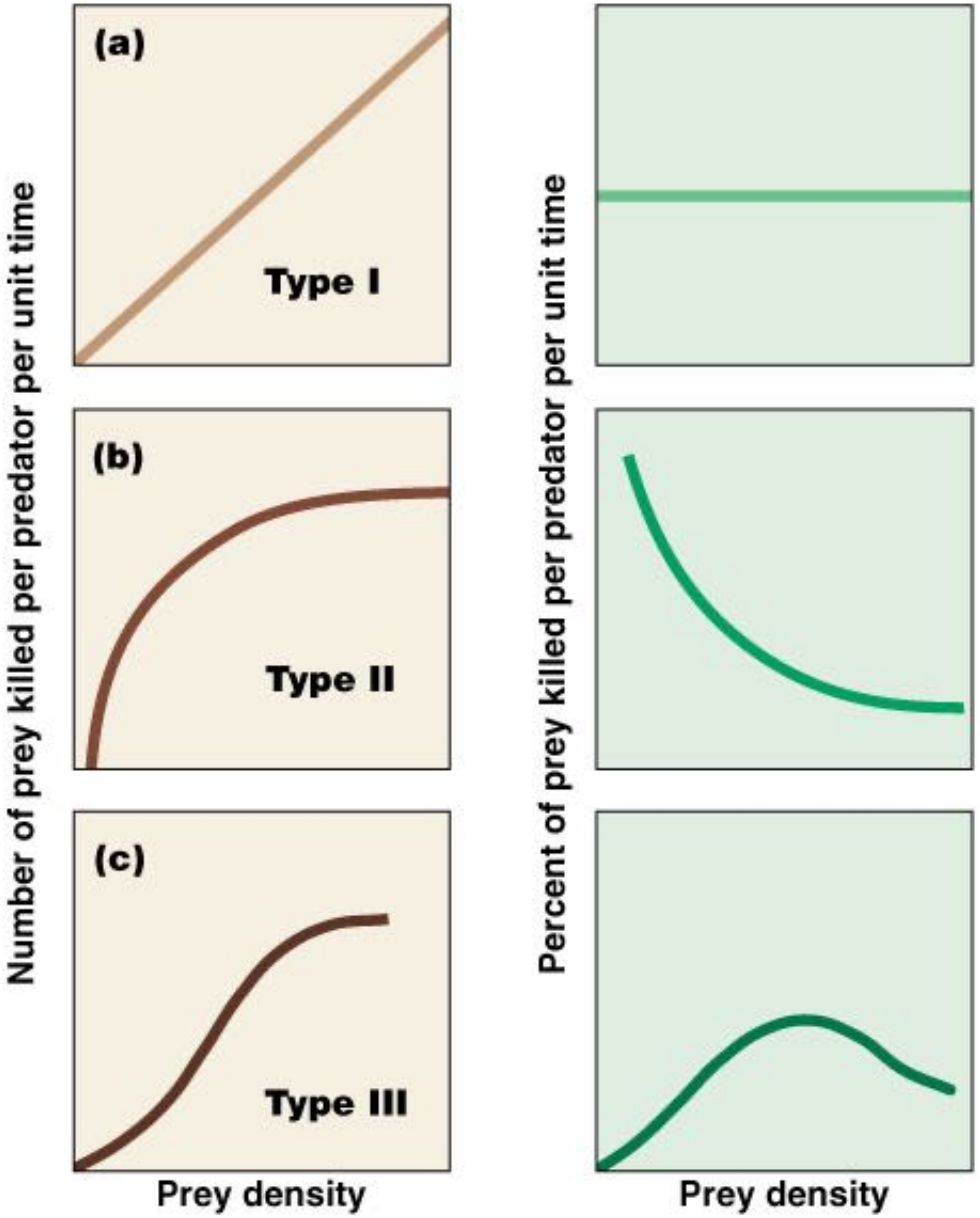
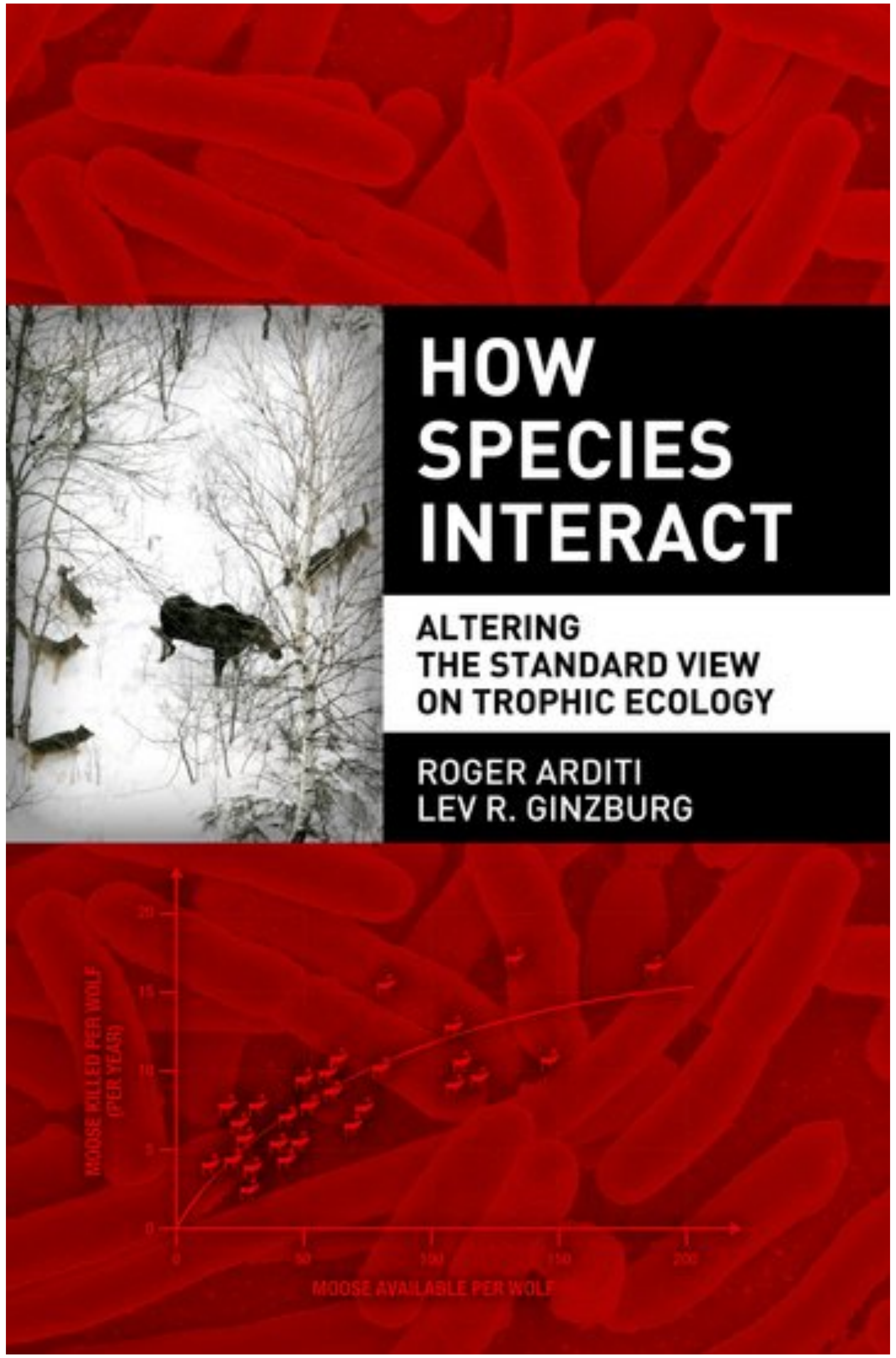
Chapter 7: Functional response





Holling's secretary: handling sand paper discs

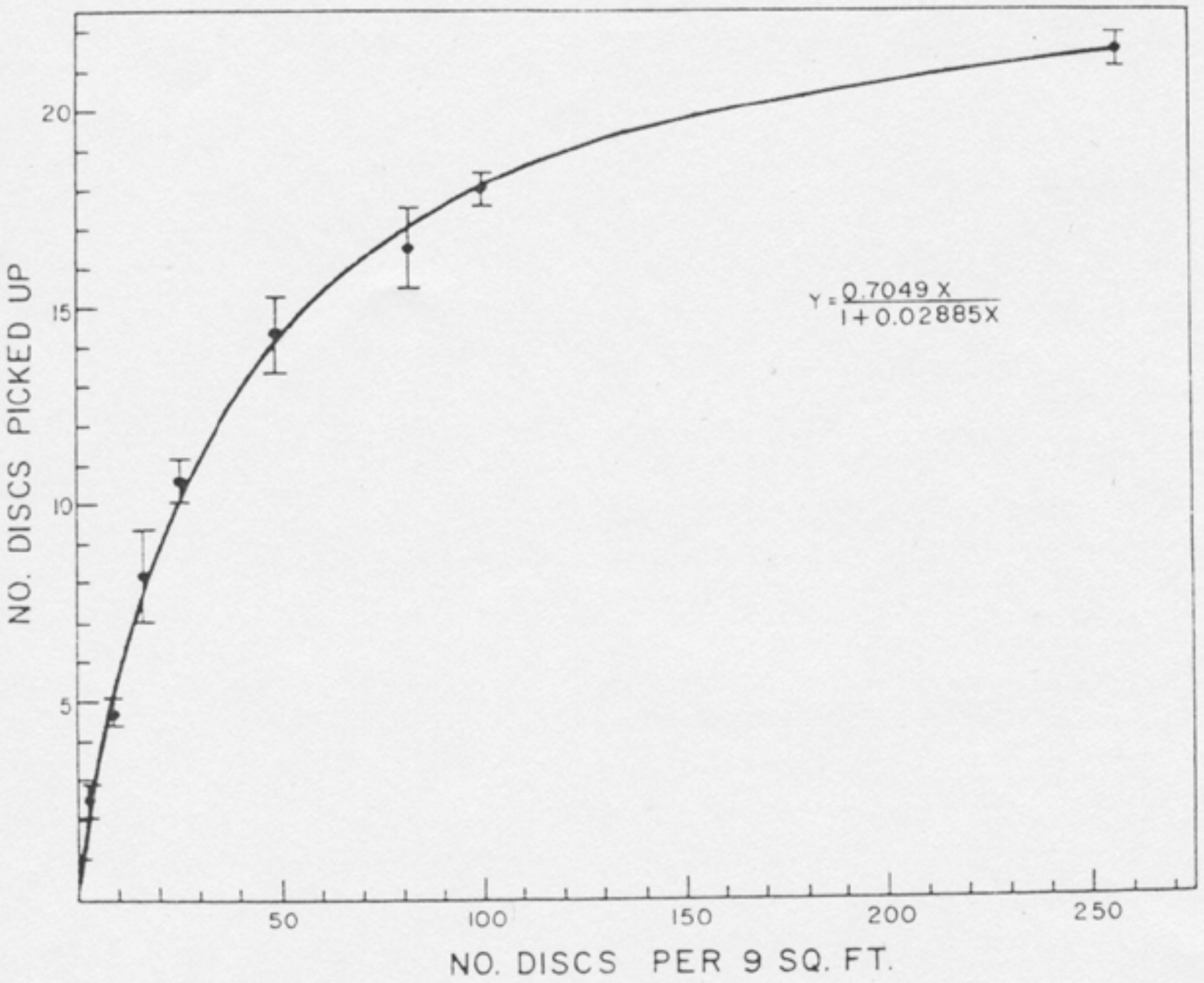


Fig. 1. Functional response of a subject searching for sandpaper discs by touch. (Averages ± 2 S.E. of 8 replicates.)

Holling's secretary: handling sand paper discs

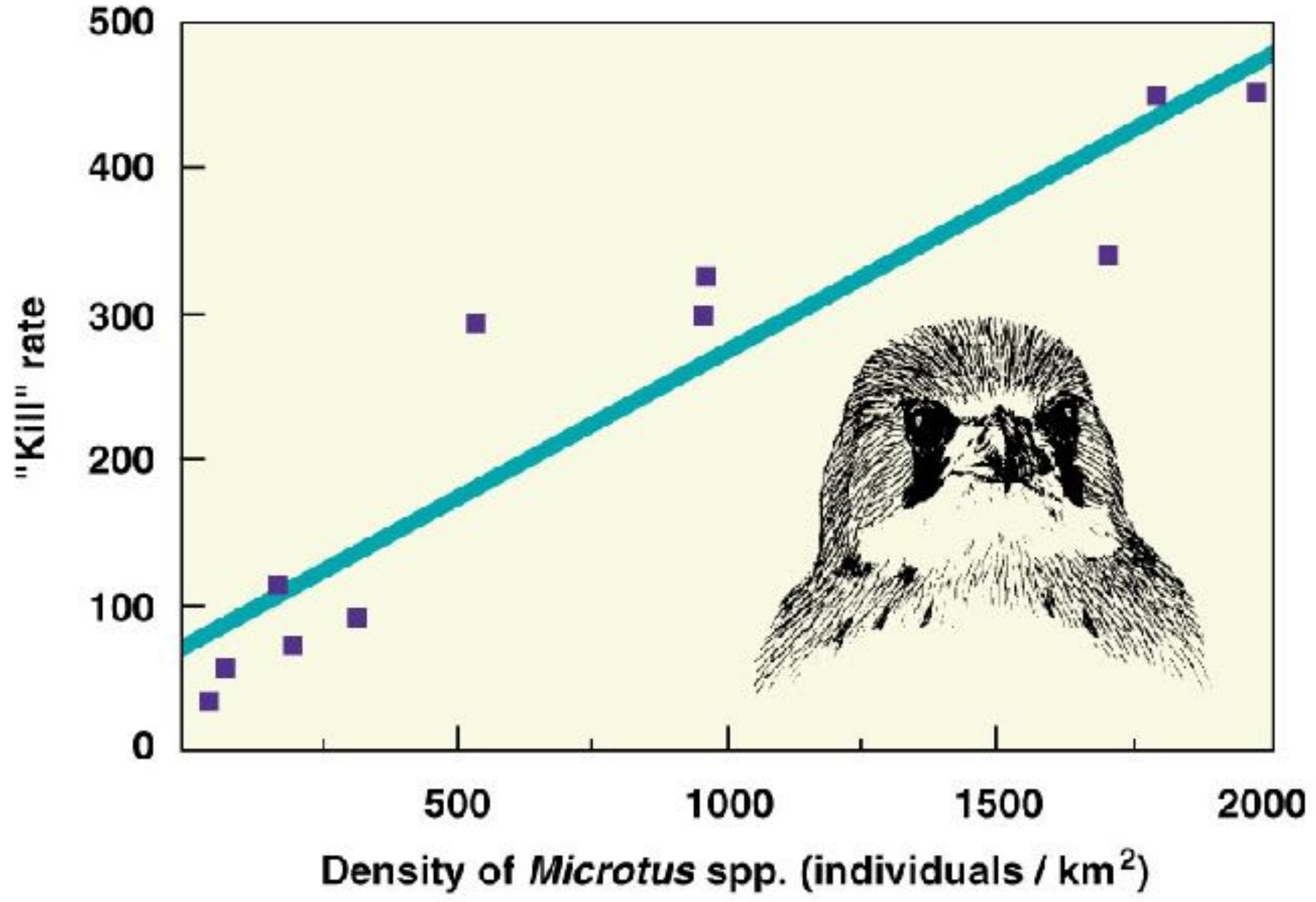
$$n = atR\ , \qquad t = T - bn$$

$$n = a(T - bn)R \quad \text{or} \quad n = \frac{aTR}{1 + abR} = \frac{a'R}{h + R}$$

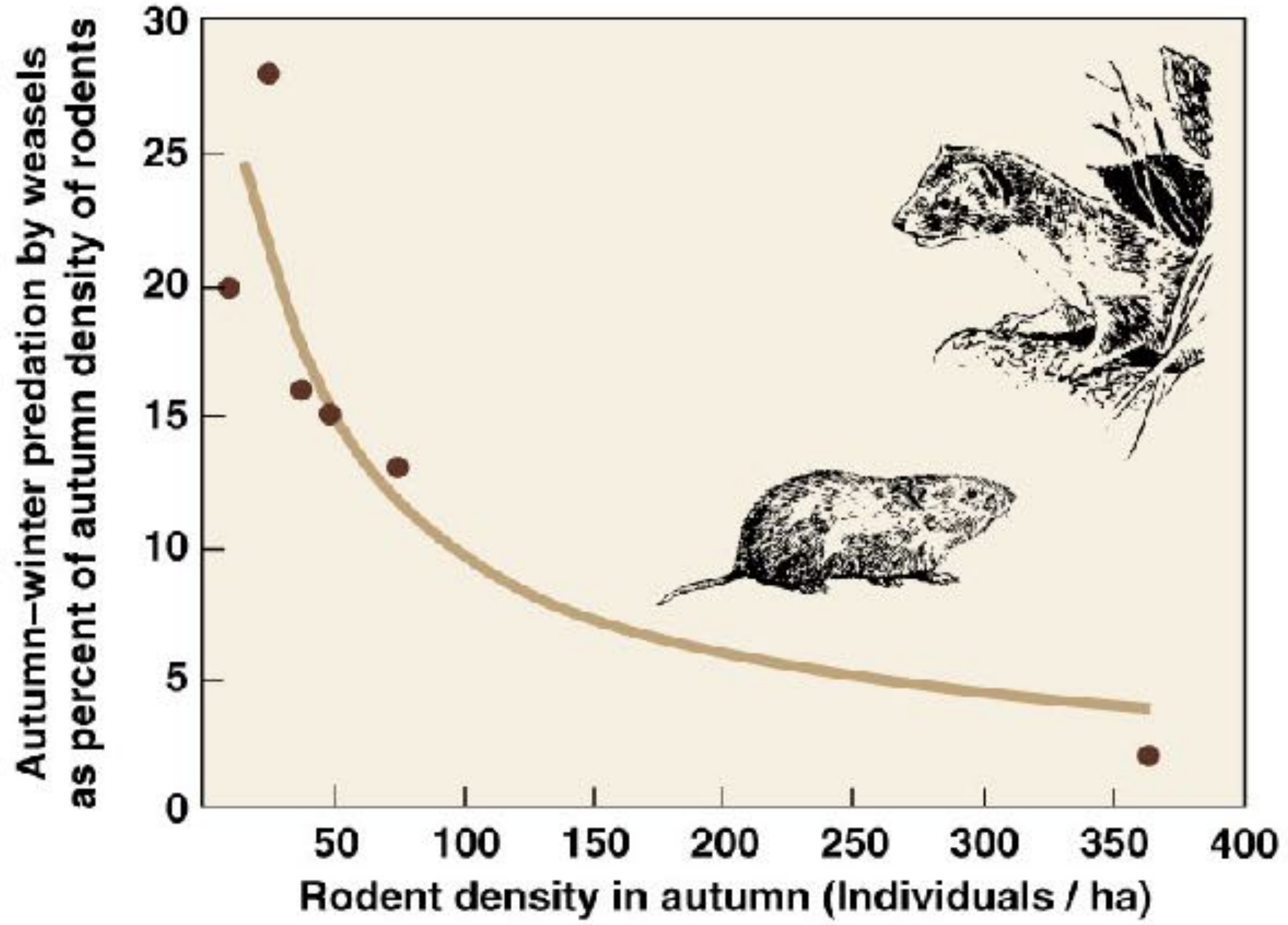
which is a general Hill function.

a'=T/b is total/handling time (max number of prey)
h=1/*(ab)* involves handling and searching times

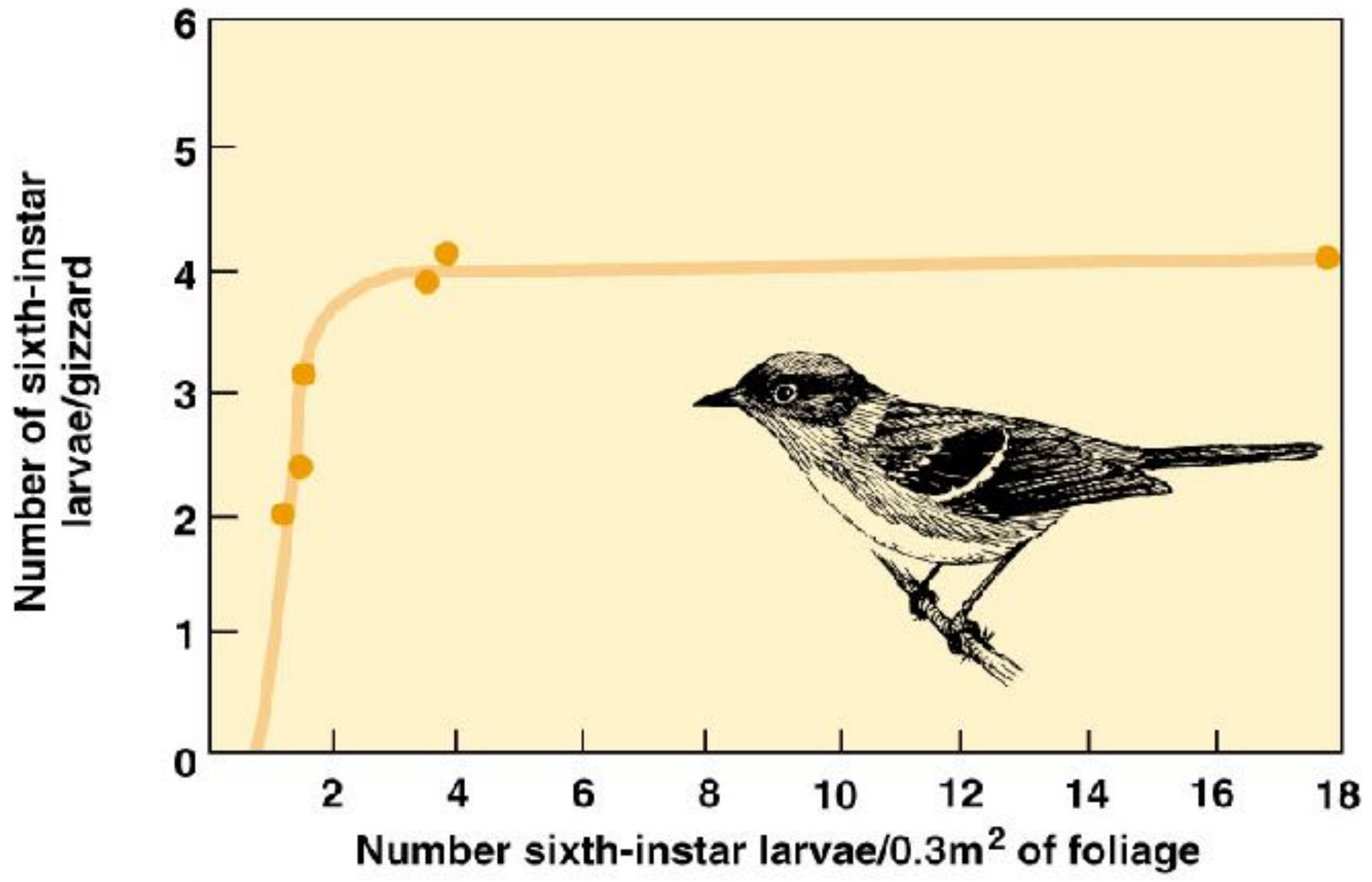
Functional response



(a)



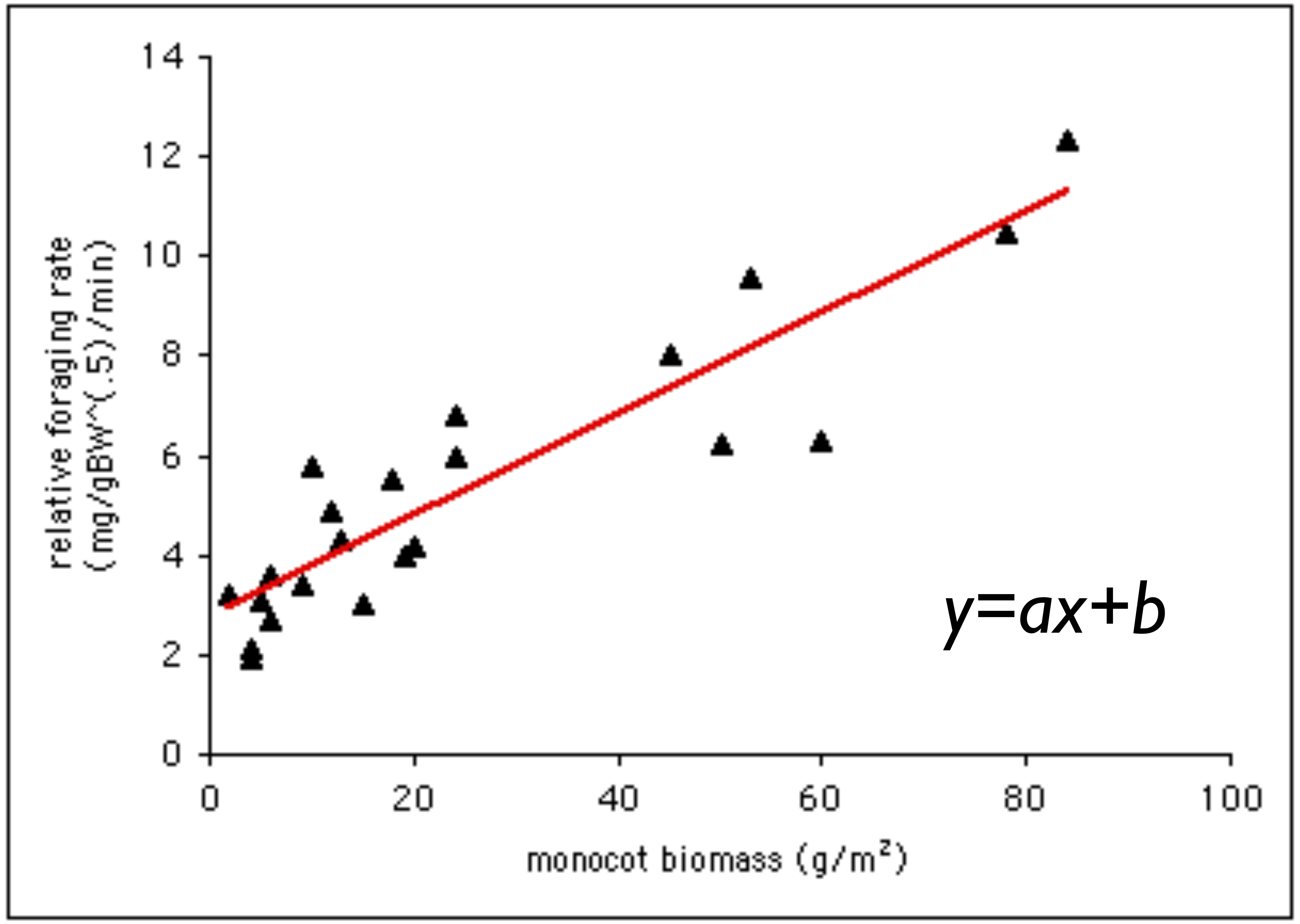
(b)



(c)

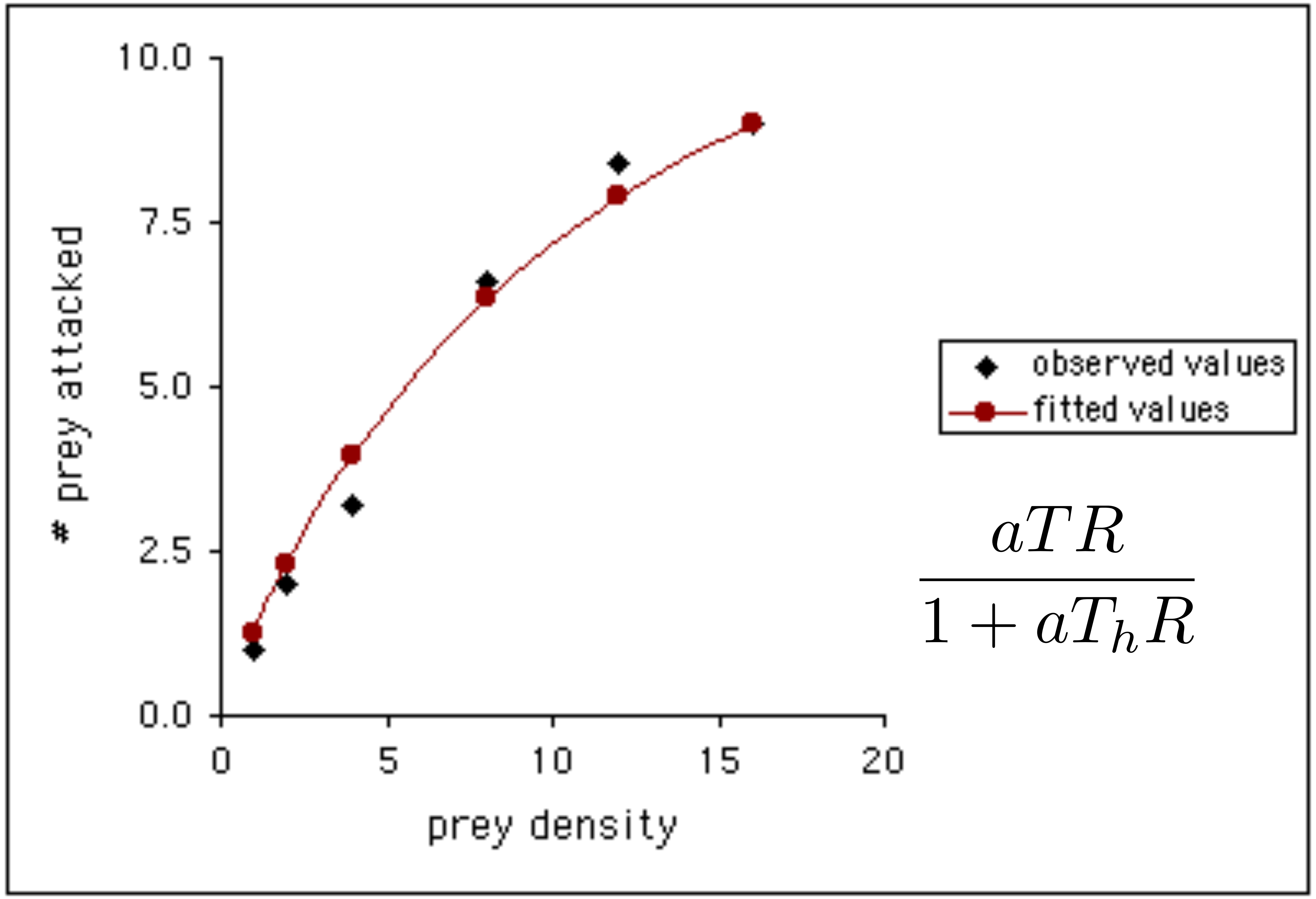
European kestral on Microtis vole (a), weasels on rodents in forests in Poland (b), and Warblers on spruce budworm larvae (c).

Functional response



Simplest type I response, where *b* is due to other prey (mosses).
Brown lemmings (*Lemmus sibericus*) foraging monocot in arctic tundra
From: Batzli *et al*, Oikos, 1981, 37: 112-116.

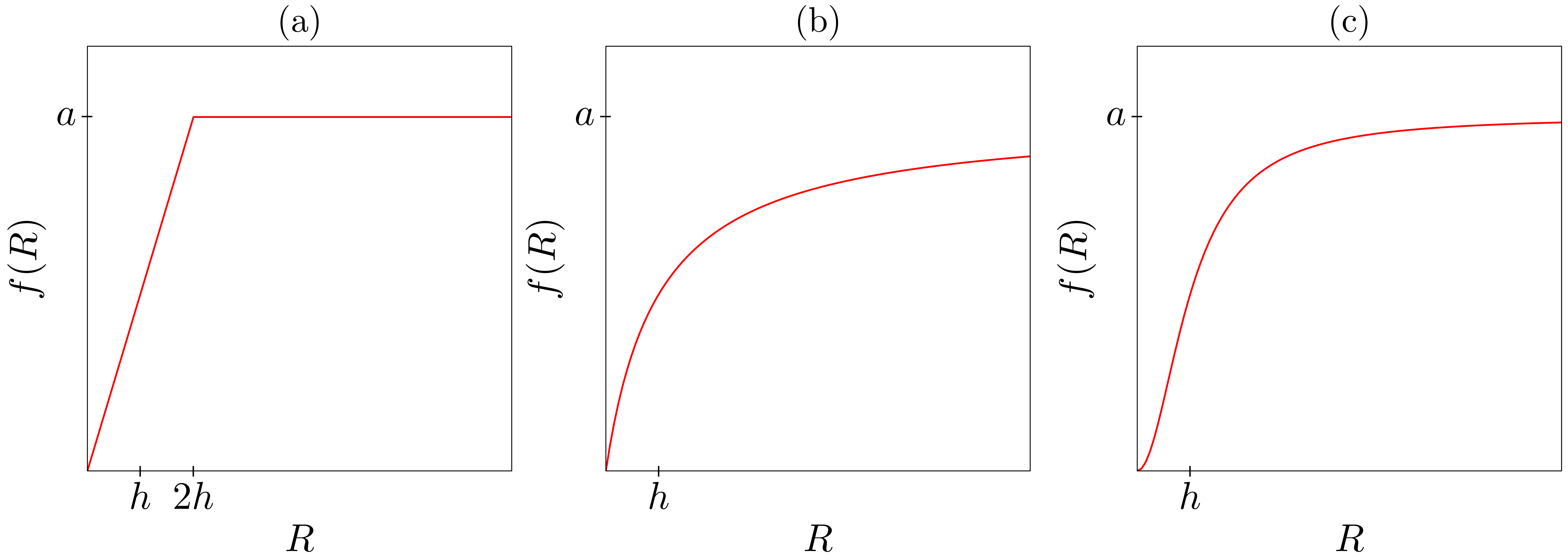
Functional response



$$\frac{aTR}{1 + aT_hR}$$

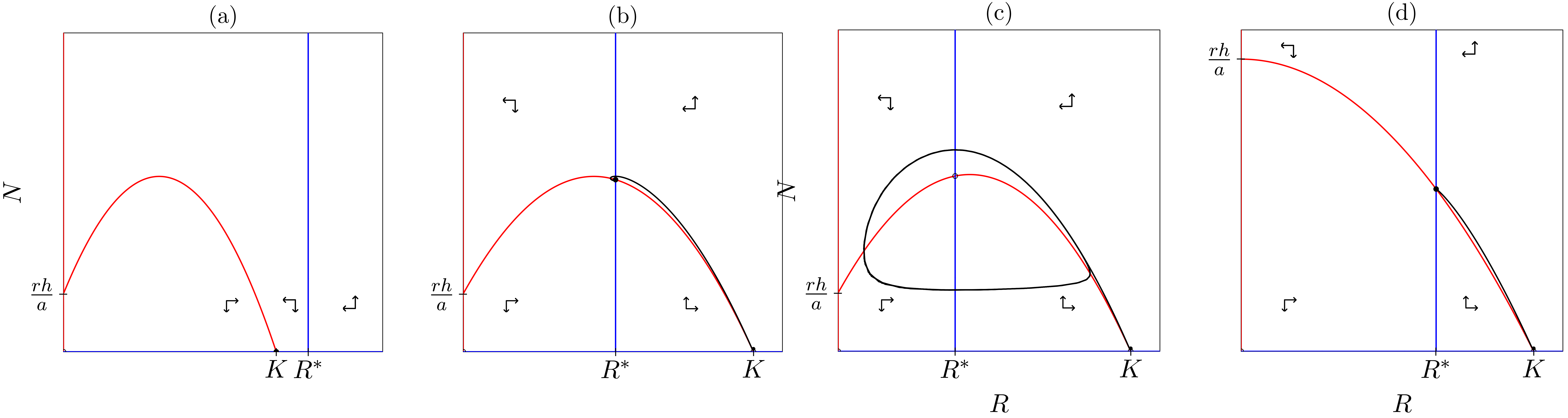
Stinkbug (*Podisus maculiventris*) in lab feeding on larvae of Mexican bean beetle.
Here a is the attack rate, T=14 h is the total time, and Th=0.9 h is the handling time.
From: Wiedenmann & O'Neil, Environ. Entomol., 1991, 20: 610-614.

Type I, II and III functional responses



$$f(R) = a\min\left(1, \frac{R}{2h}\right), \quad f(R) = a\frac{R}{h+R} \quad \text{and} \quad f(R) = a\frac{R^2}{h^2+R^2},$$

Monod functional response

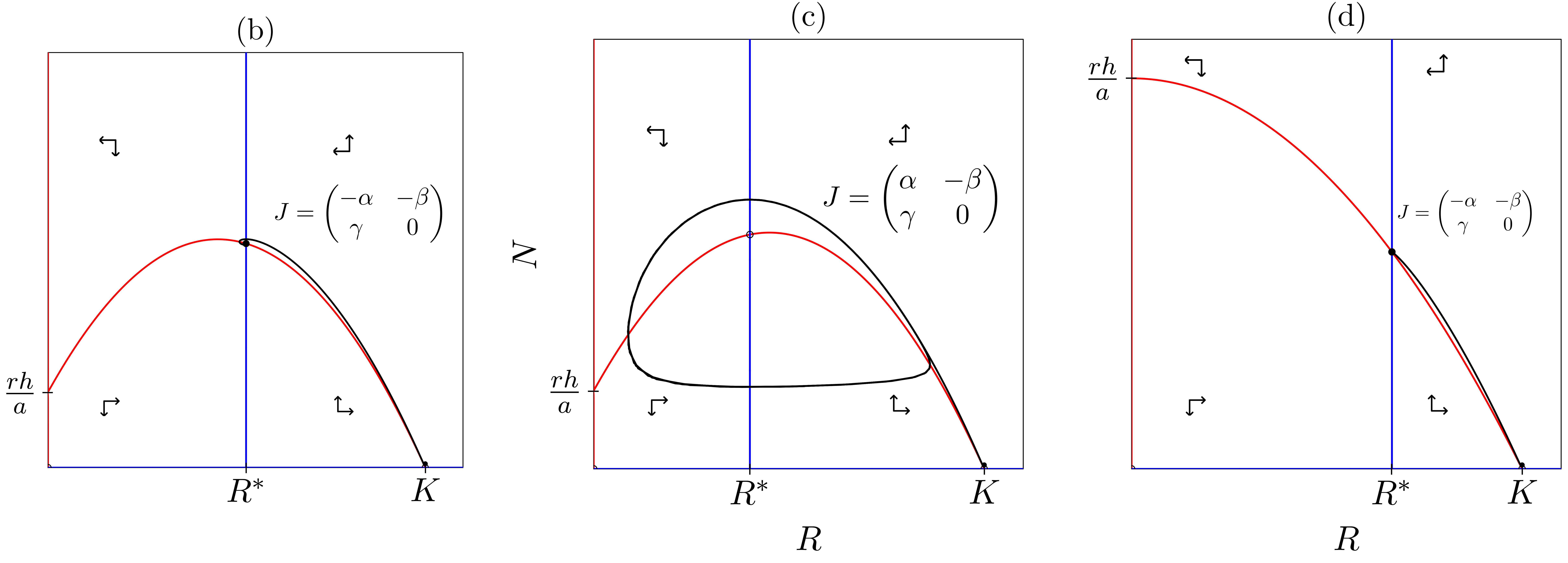


$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aRN}{h+R} = rR(1 - R/K) - \frac{a'RN}{1 + R/h}, \qquad \frac{\mathrm{d}N}{\mathrm{d}t} = \frac{caRN}{h+R} - \delta N$$

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

$$R^* = \frac{h}{R_0 - 1}$$

Monod functional response



$\text{tr} = -\alpha < 0$ and $\det = \beta\gamma > 0$

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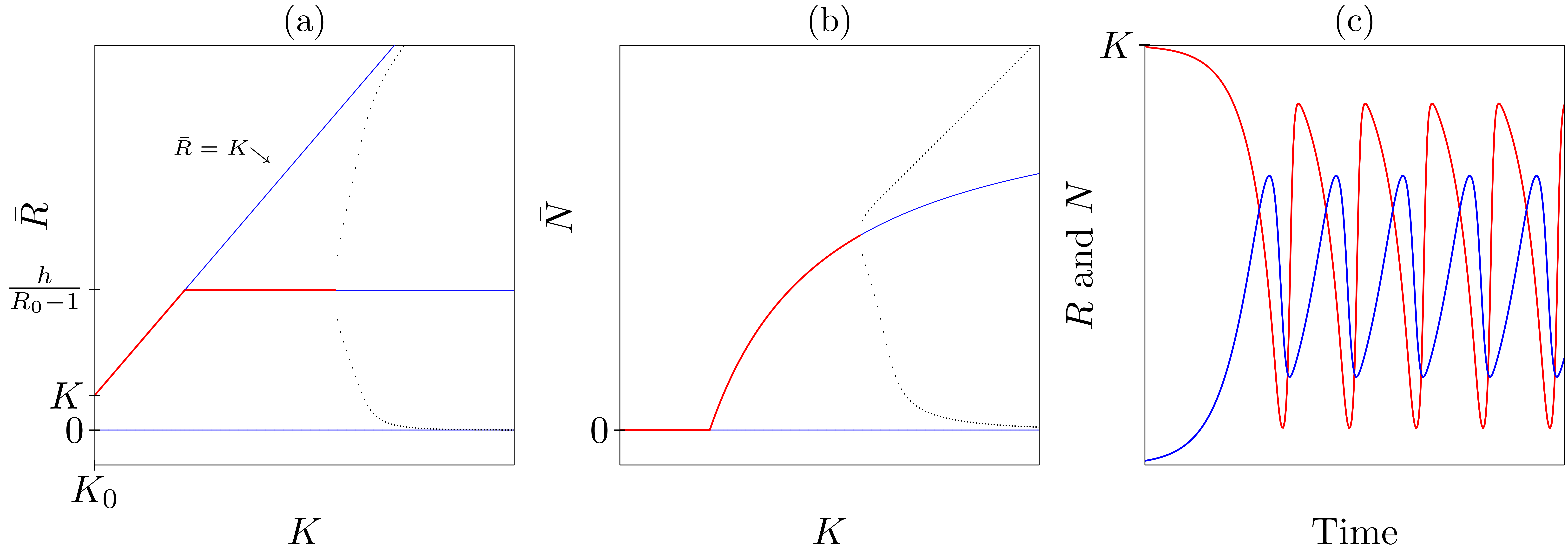
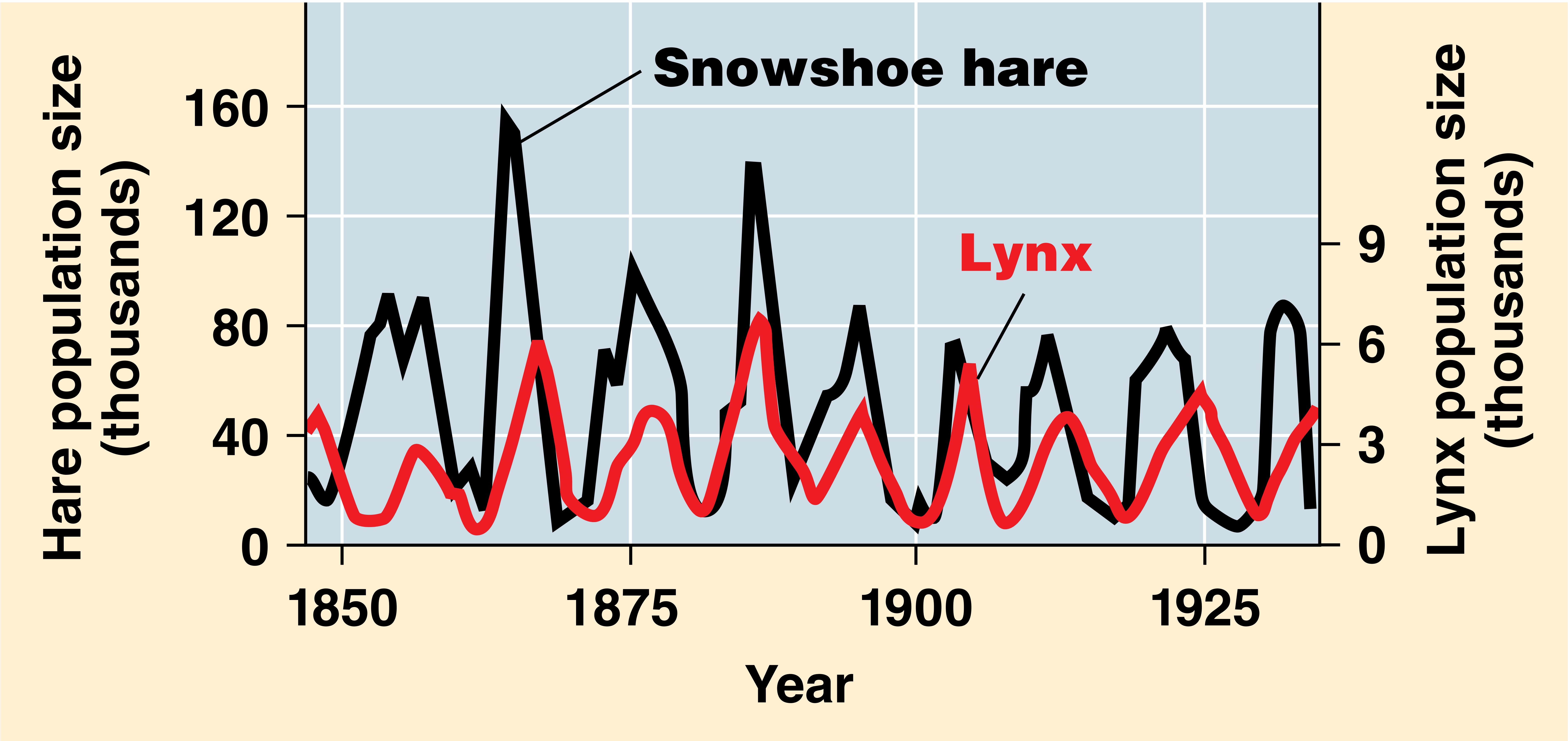
Monod functional response

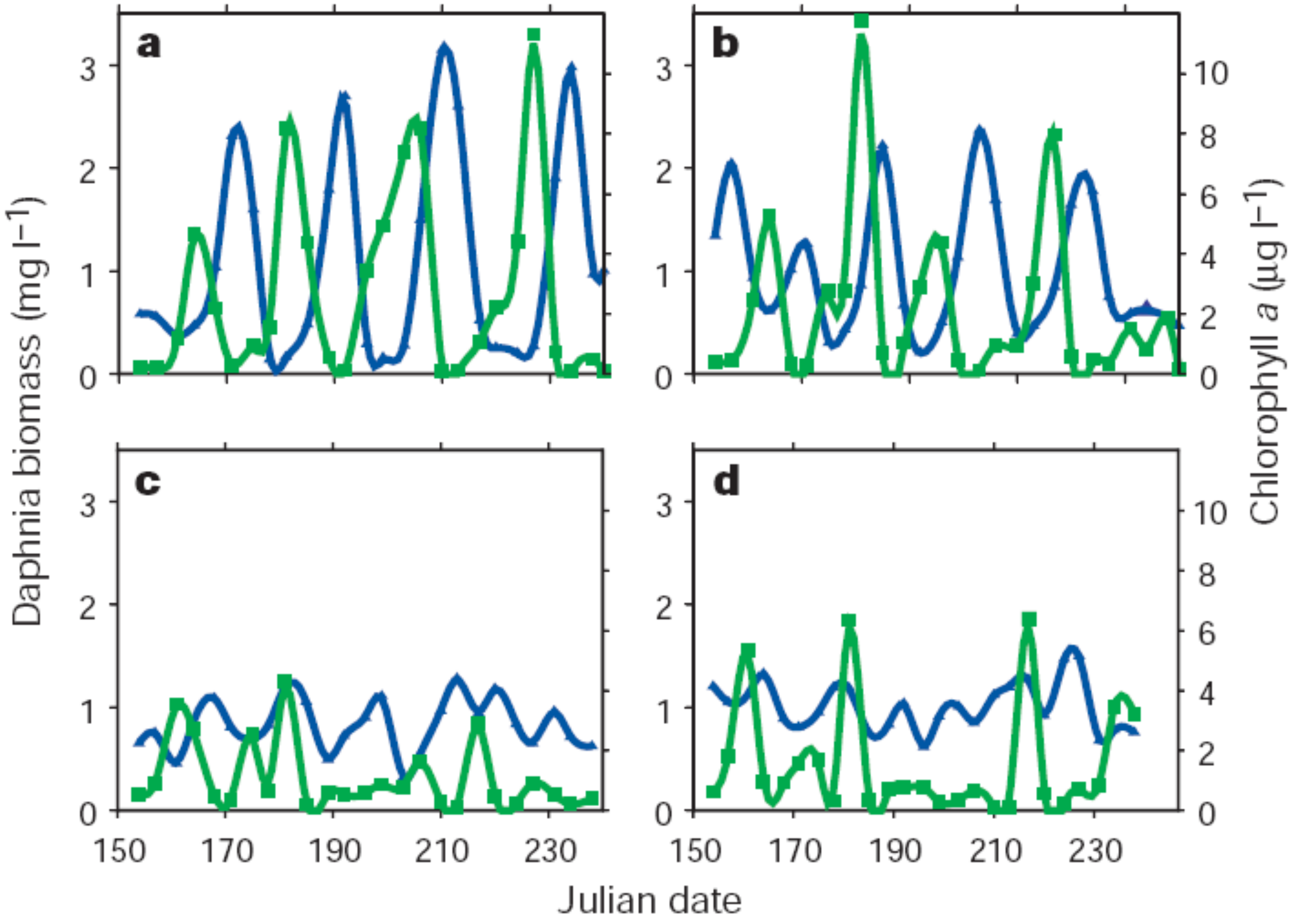


Population cycles



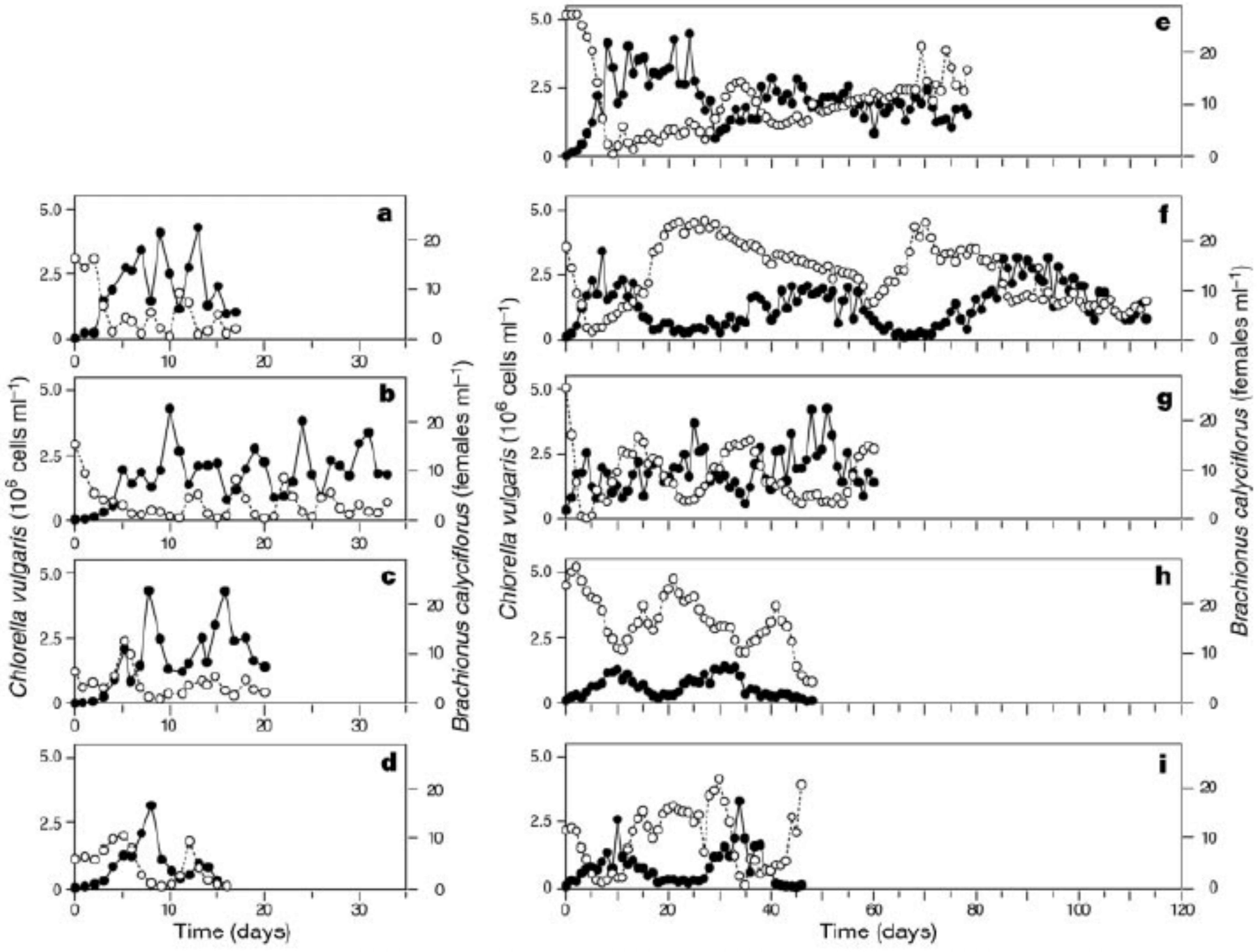
Population cycles in the snowshoe hare and the lynx.

Algae zooplankton oscillations



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

Algae zooplankton oscillations



From: Yoshida *et al*, Nature, 2003

Experimental results showing the population cycles of rotifer-alga systems. a-d, Single-clone algal populations; e-i, multiple-clone algal populations. Filled circles, *B. calyciflorus* (predator); open circles, *C. vulgaris* (prey).

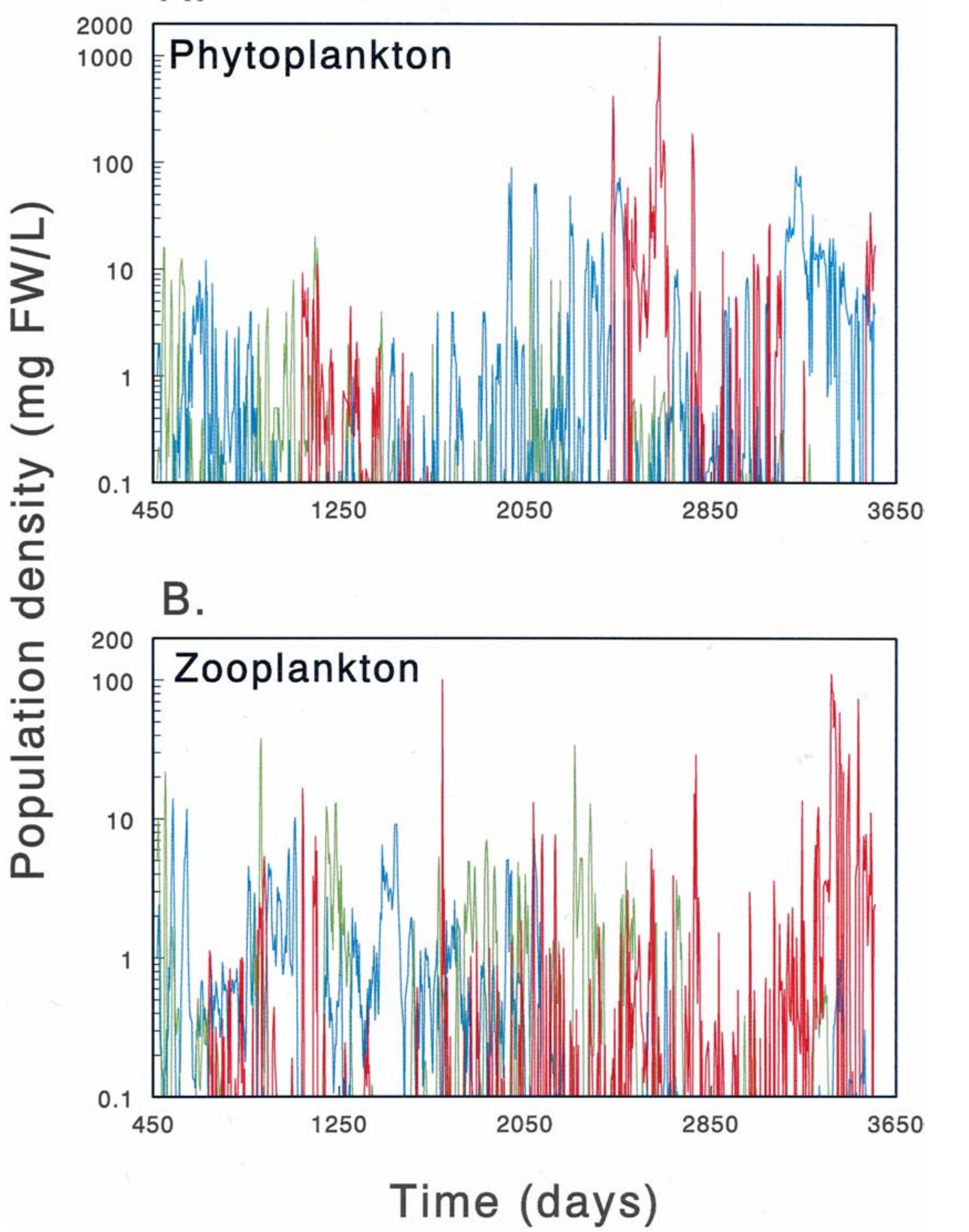


Figure 5. Non-equilibrium dynamics observed in an experimental multispecies community. The community developed in a long-term laboratory experiment under constant external conditions, and consisted of more than 20 different species. Data show the observed time course of (A) the dominant phytoplankton groups (green = green flagellates, blue = prokaryotic pico-phytoplankton, red = the diatom *Melosira*), and (B) the dominant zooplankton groups (green = the rotifer *Brachionus*, blue = the copepod *Eurytemora*, red = protozoans). Data were kindly provided by Heerkloss (unpublished), and by Heerkloss & Klinkenberg (1998), with permission from Schweizerbartsche Verlagsbuchhandlung.

Algae zooplankton oscillations

Non-equilibrium dynamics observed in an experimental multispecies community. The community developed in a long-term laboratory experiment under **constant external conditions**, and consisted of more than 20 different species. Data show the observed time course of (A) the dominant phytoplankton groups (green = green flagellates, blue = prokaryotic pico-phytoplankton, red = the diatom *Melosira*), and (B) the dominant zooplankton groups (green = the rotifer *Brachionus*, blue = the copepod *Eurytemora*, red = protozoans).

Data: Heerkloss & Klinkenberg, 1998;
Copied from Scheffer et *et al,* Hydrobiologia, 2003

Quasi steady state assumption

Split consumers into free, *F*, and handling, *C*: $N = F + C$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = aRF - hC \quad \text{or} \quad \frac{\mathrm{d}C}{\mathrm{d}t} = aR(N - C) - hC$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = 0 \quad \text{gives} \quad C = \frac{aNR}{h + aR} = \frac{NR}{h' + R}$$

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Add $\mathrm{d}C/\mathrm{d}t = 0$ to $\mathrm{d}R/\mathrm{d}t = rR(1 - R/K) - aRF$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - hC = rR(1 - R/K) - \frac{hNR}{h' + R}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = cC - dN = \frac{cNR}{h' + R} - dN$$

Consumers that eat replicate.

One consumer using several resources

$$\mathrm{d}C_i/\mathrm{d}t = a_i R_i F - hC_i = 0 \qquad N = F + \sum_i C_i$$

$$\sum_i \frac{\mathrm{d}C_i}{\mathrm{d}t} = \sum_i a_i R_i F - h \sum_i C_i = \sum_i a_i R_i \Big(N - \sum_j C_j\Big) - h \sum_i C_i = 0 \ ,$$

which can be rewritten into

$$\sum_i C_i = \frac{N \sum_i a_i R_i}{h + \sum_j a_j R_j} \quad \text{and, hence,} \quad C_i = \frac{N a_i R_i}{h + \sum_j a_j R_j} \ .$$

For each resource, i, one can again add $\mathrm{d}C_i/\mathrm{d}t = a_i R_i F - hC_i = 0$ to

$$\frac{\mathrm{d}R_i}{\mathrm{d}t} = rR_i(1 - R_i/K_i) - a_i R_i F \quad \text{giving} \quad \frac{\mathrm{d}R_i}{\mathrm{d}t} = rR_i(1 - R_i/K_i) - \frac{h a_i R_i N}{h + \sum_j a_j R_j}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = c \sum_i C_i - dN = \frac{cN \sum_i a_i R_i}{h + \sum_j a_j R_j} - dN$$

Saturated birth rate

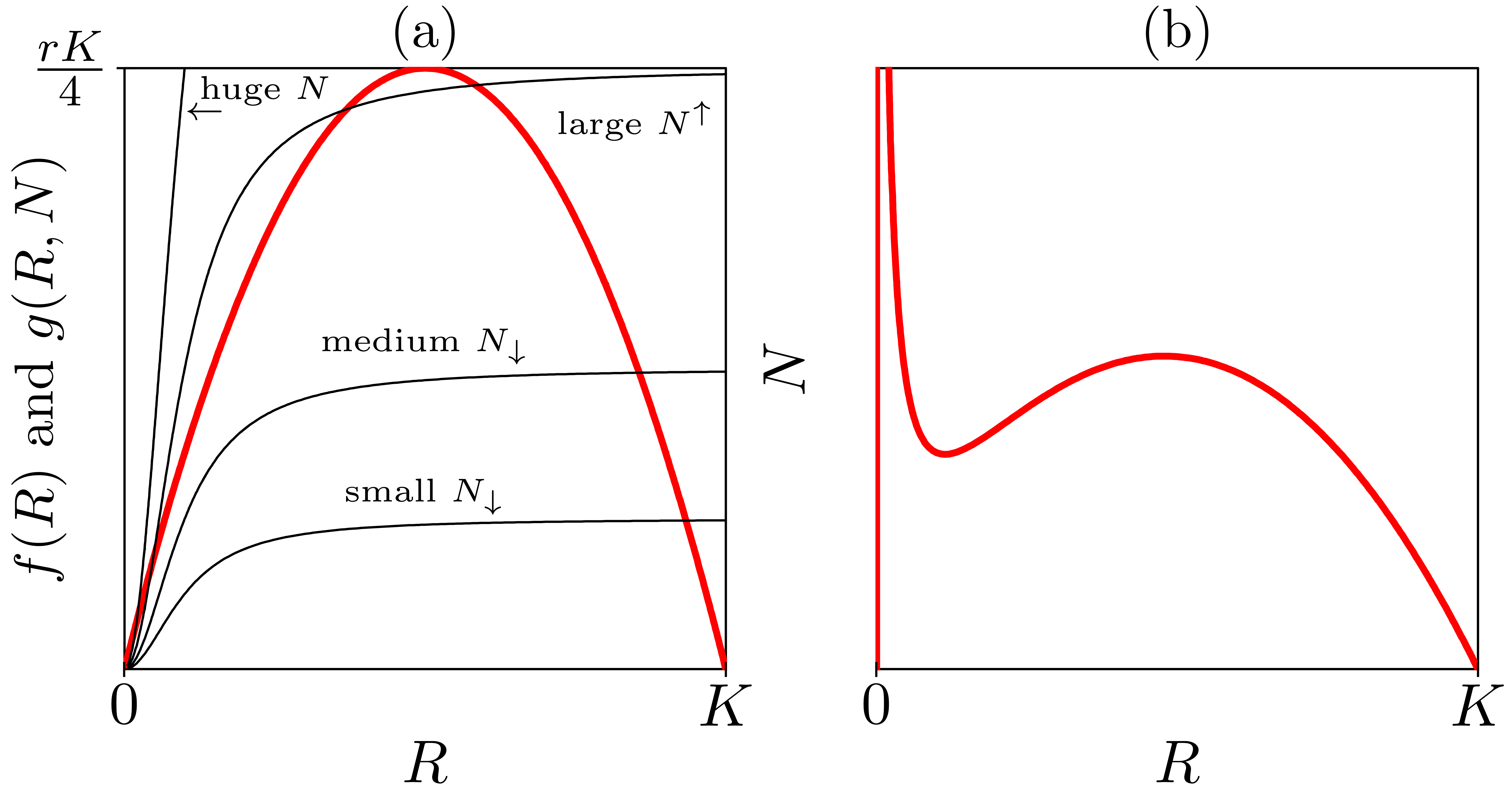
$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aRN}{h + R} \quad \text{consumption} \quad \frac{aR}{h + R}$$

$$g(R) = \frac{c\frac{aR}{h+R}}{H + \frac{aR}{h+R}} = \frac{caR}{H(h + R) + aR} = \frac{\beta R}{h' + R}$$

$$\beta = ca/(H + a) \quad \text{and} \quad h' = hH/(H + a) < h$$

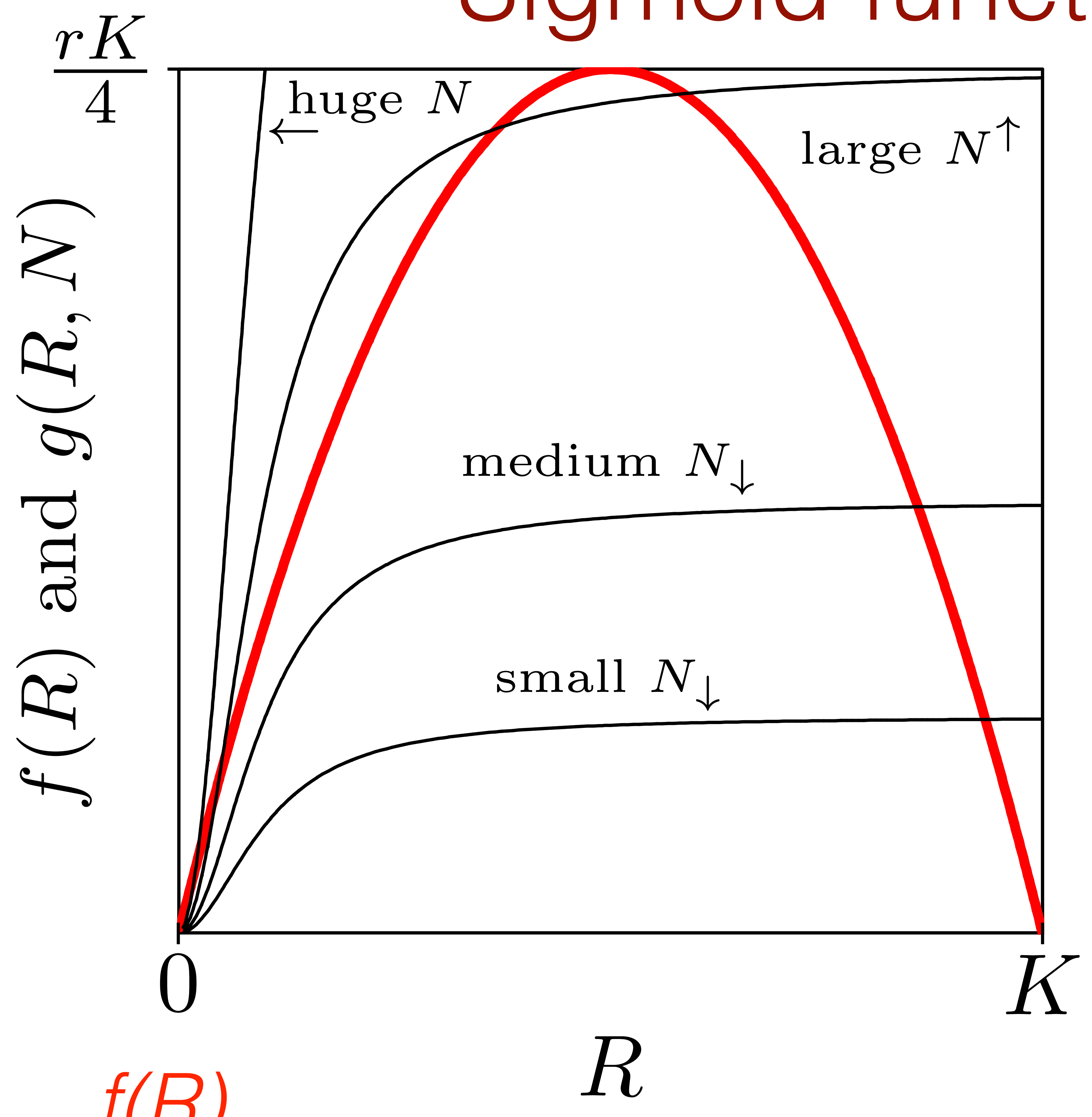
$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{\beta RN}{h' + R} - \delta N$$

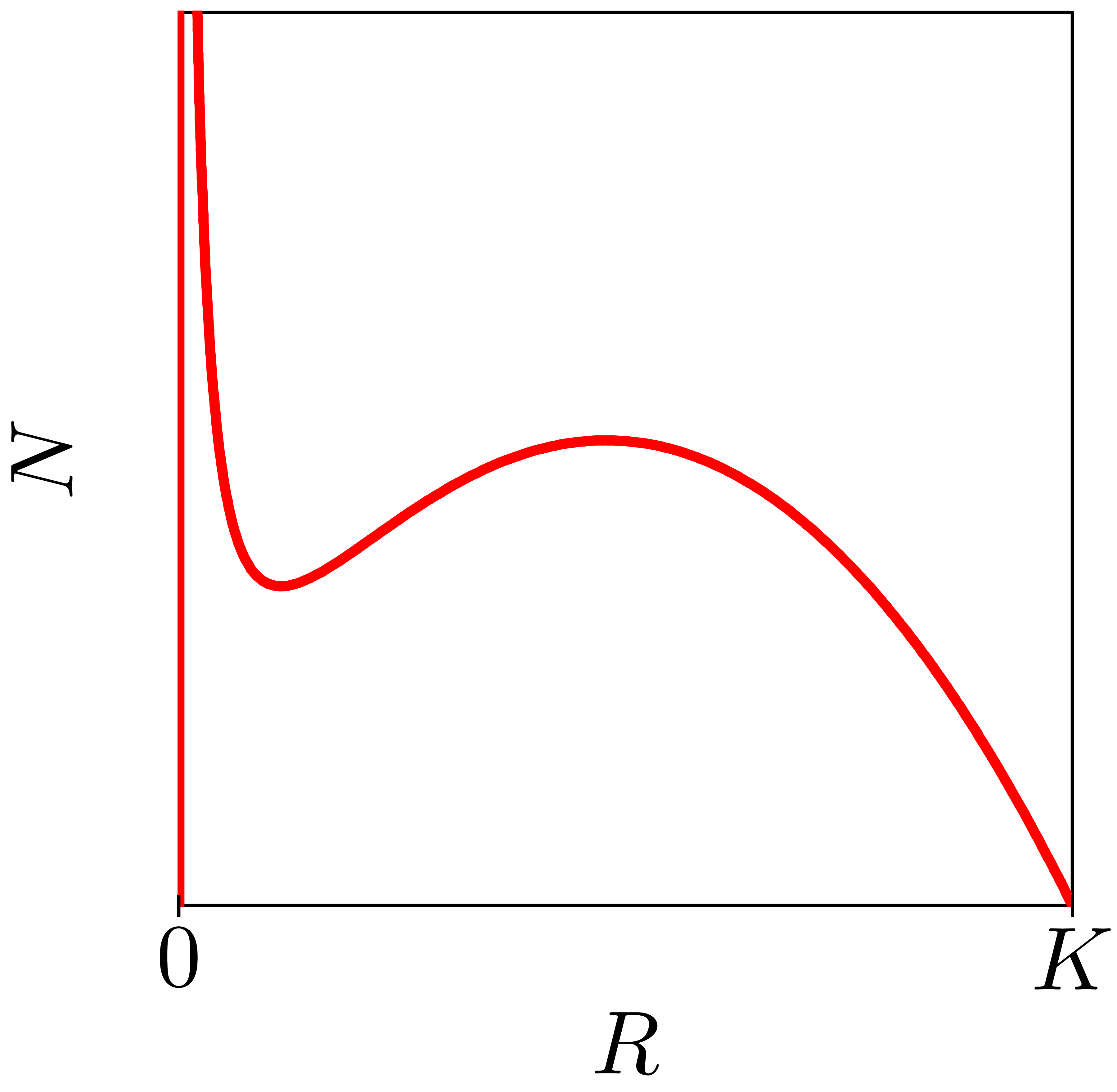
Sigmoid functional response



$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aR^2N}{h^2 + R^2} \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = \frac{caR^2N}{h^2 + R^2} - \delta N$$

Sigmoid functional response





f(R)

g(R,N)

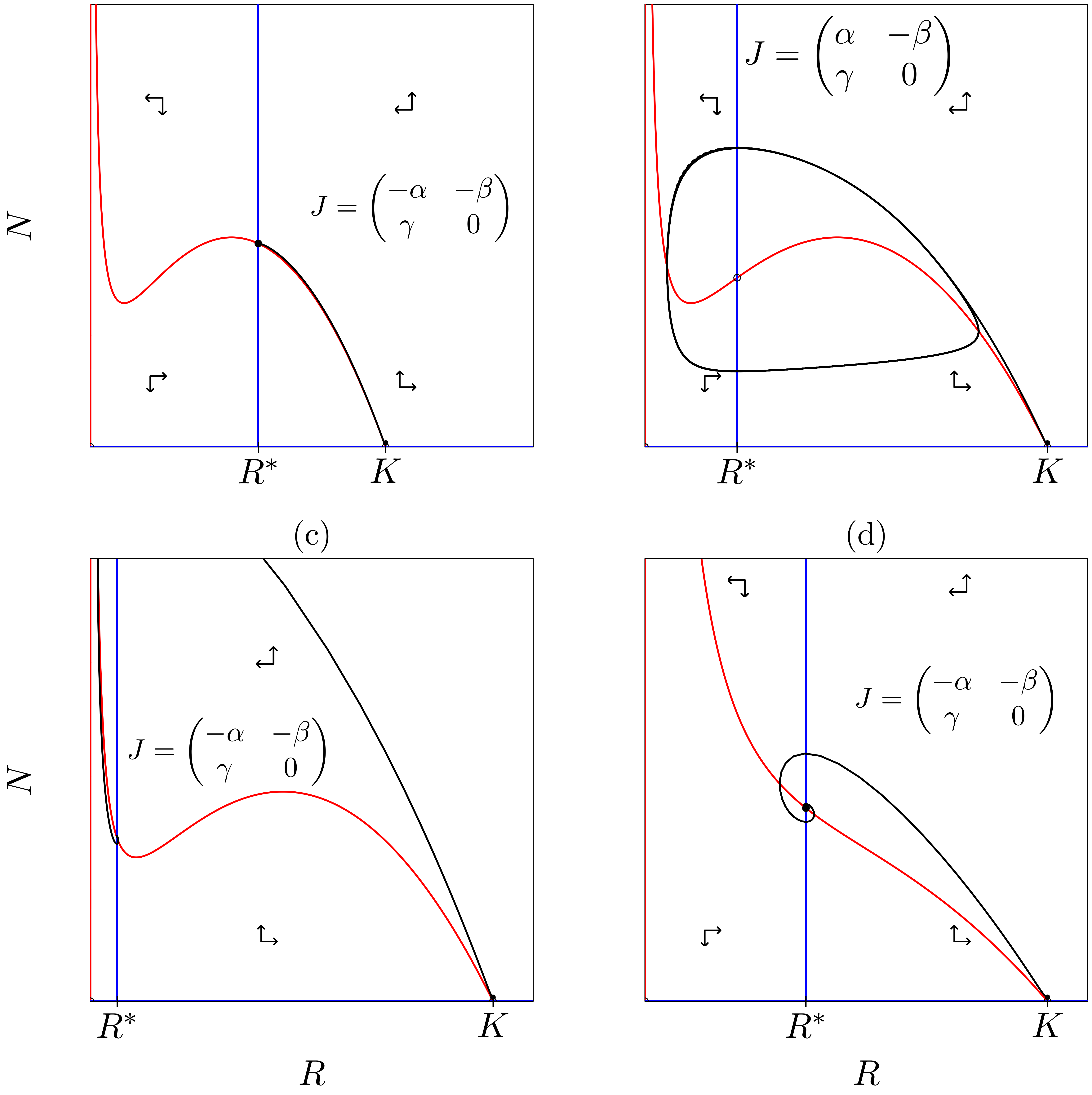
$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - \frac{aR^2N}{h^2 + R^2}$$

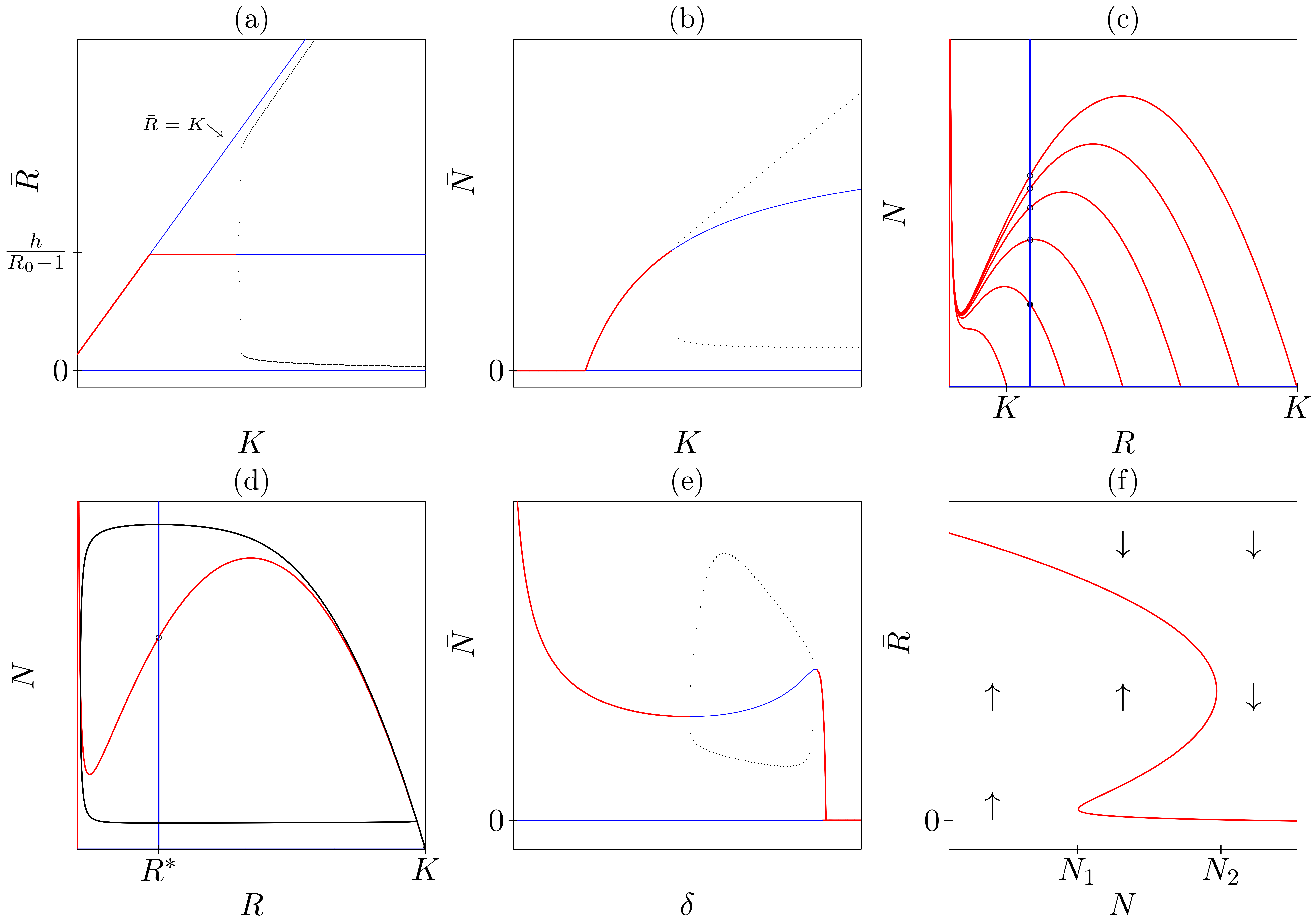
$$N = \frac{r(h^2 + R^2)}{aR}\left(1 - \frac{R}{K}\right)$$

$$\partial_R\, f(R) = r - 2rR/K$$

$$\partial_R\, g(R,N) = \frac{2aRN}{h^2 + R^2} - \frac{2aR^3N}{(h^2 + R^2)^2}$$

Sigmoid functional response





Sigmoid functional response

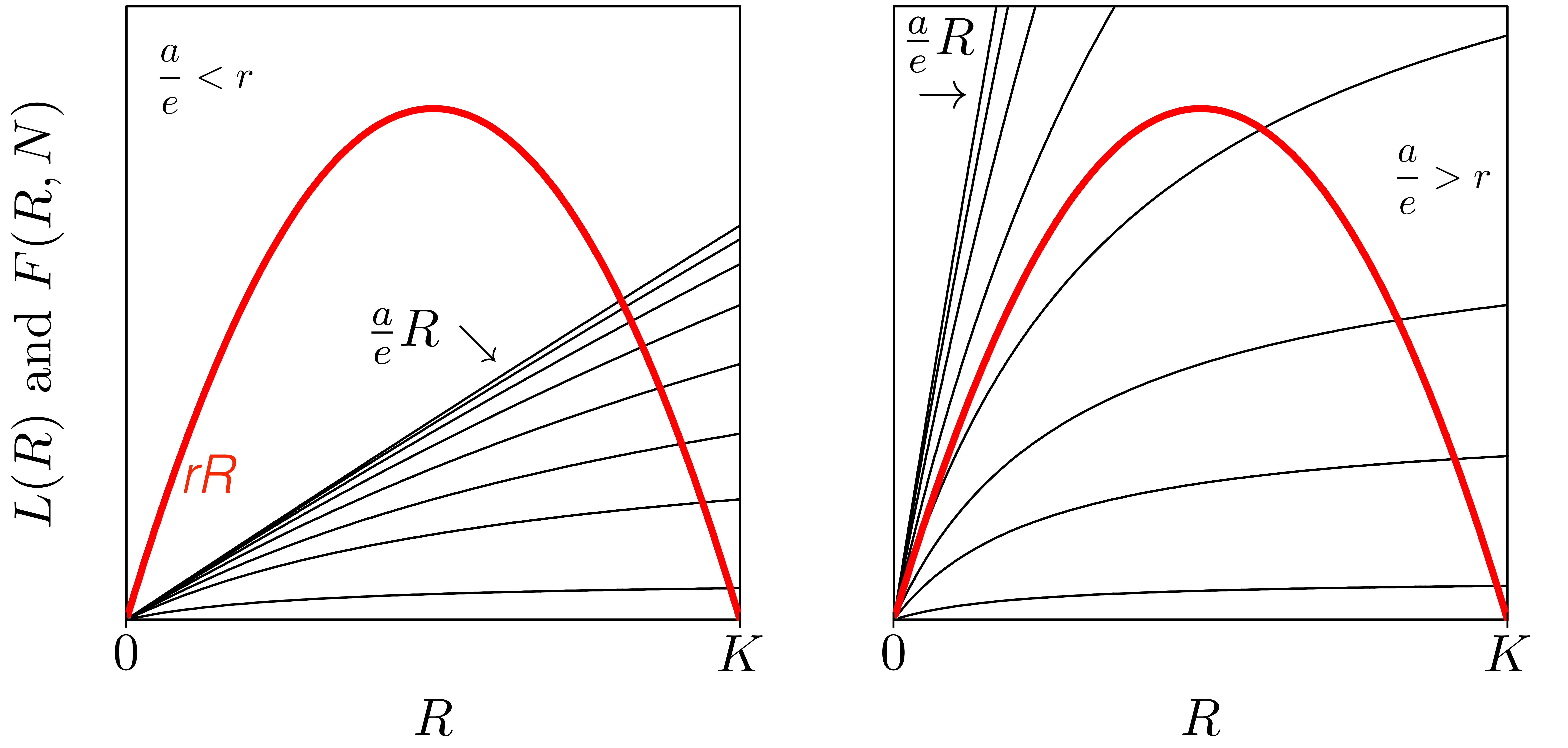
Beddington functional response

$$\begin{aligned}\frac{\mathrm{d}R}{\mathrm{d}t} &= rR(1-R/K) - \frac{aRN}{h+eN+R} \\ \frac{\mathrm{d}N}{\mathrm{d}t} &= \frac{caRN}{h+eN+R} - dN\ .\end{aligned}$$

$$\lim_{R\to\infty} \frac{aR}{h+eN+R} = a$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = 0 \to N = 0 \quad \text{and} \quad N = \frac{ca-d}{de}\ R - \frac{h}{e} = \frac{R_0 - 1}{e}\ R - \frac{h}{e}\ .$$

Constructing the R'=0 nullcline



L(R) F(R,N)

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

$$\lim_{N\to\infty} \frac{aRN}{h + eN + R} = \frac{a}{e} R$$

$$\partial_R \, F(R,N) = \frac{aN}{h + eN + R} - \frac{aRN}{(h + eN + R)^2} \quad \text{which for } R = 0 \text{ yields} \quad \frac{aN}{h + eN}$$

Beddington functional response

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

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{caRN}{h + eN + R} - dN \ .$$

Beddington functional response

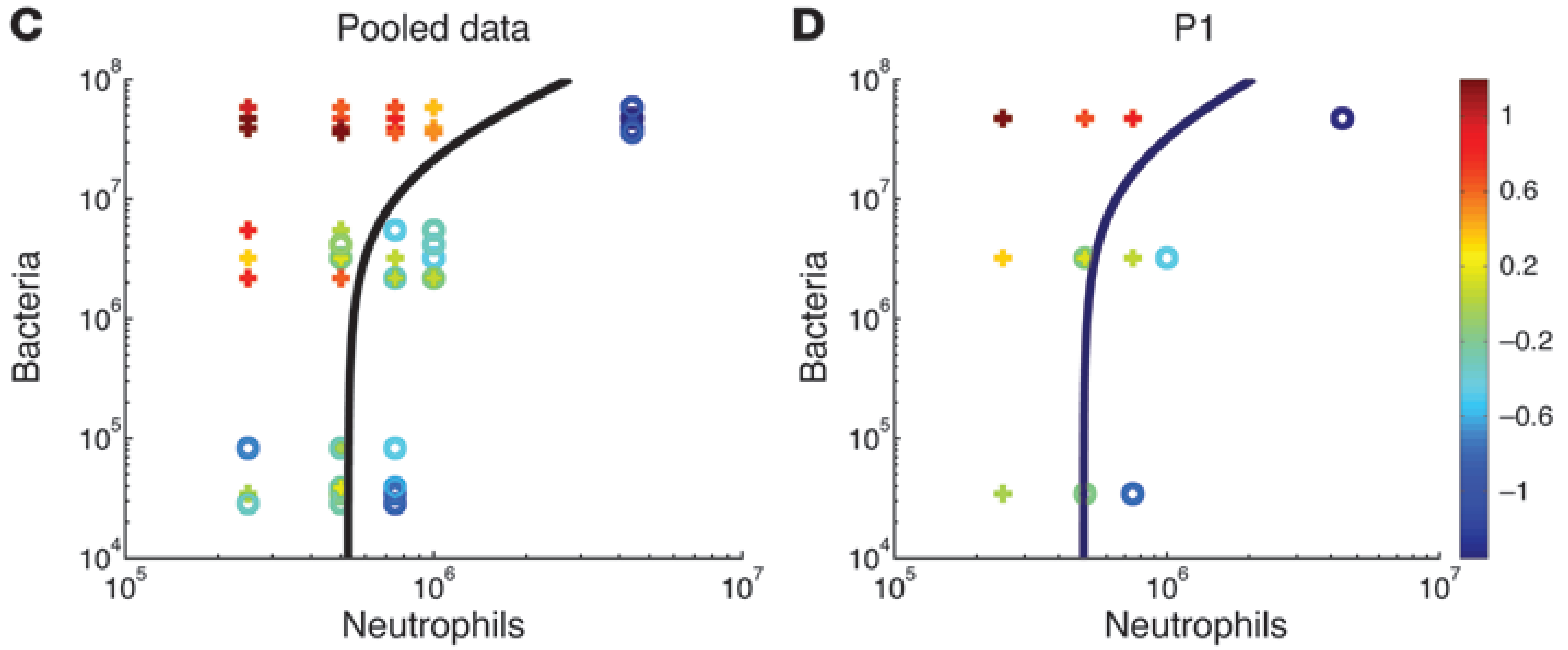
Total Quasi Steady State Assumption

$$\frac{\mathrm{d}C}{\mathrm{d}t} = aR_F N_F - hC \quad \text{or} \quad \frac{\mathrm{d}C}{\mathrm{d}t} = a(R-C)(N-C) - hC$$

$$aC^2 - C(aR + aN + h) + aRN = C^2 - C(R + N + h') + RN = 0 \;\text{ where } h' = \frac{h}{a}$$

$$C = \frac{RN}{h' + R + N}$$

Neutrophils killing bacteria



$$\frac{dB(t)}{dt} = \rho B(t) - \frac{\alpha N B(t)}{1 + \gamma B(t) + \eta N}$$

Color killing
Log[B(60)/B(0)]

Malka et al., J. Clin Invest. 2012