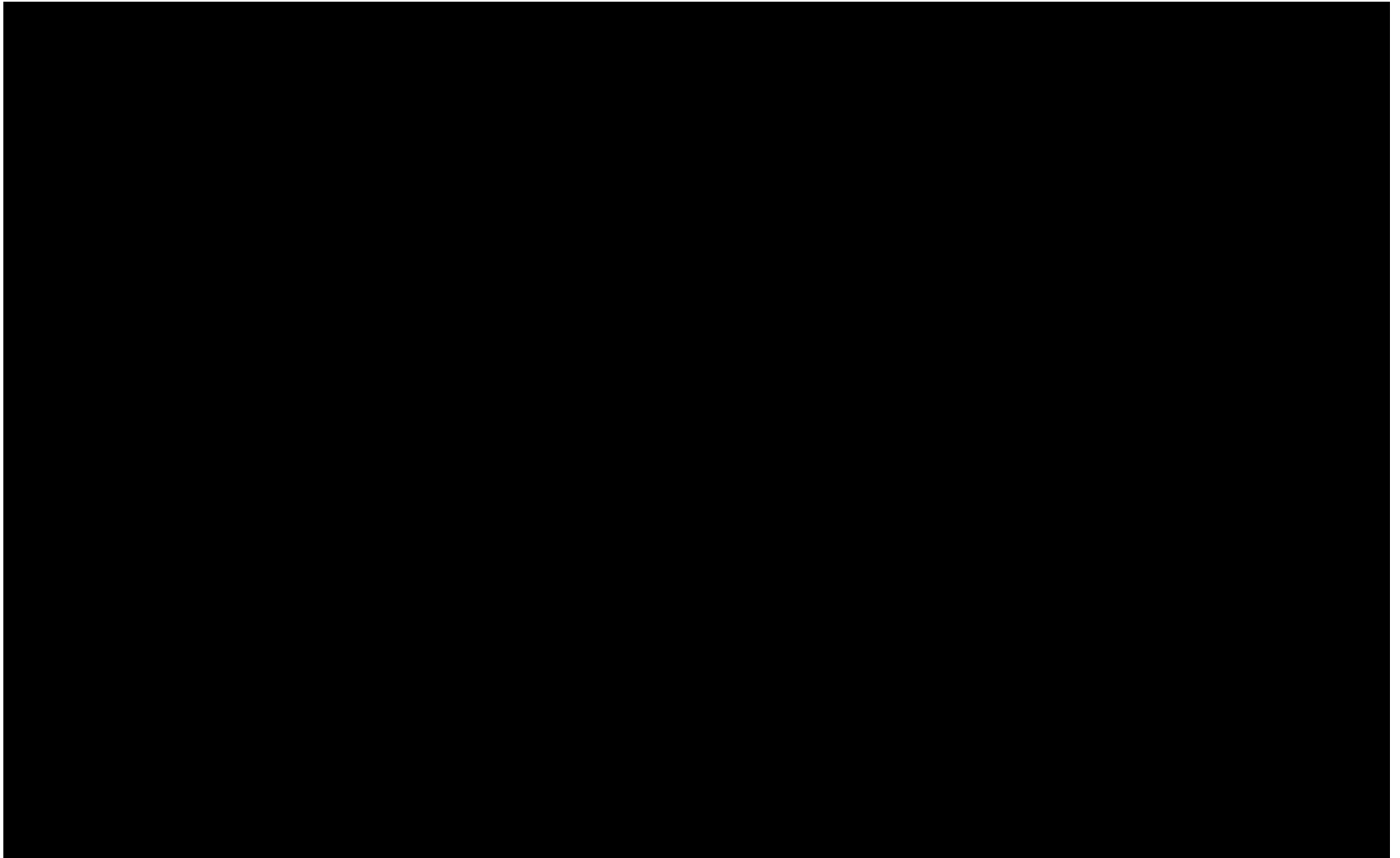


Space 1

Space 2

- The model equations are very much like two coupled pendulums

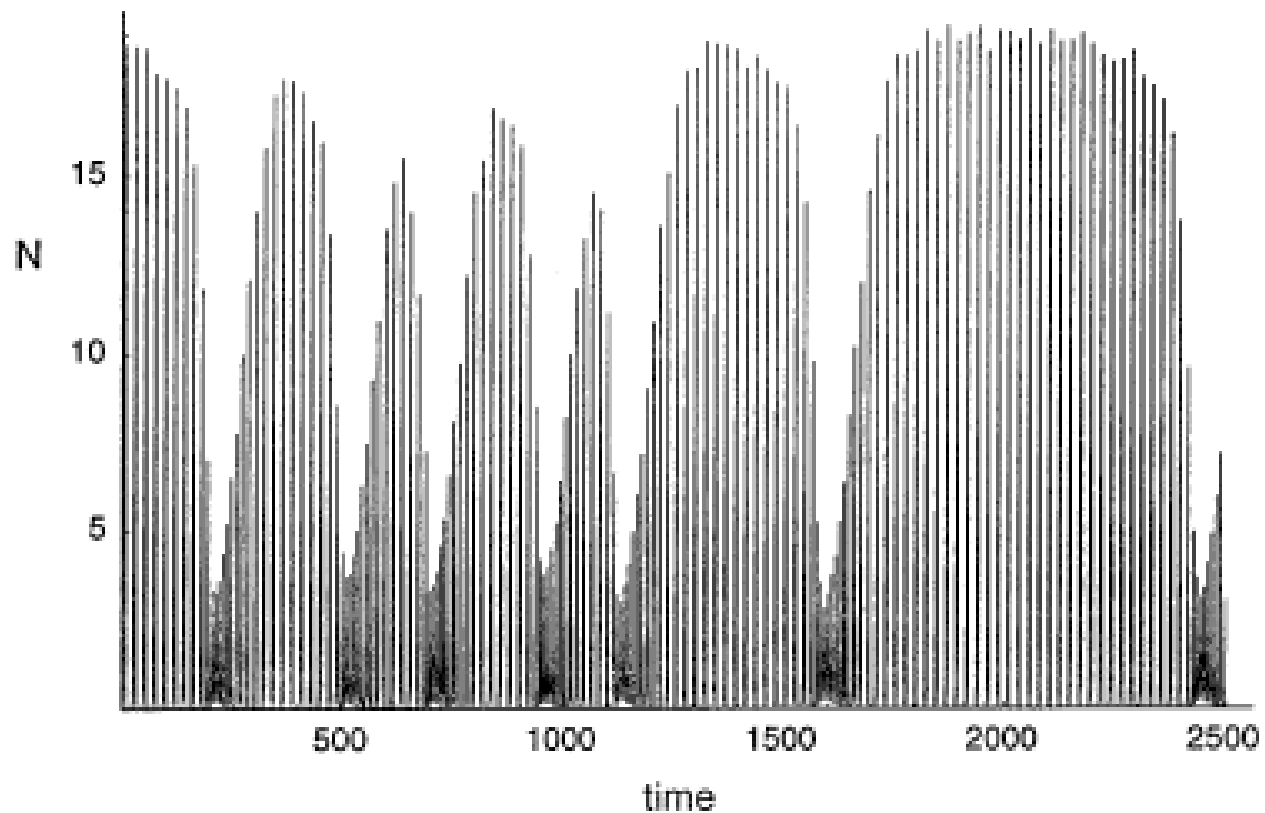
Video 2 coupled pendulums here



Exercise

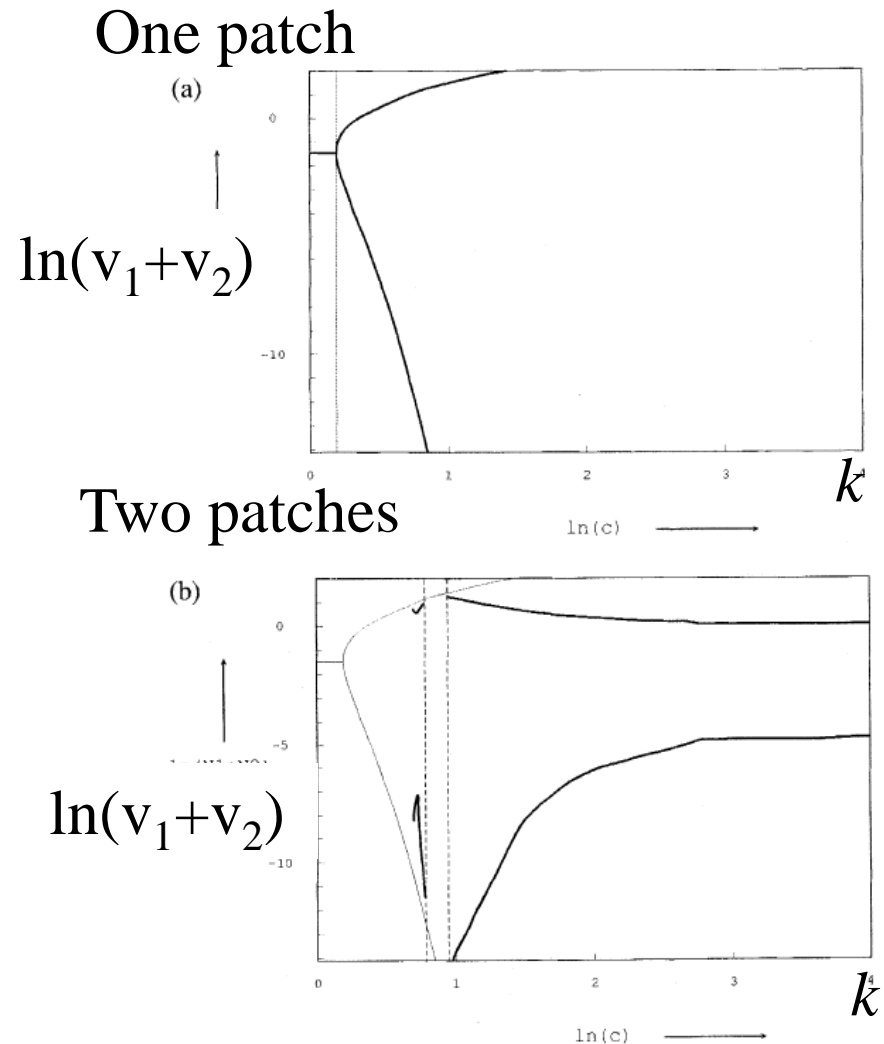
The effect of space on the dynamics of a predator-prey model.

Spatial interactions

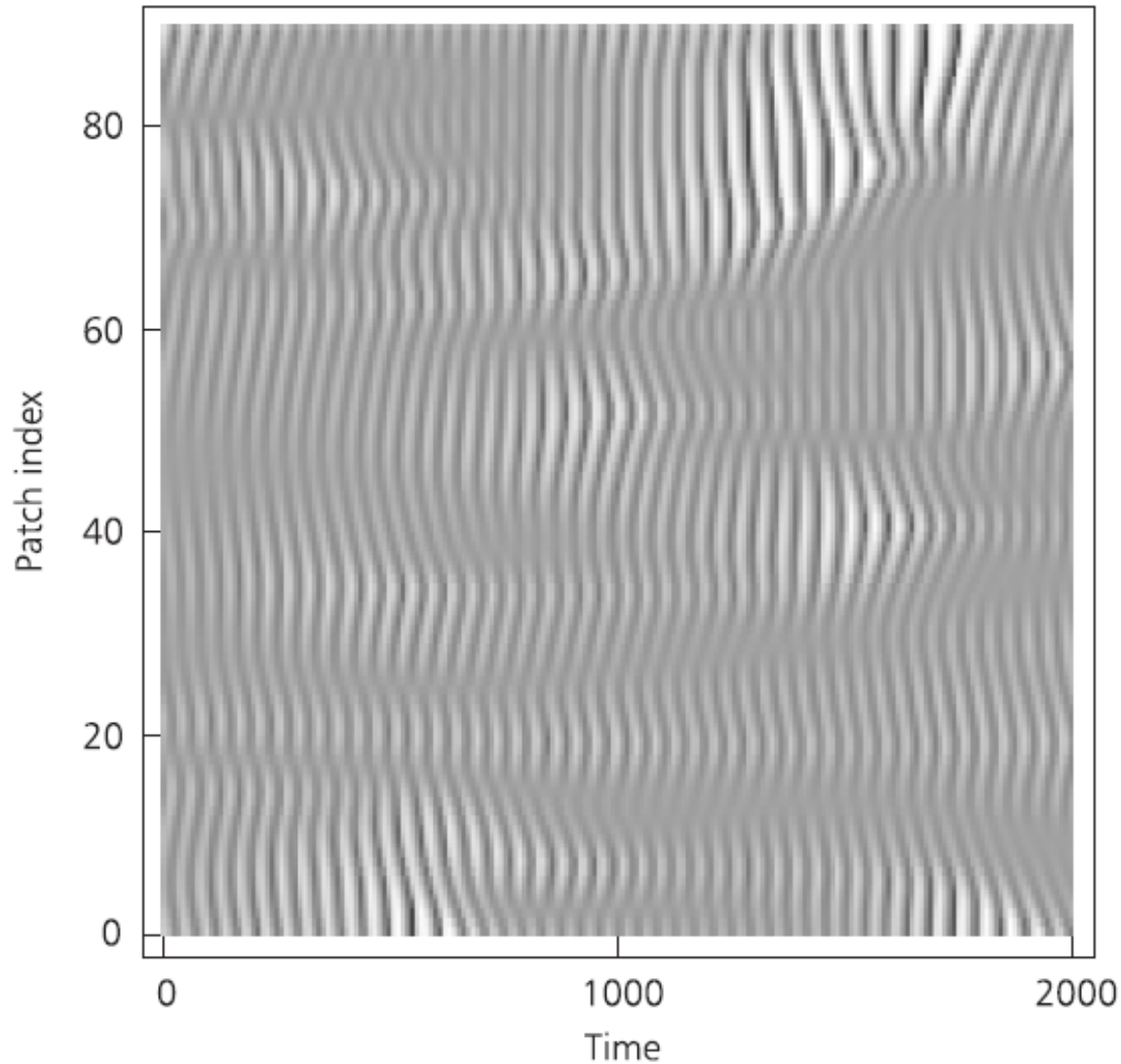


Spatial interactions

- This offers a solution to the paradox of enrichment

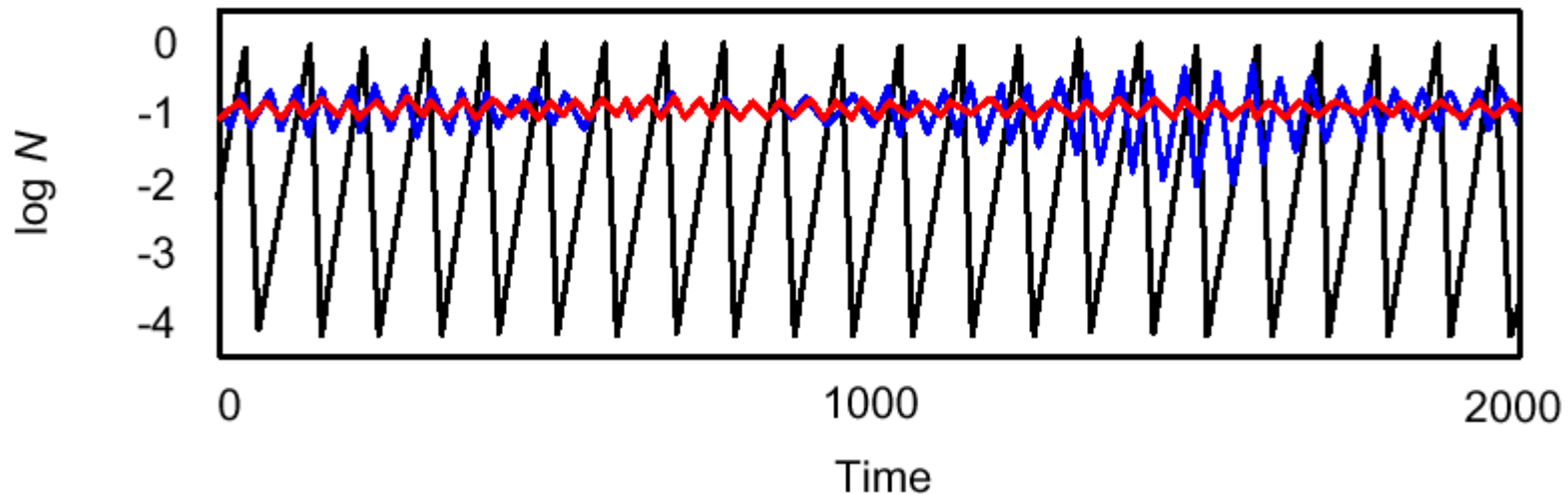


With many patches:



Predators and prey in space

- The isolated, coupled and mean dynamics:



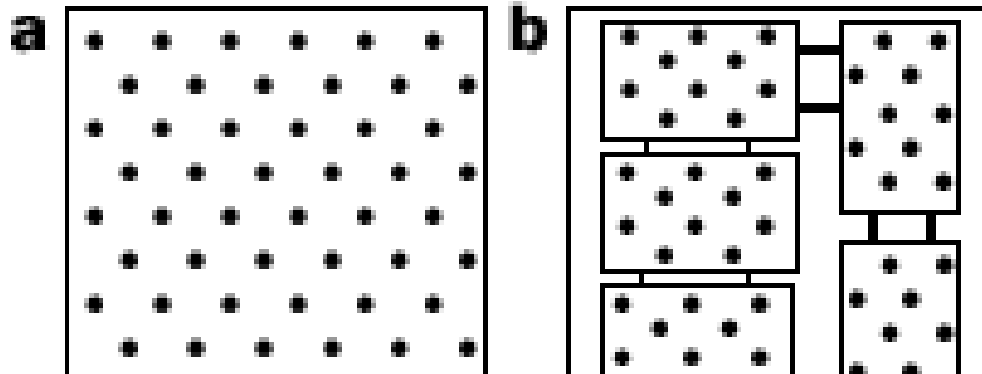
In a spatial system predator and prey populations do not oscillate as much and are less likely to become extinct

Spatial interactions

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

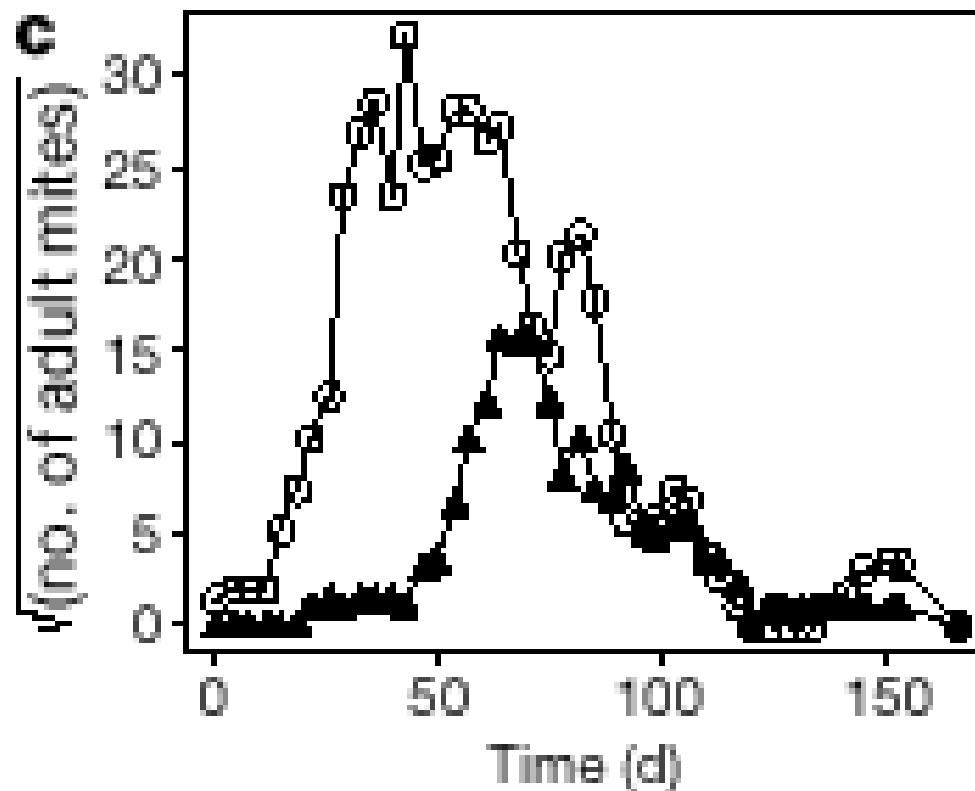
Spatial interactions

- Description of Janssen's experiment



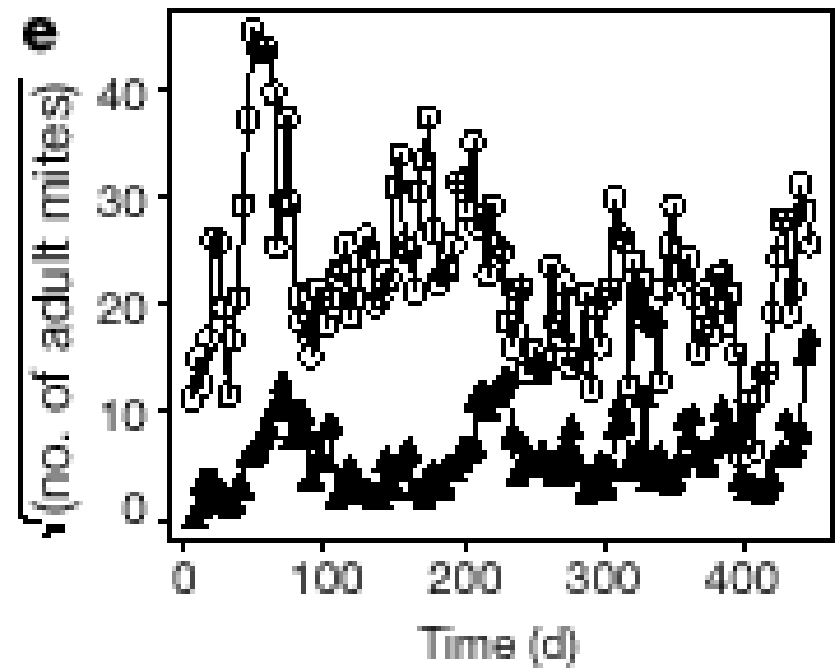
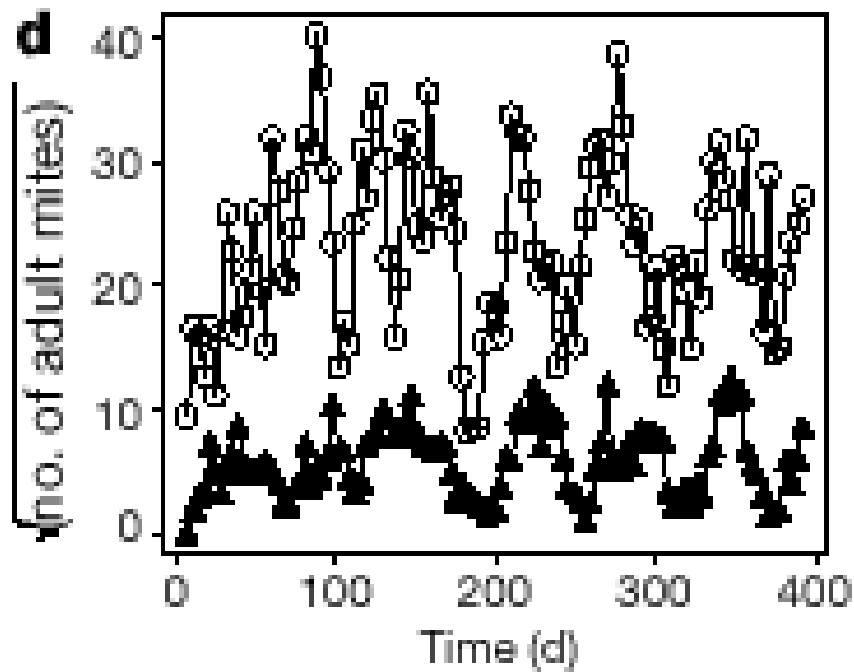
Spatial interactions

- Result in the single island system



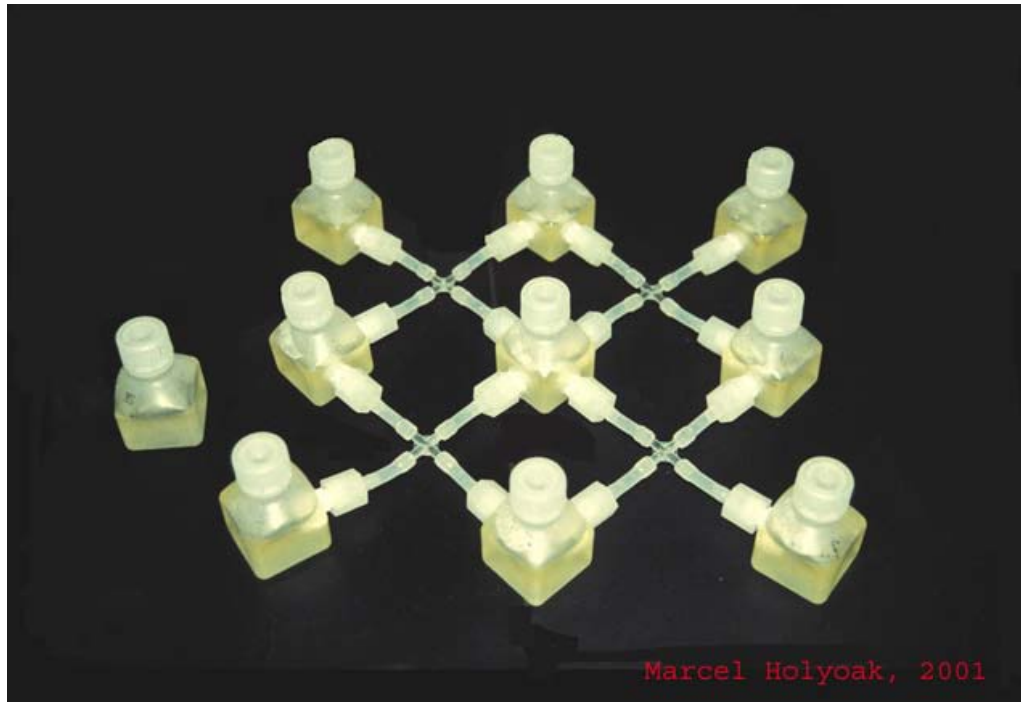
Spatial interactions

- Result in the coupled islands system



Spatial interactions

- Another example:



Prey: *Colpidium striatum*



Predator: *Didinium nasutum*

- 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