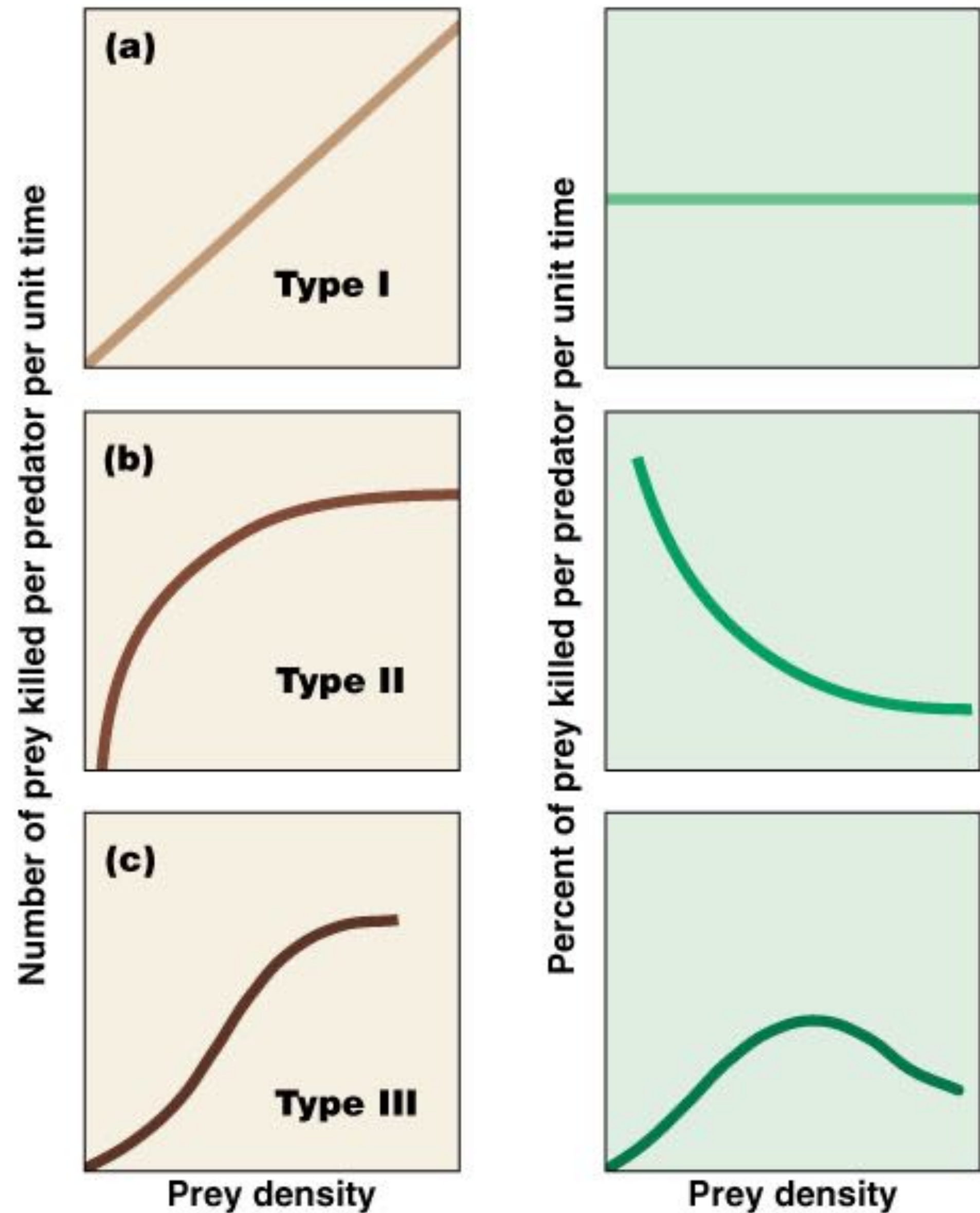
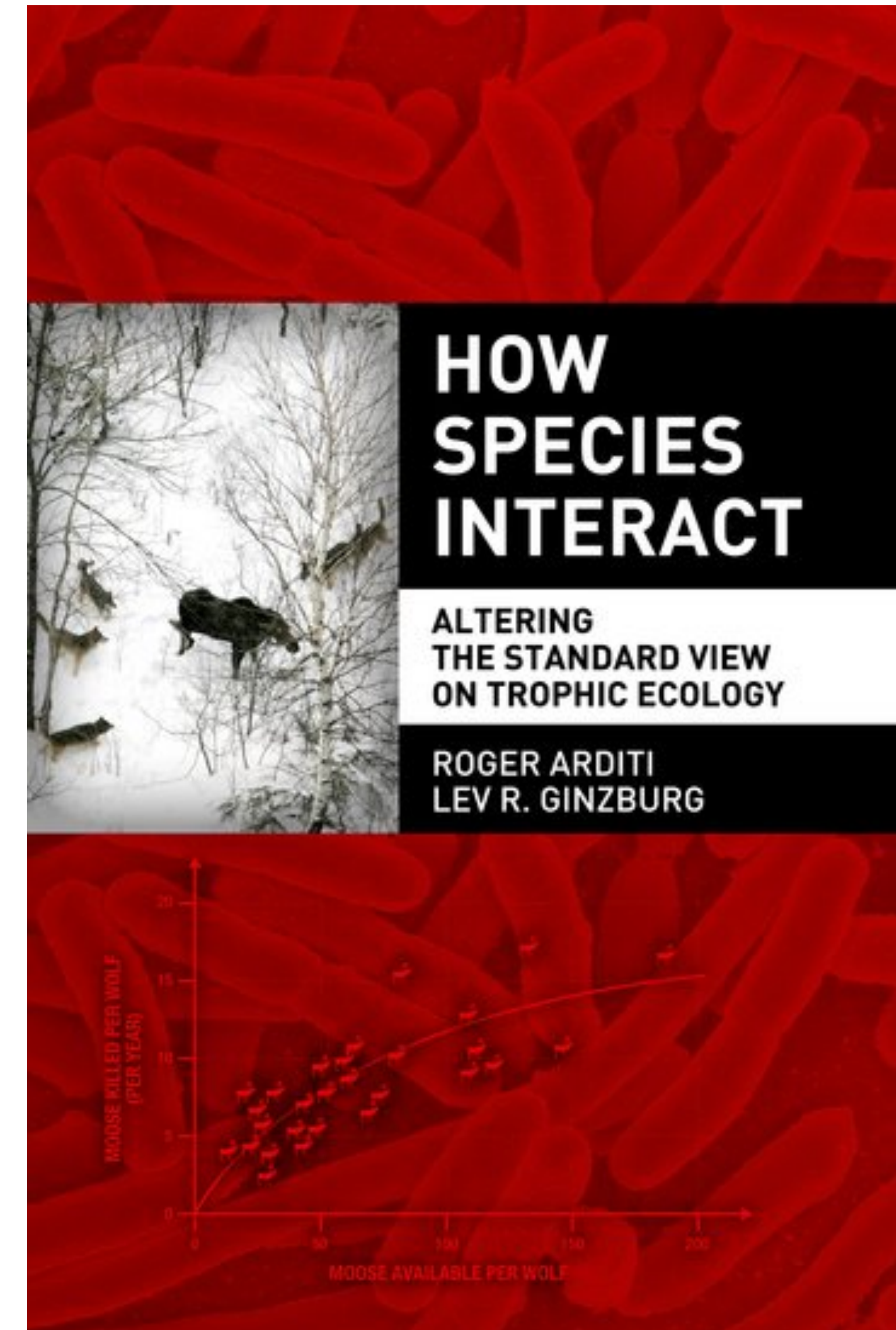


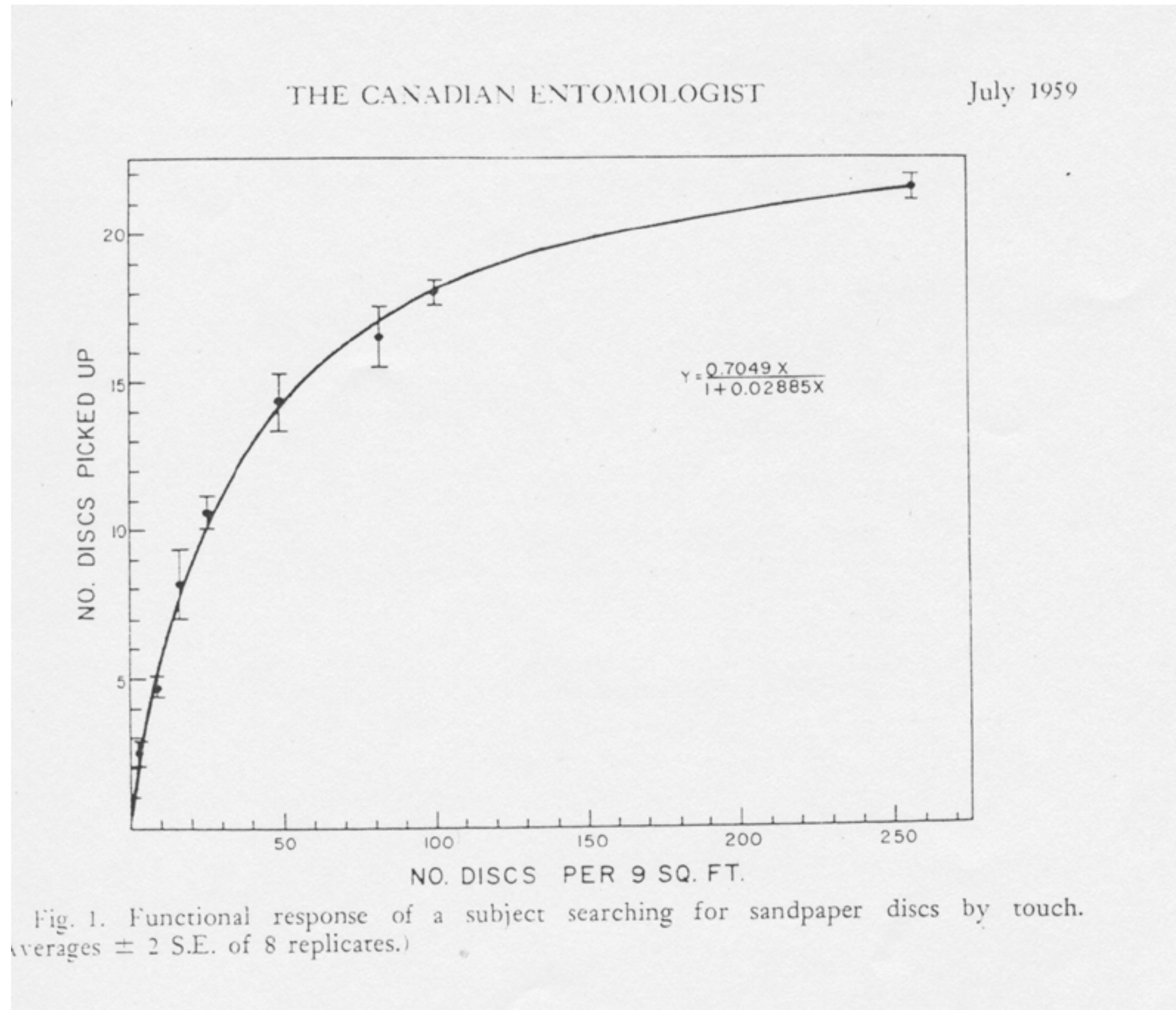
Chapter 7: Functional response



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Holling's secretary: handling sand paper discs



Holling's secretary: handling sand paper discs

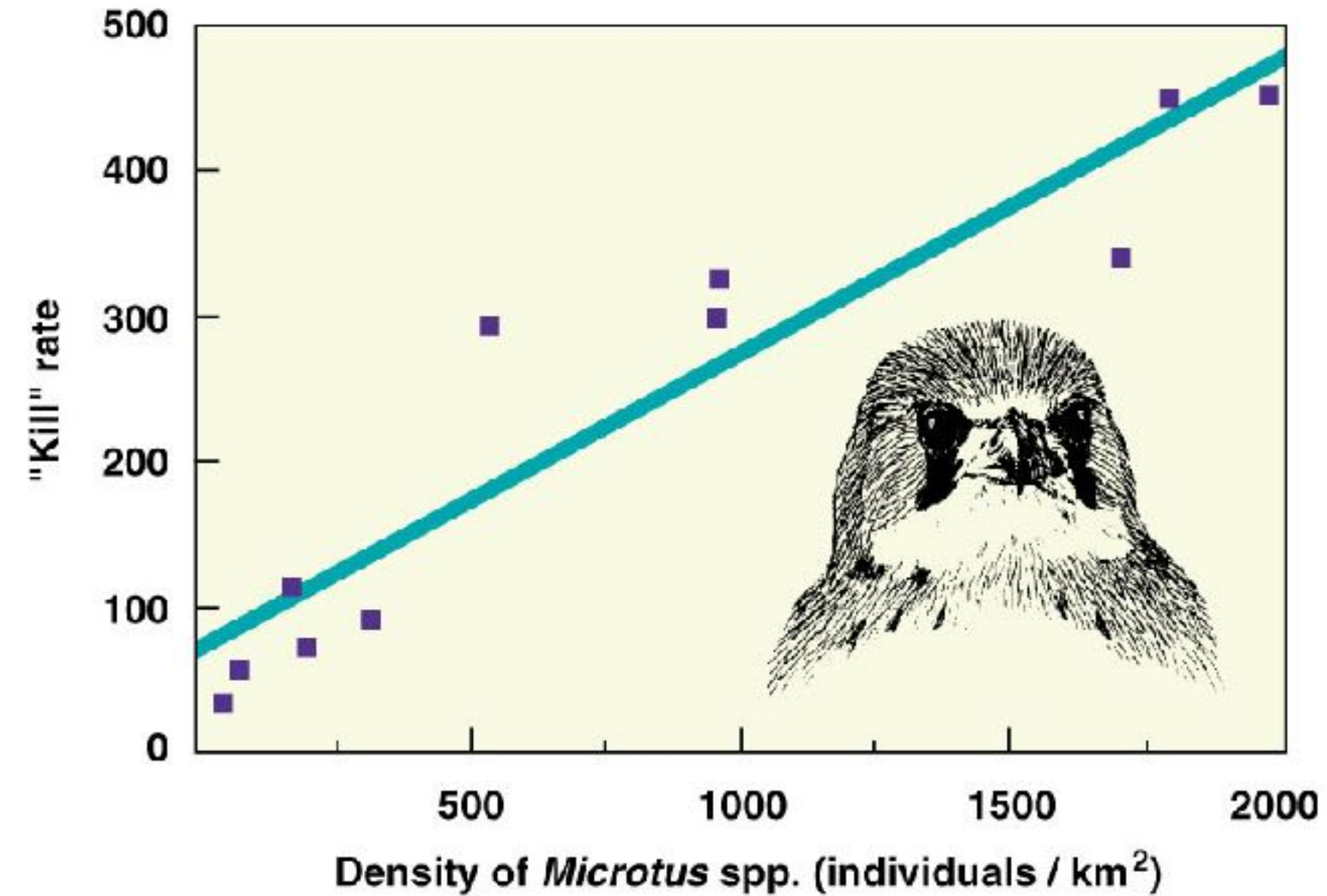
$$n = atR, \quad t = T - bn$$

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

which is a general Hill function.

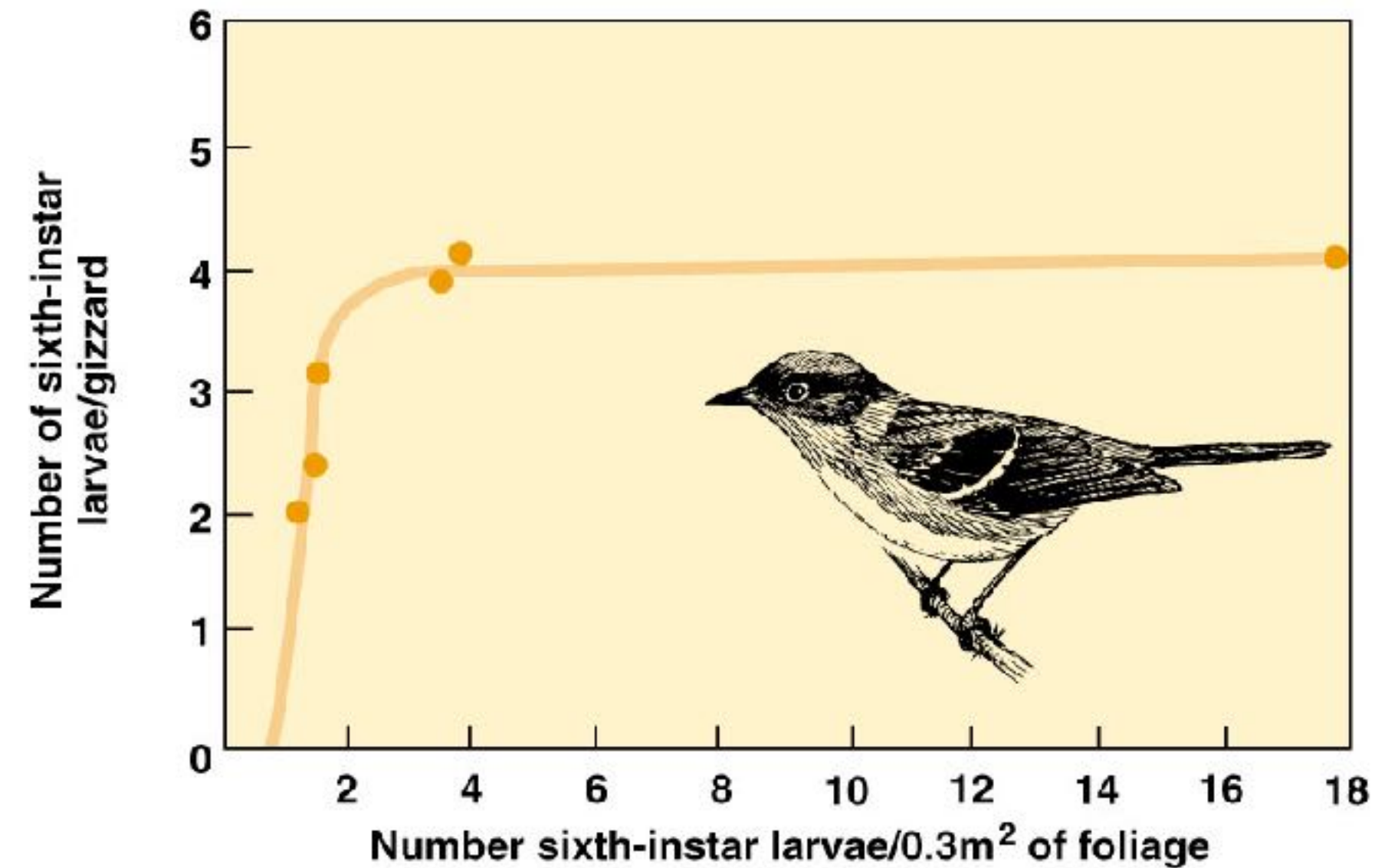
$a' = T/b$ is total/handling time (max number of prey, dimensionless)
 $h = 1/(ab)$ involves handling and searching times (dimensionless)

Functional response



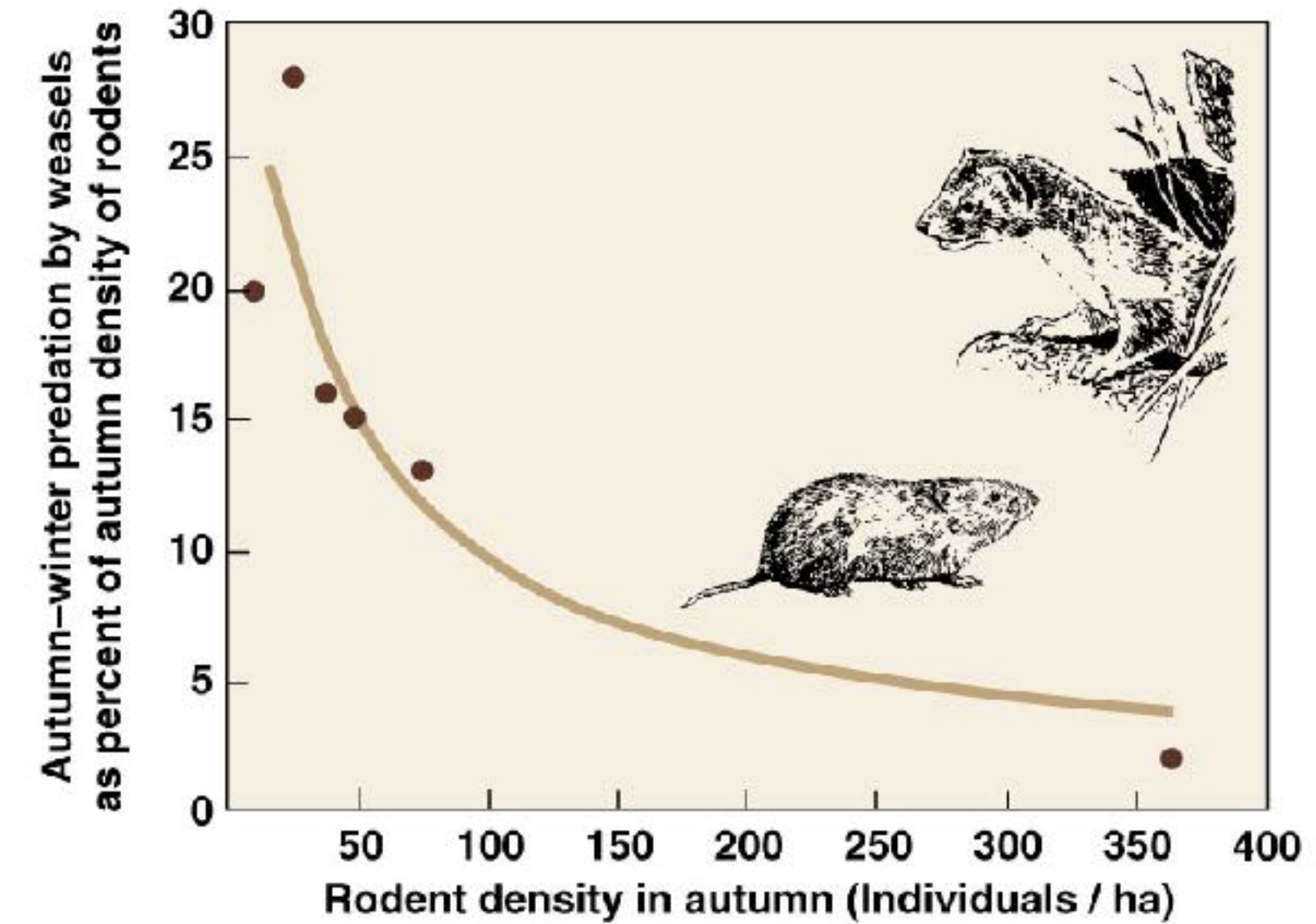
(a)

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(c)

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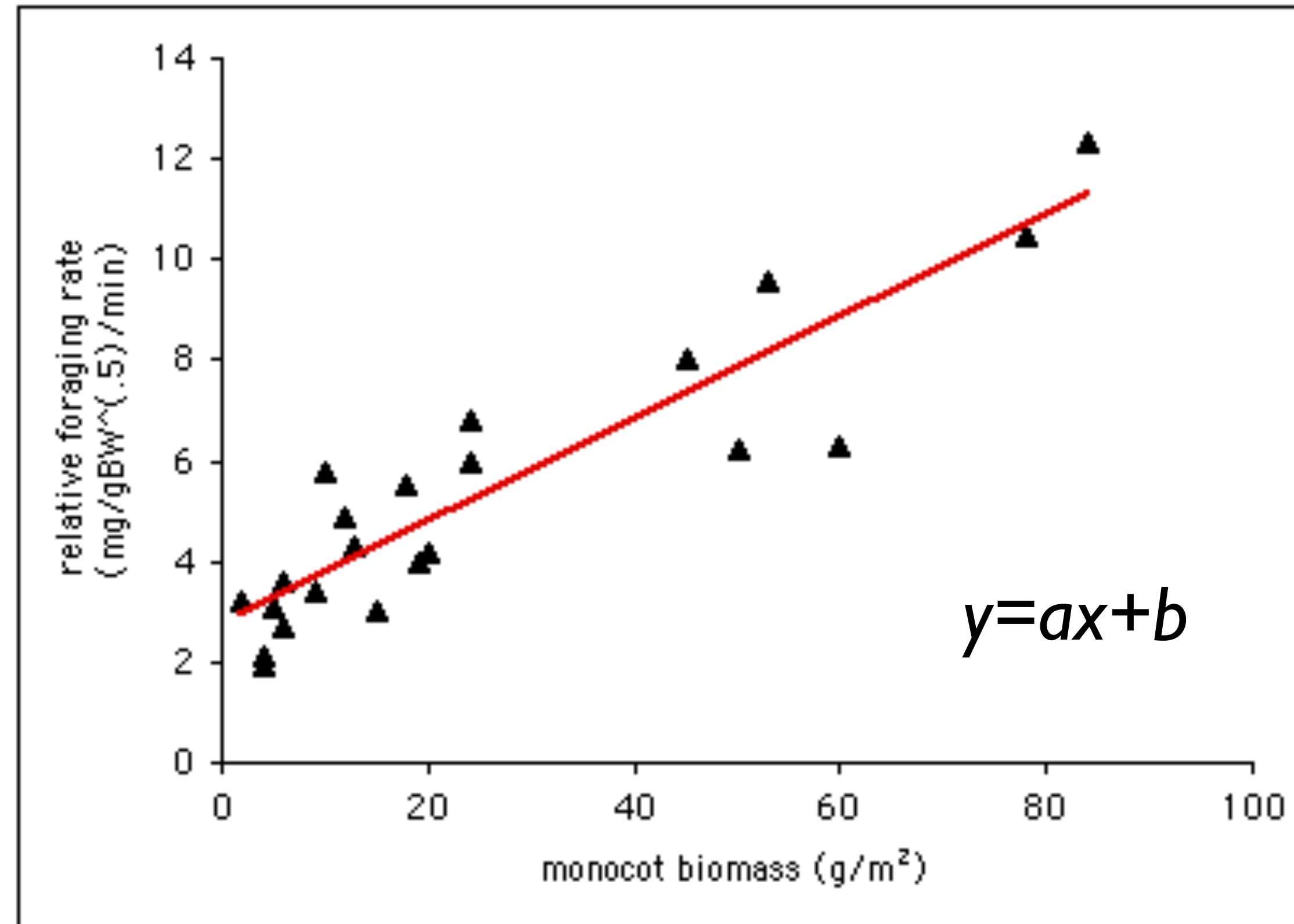


(b)

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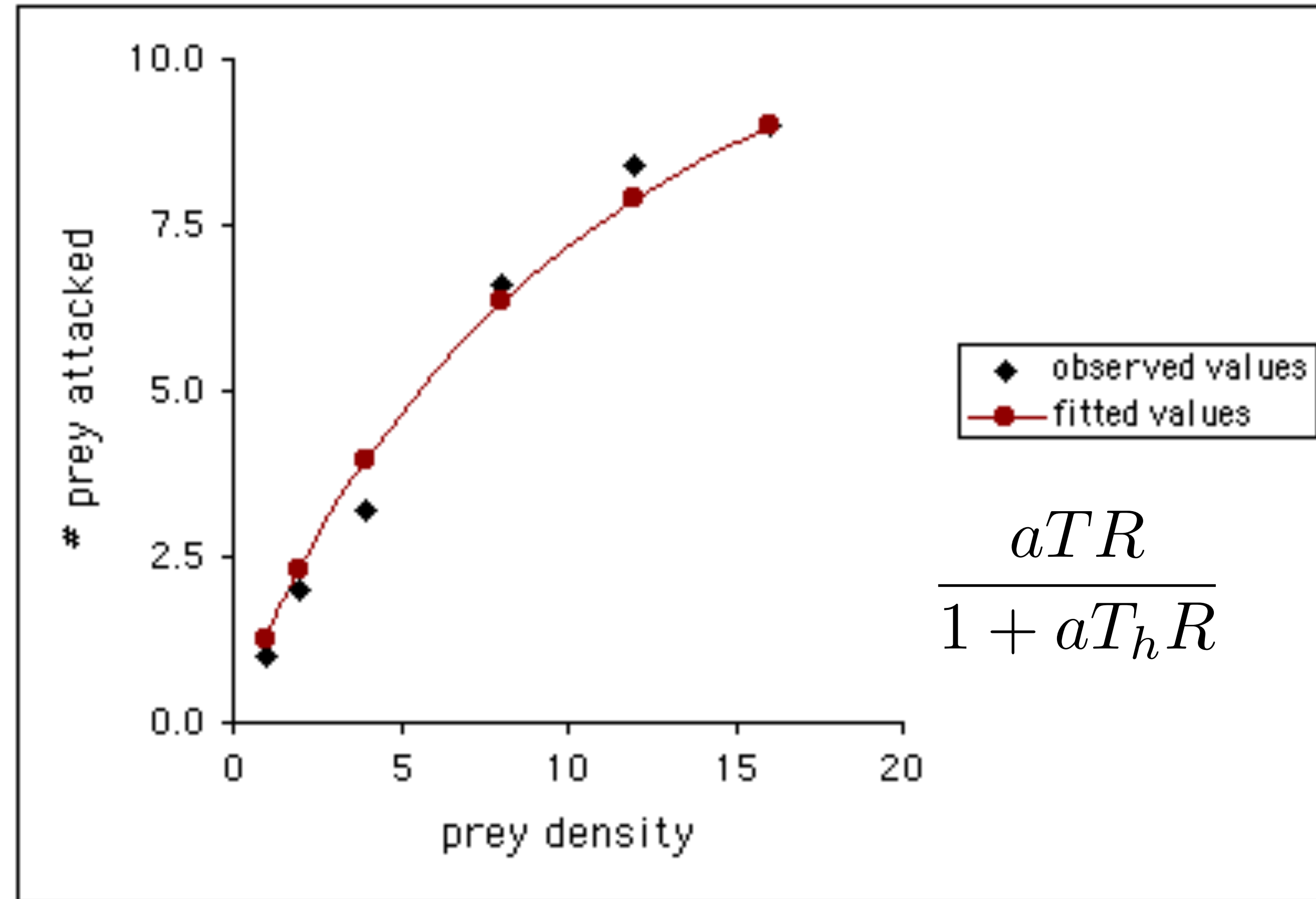
European kestrel on *Microtis* vole (a),
weasels on rodents in forests in Poland (b),
and Warblers on spruce budworm larvae (c).

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.

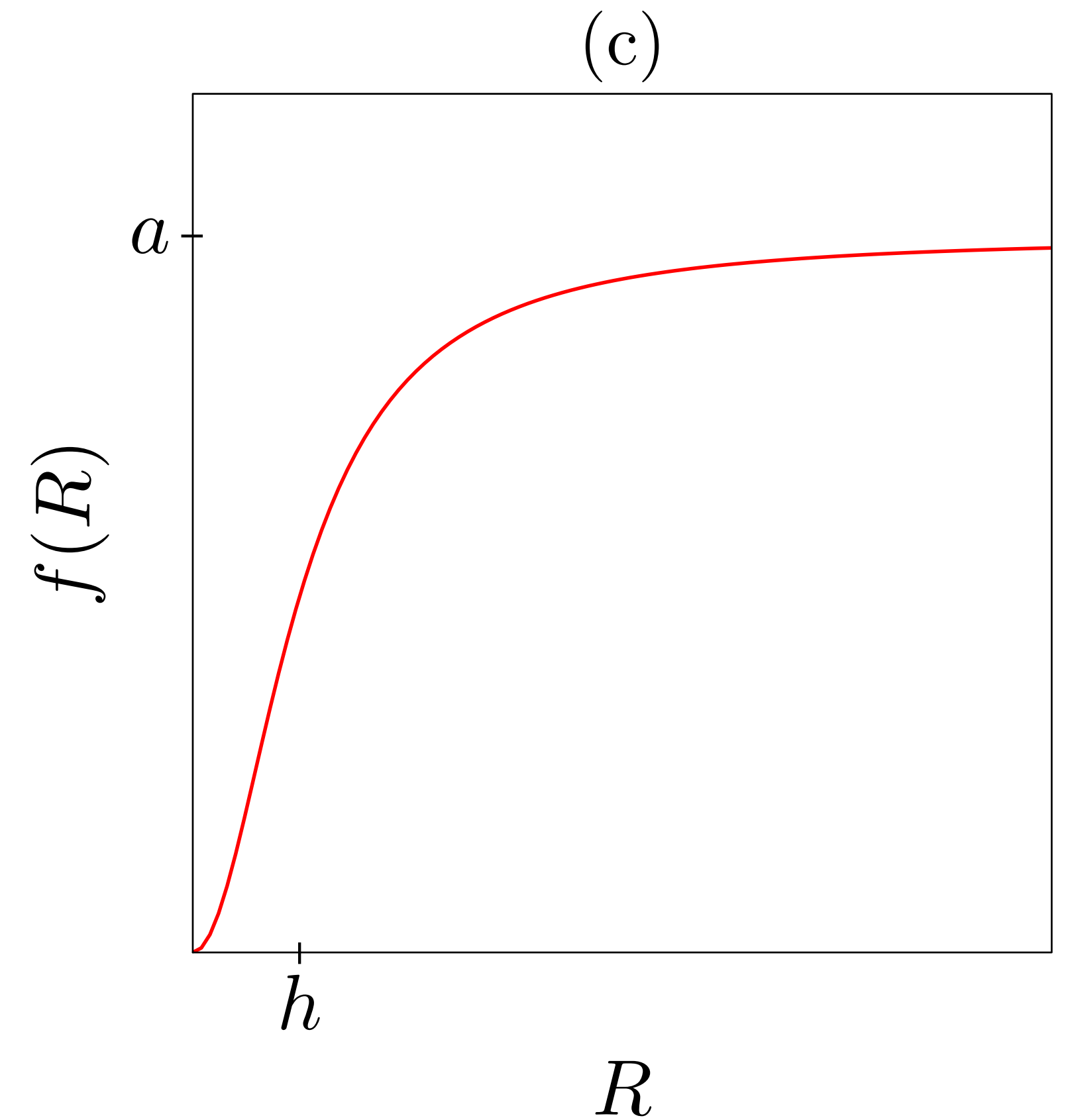
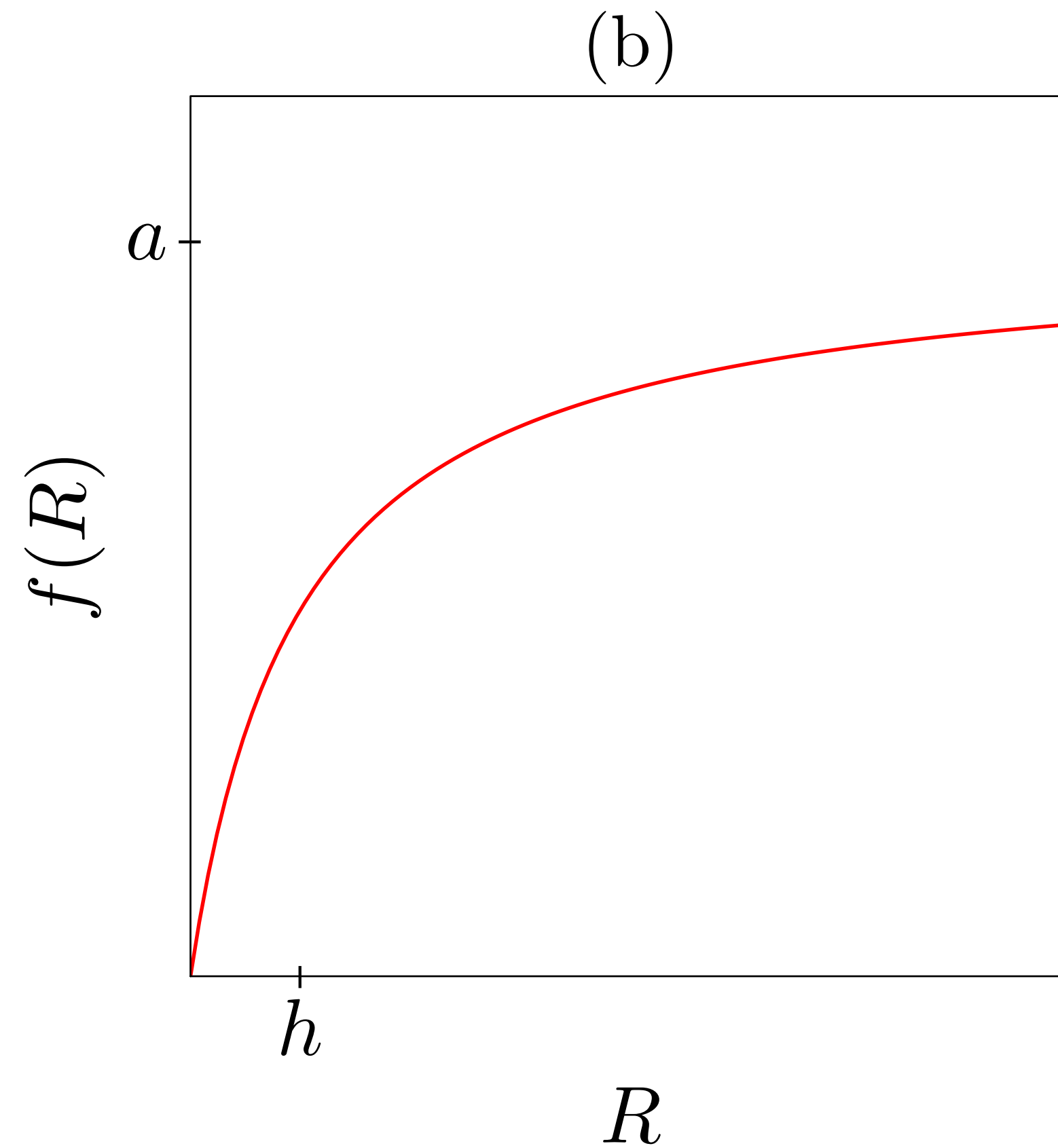
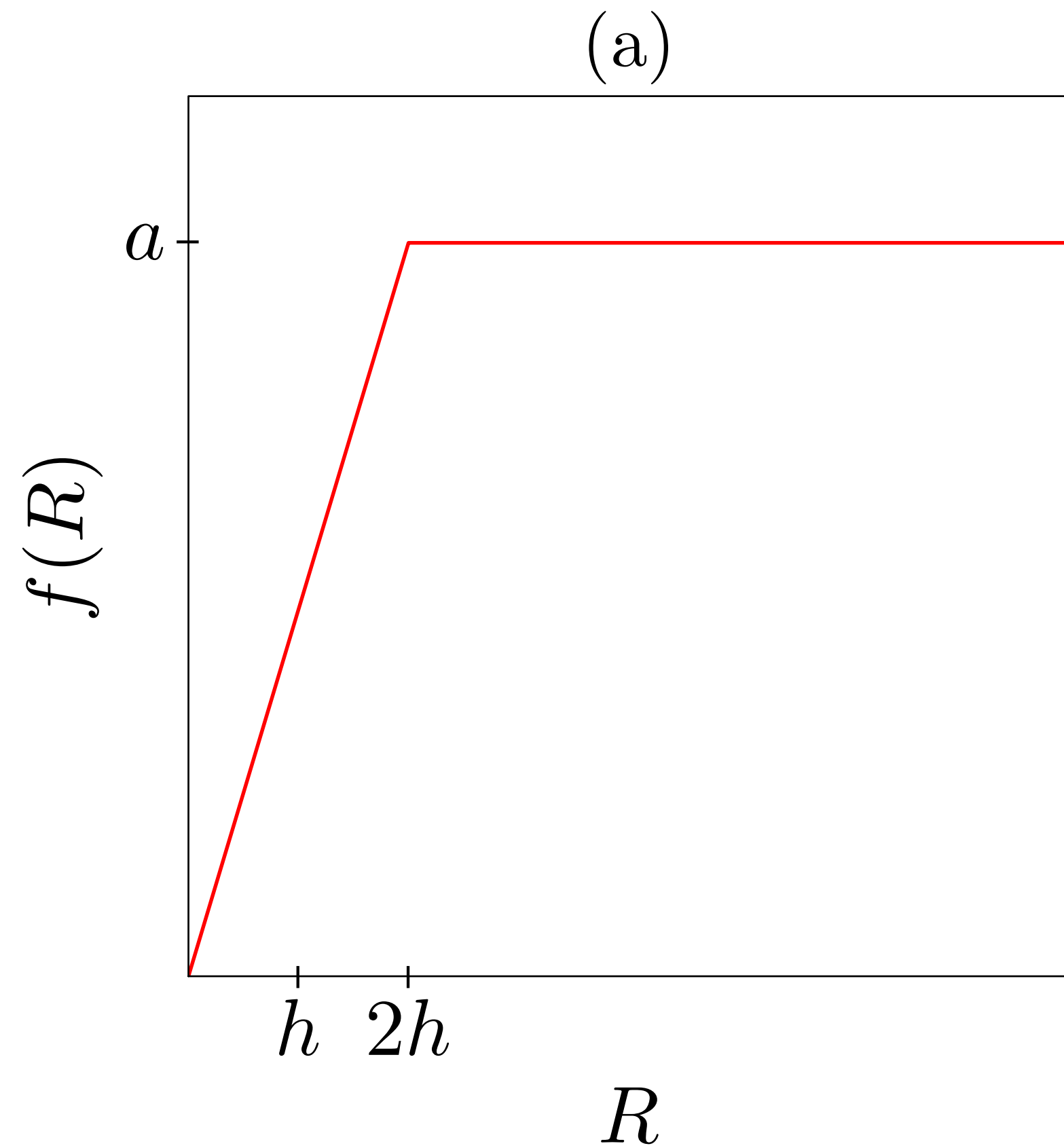
Functional response



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 $T_h=0.9$ h is the handling time.

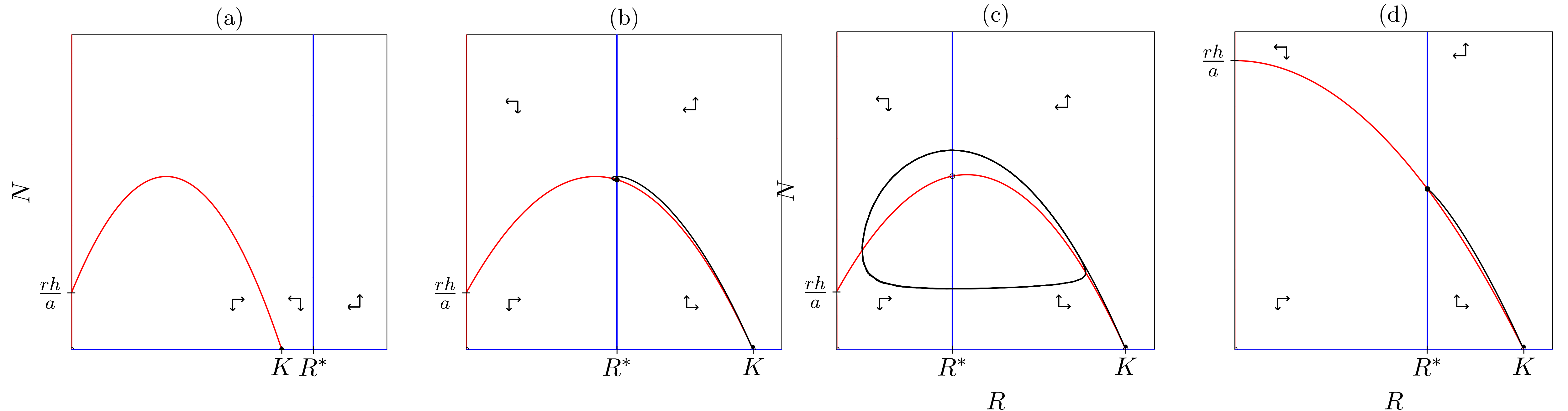
From: Wiedenmann & O'Neil, Environ. Entomol., 1991, 20: 610-614.

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

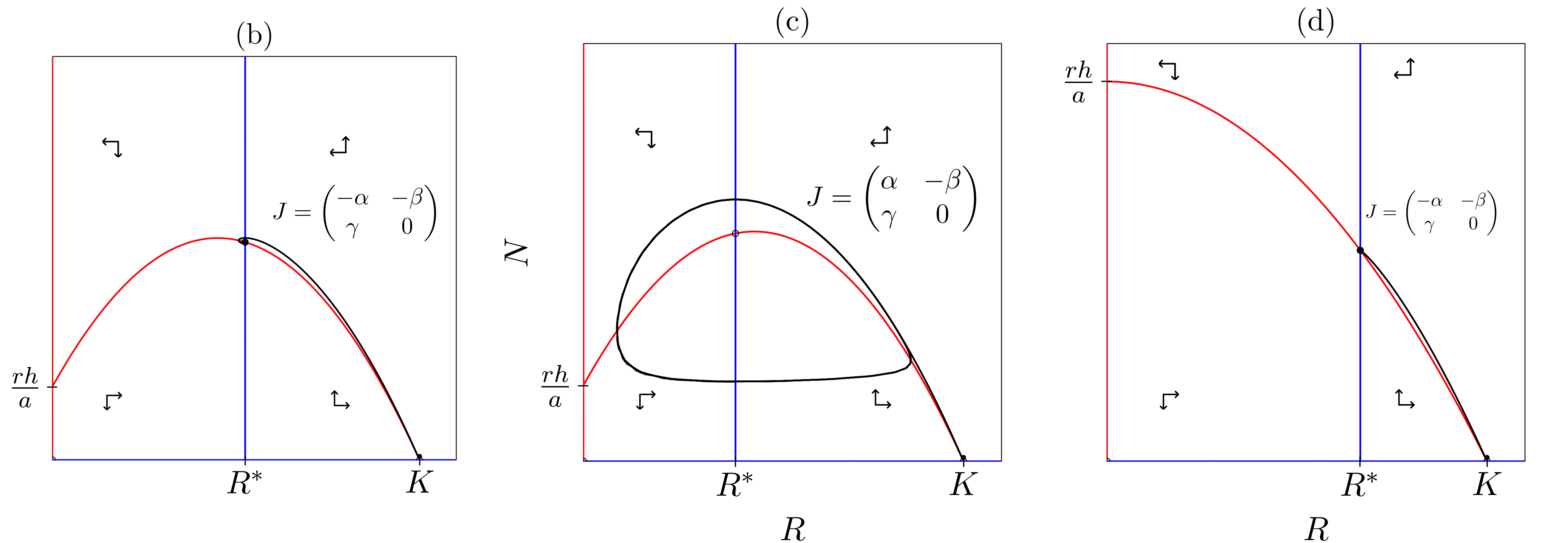


$$\frac{dR}{dt} = rR(1 - R/K) - \frac{aRN}{h + R} = rR(1 - R/K) - \frac{a'RN}{1 + R/h}, \quad \frac{dN}{dt} = \frac{caRN}{h + R} - \delta N$$

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

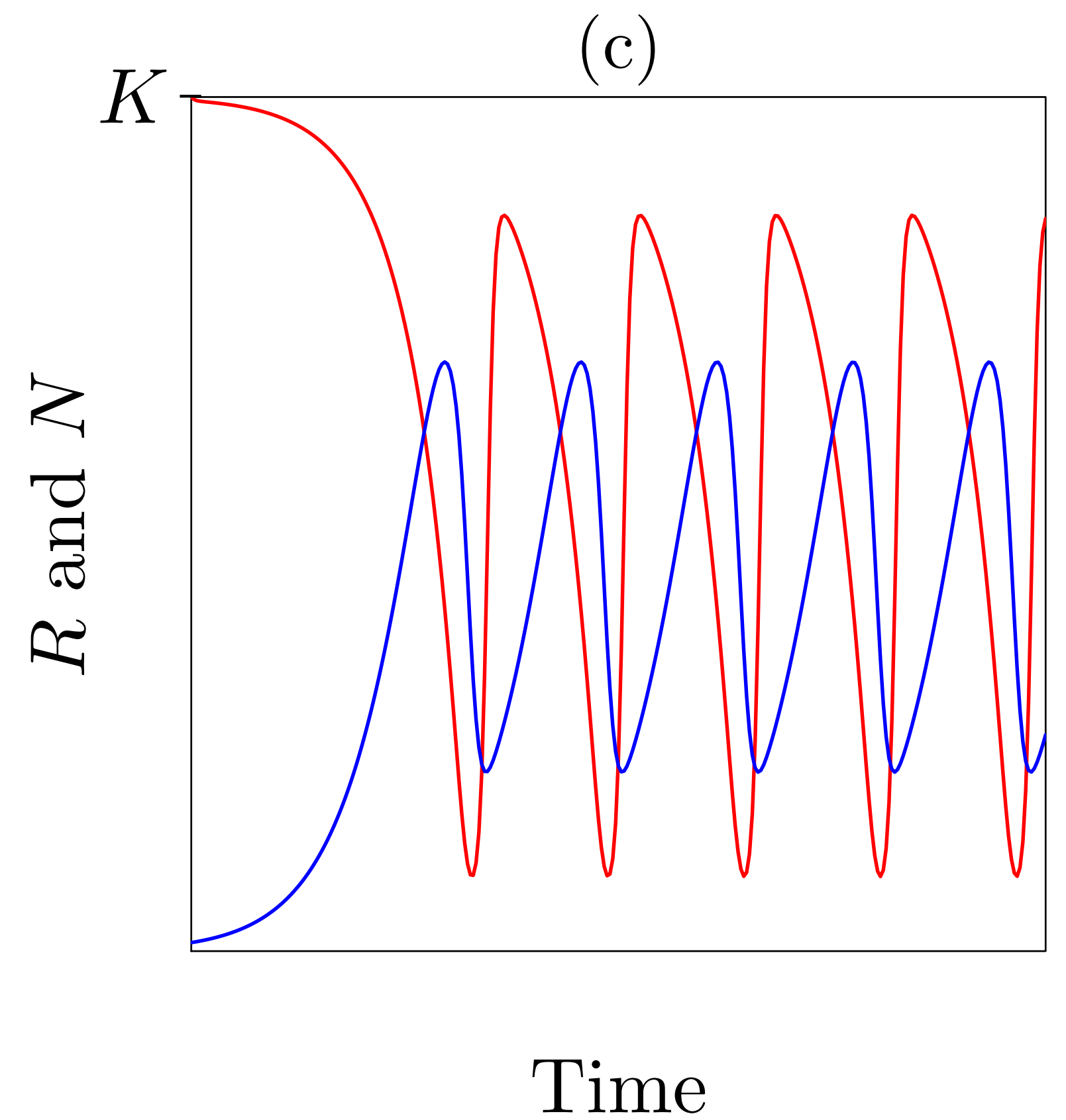
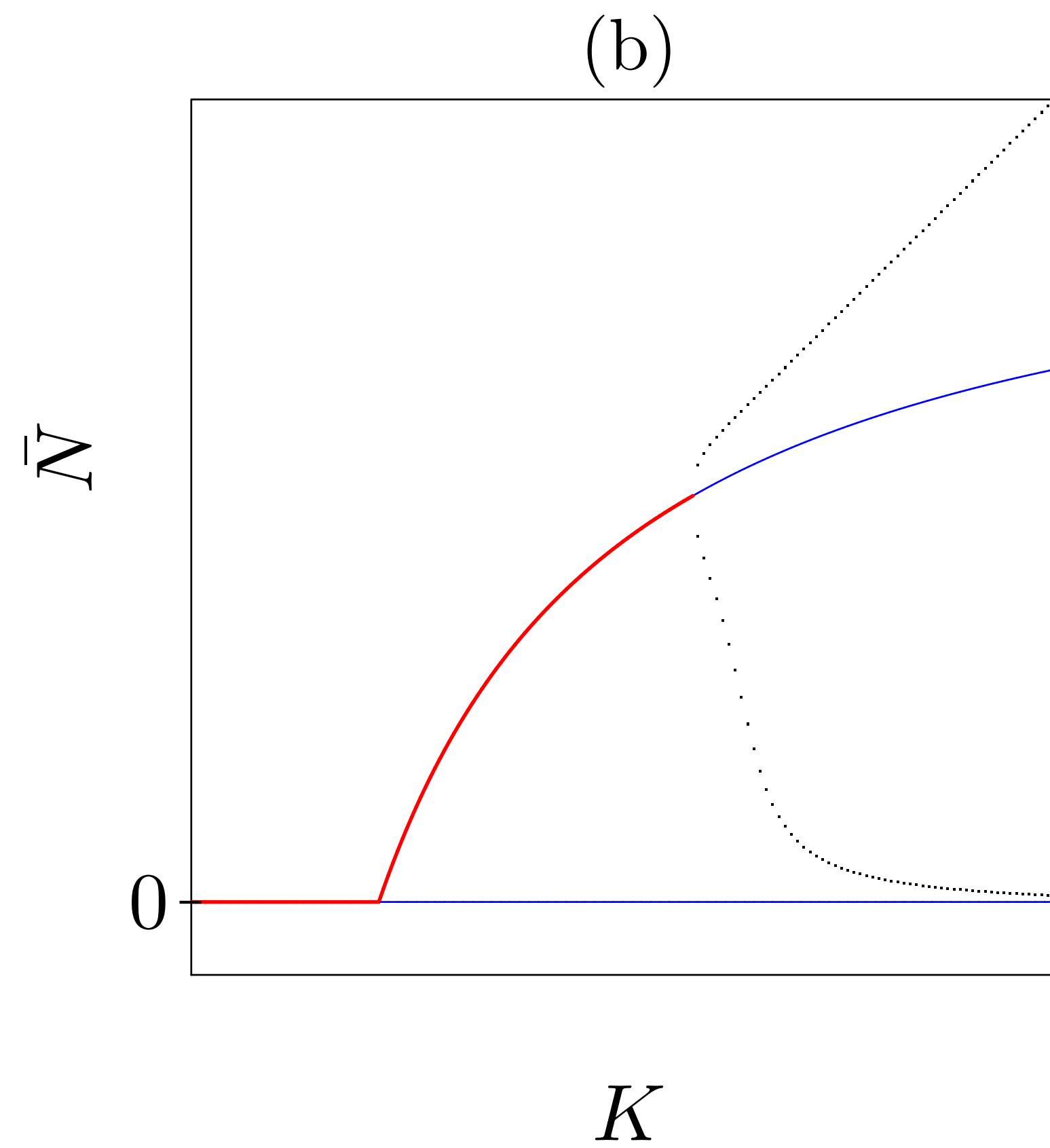
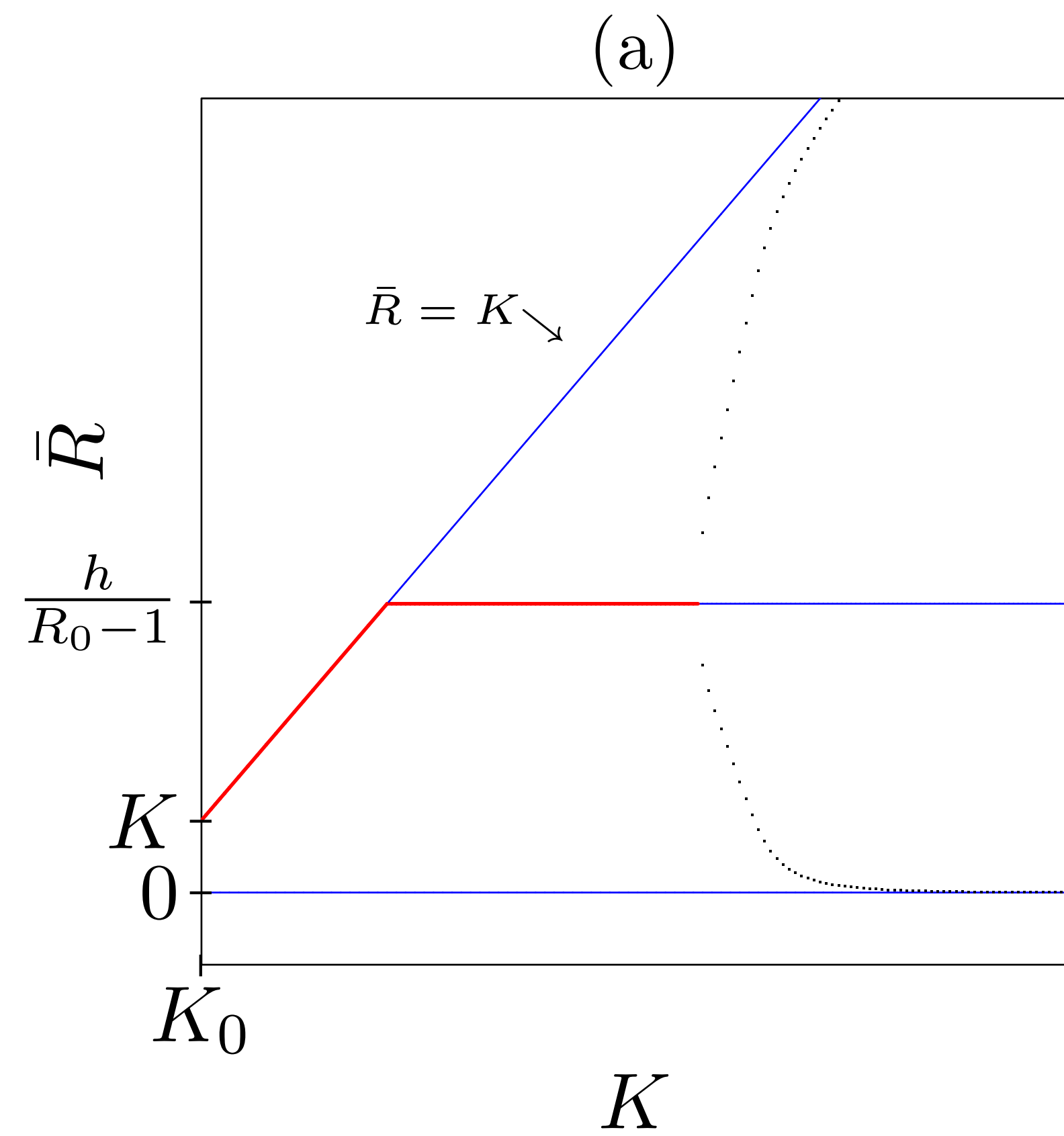
$$R^* = \frac{h}{R_0 - 1}$$

Monod functional response

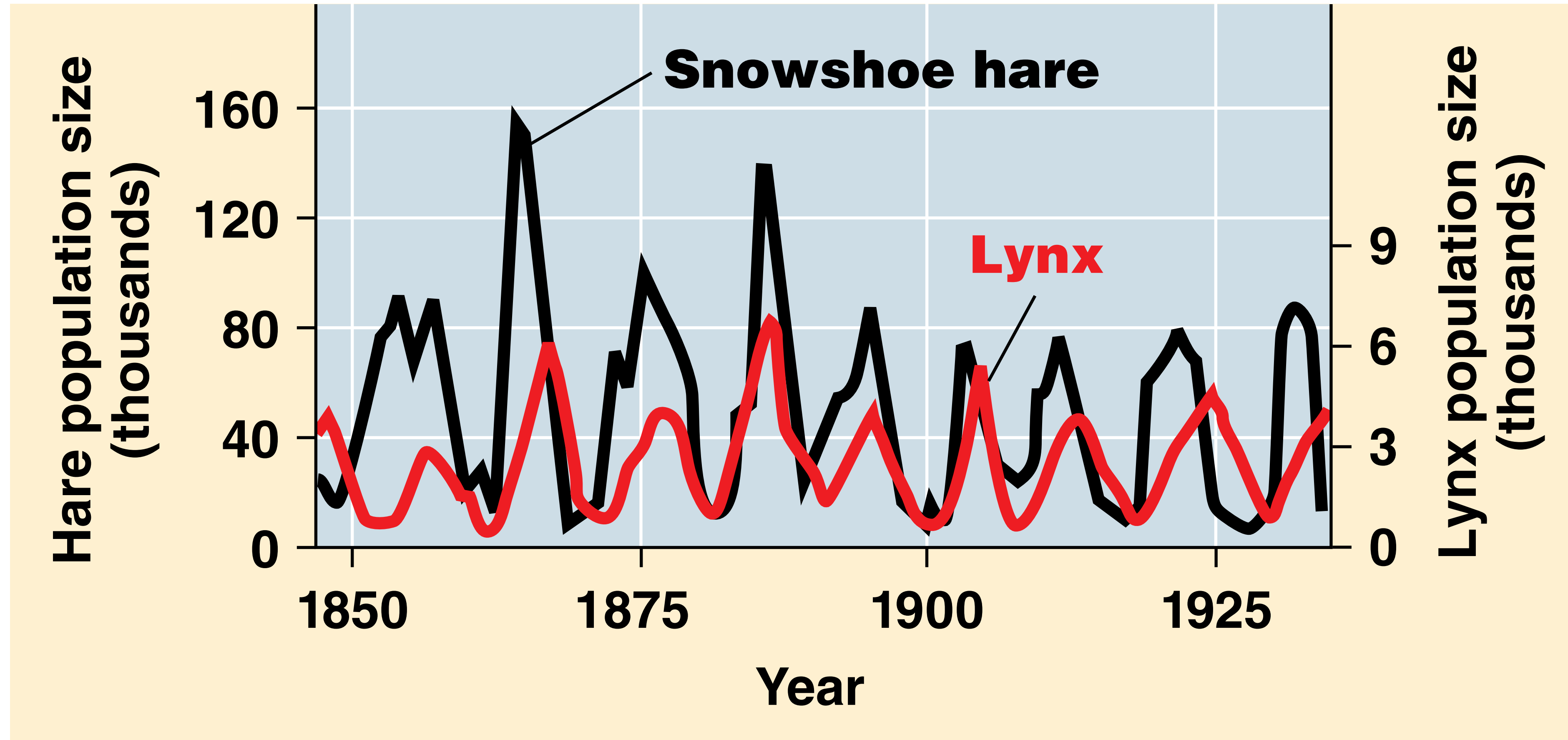


$$\text{tr} = -\alpha < 0 \quad \text{and} \quad \det = \beta\gamma > 0 \quad \text{tr} = \alpha > 0 \quad \text{and} \quad \det = \beta\gamma > 0 \quad \text{tr} = -\alpha < 0 \quad \text{and} \quad \det = \beta\gamma > 0$$

Monod functional response



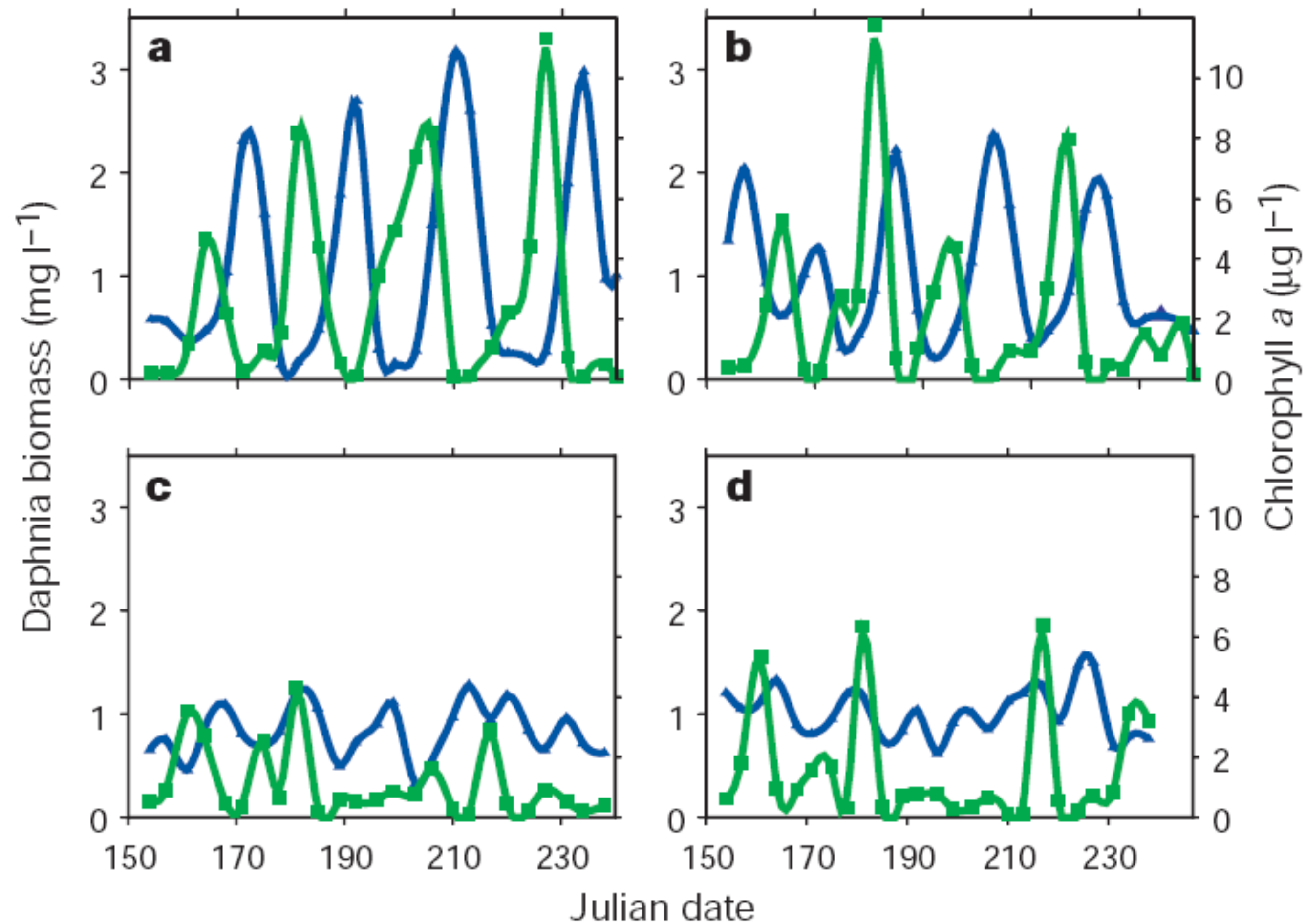
Population cycles



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Population cycles in the snowshoe hare and the lynx.

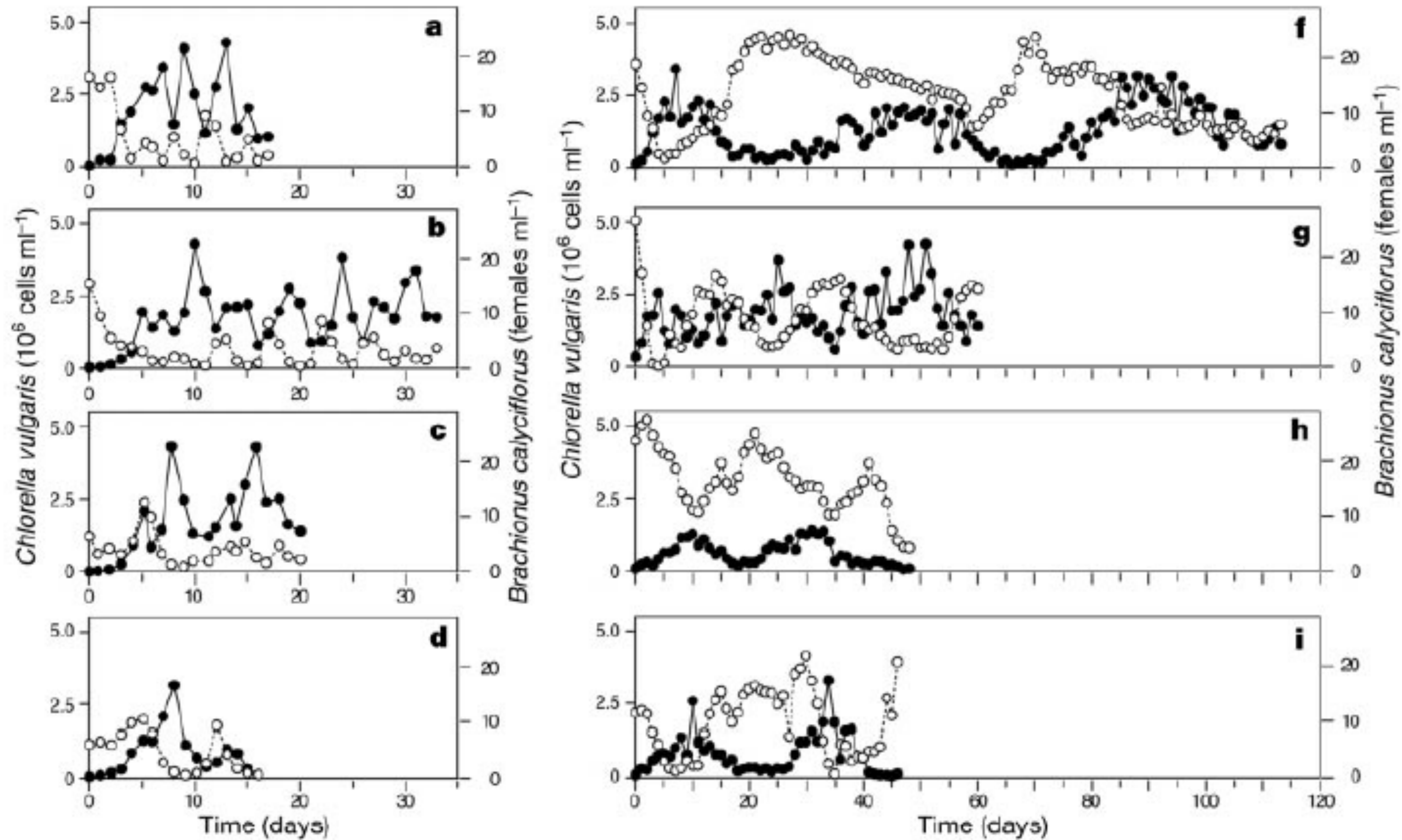
Algae zooplankton oscillations



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).

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).

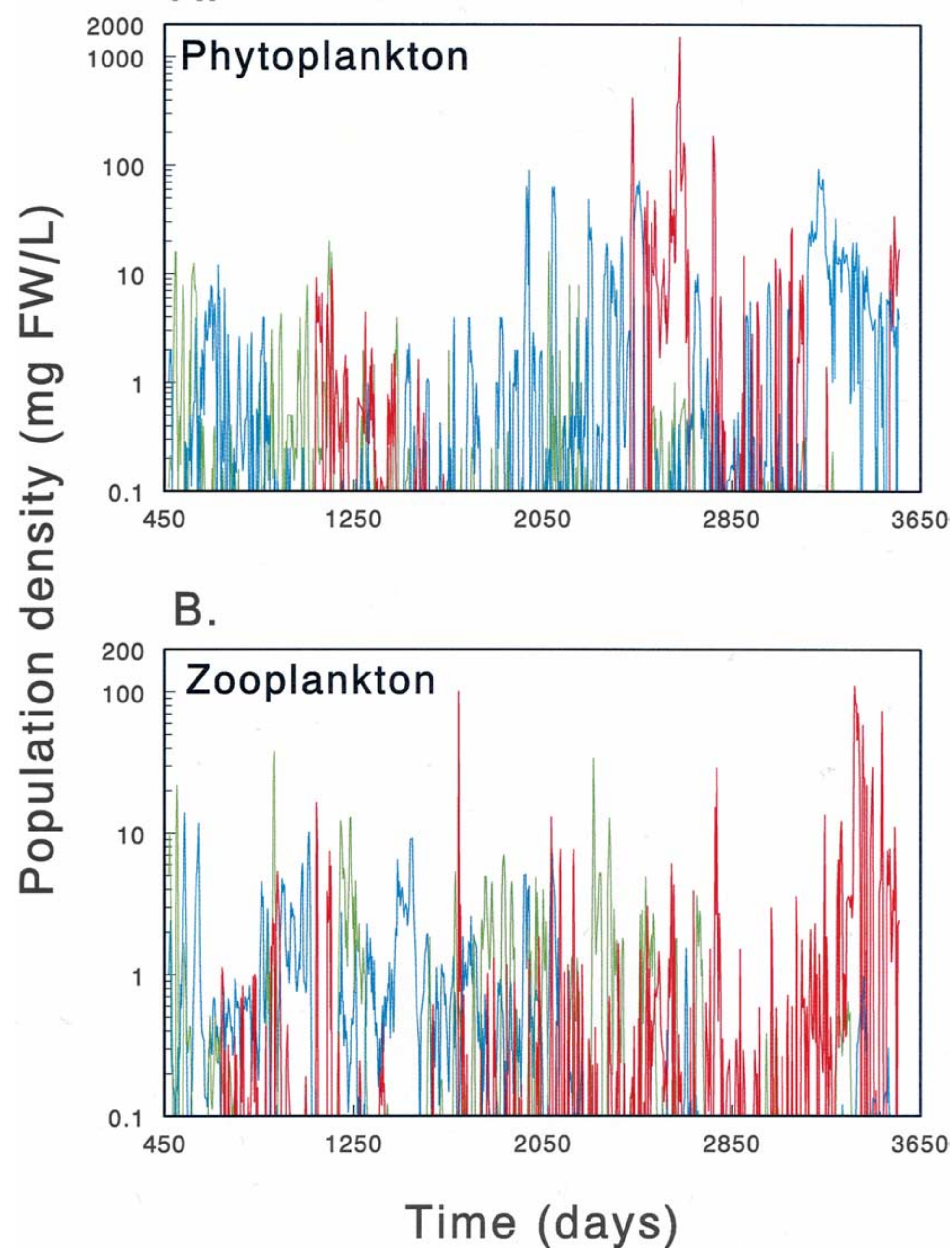


Figure 5. Non-equilibrium dynamics observed in an experimental multispecies community. The community developed in a long-term laboratory experiment under constant external conditions, and consisted of more than 20 different species. Data show the observed time course of (A) the dominant phytoplankton 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.

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

Quasi steady state assumption

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

$$\frac{dC}{dt} = aRF - hC \quad \text{or} \quad \frac{dC}{dt} = aR(N - C) - hC$$

$$\frac{dC}{dt} = 0 \quad \text{gives} \quad C = \frac{aNR}{h + aR} = \frac{NR}{h' + R}$$

Quasi steady state assumption

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

$$\frac{dC}{dt} = aRF - hC \quad \text{or} \quad \frac{dC}{dt} = aR(N - C) - hC$$

$$\frac{dC}{dt} = 0 \quad \text{gives} \quad C = \frac{aNR}{h + aR} = \frac{NR}{h' + R}$$

Add $dC/dt = 0$ to $dR/dt = rR(1 - R/K) - aRF$

$$\frac{dR}{dt} = rR(1 - R/K) - hC = rR(1 - R/K) - \frac{hNR}{h' + R}$$

$$\frac{dN}{dt} = cC - dN = \frac{cNR}{h' + R} - dN \quad \text{Consumers that eat replicate.}$$

One consumer using several resources

$$\frac{dC_i}{dt} = a_i R_i F - h C_i = 0 \quad \Leftrightarrow \quad a_i R_i \left(N - \sum_j C_j \right) = h C_i$$

Write as a sum $\sum_i a_i R_i \left(N - \sum_j C_j \right) = h \sum_i C_i$ or

$$\sum_i a_i R_i N = \sum_i a_i R_i \sum_j C_j + h \sum_j C_j = \sum_j C_j \left(\sum_i a_i R_i + h \right)$$

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

For each resource, i , one can again add $dC_i/dt = a_i R_i F - h C_i = 0$ to

$$\begin{aligned} \frac{dR_i}{dt} &= r R_i (1 - R_i/K_i) - a_i R_i F \quad \text{giving} \quad \frac{dR_i}{dt} = r R_i (1 - R_i/K_i) - \frac{h a_i R_i N}{h + \sum_j a_j R_j} \\ \frac{dN}{dt} &= c \sum_i C_i - dN = \frac{c N \sum_i a_i R_i}{h + \sum_j a_j R_j} - dN \end{aligned}$$

Saturated birth rate

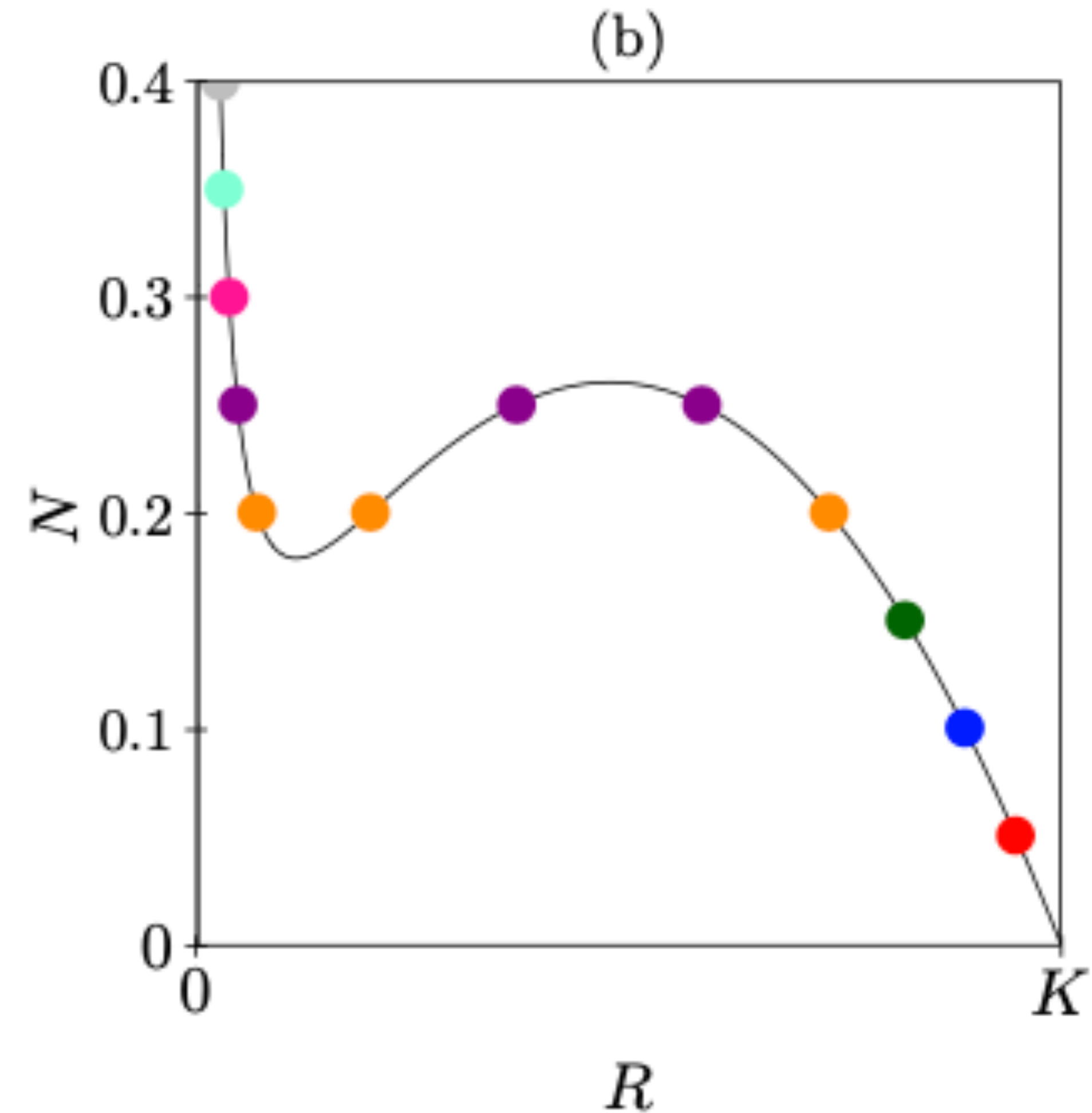
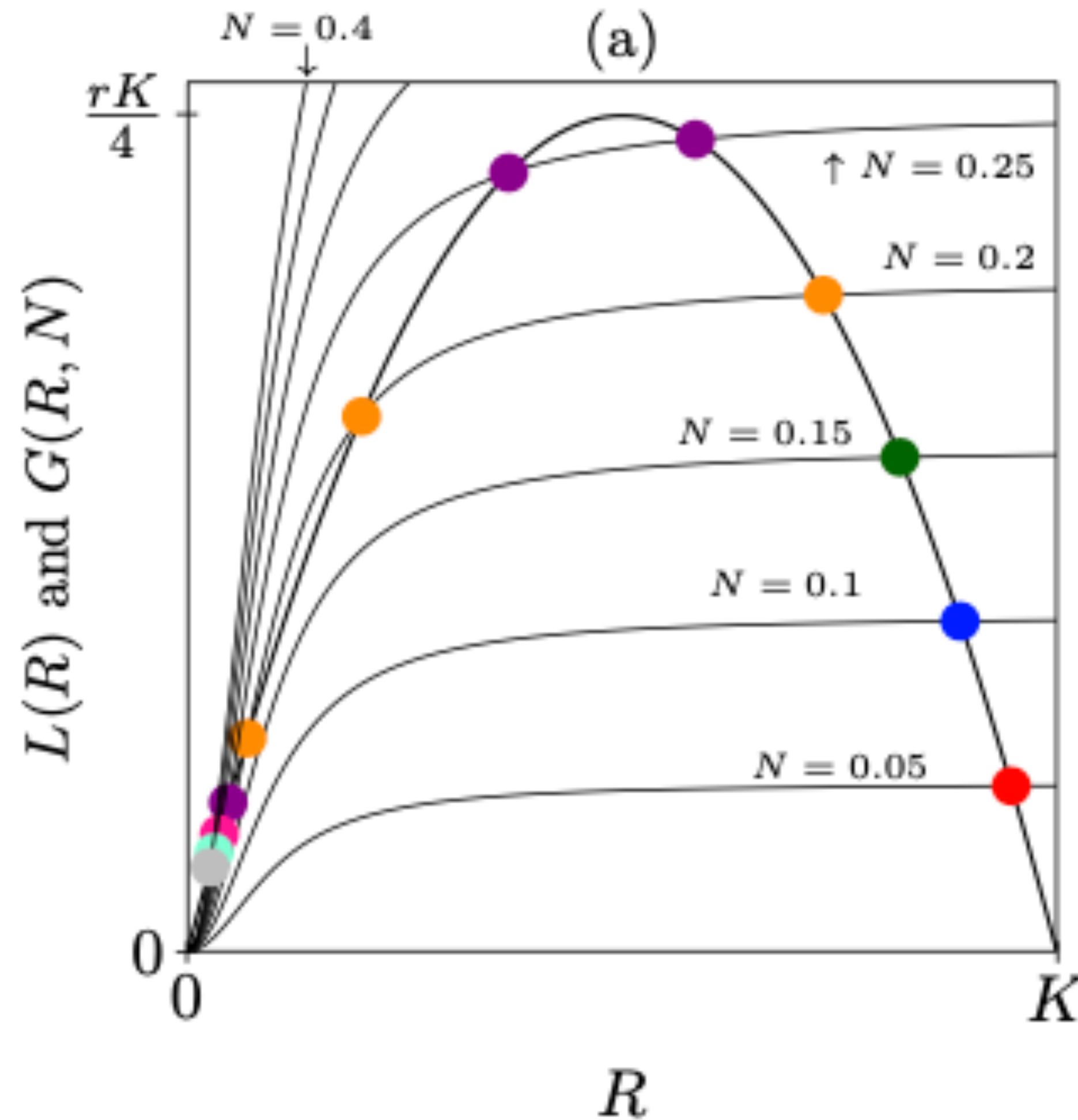
$$\frac{dR}{dt} = rR(1 - R/K) - \frac{aRN}{h + R} \quad \text{consumption} \quad \frac{aR}{h + R}$$

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

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

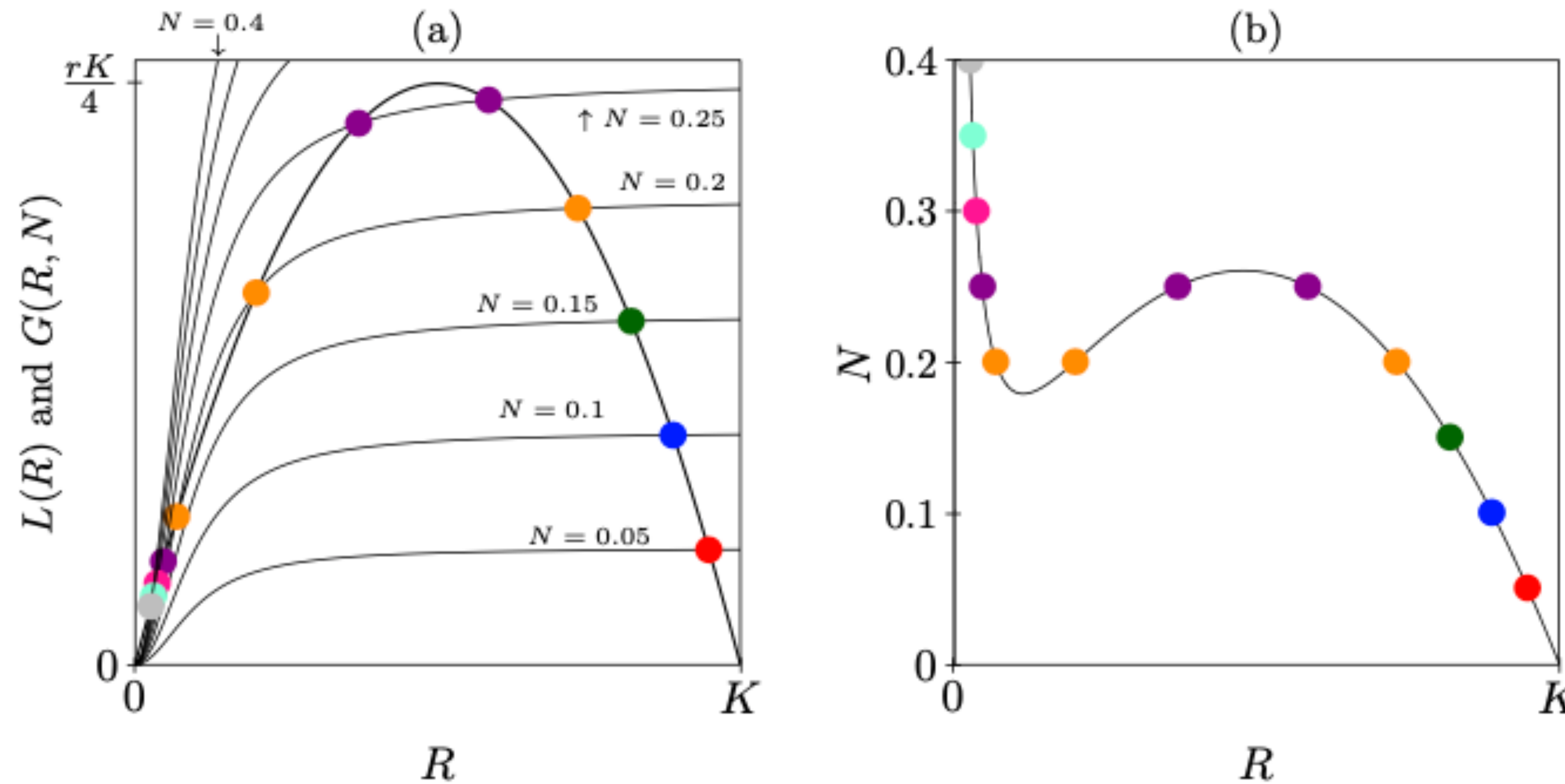
$$\frac{dN}{dt} = \frac{\beta RN}{h' + R} - \delta N$$

Sigmoid functional response



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

Sigmoid functional response



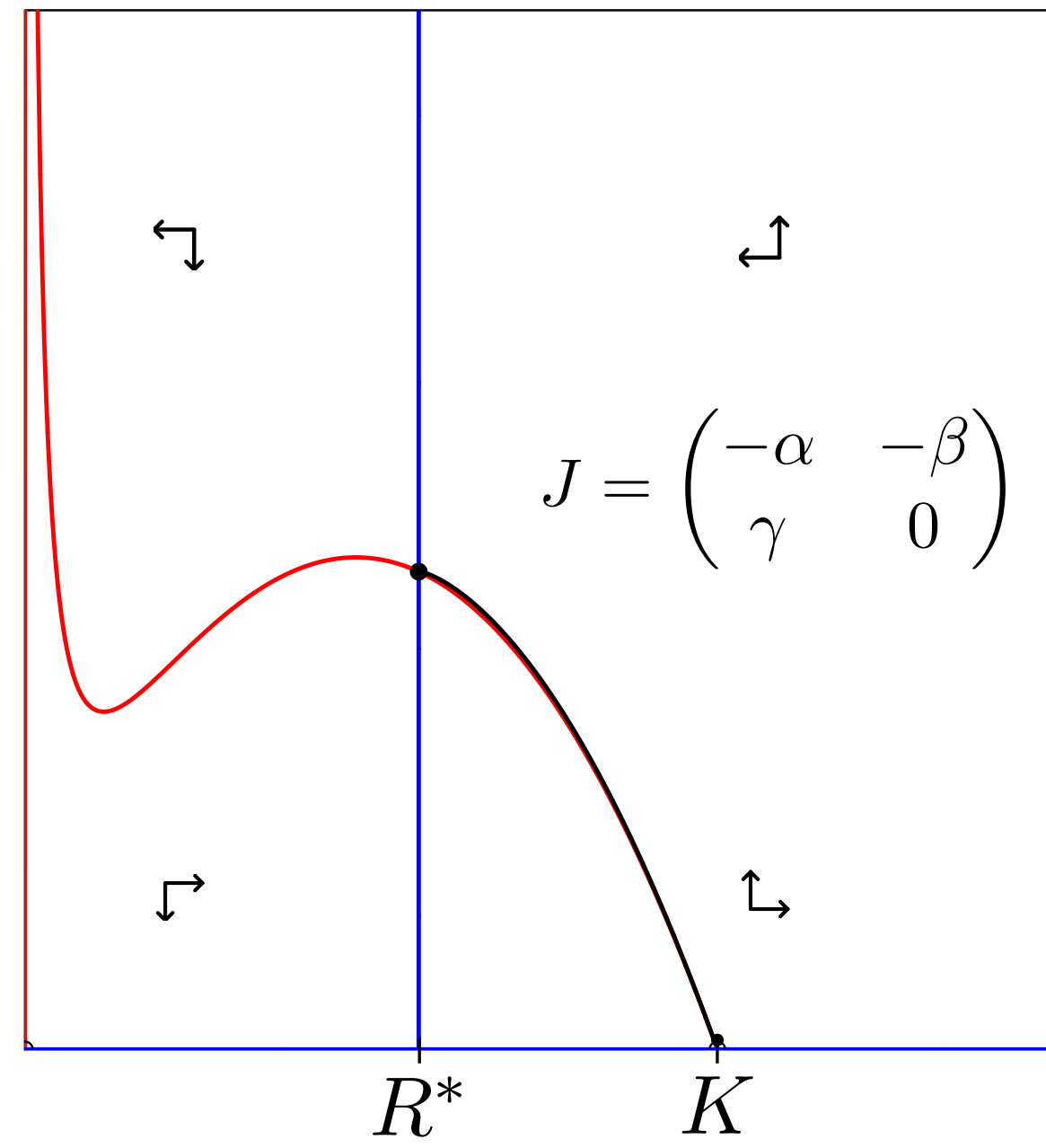
$$\frac{dR}{dt} = \overbrace{rR(1 - R/K)}^{f(R)} - \overbrace{\frac{aR^2 N}{h^2 + R^2}}^{g(R, N)}$$

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

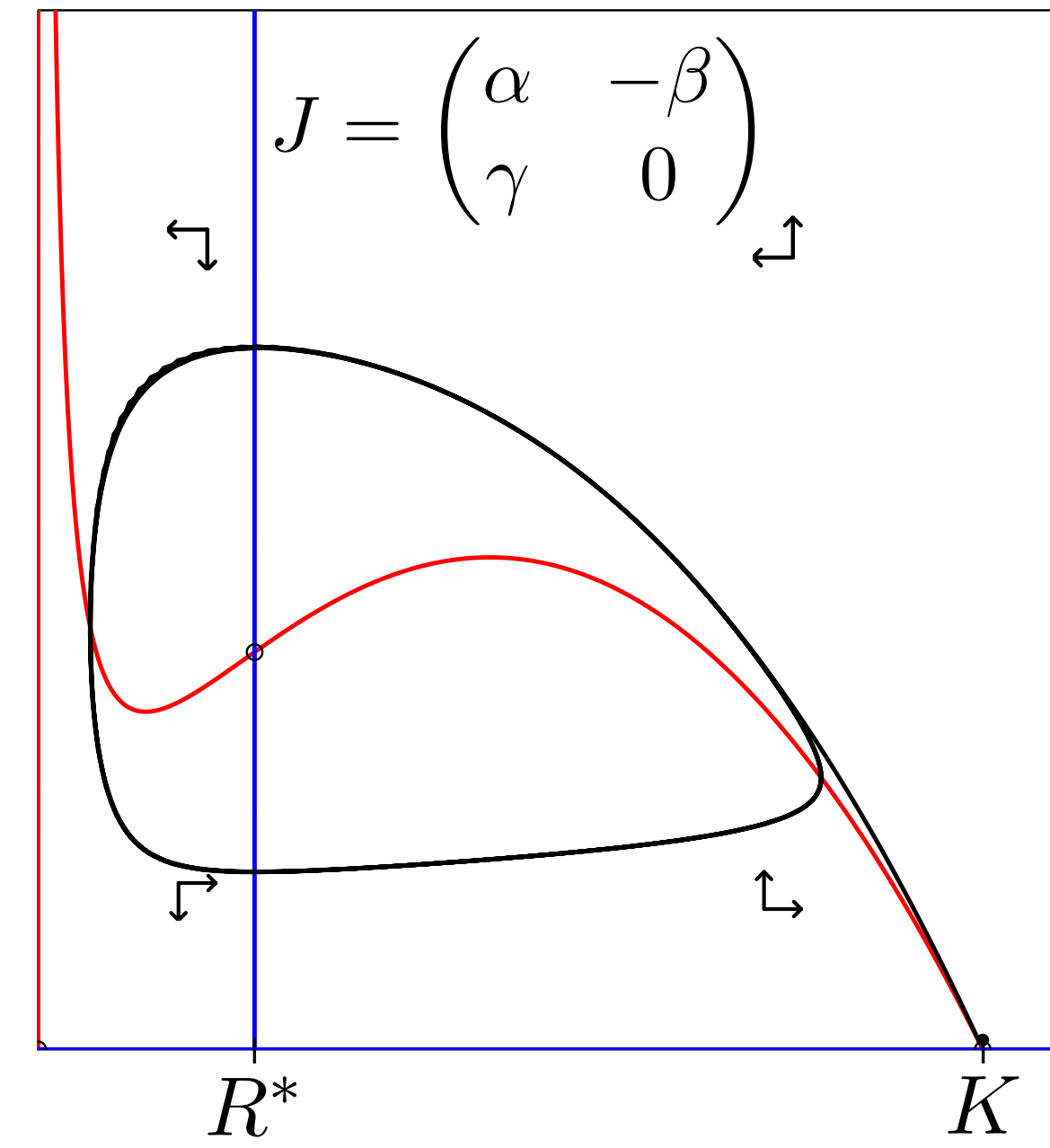
$$\partial_R \overbrace{f(R)}^{f(R)} = r - 2rR/K$$

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

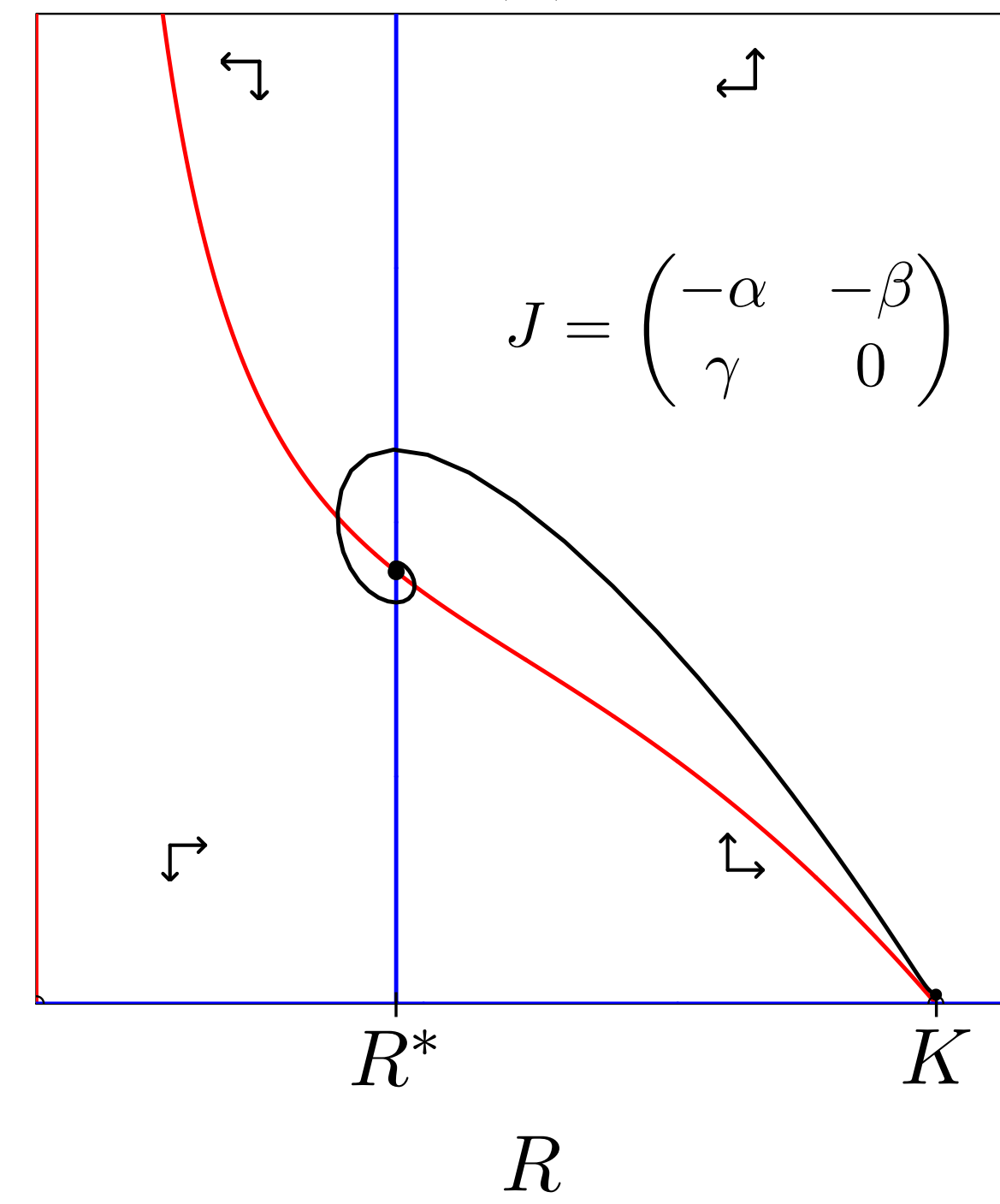
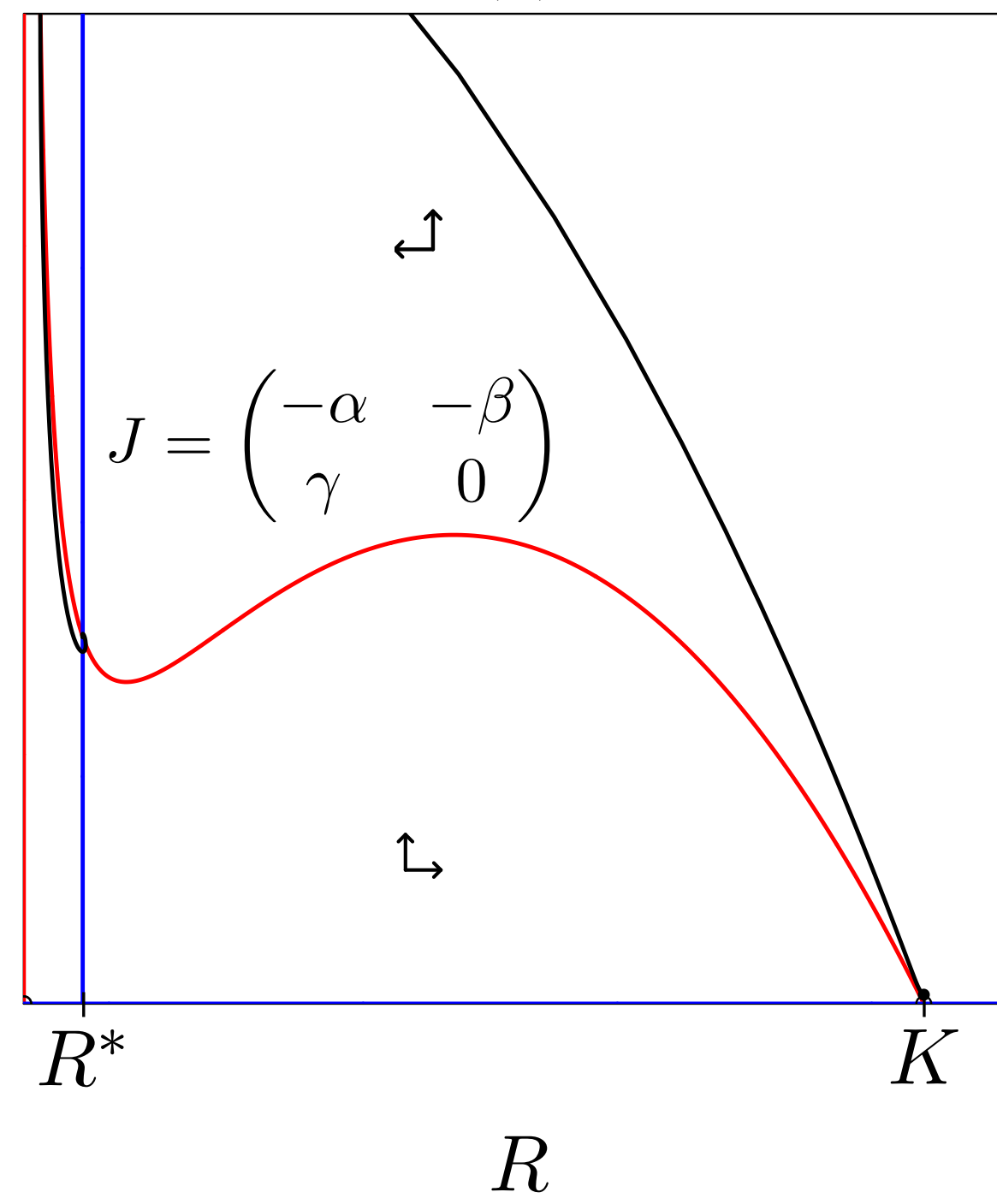
Sigmoid functional response

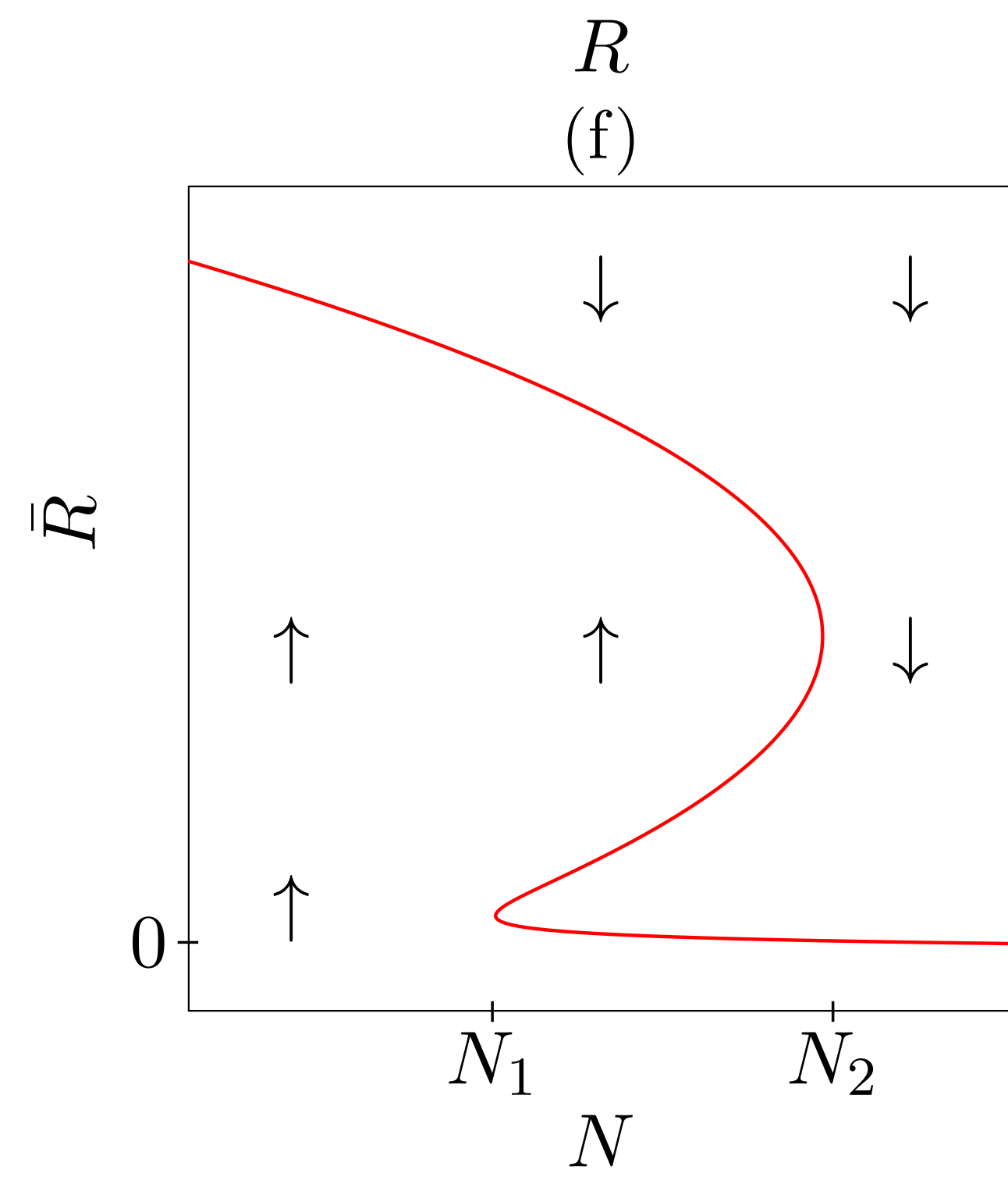
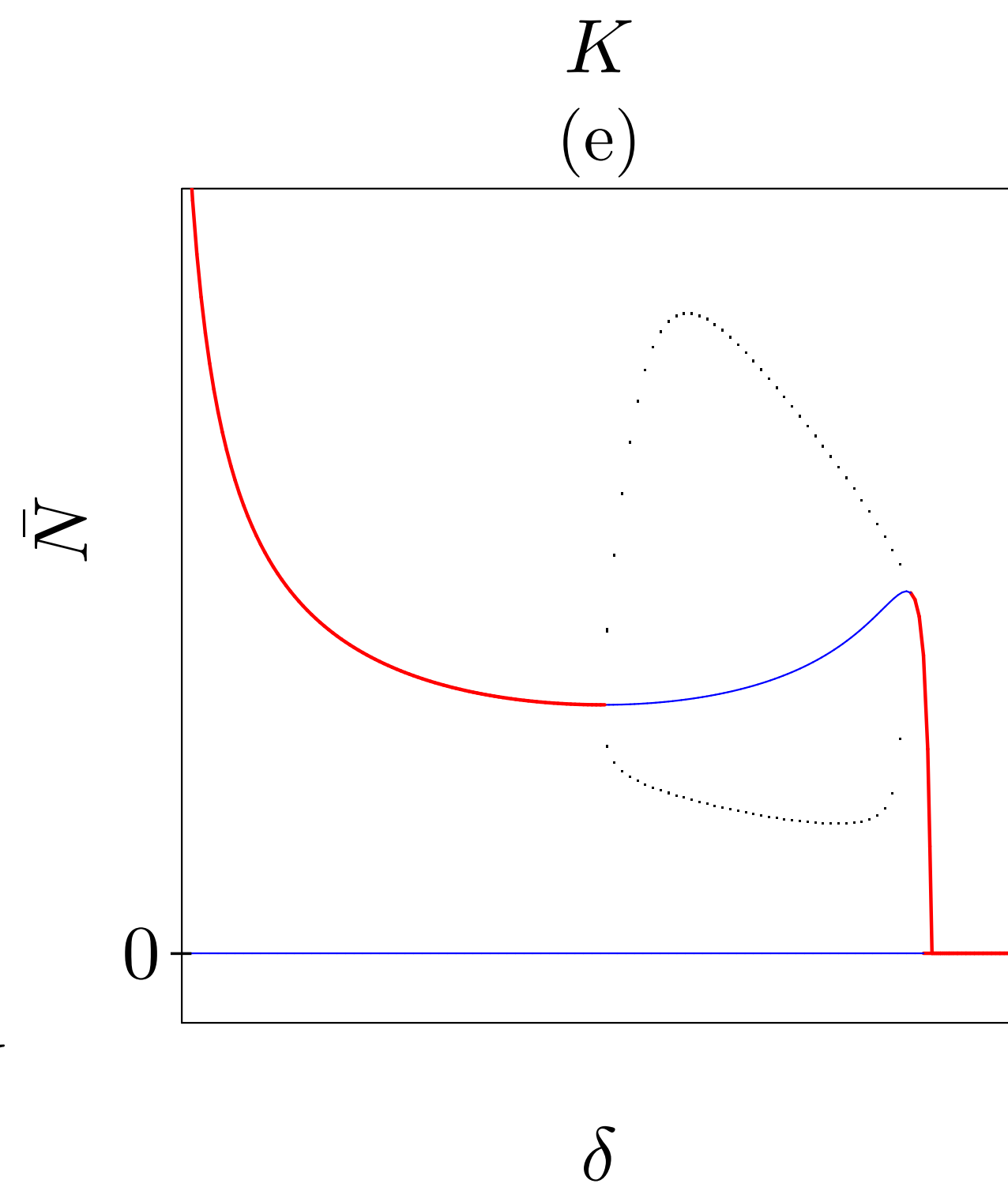
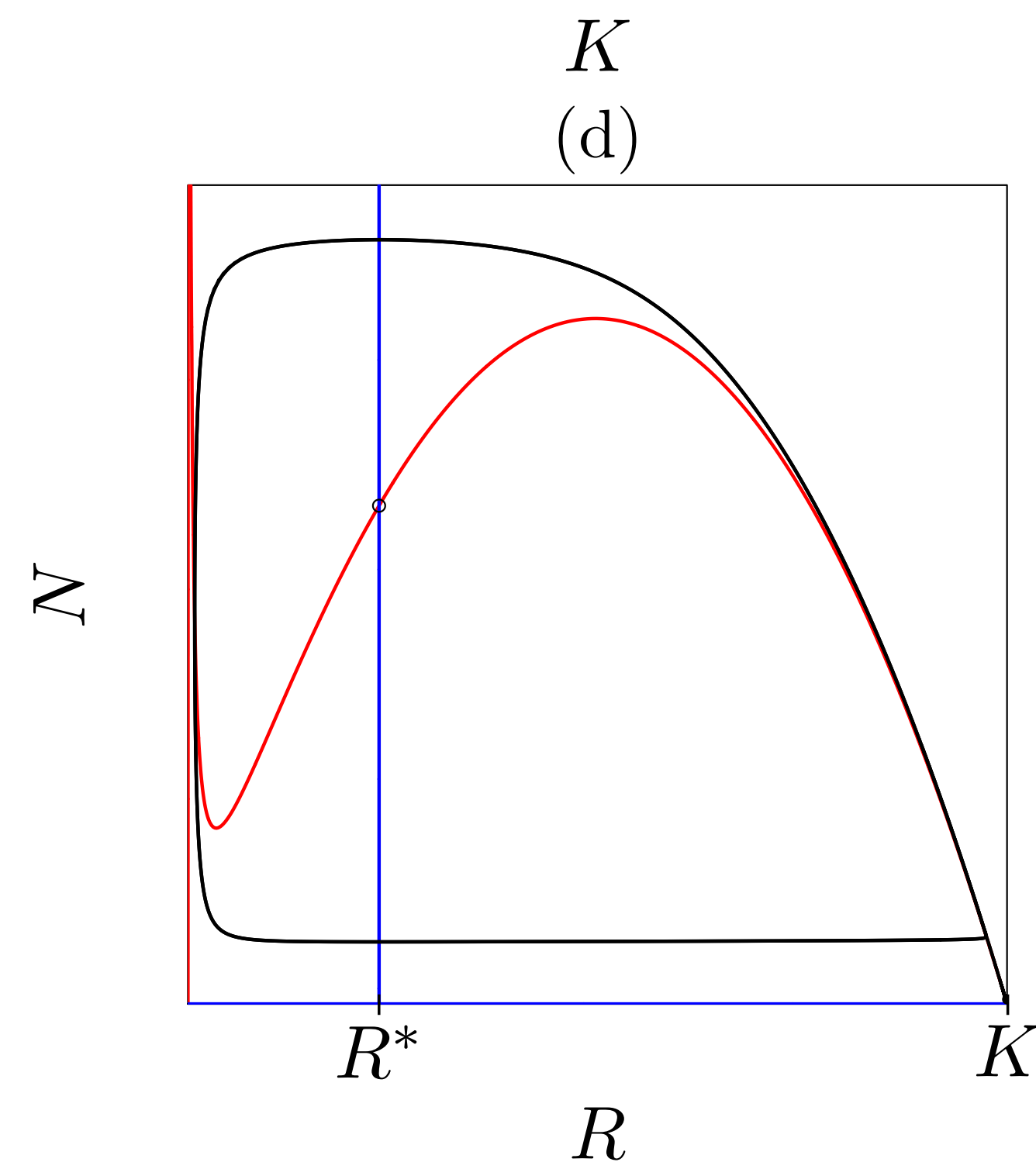
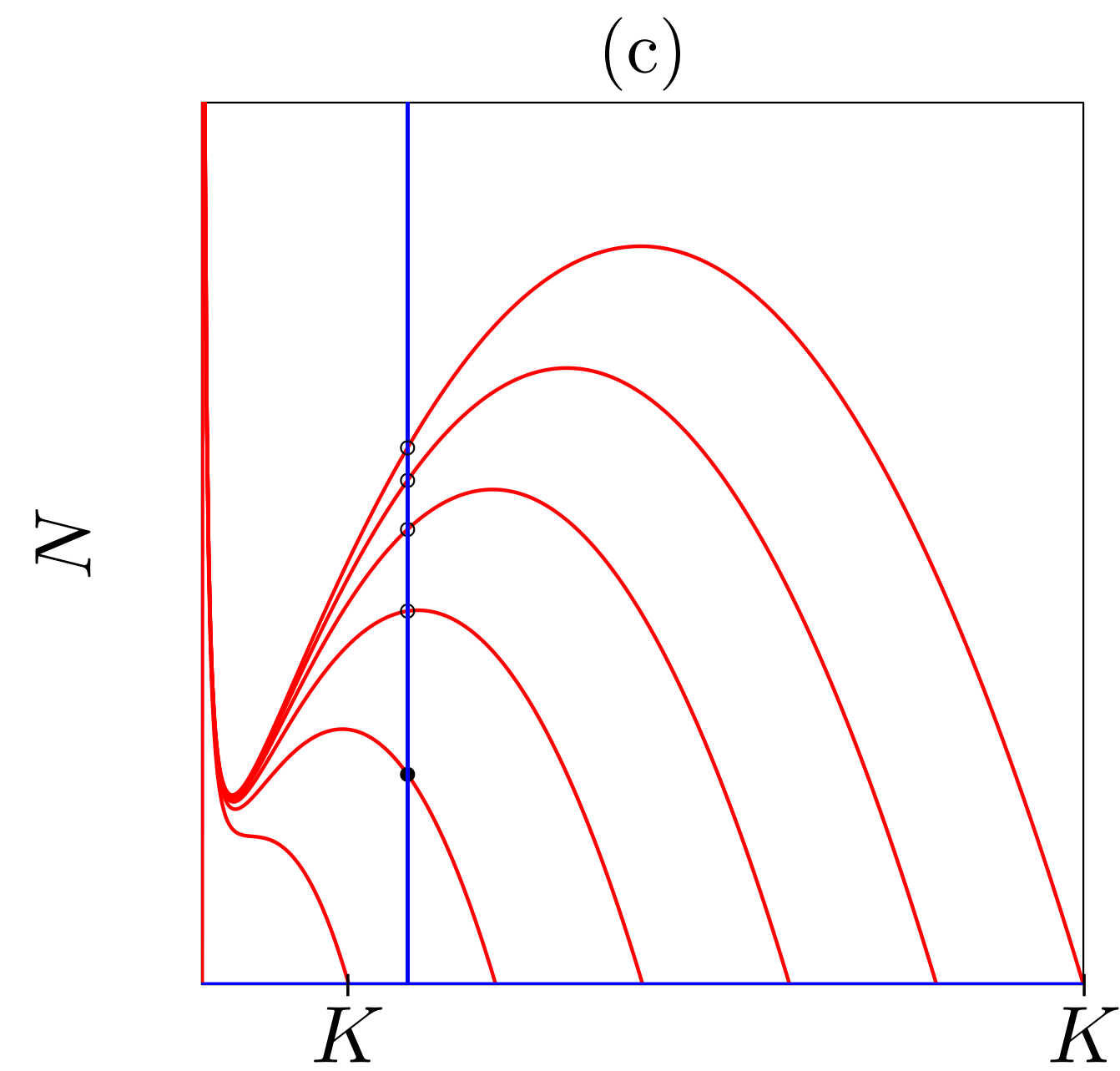
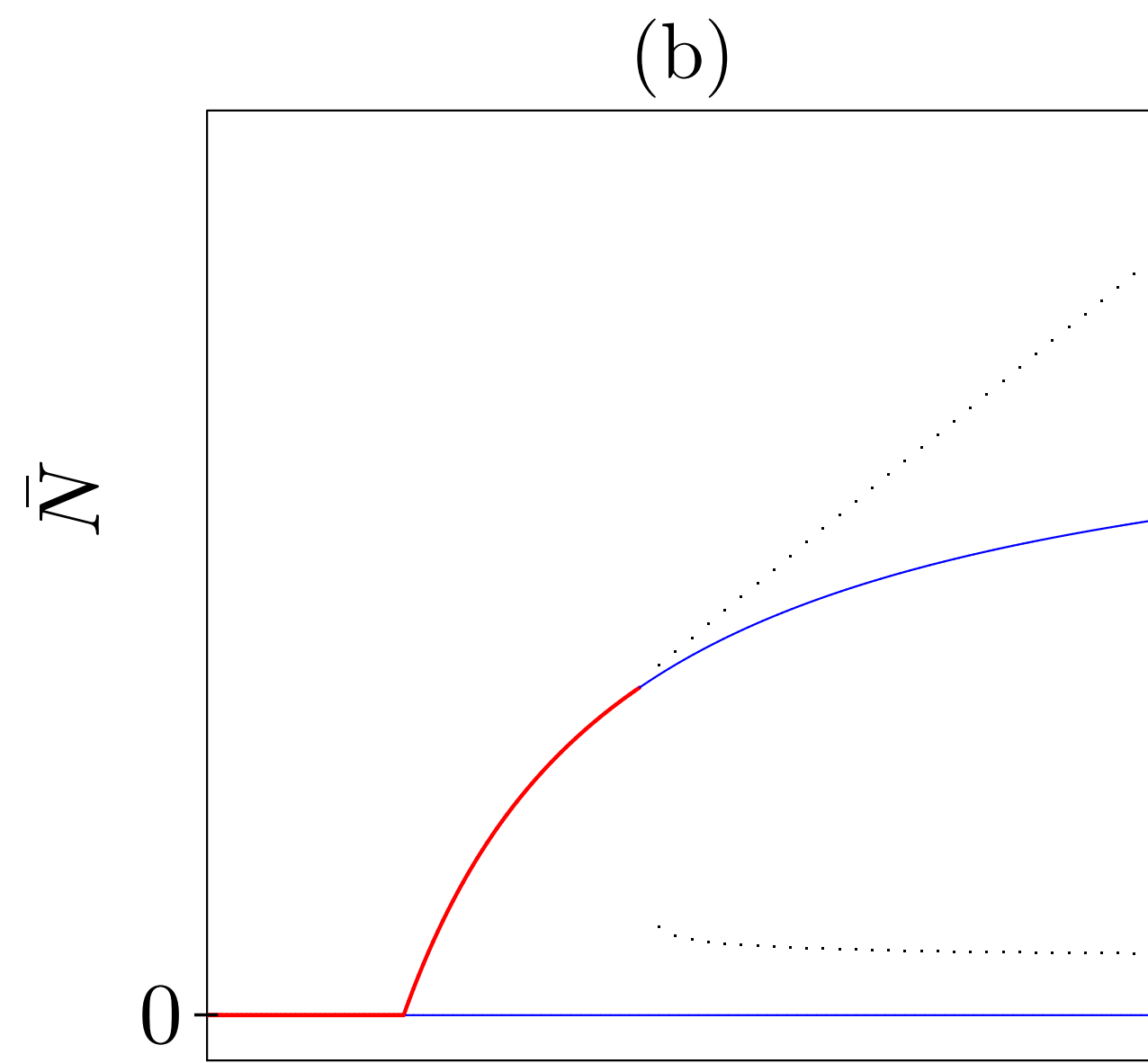
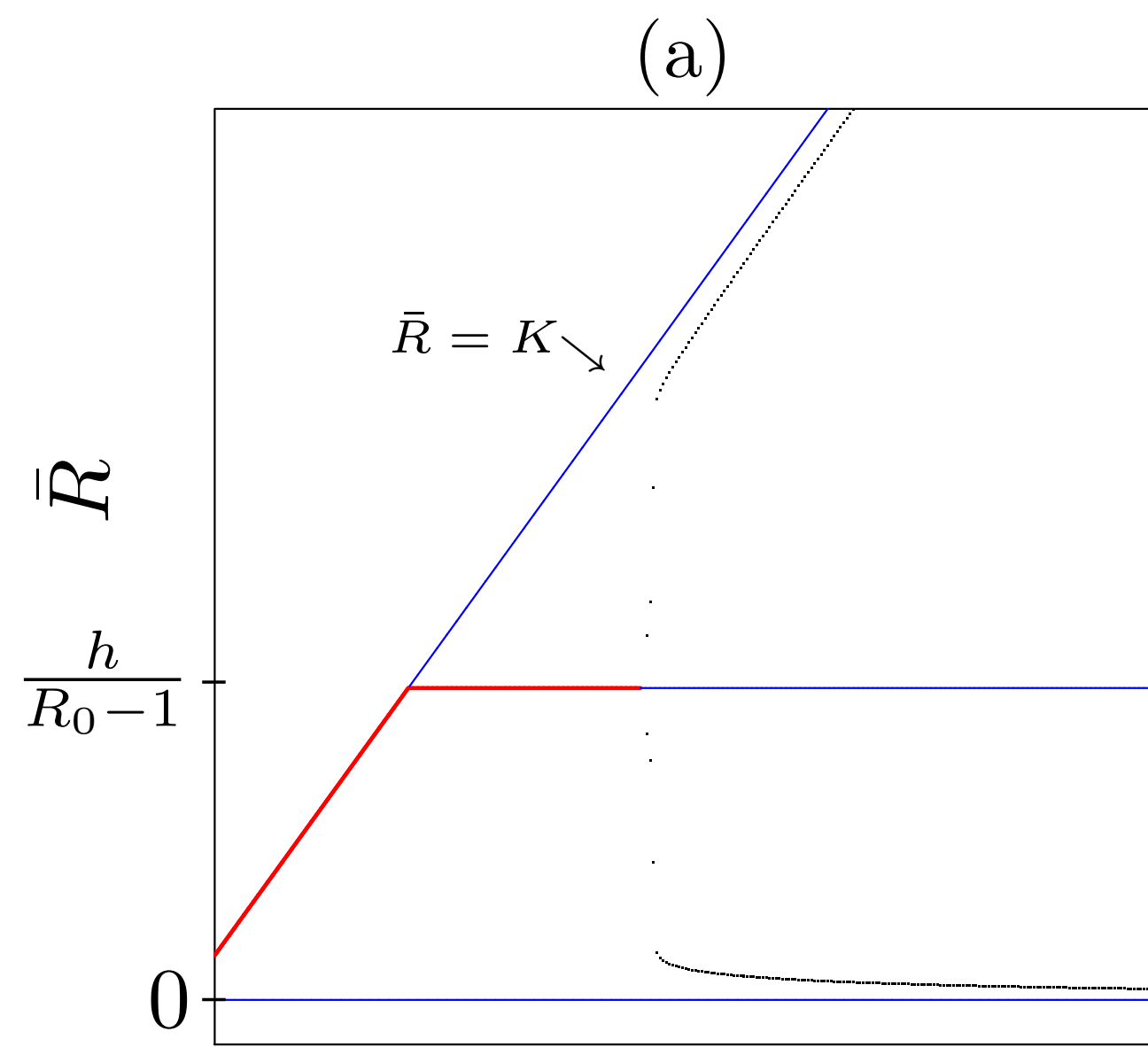


(c)



(d)





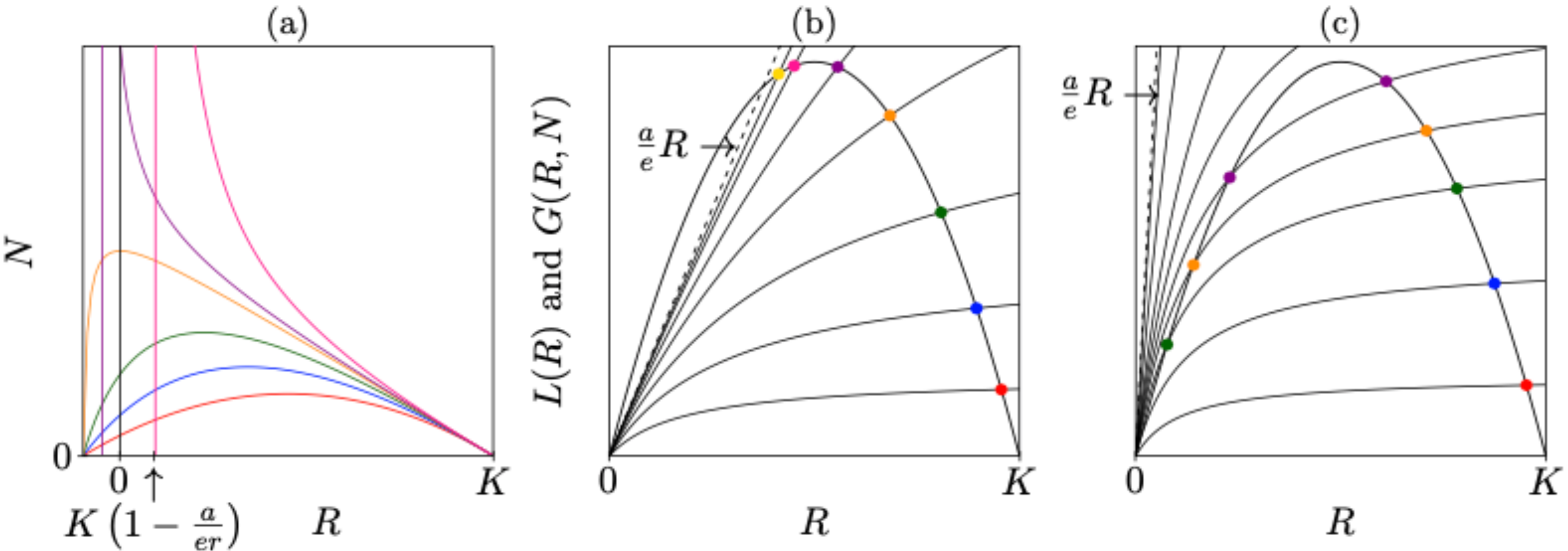
Sigmoid functional response

Beddington functional response

$$\begin{aligned}\frac{dR}{dt} &= rR(1 - R/K) - \frac{aRN}{h + eN + R} \\ \frac{dN}{dt} &= \frac{caRN}{h + eN + R} - dN .\end{aligned}\quad \lim_{R \rightarrow \infty} \frac{aR}{h + eN + R} = a$$

$$\frac{dN}{dt} = 0 \rightarrow N = 0 \quad \text{and} \quad N = \frac{ca - d}{de} R - \frac{h}{e} = \frac{R_0 - 1}{e} R - \frac{h}{e} .$$

Constructing the $R'=0$ nullcline



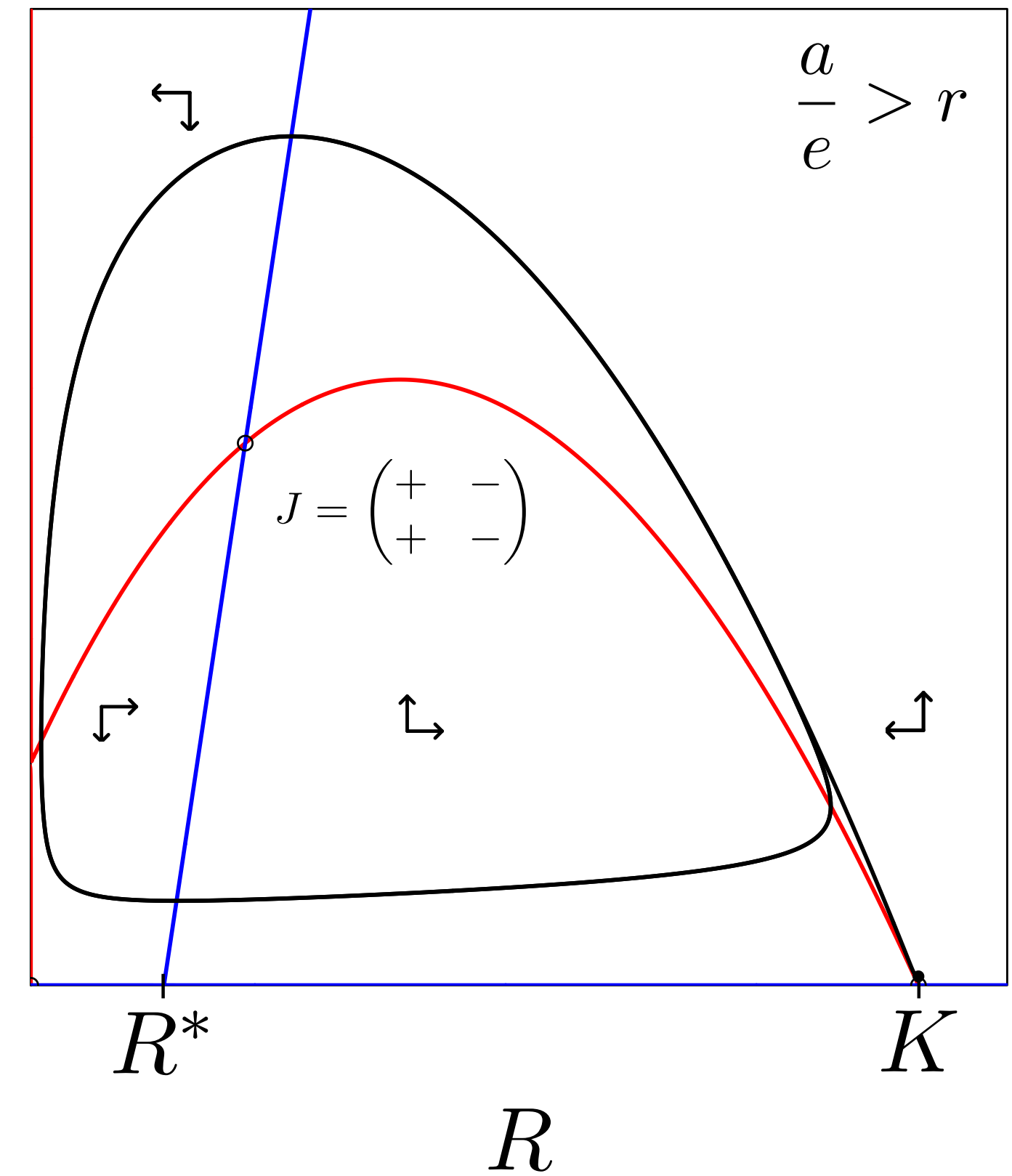
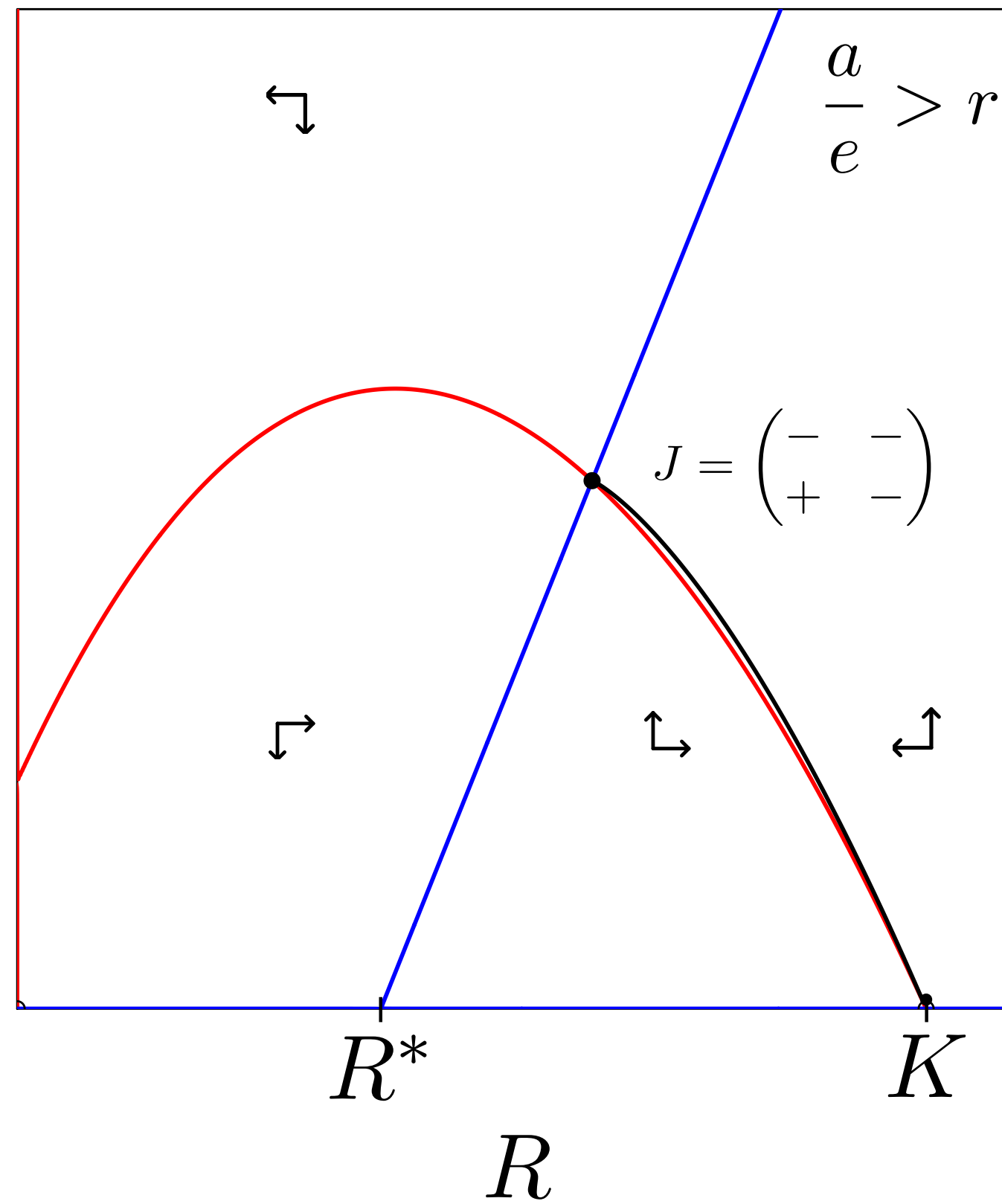
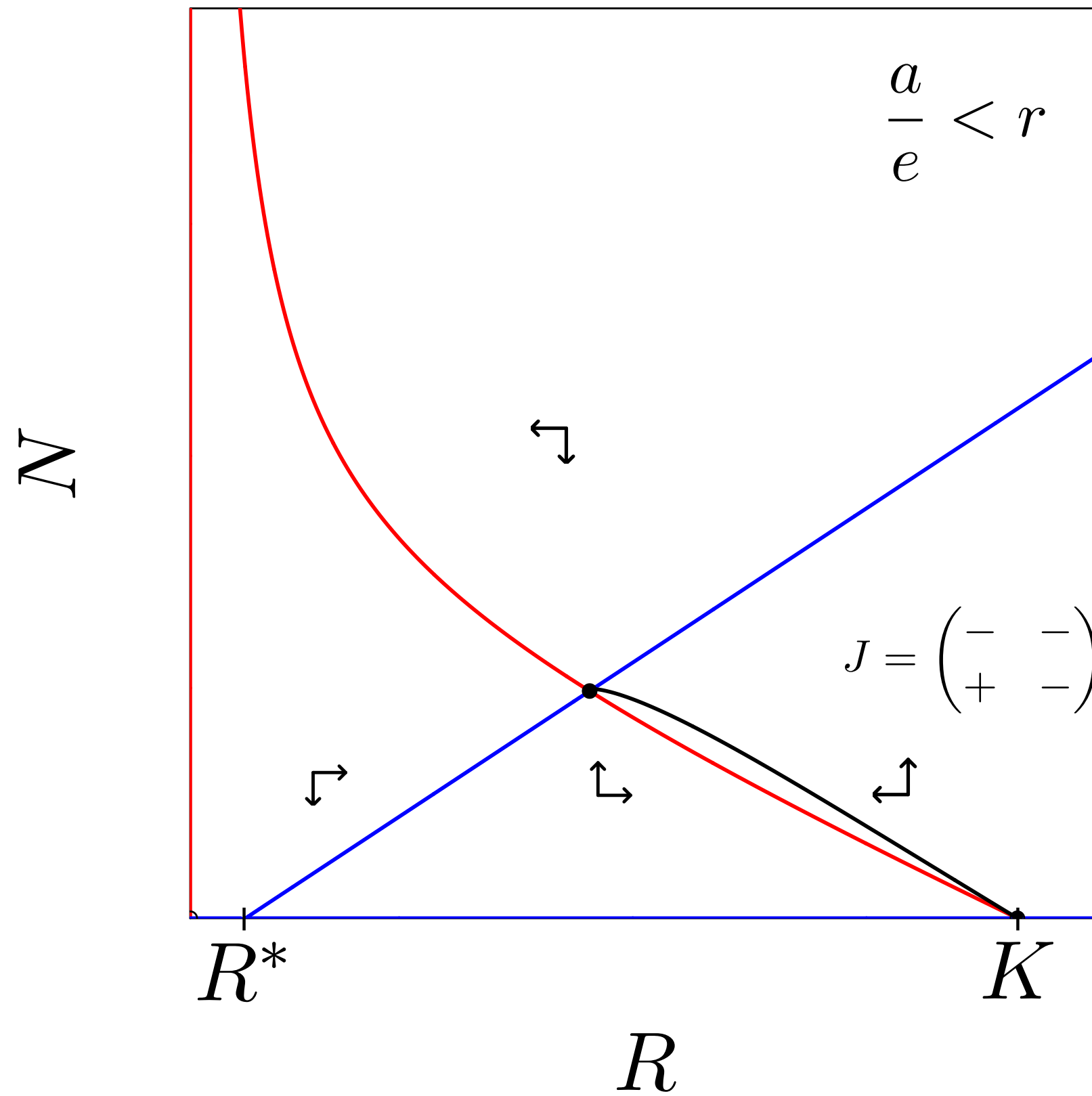
$$\frac{dR}{dt} = rR(1 - R/K) - \frac{aRN}{h + eN + R}$$

$$N = \frac{r(1 - R/K)(h + R)}{a - er(1 - R/K)}$$

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

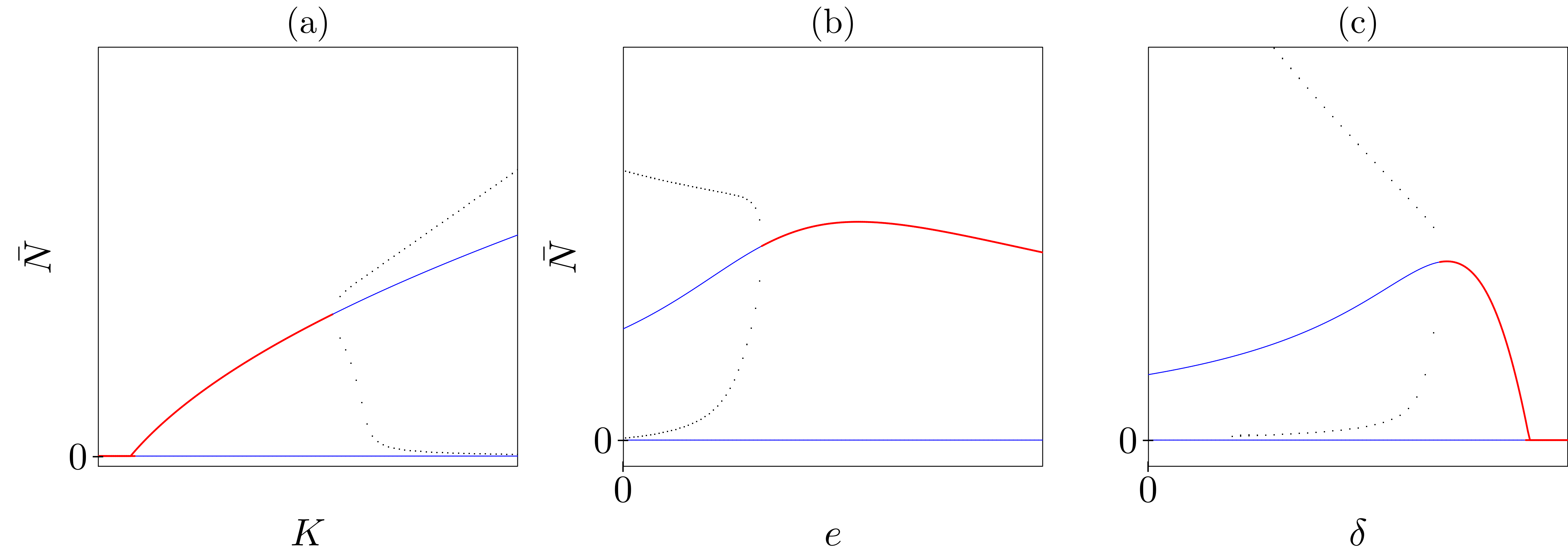
$$\partial_R F(R, N) = \frac{aN}{h + eN + R} - \frac{aRN}{(h + eN + R)^2} \quad \text{which for } R = 0 \text{ yields } \frac{aN}{h + eN}$$

Beddington functional response



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

Beddington functional response



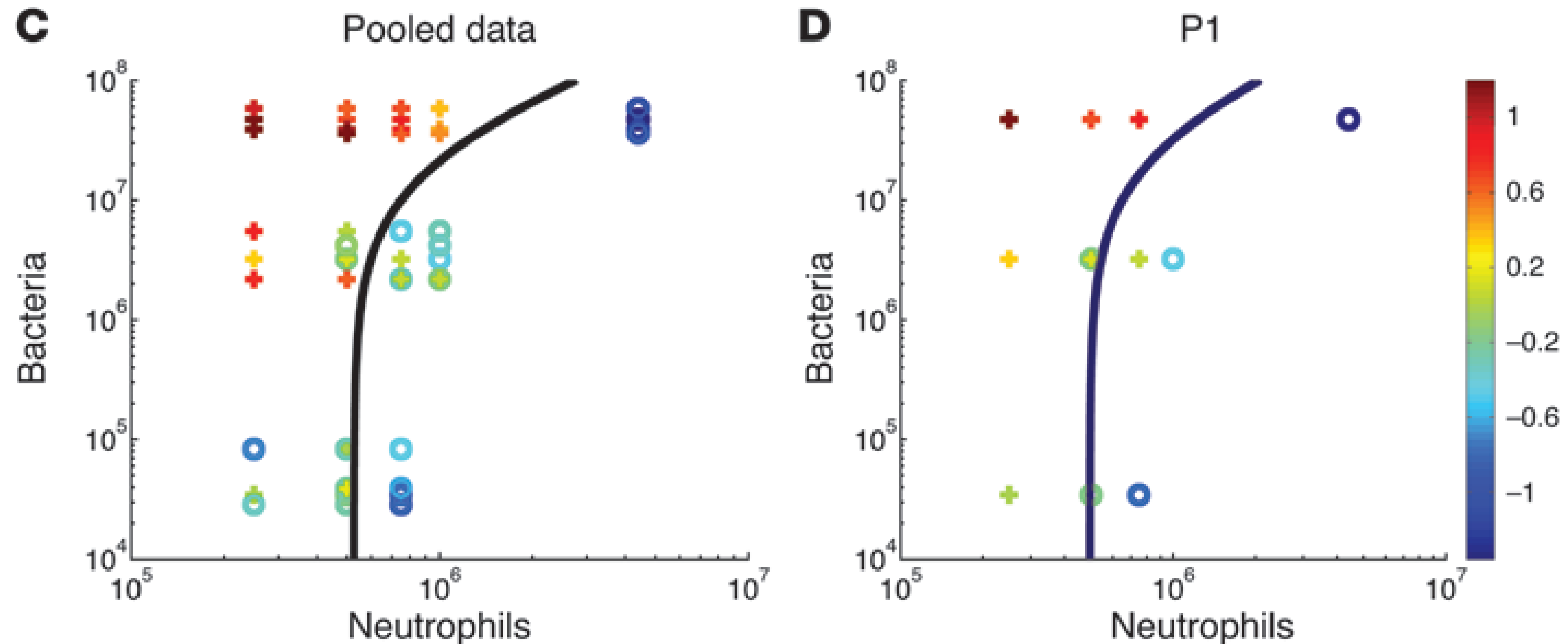
Total Quasi Steady State Assumption

$$\frac{dC}{dt} = aR_F N_F - hC \quad \text{or} \quad \frac{dC}{dt} = a(R - C)(N - C) - hC$$

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

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

Neutrophils killing bacteria



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