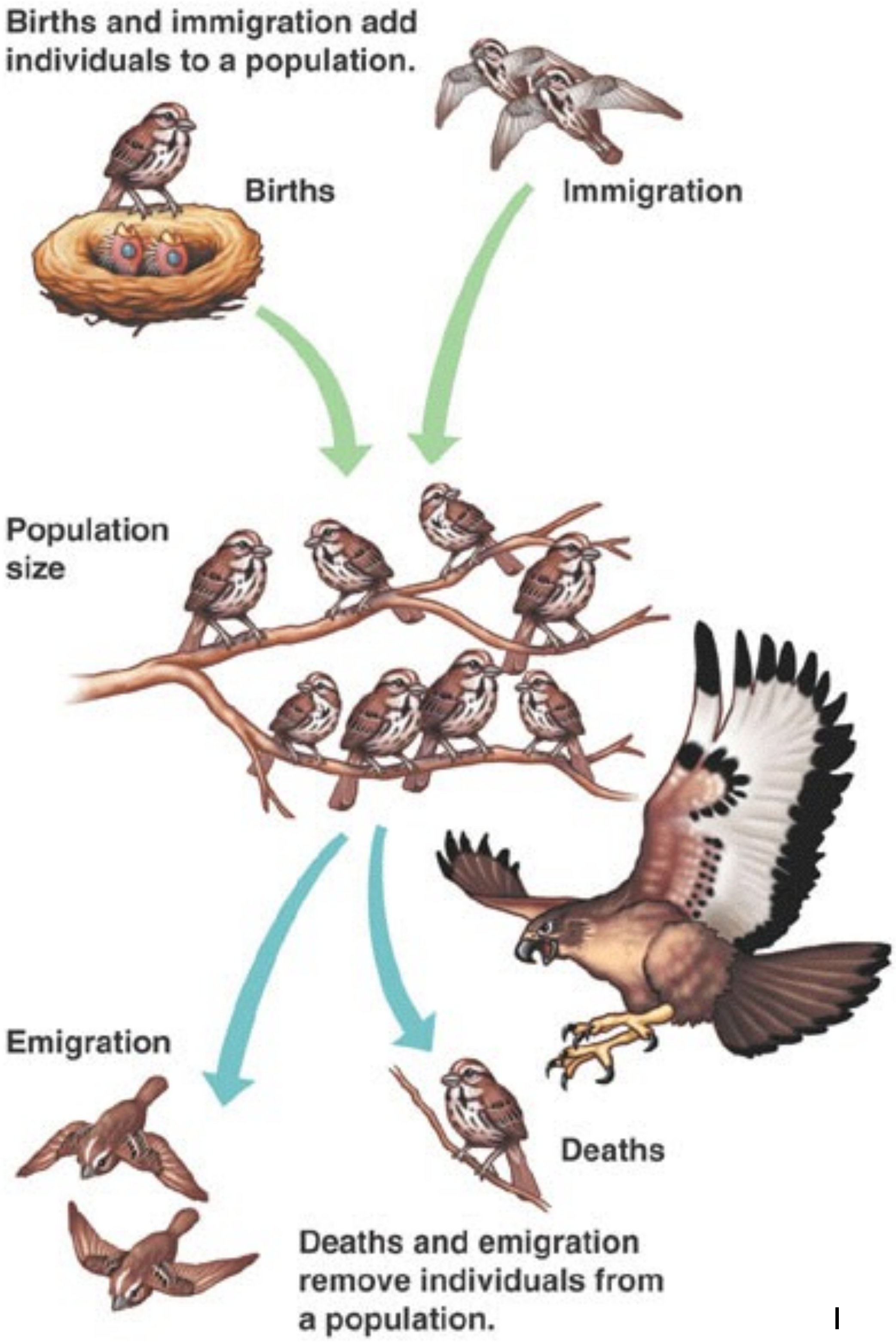


Chapter 4

Functional Response

Theoretical Biology 2016

What will your learn today?

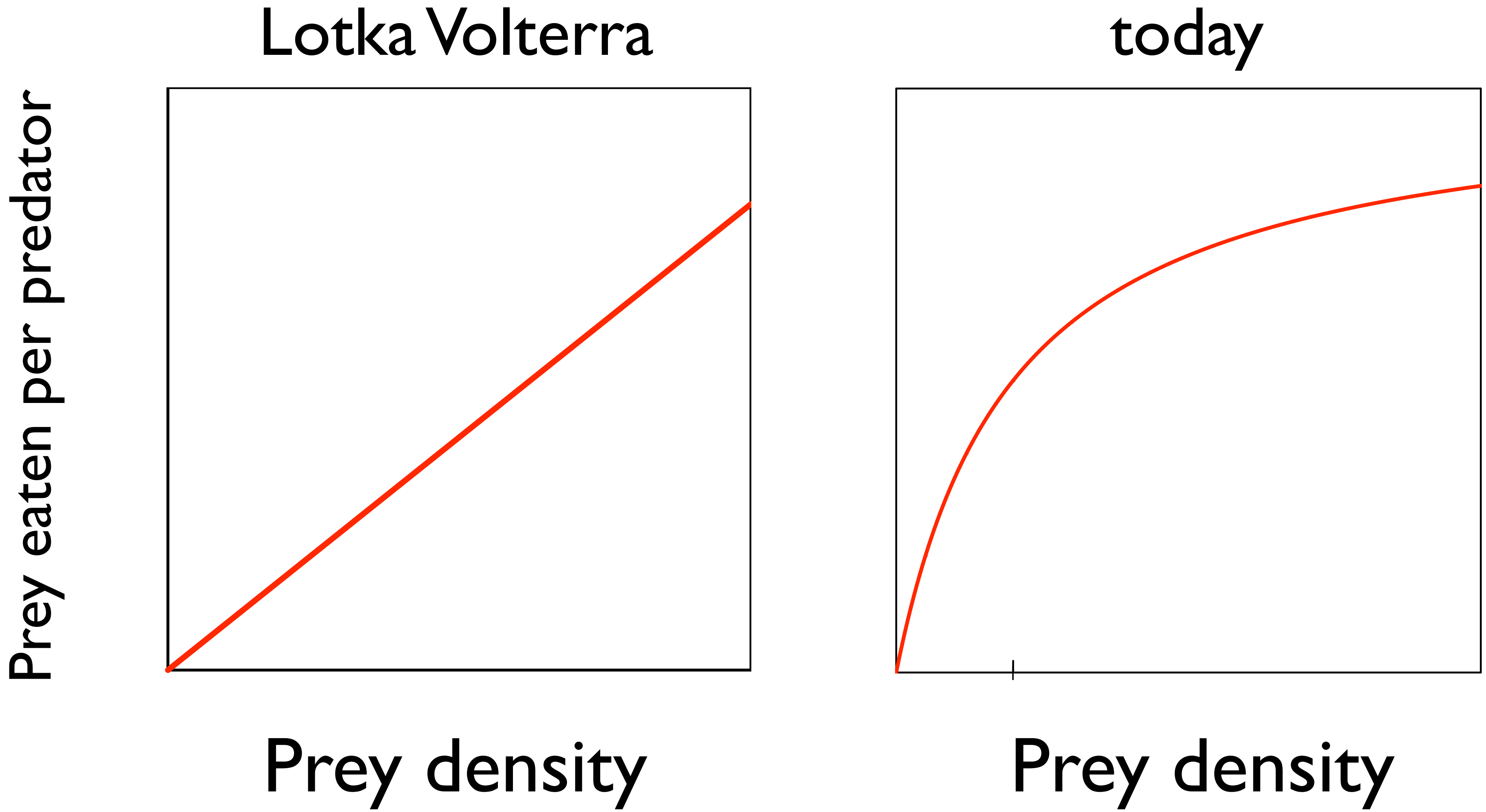
To work with a saturated functional response.

The humped prey nullcline.

To understand the nature of oscillations.

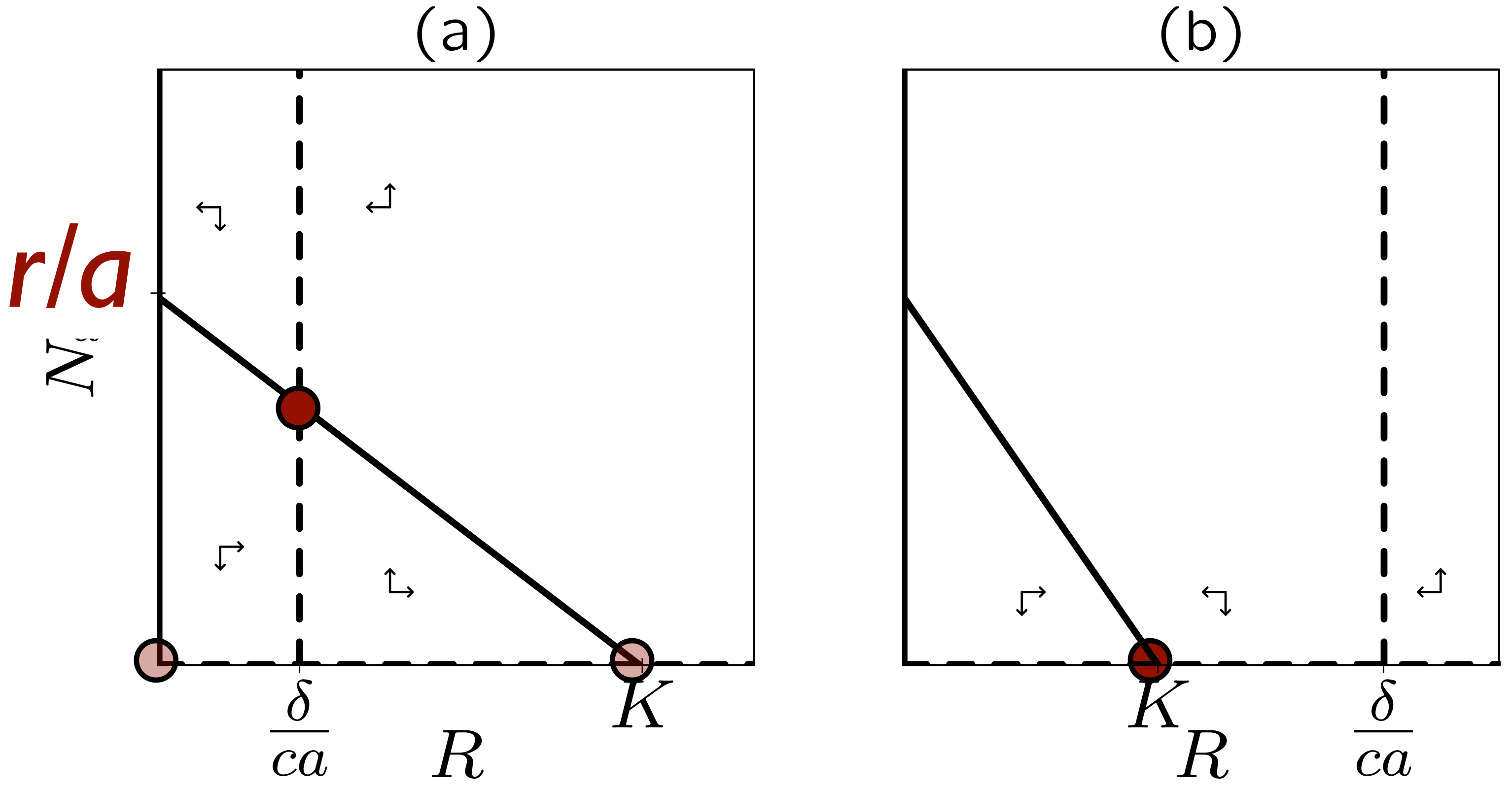
A new R_0 of the predator.

Number of prey eaten per predator



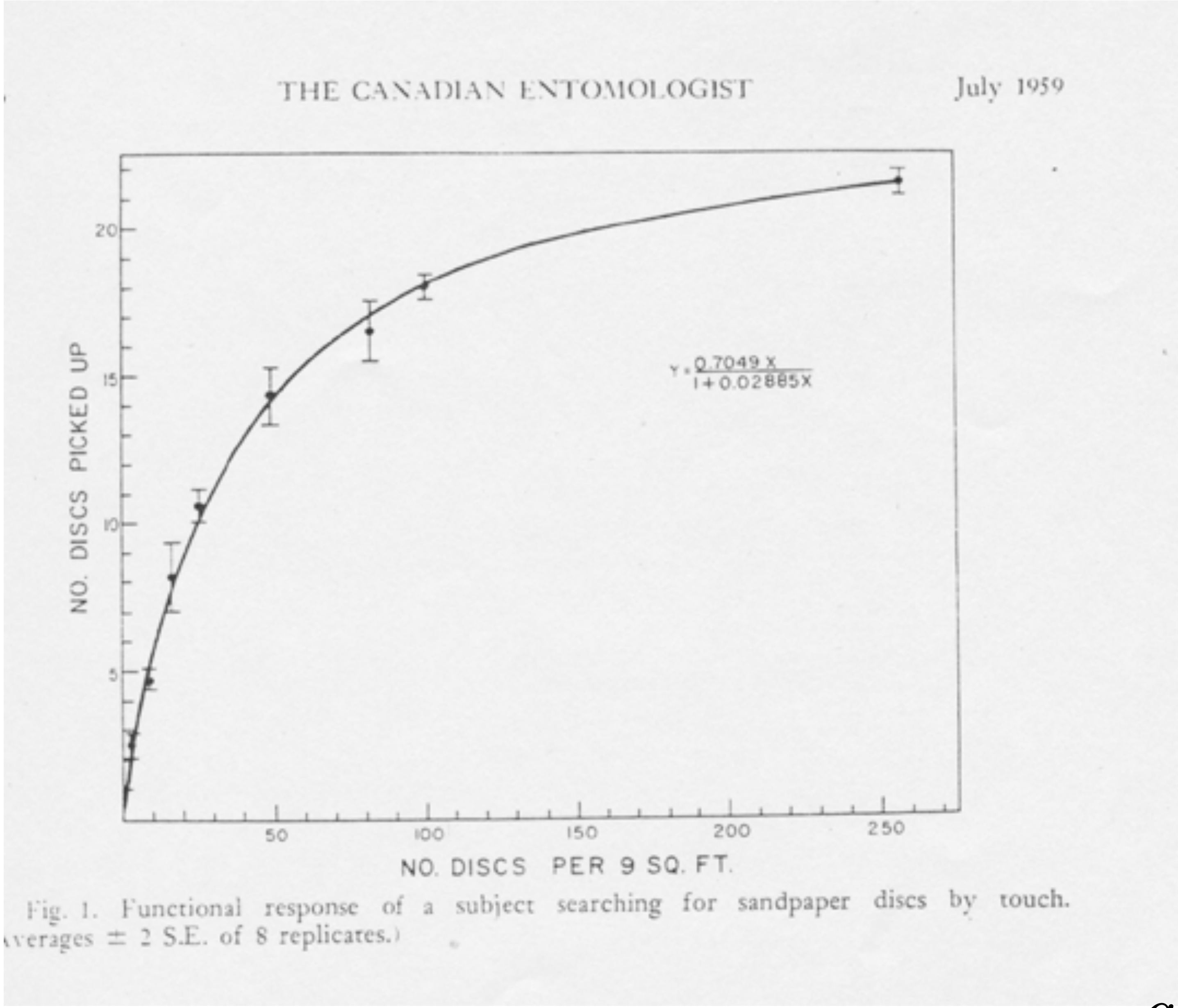
At some prey density the predator should become satiated, and/or become limited by the time to handle all the prey

LV-model has a linear functional response



$$\frac{\mathrm{d}R}{\mathrm{d}t} = [r(1 - R/K) - aN]R \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

Holling's secretary: handling sand paper discs

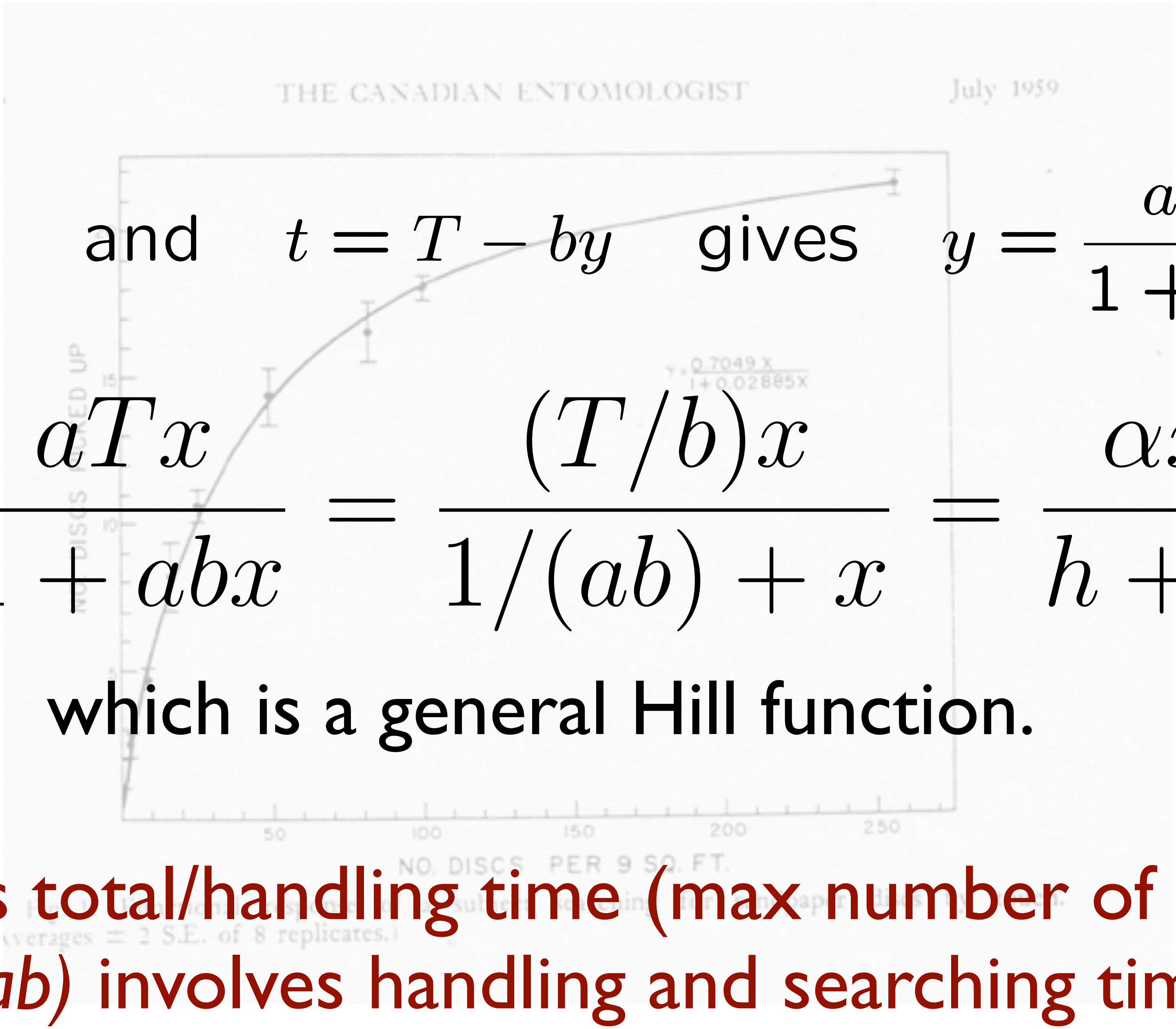


THE CANADIAN ENTOMOLOGIST July 1959

Fig. 1. Functional response of a subject searching for sandpaper discs by touch. verages ± 2 S.E. of 8 replicates.)

$y = atx$ and $t = T - by$ gives $y = \dfrac{aTx}{1 + abx}$

Holling's secretary: handling sand paper discs



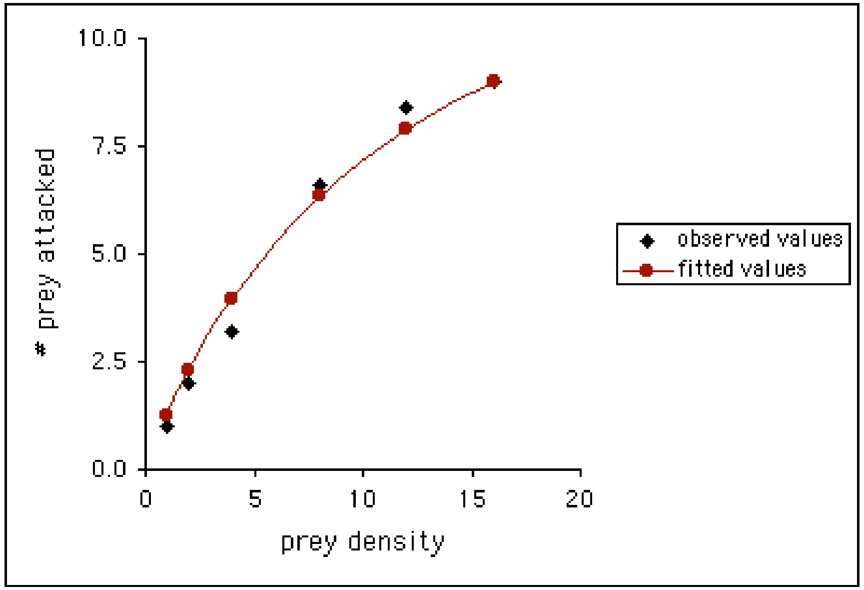
$y = atx$ and $t = T - by$ gives $y = \dfrac{aTx}{1 + abx}$

$$y = \frac{aTx}{1 + abx} = \frac{(T/b)x}{1/(ab) + x} = \frac{\alpha x}{h + x}$$

which is a general Hill function.

α=*T*/*b* is total/handling time (max number of prey)
h=1/(*ab*) involves handling and searching times

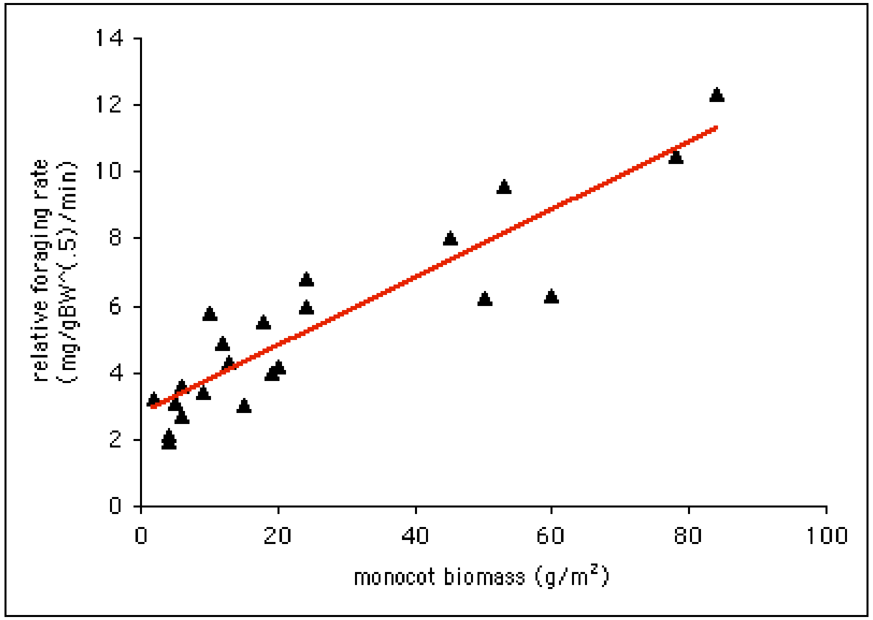
Monod functional response (type II)



Predatory stinkbug (*Podisus maculiventris*) in the lab feeding on larvae of Mexican bean beetle.

Fitted to: $y = \frac{aTR}{1+aT_hR}$ where a is attack rate, $T = 14$ h is total time, and $T_h = 0.9$ h is handling time.

Linear functional response (type I)



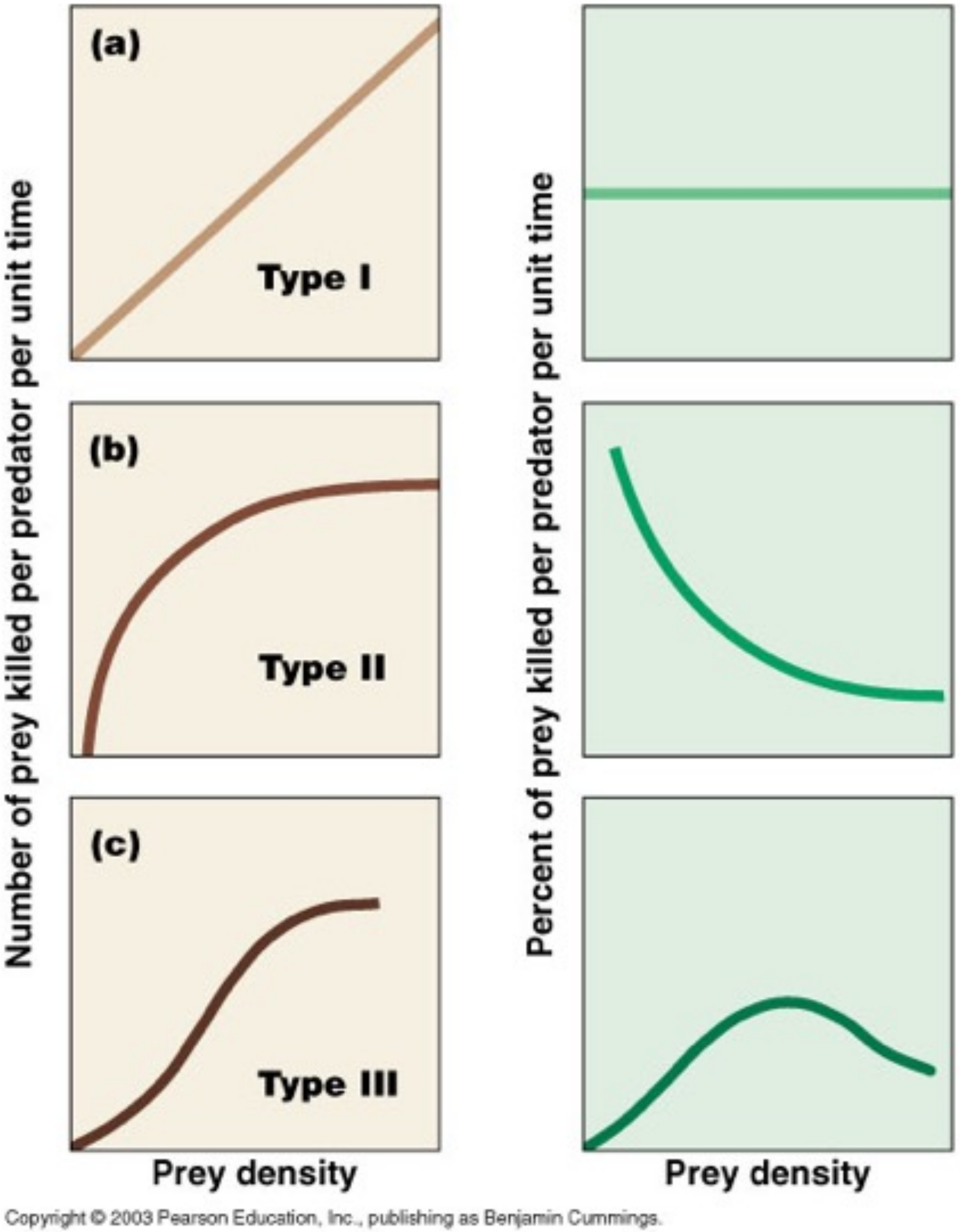
Simplest type I response, $y = ax + b$, where b is due to other prey (mosses).

Brown lemmings (*Lemmus sibericus*) foraging monocot in artic tundra.

From: Batzli *et al.*, Oikos, 1981, 37: 112-116.

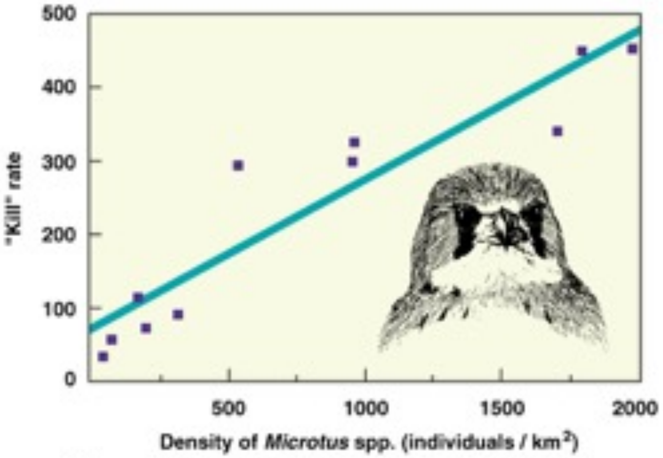
From: Wiedenmann & O'Neil, Environ. Entomol., 1991, 20: 610-614.

Holling's functional responses

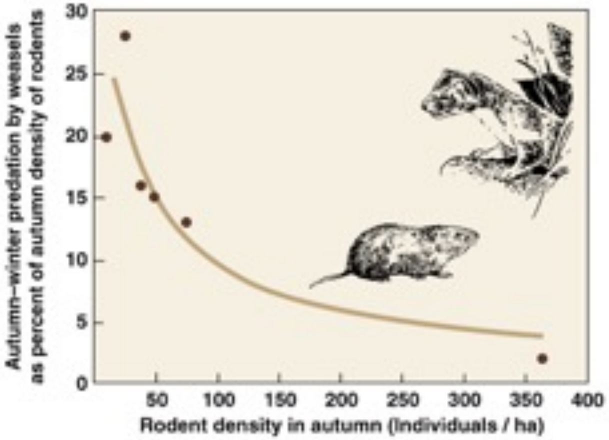


From:
Smith & Smith
Elements of
Ecology

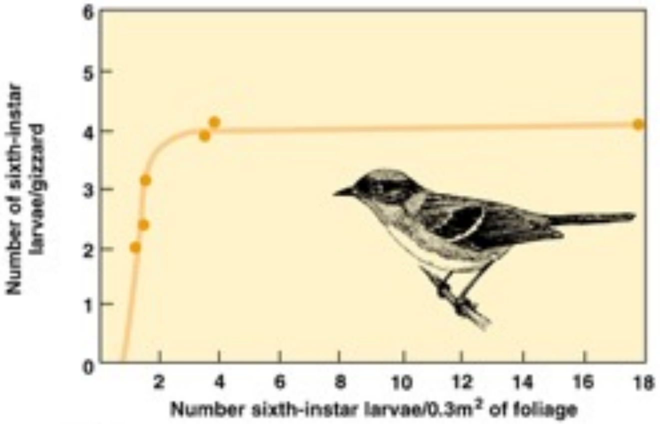
Holling’s functional responses



(a)



(b)

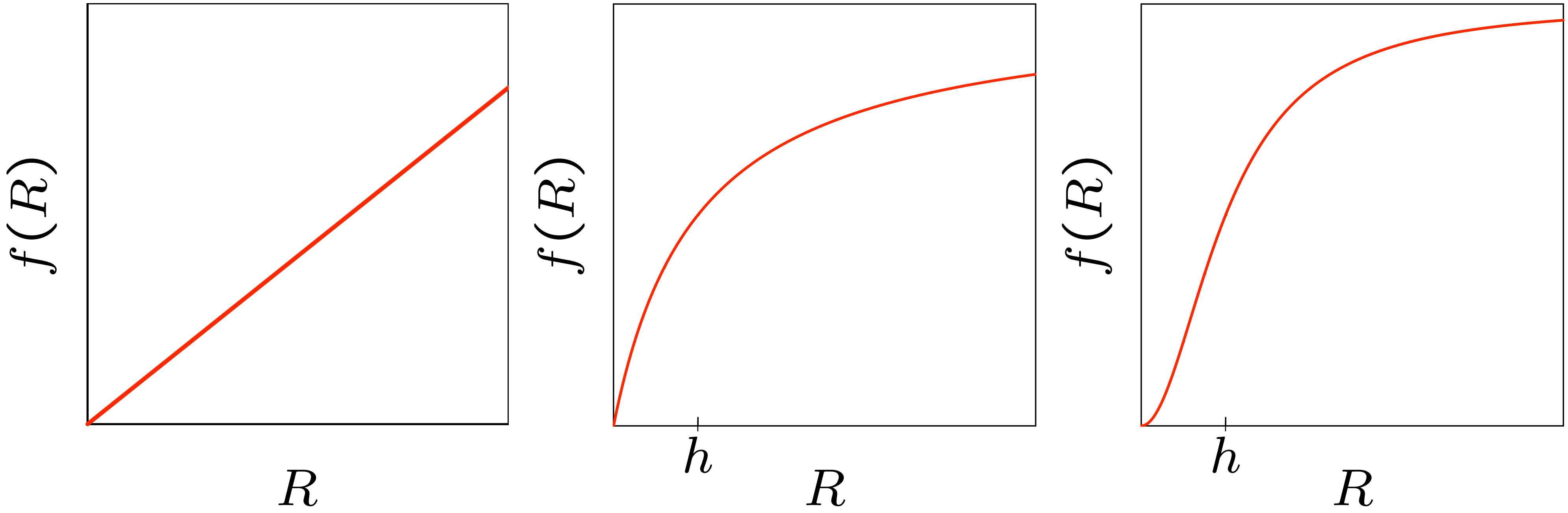


(c)

European kestrel on *Microtis* vole (a),
weasels on rodents in forests in Poland (b),
and warblers on spruce budworm larvae (c).

From:
Smith & Smith
Elements of Ecology

Today: three formal functional responses



Plotting the number of prey eaten per predator as a function of the prey density R.

$$f(R) = aR\ , \quad f(R) = \frac{aR}{h+R} \quad \text{and} \quad f(R) = \frac{aR^2}{h^2+R^2}$$

Monod predator prey model

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aNR}{h+R}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{caNR}{h+R} - dN$$

No R_0 of the prey.

For the predator we take $R_0 = ca/d$,

which is realized at large prey densities.

(instead of $R_0 = caK/[d(h+K)]$)

Nullclines

To sketch the nullclines we write dR/d$t = 0$ to find

$$R = 0 \quad \text{and} \quad N = (r/a)(h + R)(1 - R/K)$$

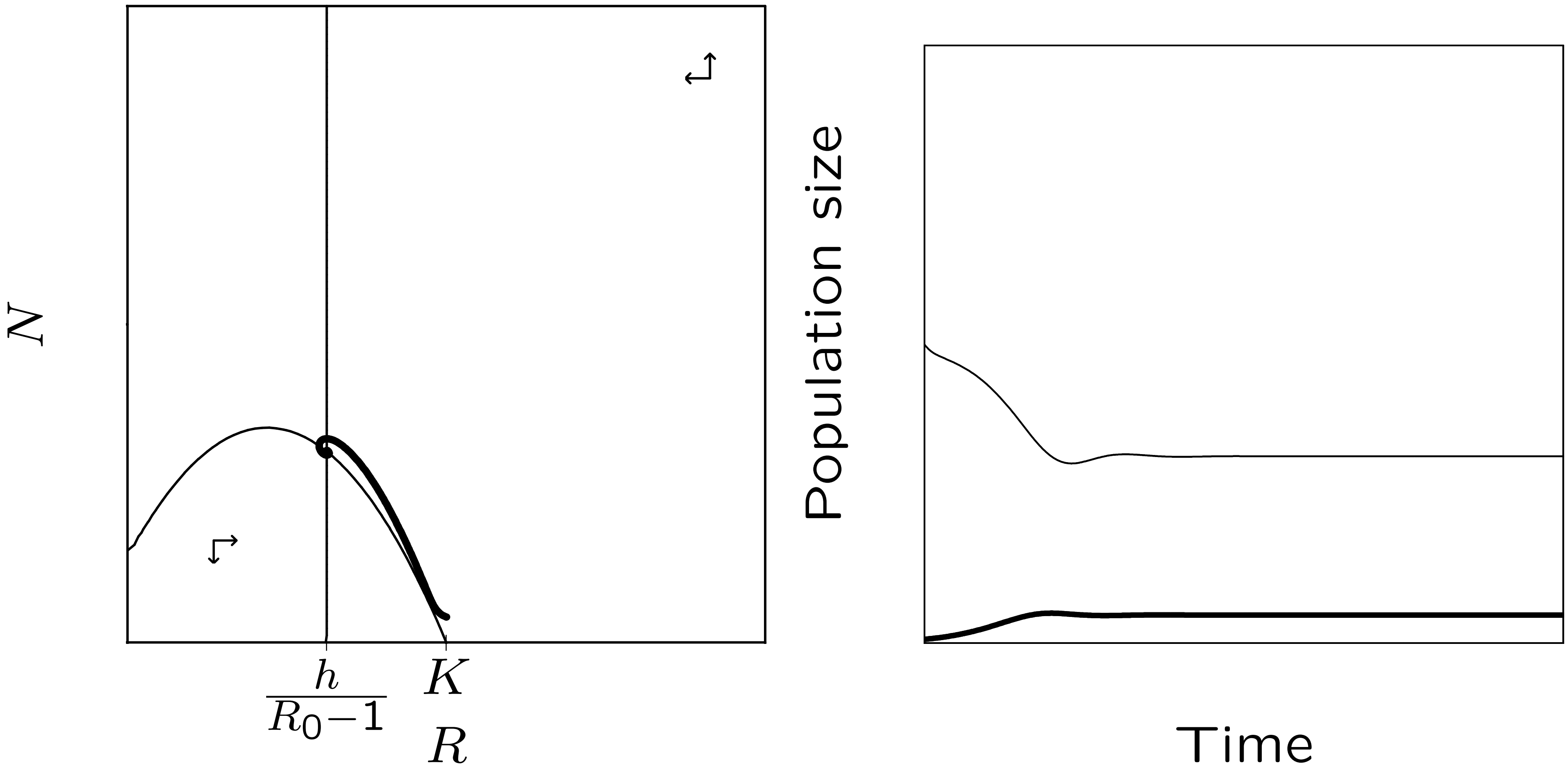
where the latter describes a parabola that equals zero when $R = -h$ and $R = K$.

For the predator nullcline we write dN/d$t = 0$ to find

$$N = 0 \quad \text{or} \quad R = \frac{h}{ac/d - 1}$$

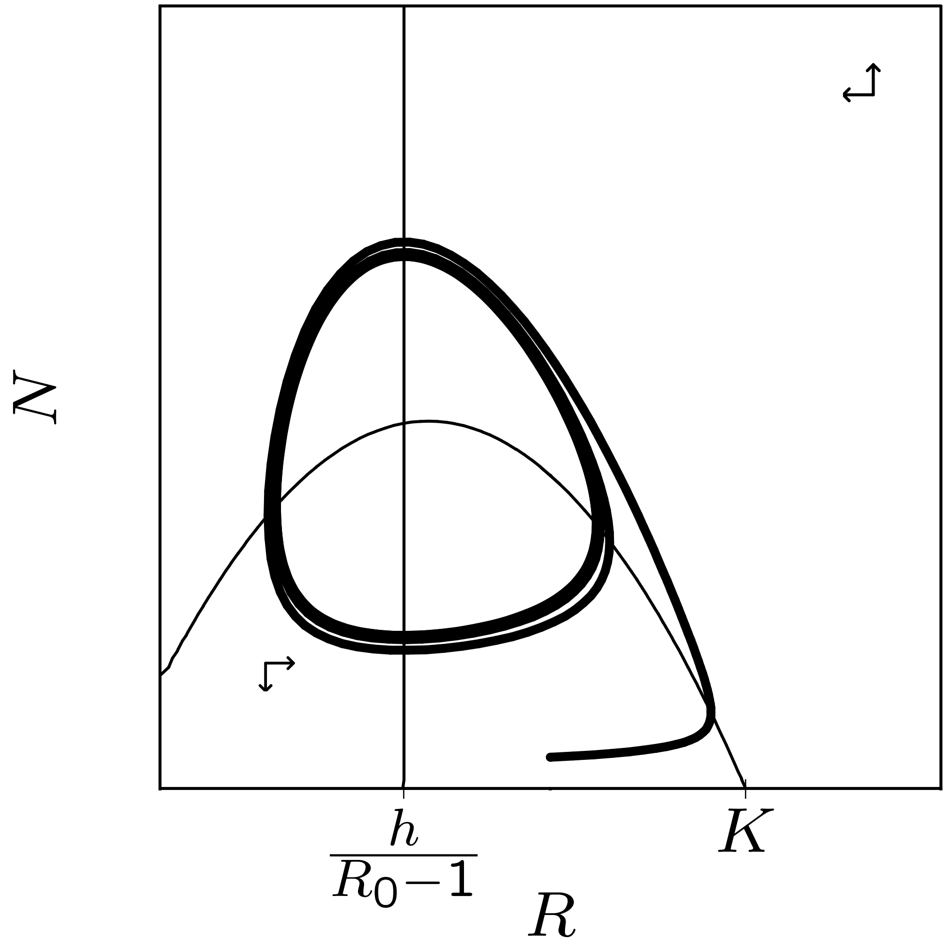
which are horizontal and vertical lines in the phase space.

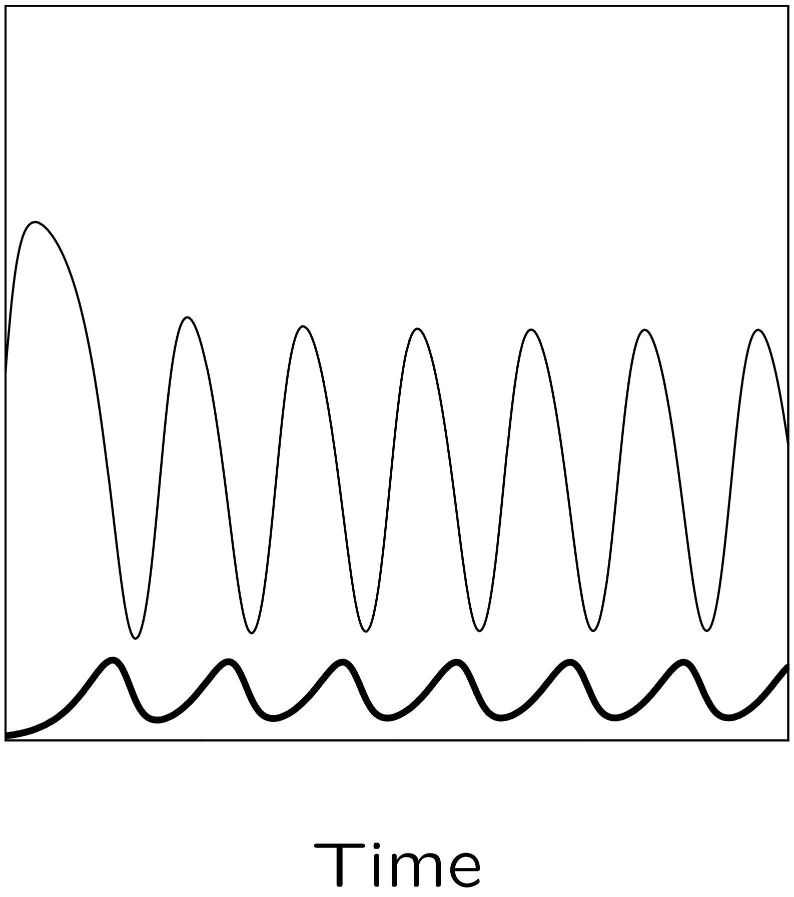
Nullclines



Predator nullcline on the right slope of parabola:
Stable steady state

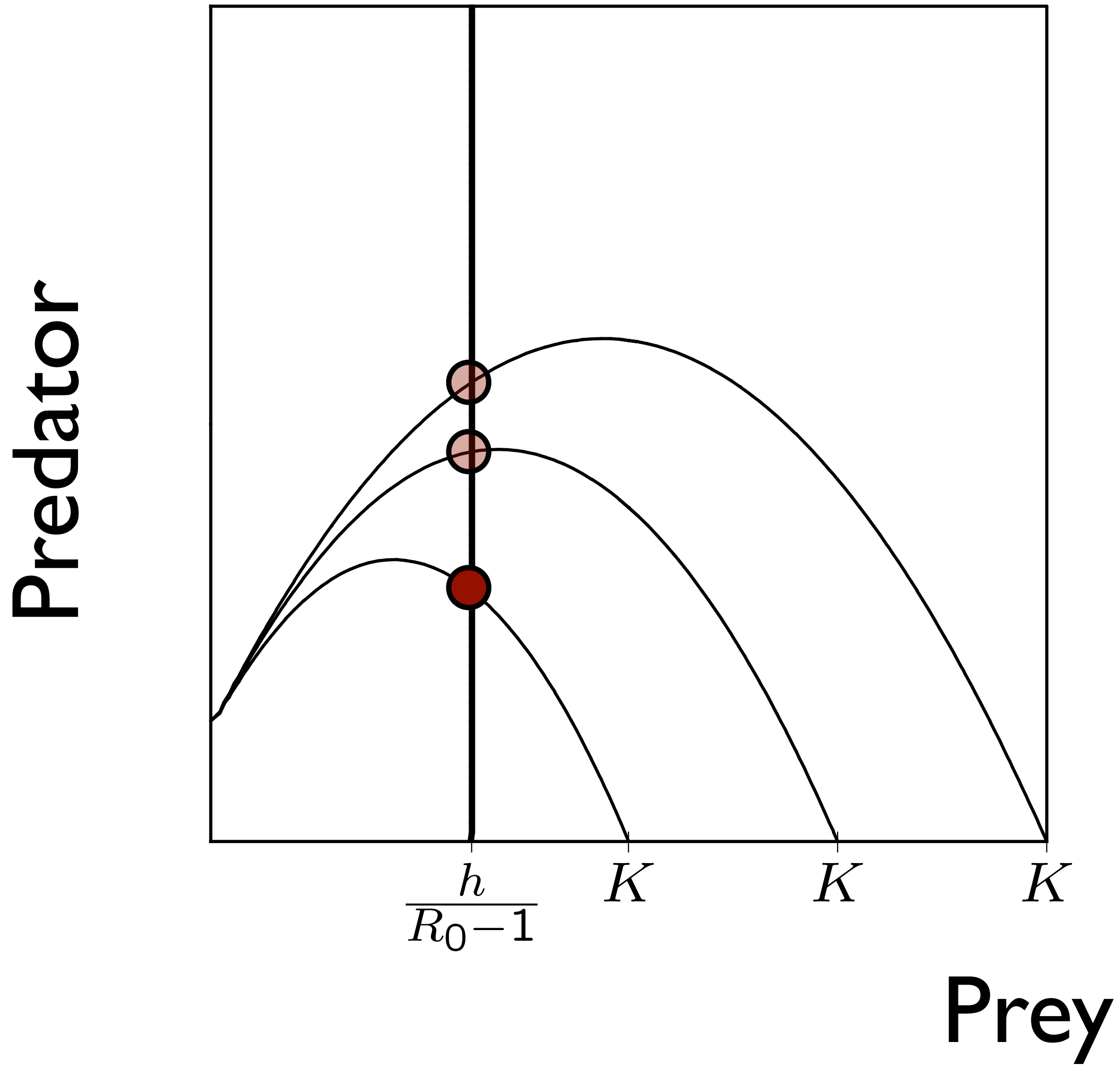
Nullclines





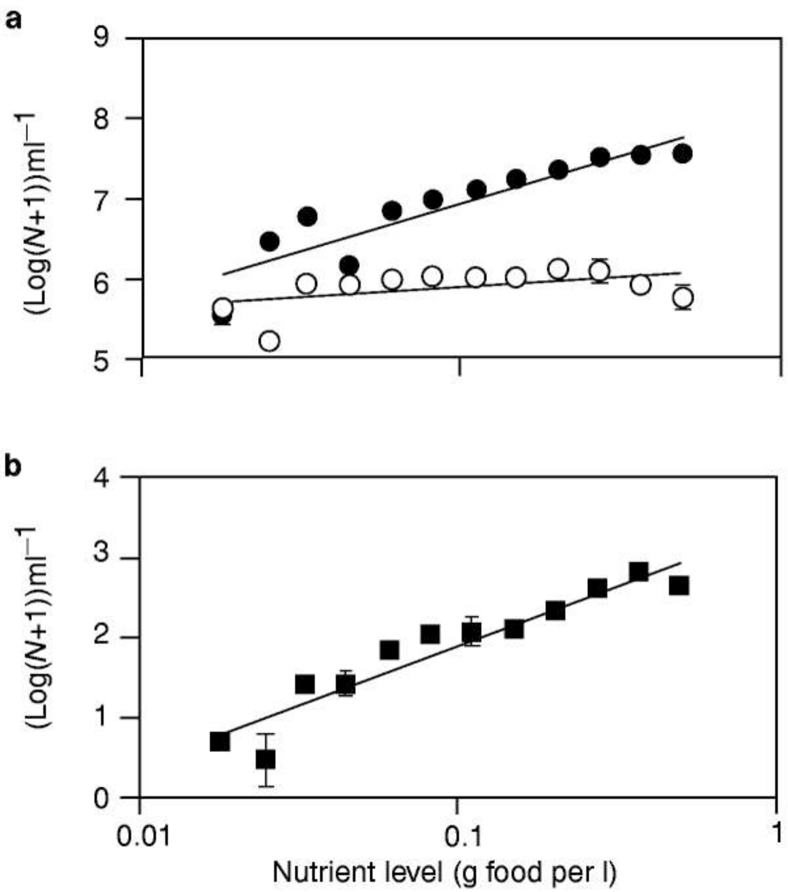
Predator nullcline on the left slope of parabola:
Unstable steady state & stable limit cycle

Paradox of enrichment



Increasing the prey's carrying capacity increases the predator's steady state level

Paradox of enrichment: bacterial food chain



← Predator

Colpidium striatium

← Prey with predator

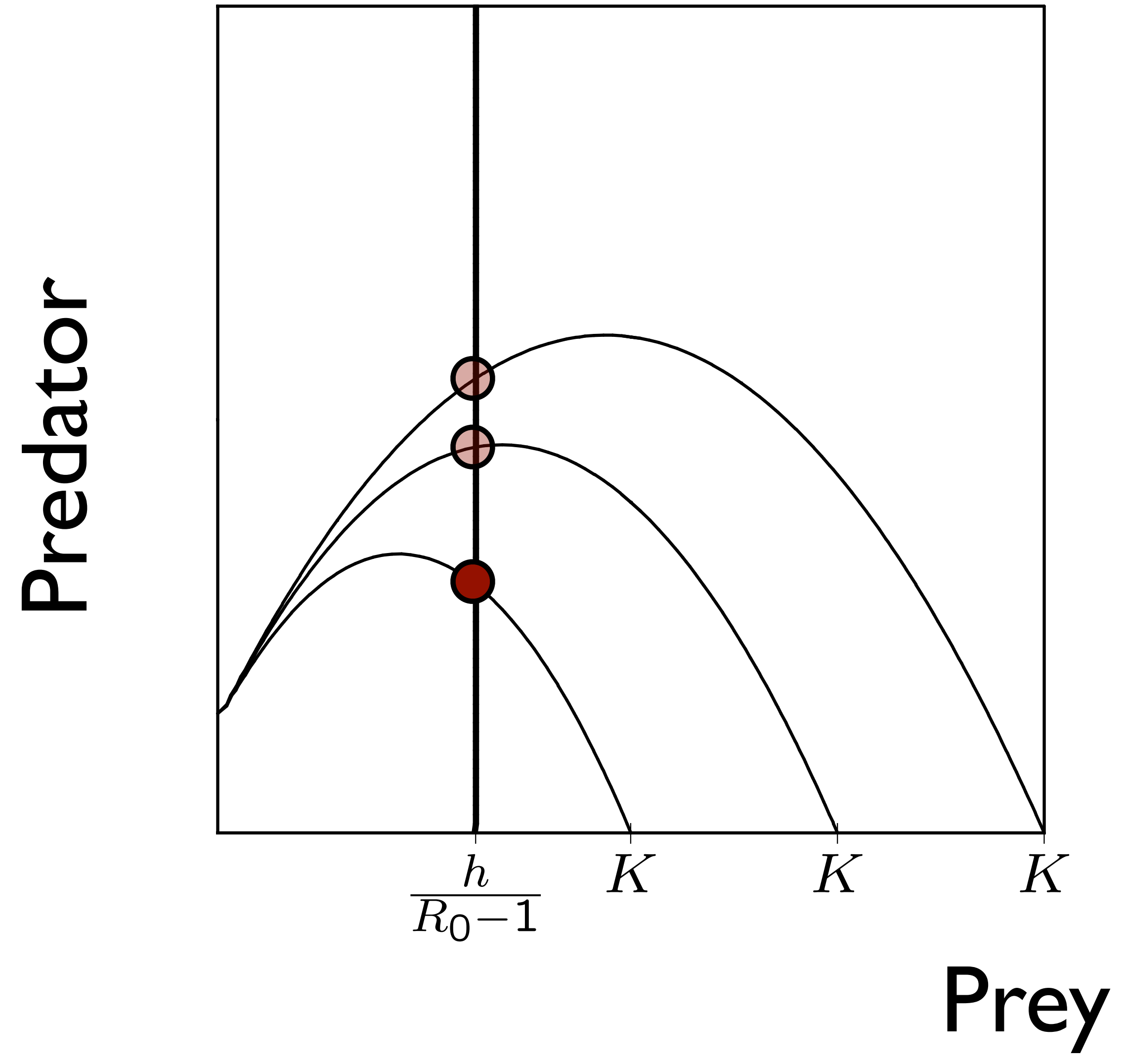
Serratia marcescens

← Prey alone

Serratia marcescens

(b): The effect of nutrients on the density of *prey*
(a): The same for prey (a: open circles) and a predator (a: closed circles).
From: Kaunzinger et al. Nature 1998.

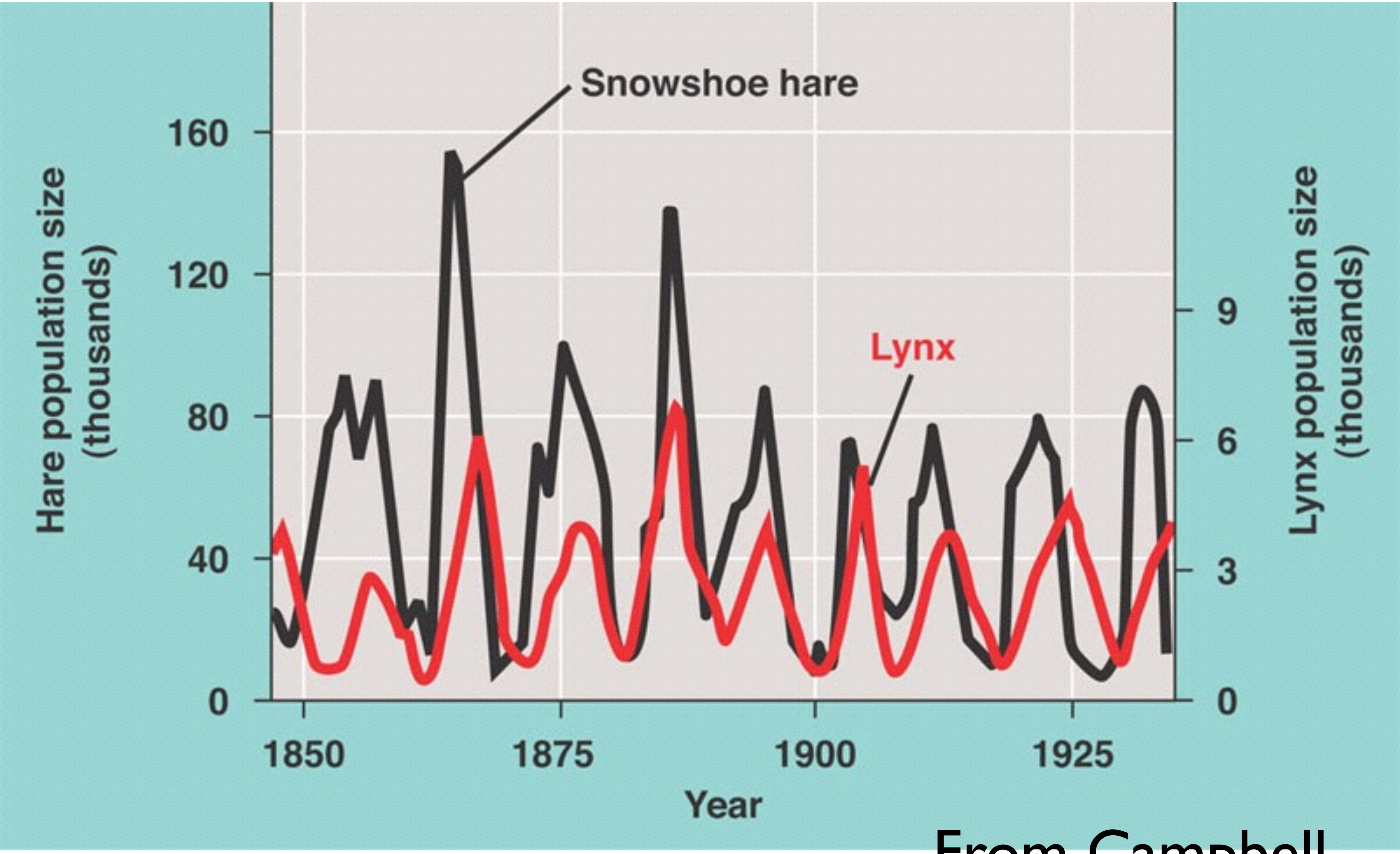
Enrichment leads to destabilization



Steady state goes from stable spiral to unstable spiral

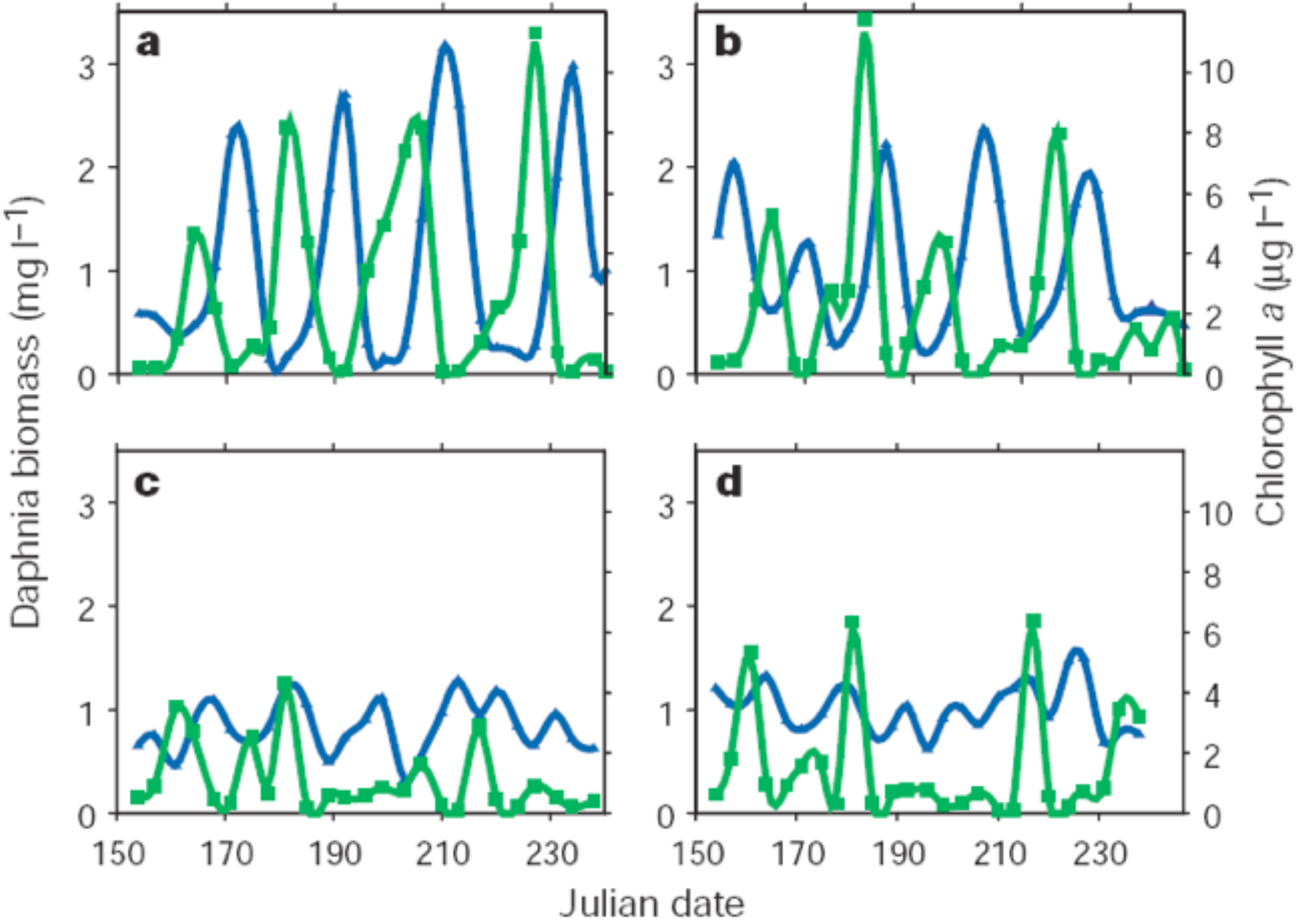
Hopf bifurcation

Population cycles: periodic behavior



From Campbell

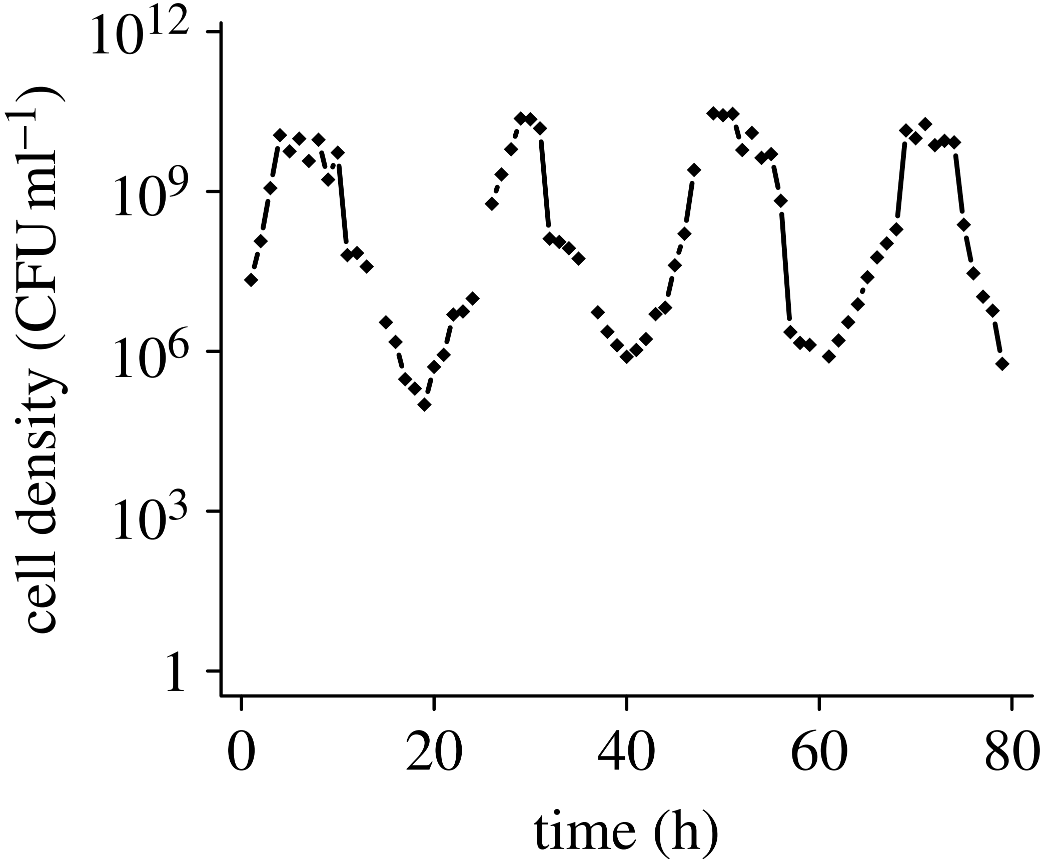
Algae zooplankton oscillations



Daphnia (blue triangles) and their edible algal prey (green squares) in four nutrient-rich systems. From: McCauley et al, Nature, 1999

Oscillations in continuous culture populations of *Streptococcus pneumoniae*: population dynamics and the evolution of clonal suicide

Omar E. Cornejo[1], Daniel E. Rozen[1,2], Robert M. May[3] and Bruce R. Levin[1,*]



PROCEEDINGS OF THE ROYAL SOCIETY B 2009

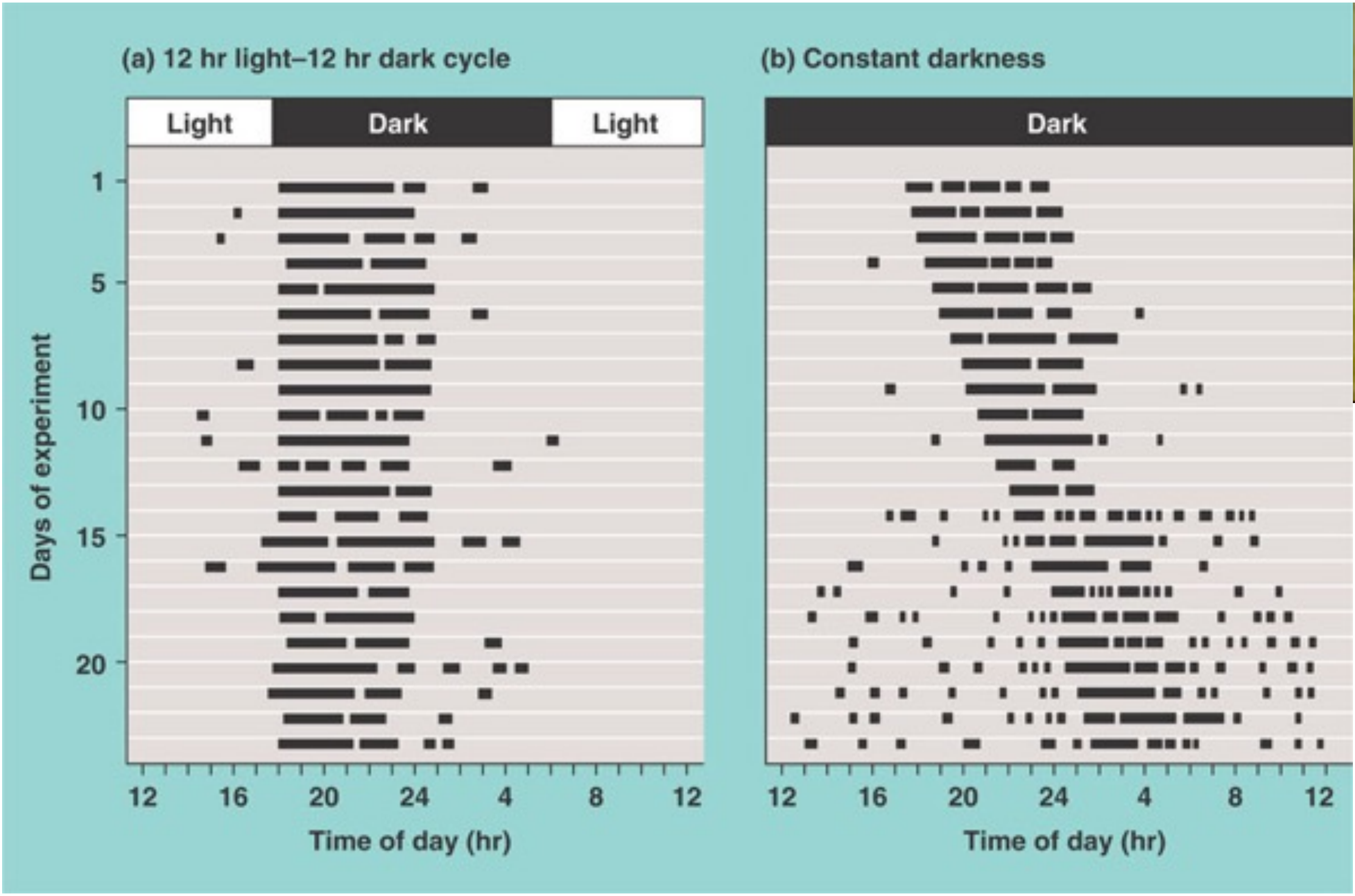
$$\frac{dR}{dt} = w(C-R) - \Psi(R)Be,$$

$$\frac{dB}{dt} = \Psi(R)B - xBT - wB,$$

$$\frac{dT}{dt} = yBT - dT - wT.$$

Resource flows in and out by chemostat, Bacteria consume resource by a Monod function, and have an autocatalytic production of a toxin. See question 4.3 (and the GRIND files toxin.grd and toxin.txt)

Circadian rhythm: rodent running


(a) 12 hr light–12 hr dark cycle

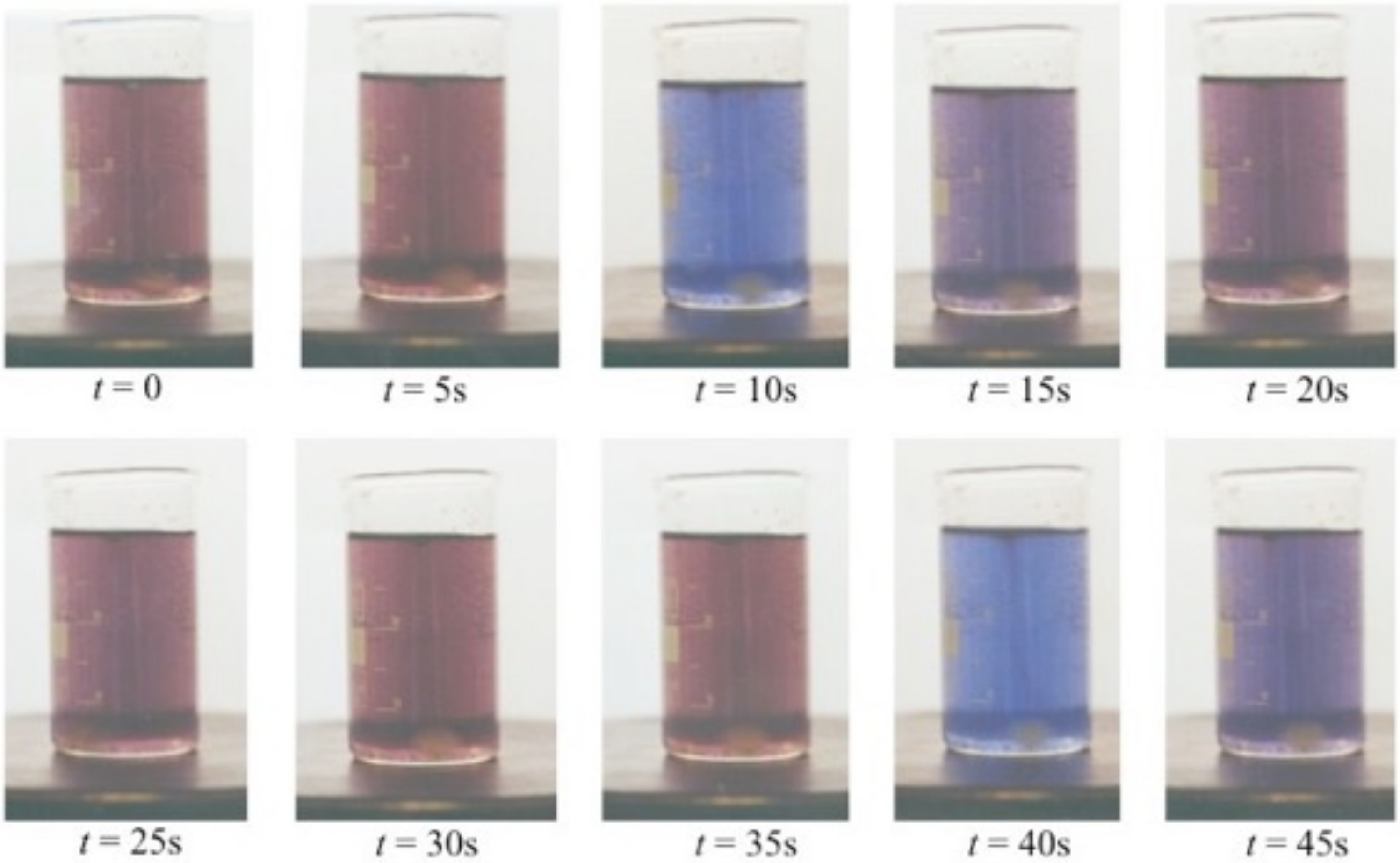
(b) Constant darkness


From: YouTube

Entrainment to external light

From: Campbell

Belousov Zhabotinsky reaction



$t = 0$ $t = 5s$ $t = 10s$ $t = 15s$ $t = 20s$

$t = 25s$ $t = 30s$ $t = 35s$ $t = 40s$ $t = 45s$

From: YouTube

Potassium bromate, cerium (IV) sulfate, propanedioic acid and citric acid in dilute sulfuric acid. The ratio of the cerium (IV) and cerium (III) ions oscillates, causing the color of the solution to oscillate between yellow colorless.

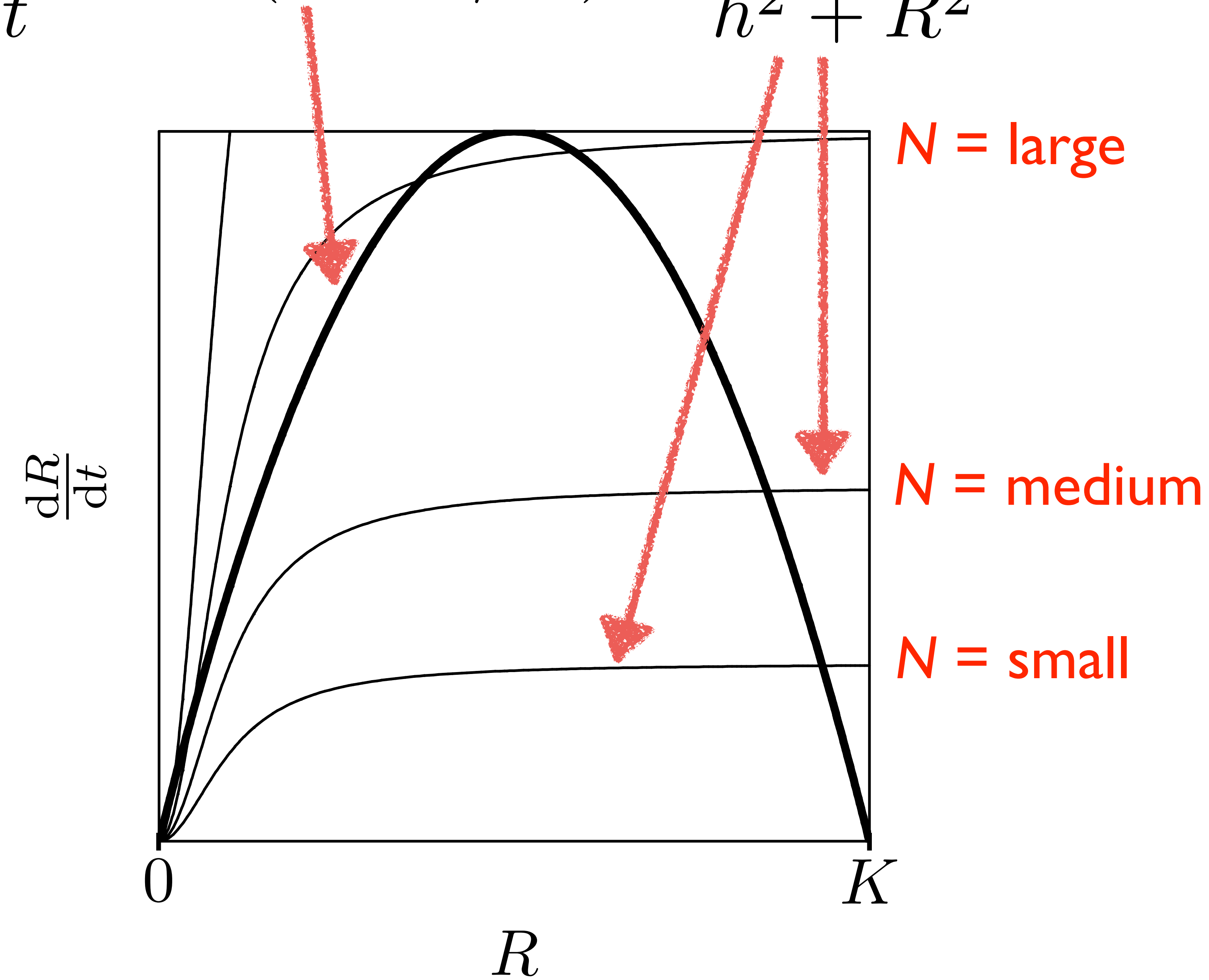
Various biological rhythms

Rhythm	Period
Neurons	0.01 to 10 sec
Heart	1 sec
Cell division	10 min to hours
Circadian	24 hours
Ovulation cycle	28 days
Ecology	years

From: YouTube

Sigmoid predator prey model

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aNR^2}{h^2 + R^2}$$



Sigmoid predator prey model

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aNR^2}{h^2 + R^2}$$