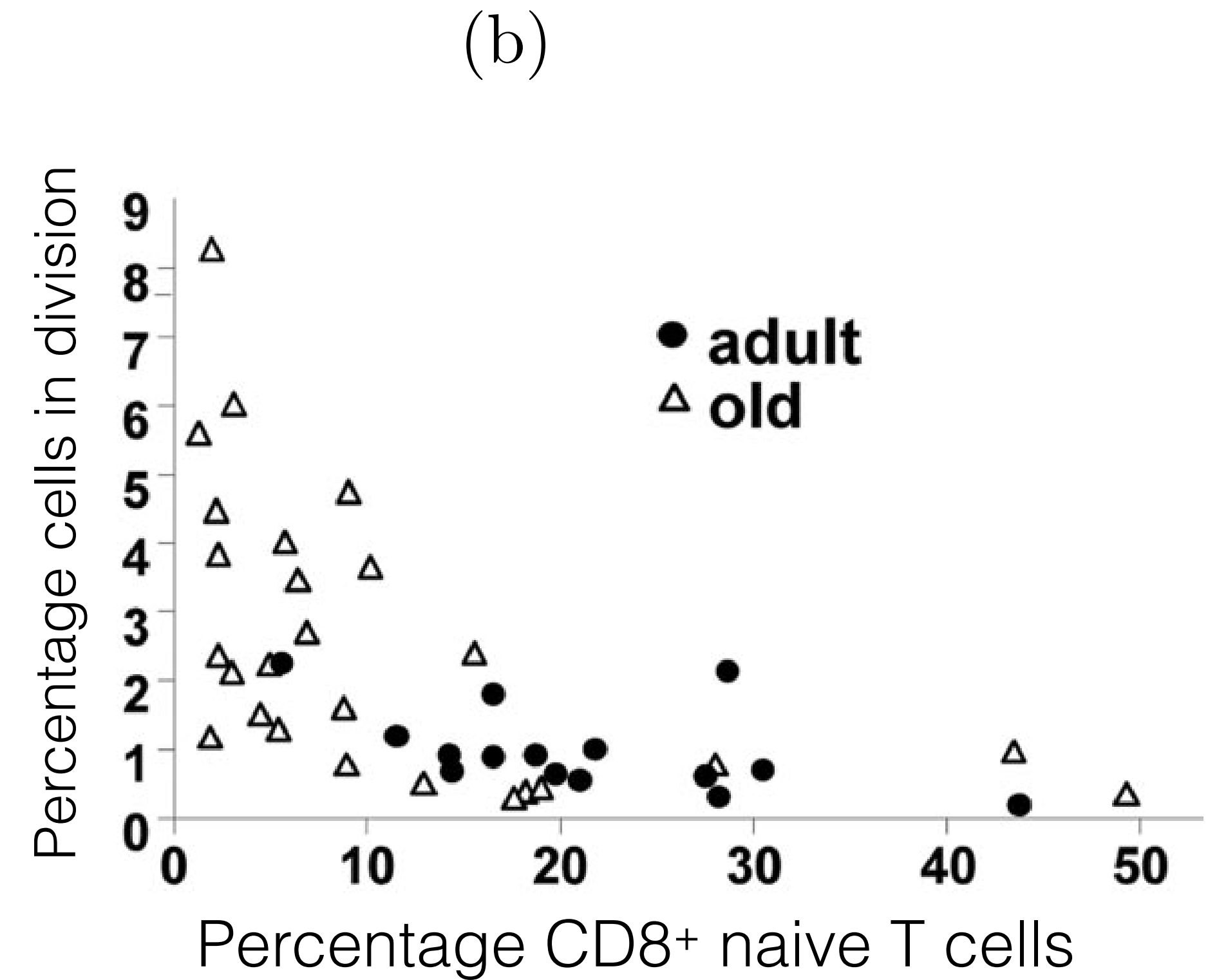
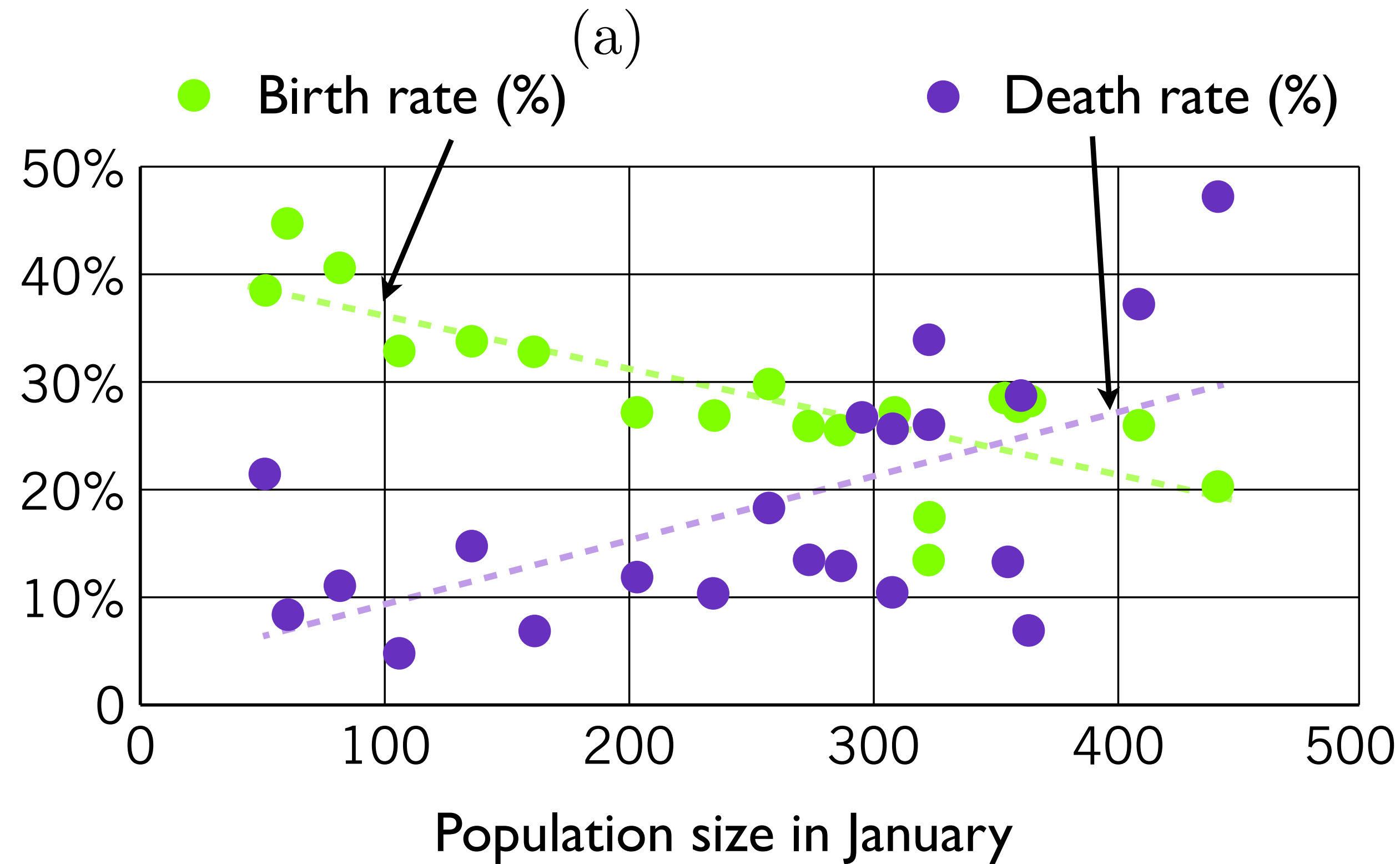


Chapter 3: Density dependence



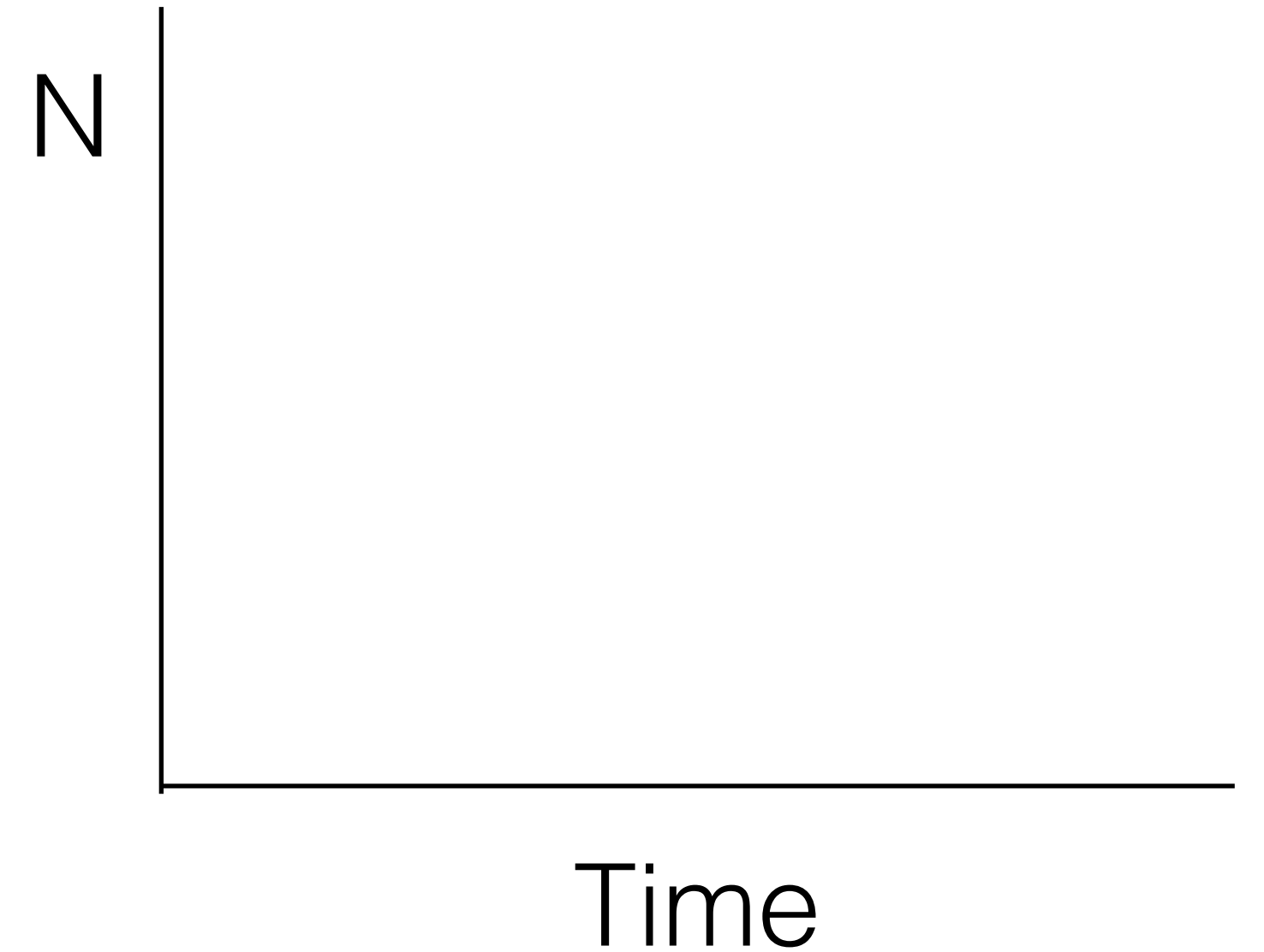
$$\frac{dN}{dt} = sf(N) + [bg(N) - dh(N)]N$$

Populations change by immigration, birth, and death processes, which could all depend on the density of the population itself

Typically source death or Logistic growth

Logistic growth

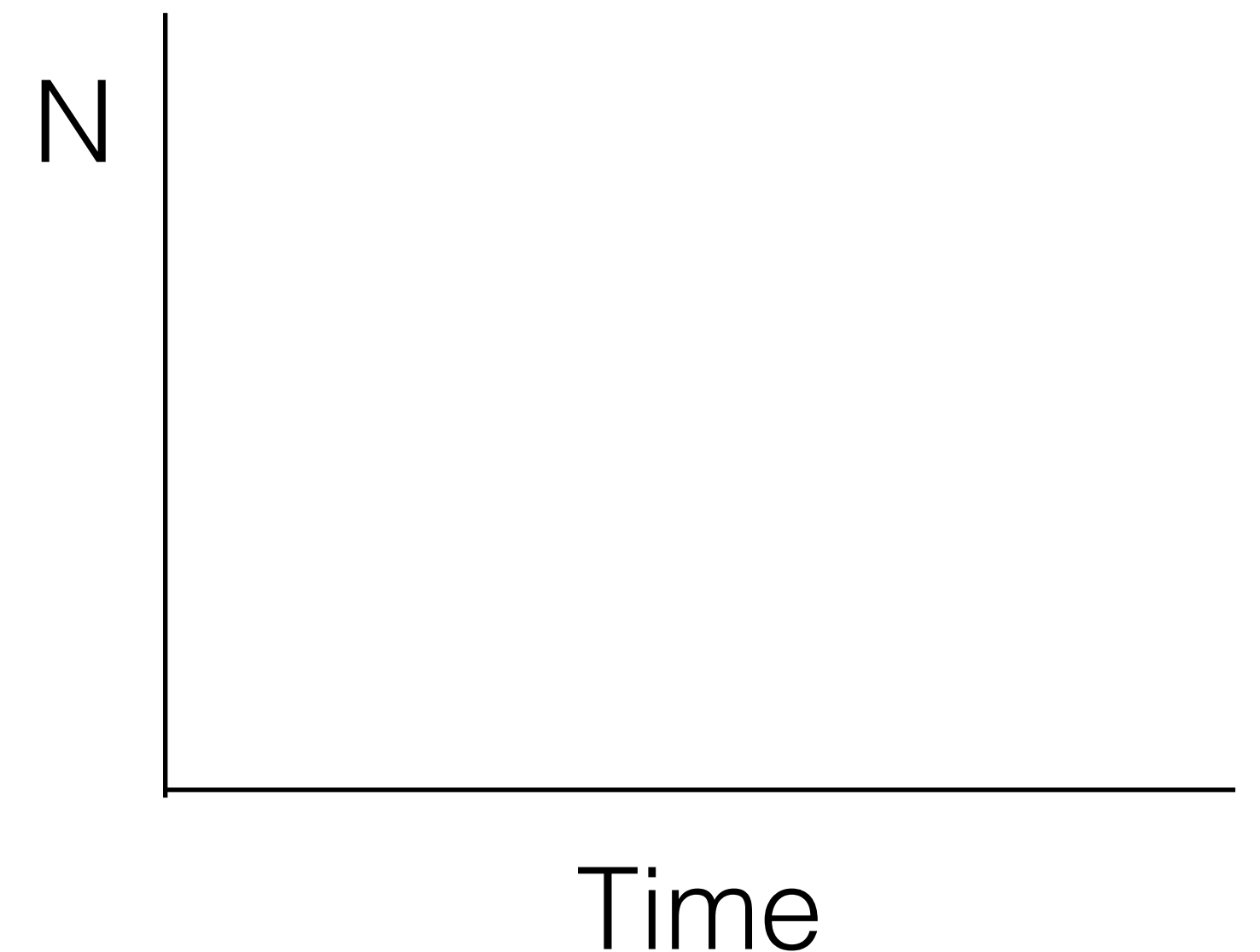
$$\frac{dN}{dt} = rN(1 - N/K) \quad \text{with} \quad \bar{N} = 0 \quad \text{or} \quad \bar{N} = K$$



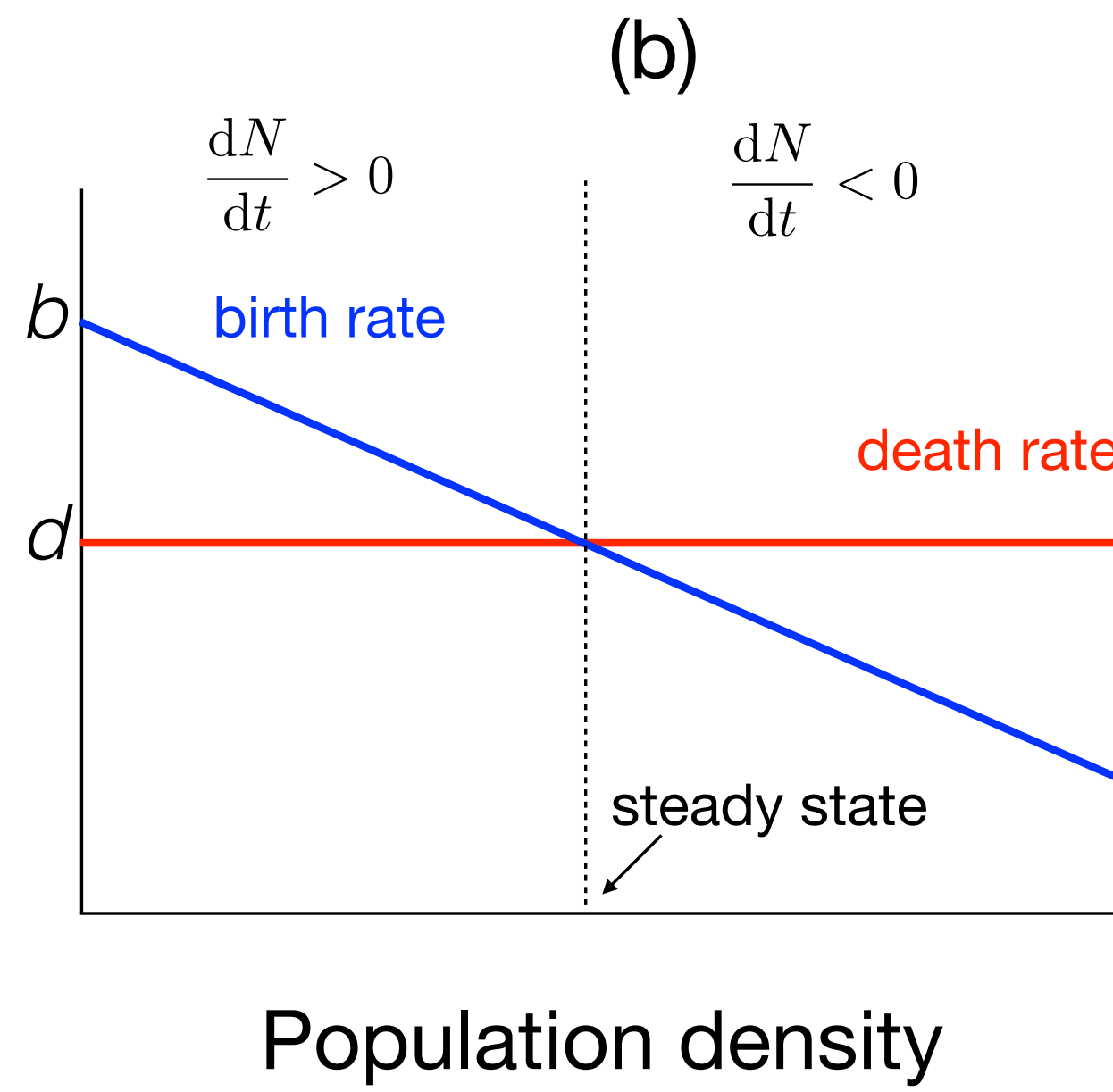
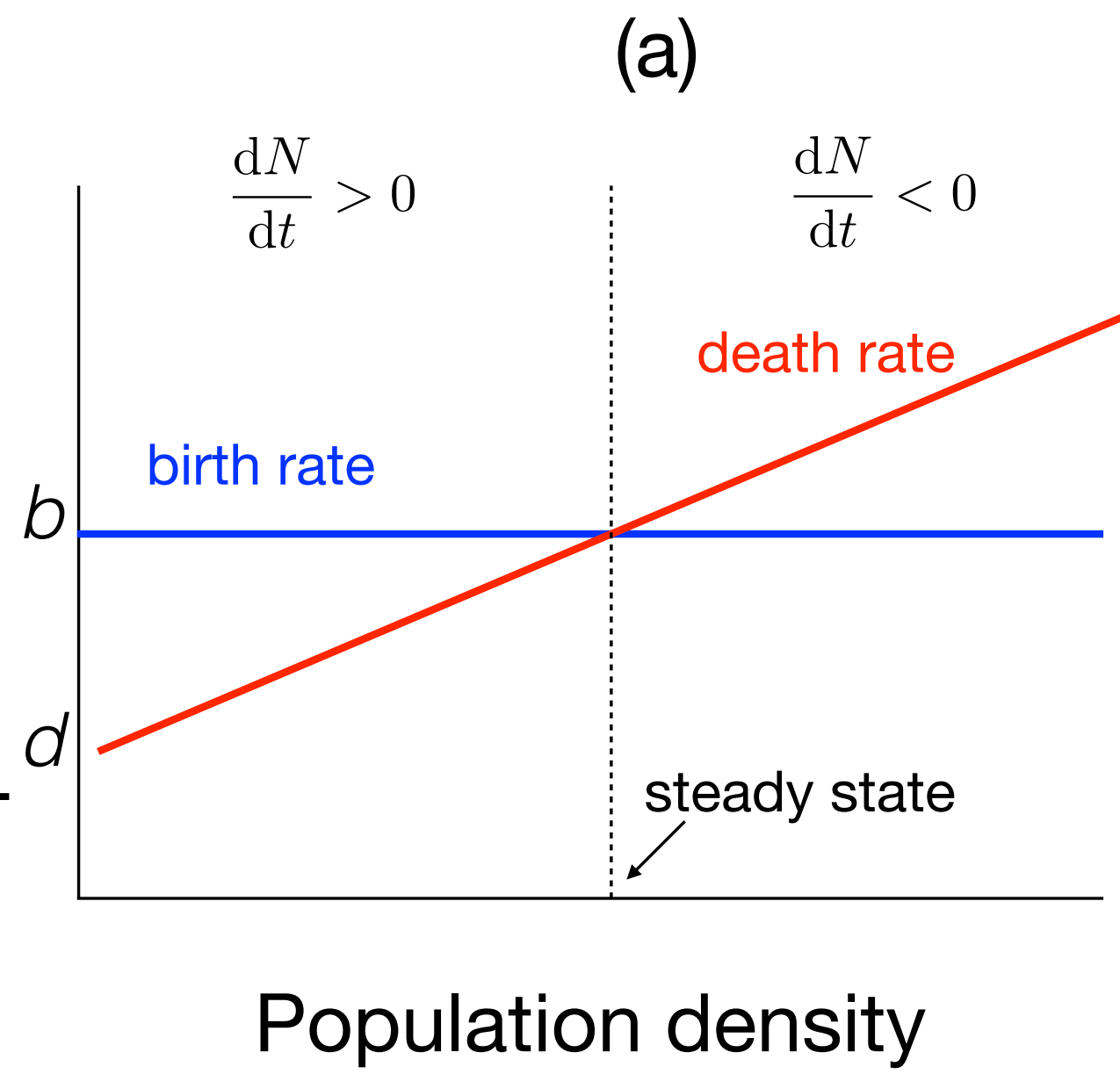
Source death

$$\frac{dN}{dt} = s - dN \quad \text{with} \quad \bar{N} = \frac{s}{d}$$

$$\frac{dN}{dt} = sf(N) + [bg(N) - dh(N)]N$$



Per capita birth or death rate



Death rate: $F(N)$

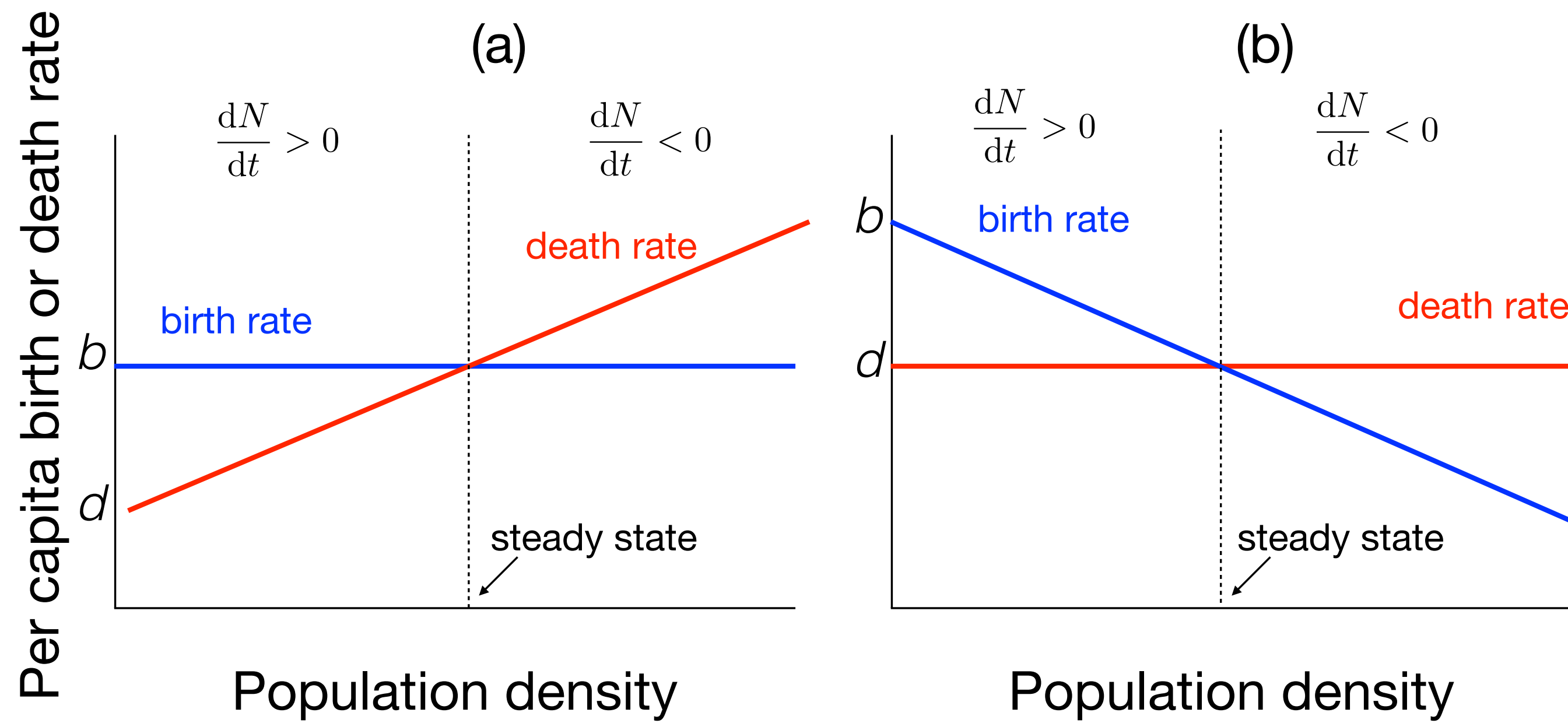
Population density

$$\frac{dN}{dt} = [b - df(N)]N$$

$$F(N) = d + cN = df(N) \quad \Leftrightarrow \quad f(N) = 1 + N/k$$

$$\frac{dN}{dt} = \left[b - d \left(1 + \frac{N}{k} \right) \right] N$$

$$\bar{N} = k \frac{b - d}{d} = k(R_0 - 1)$$



Birth rate: $F(N)$

Population density

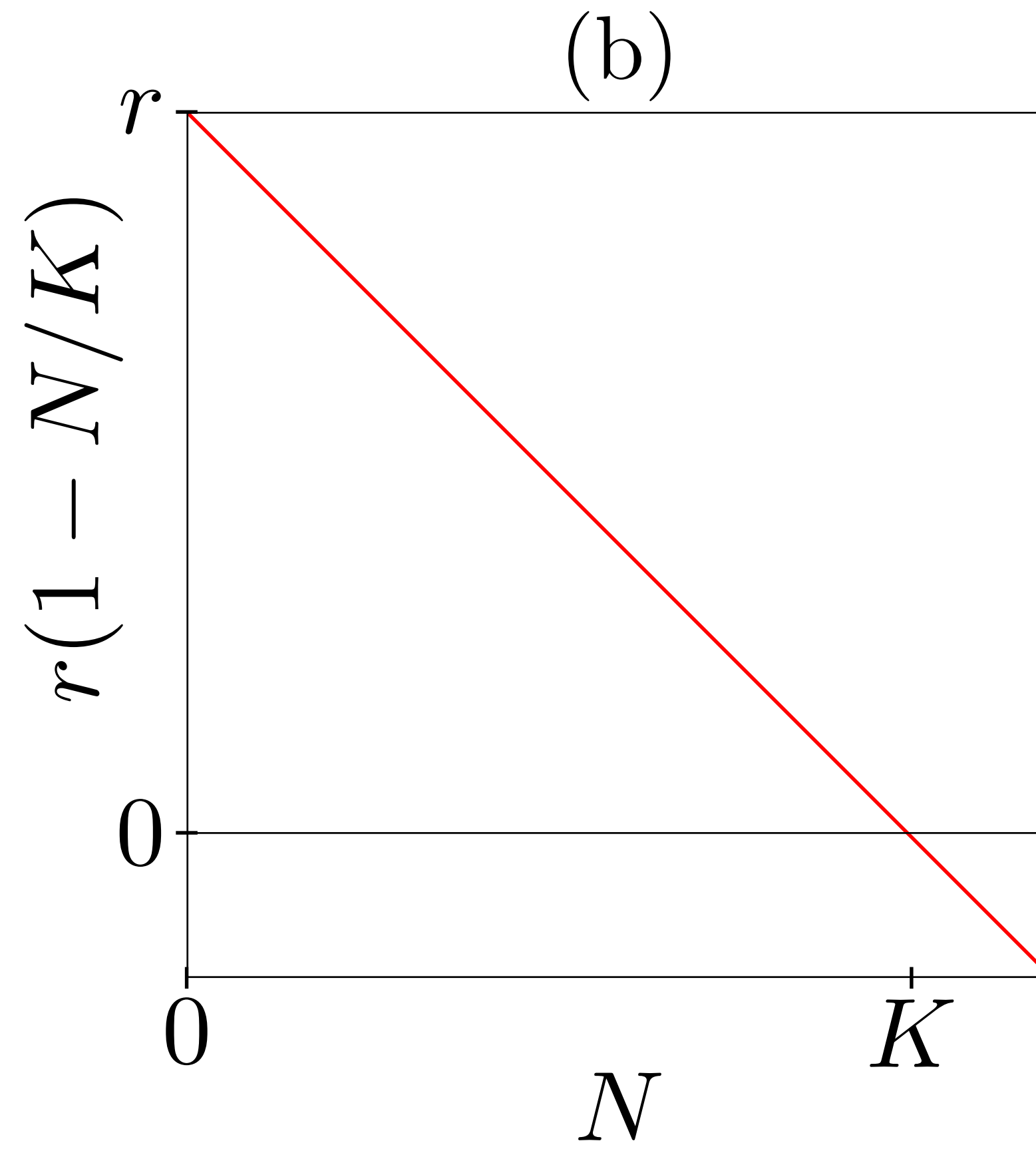
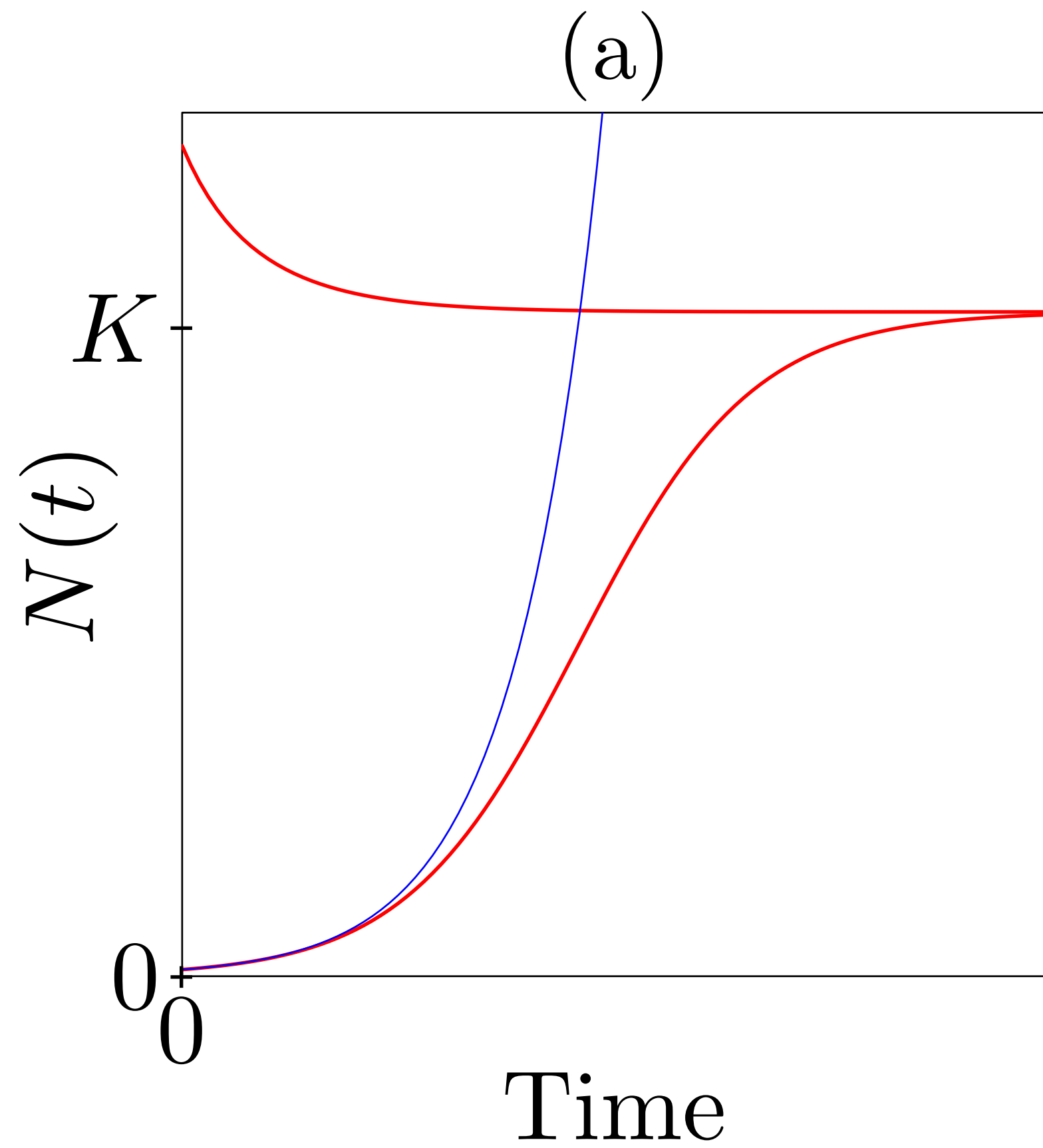
$$\frac{dN}{dt} = [bf(N) - d]N$$

$$F(N) = b - cN = bf(N) \quad \Leftrightarrow \quad f(N) = 1 - N/k$$

$$\frac{dN}{dt} = \left[b \left(1 - \frac{N}{k} \right) - d \right] N$$

$$\bar{N} = k \left(1 - \frac{d}{b} \right) = k \left(1 - \frac{1}{R_0} \right)$$

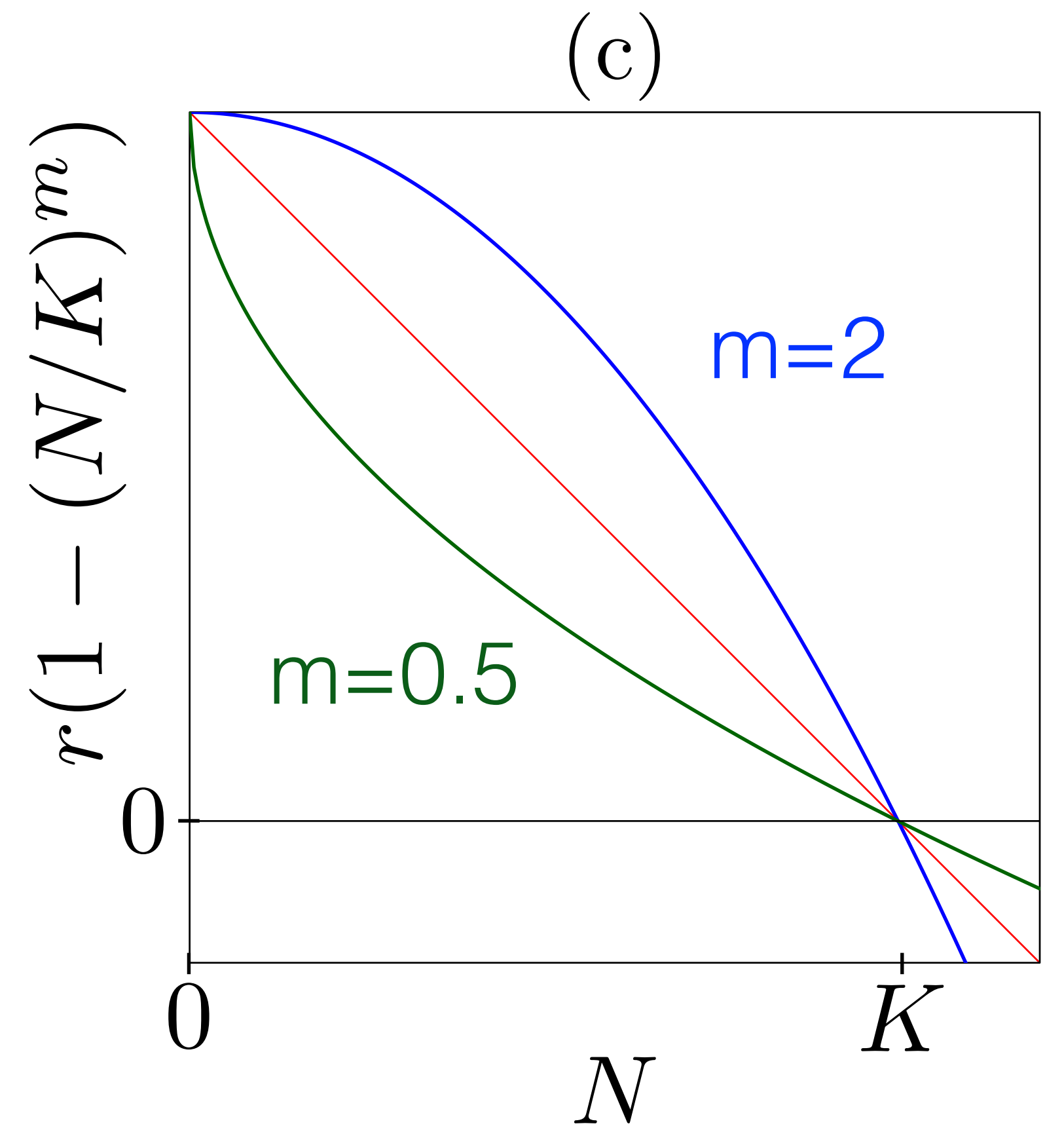
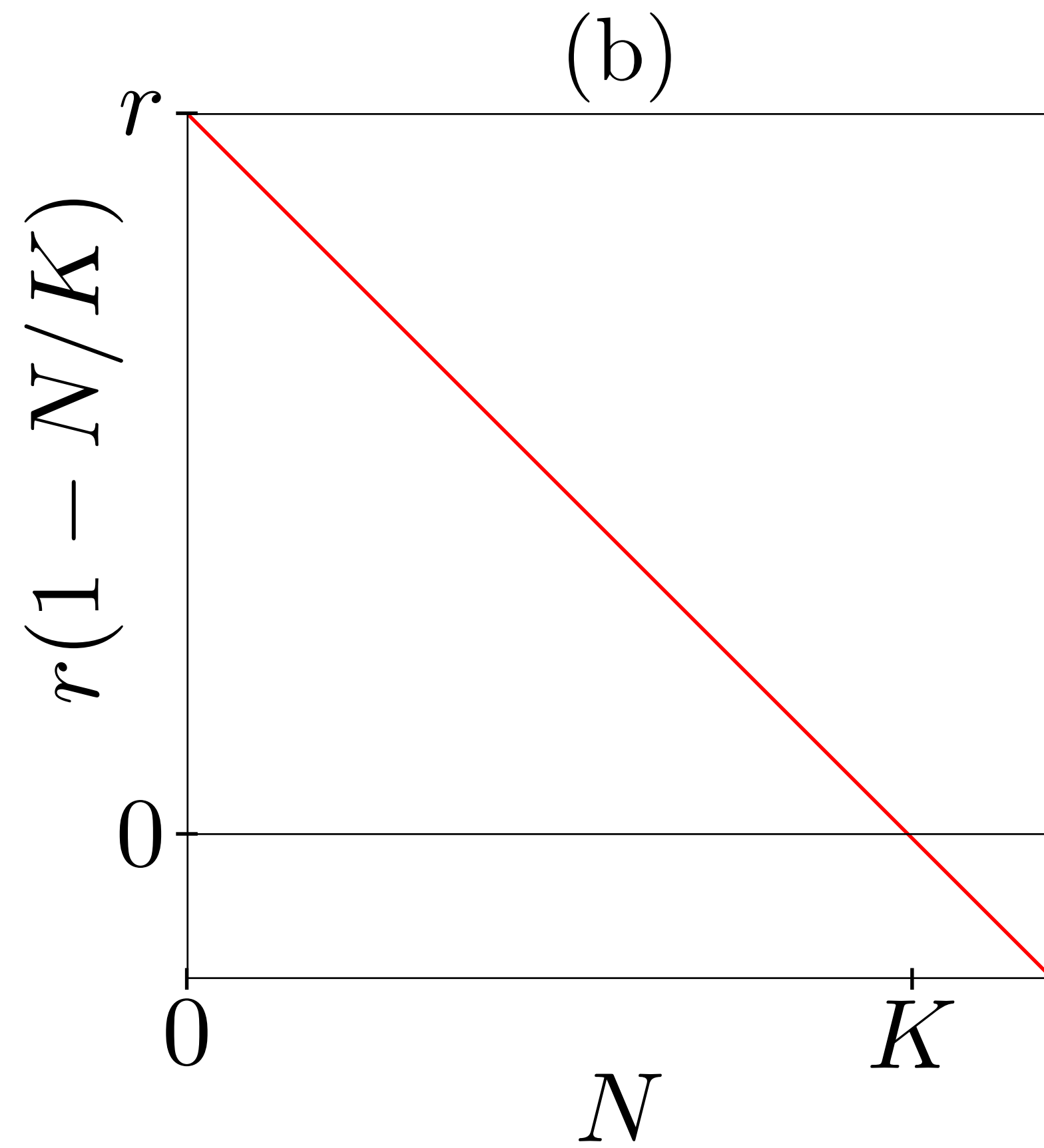
Logistic growth: $\frac{dN}{dt} = rN(1 - N/K)$, with solution $N(t) = \frac{KN(0)}{N(0) + e^{-rt}(K - N(0))}$



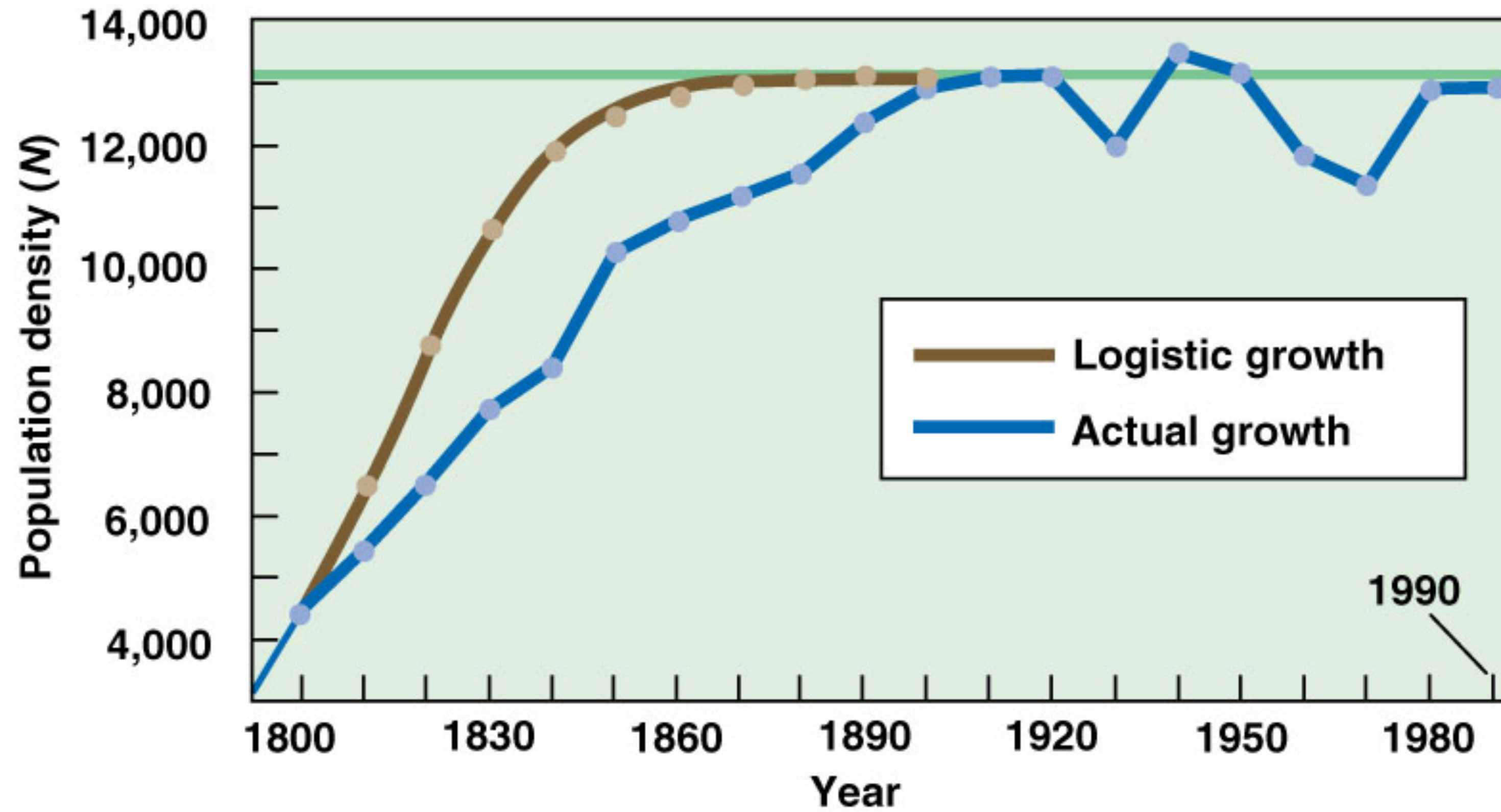
$$\frac{dN}{dt} = \left[b - d \left(1 + \frac{N}{k} \right) \right] N$$

$$\frac{dN}{dt} = \left[b \left(1 - \frac{N}{k} \right) - d \right] N$$

Generalized logistic growth: $\frac{dN}{dt} = rN(1 - (N/K)^m)$, with $N(t) = \frac{K}{[1 - (1 - [K/N(0)]^m)e^{-rmt}]^{1/m}}$

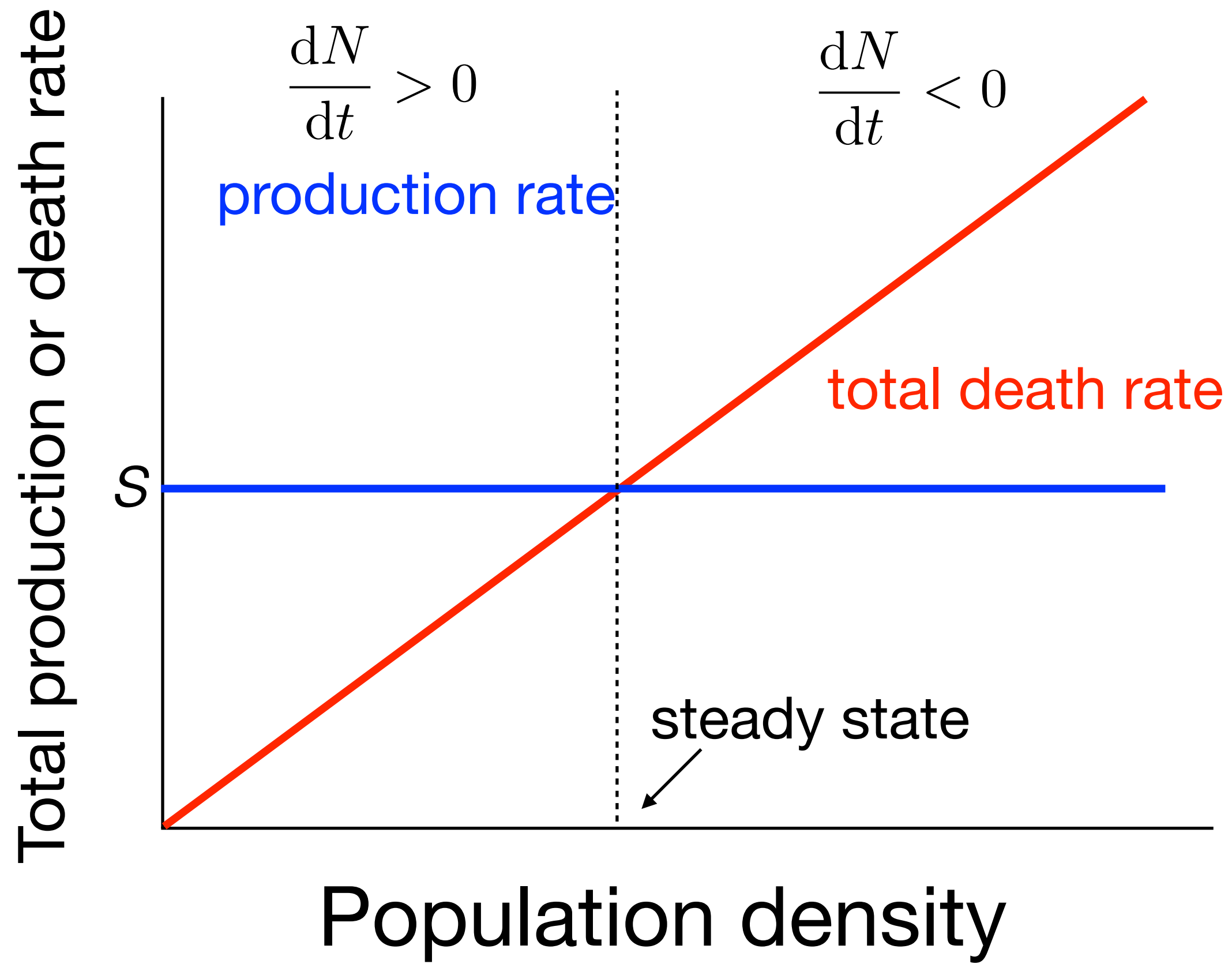


Human logistic growth



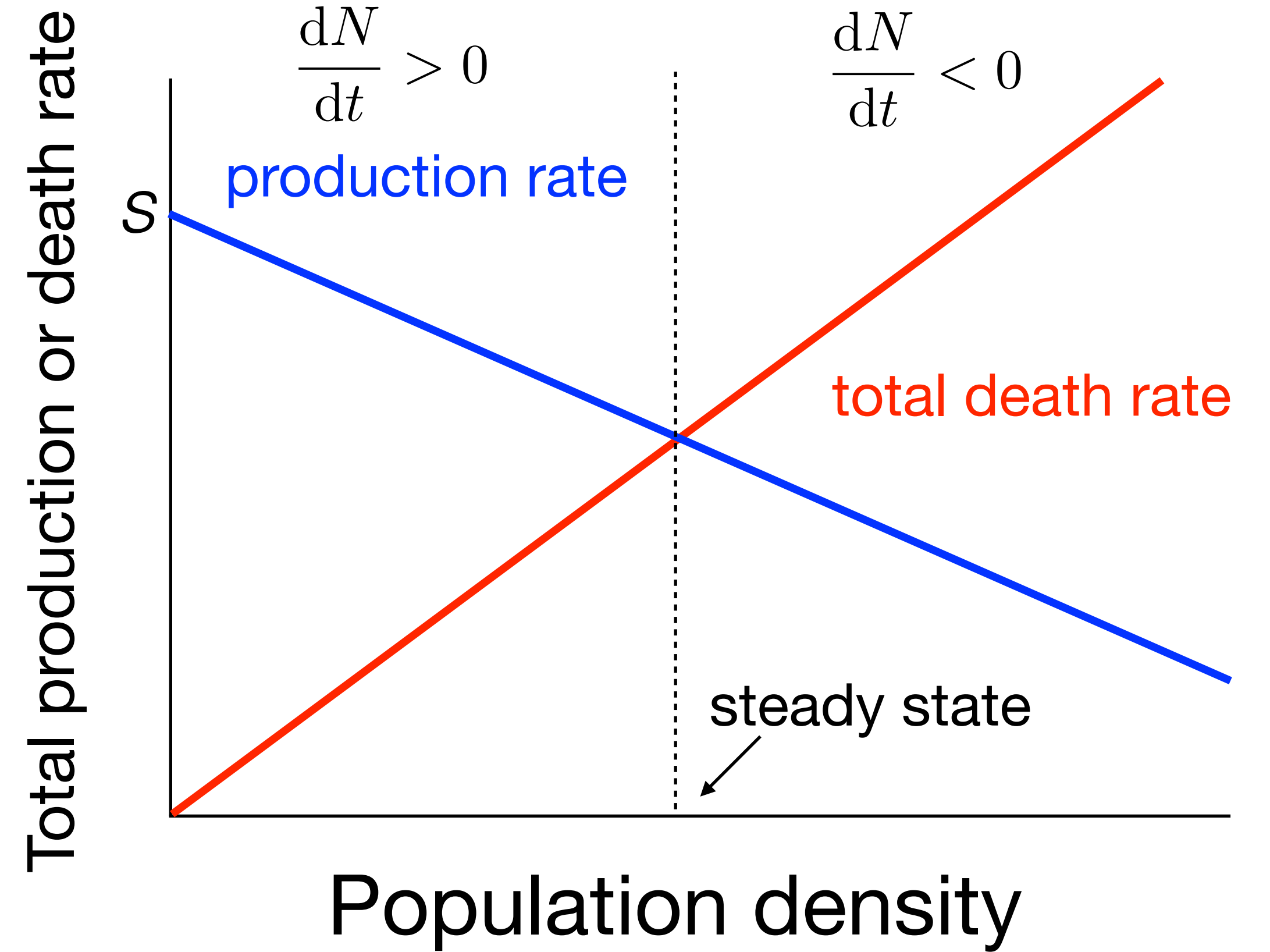
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Human population in Monroe County, West Virginia



$$\frac{dN}{dt} = s - d \left(1 + \frac{N}{k} \right) N$$

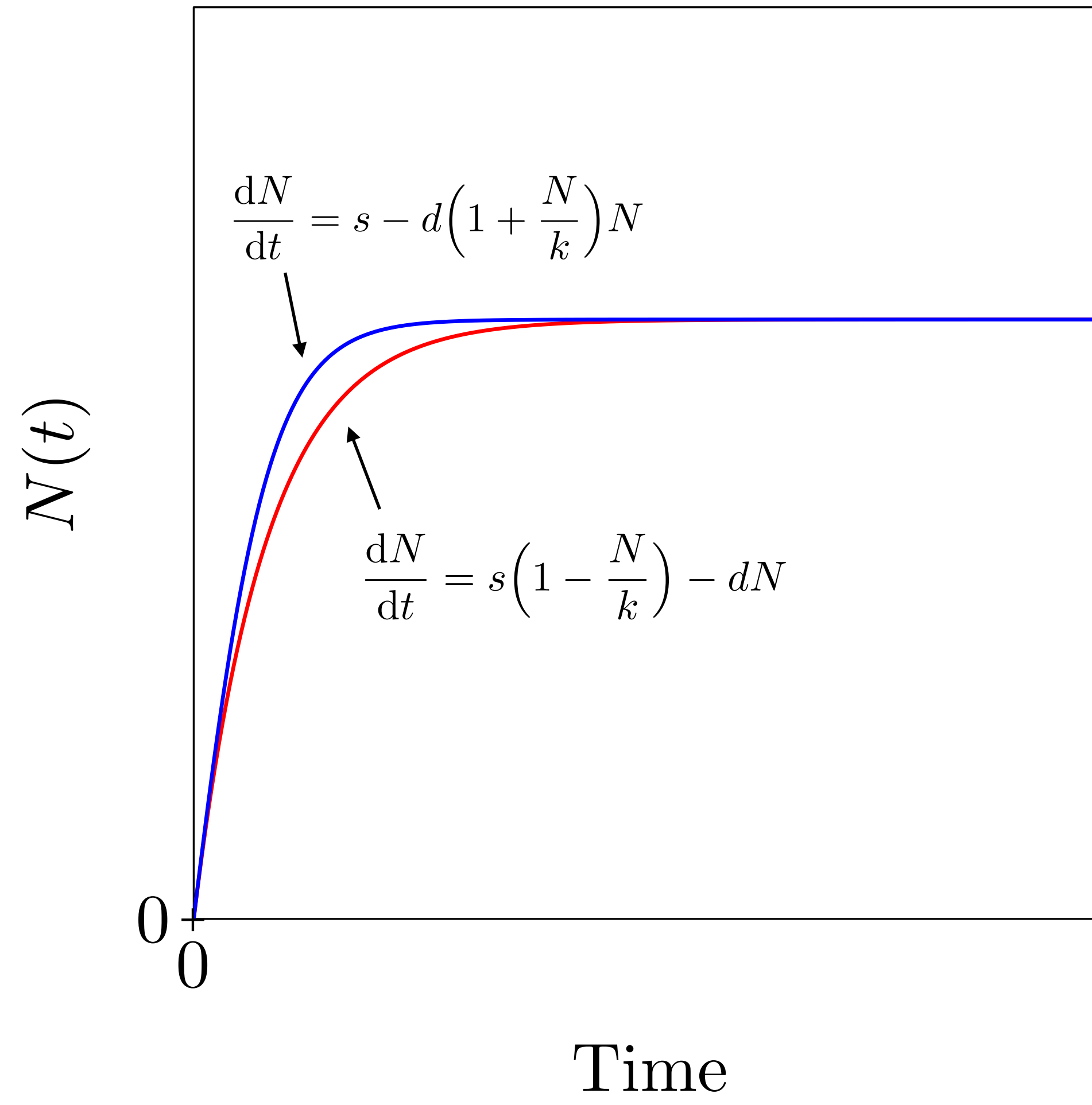
$$\bar{N} = \frac{-dk \pm \sqrt{dk(dk + 4s)}}{2d}$$



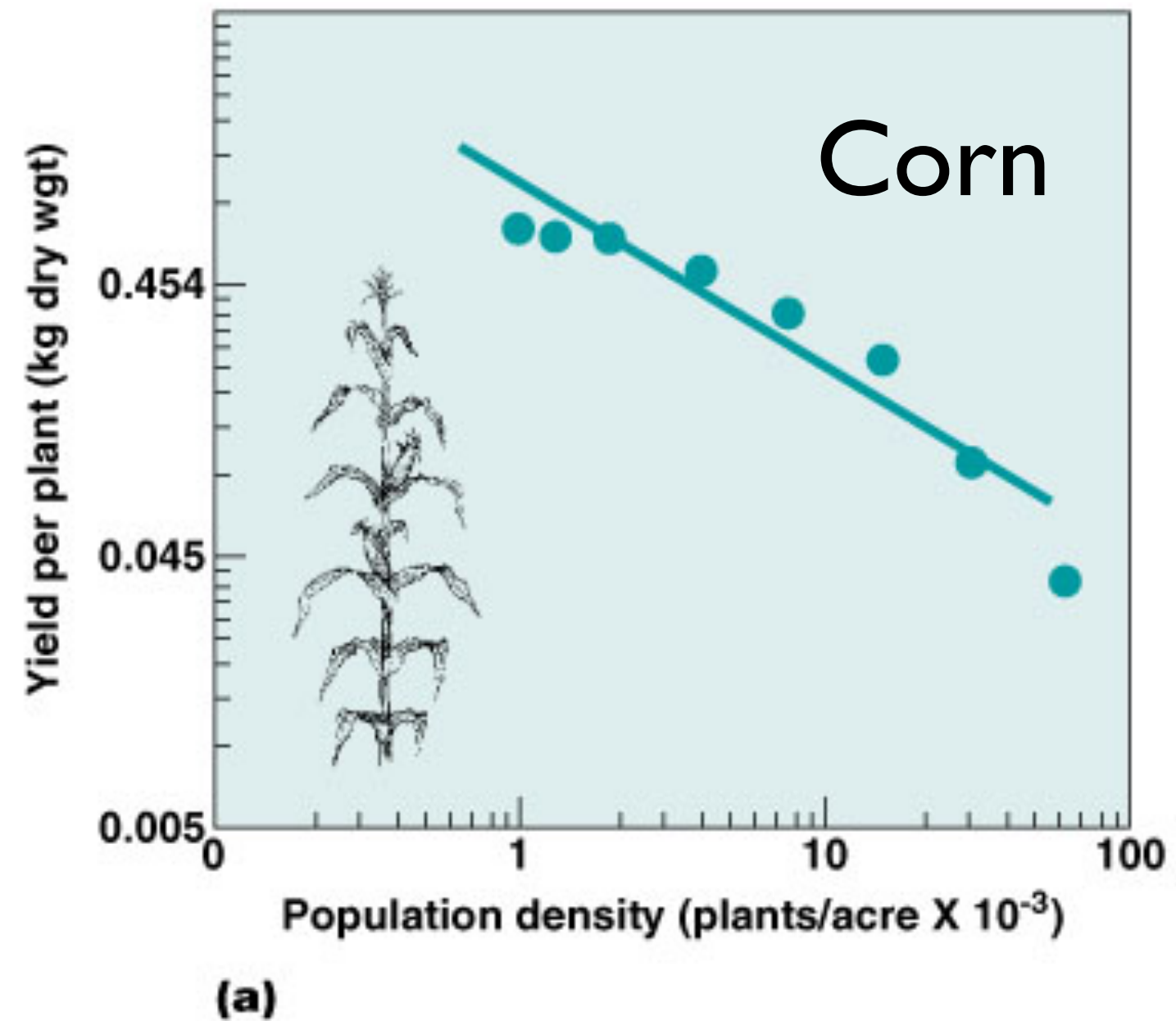
$$\frac{dN}{dt} = s \left(1 - \frac{N}{k} \right) - dN$$

$$\bar{N} = \frac{sk}{dk + s}$$

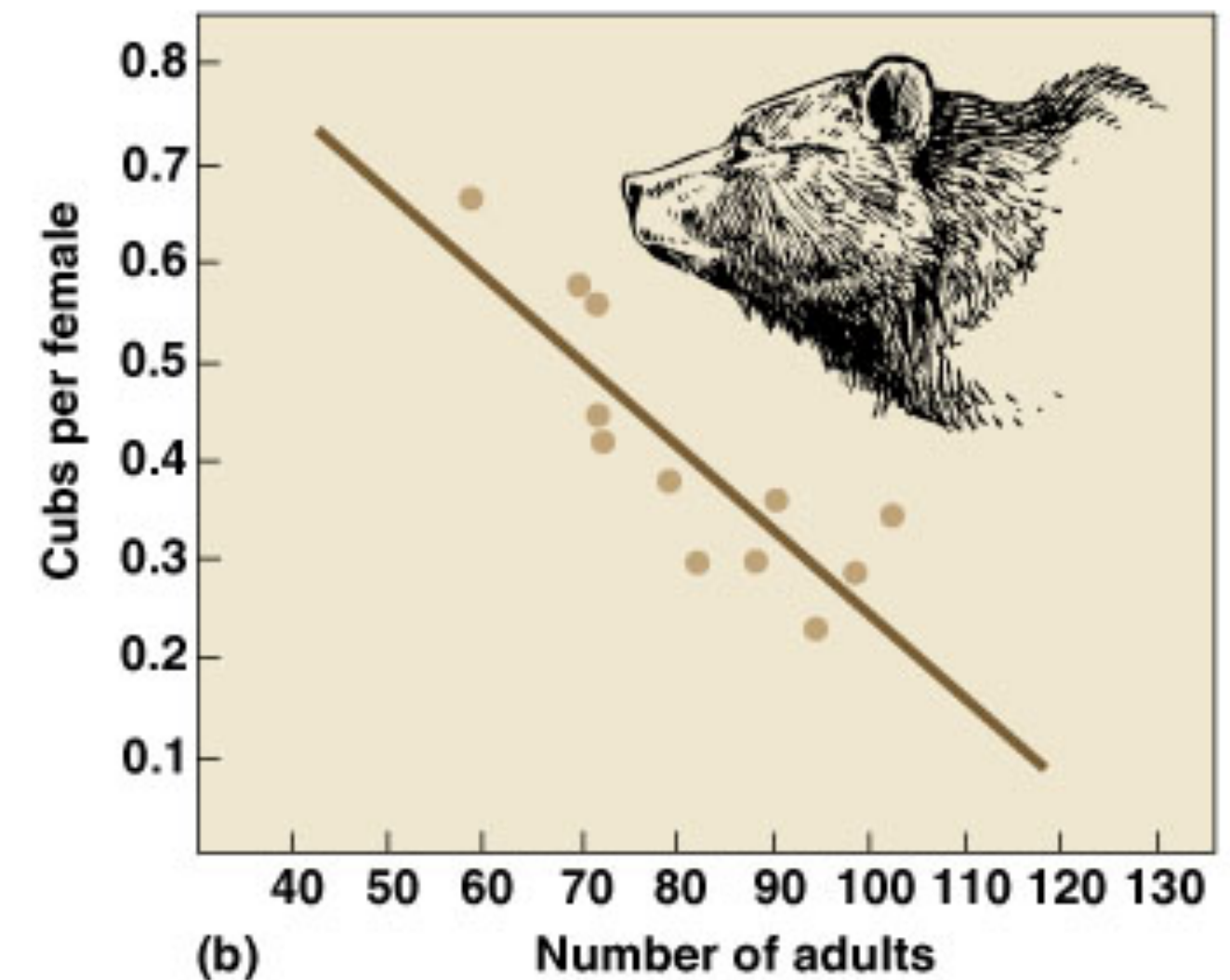
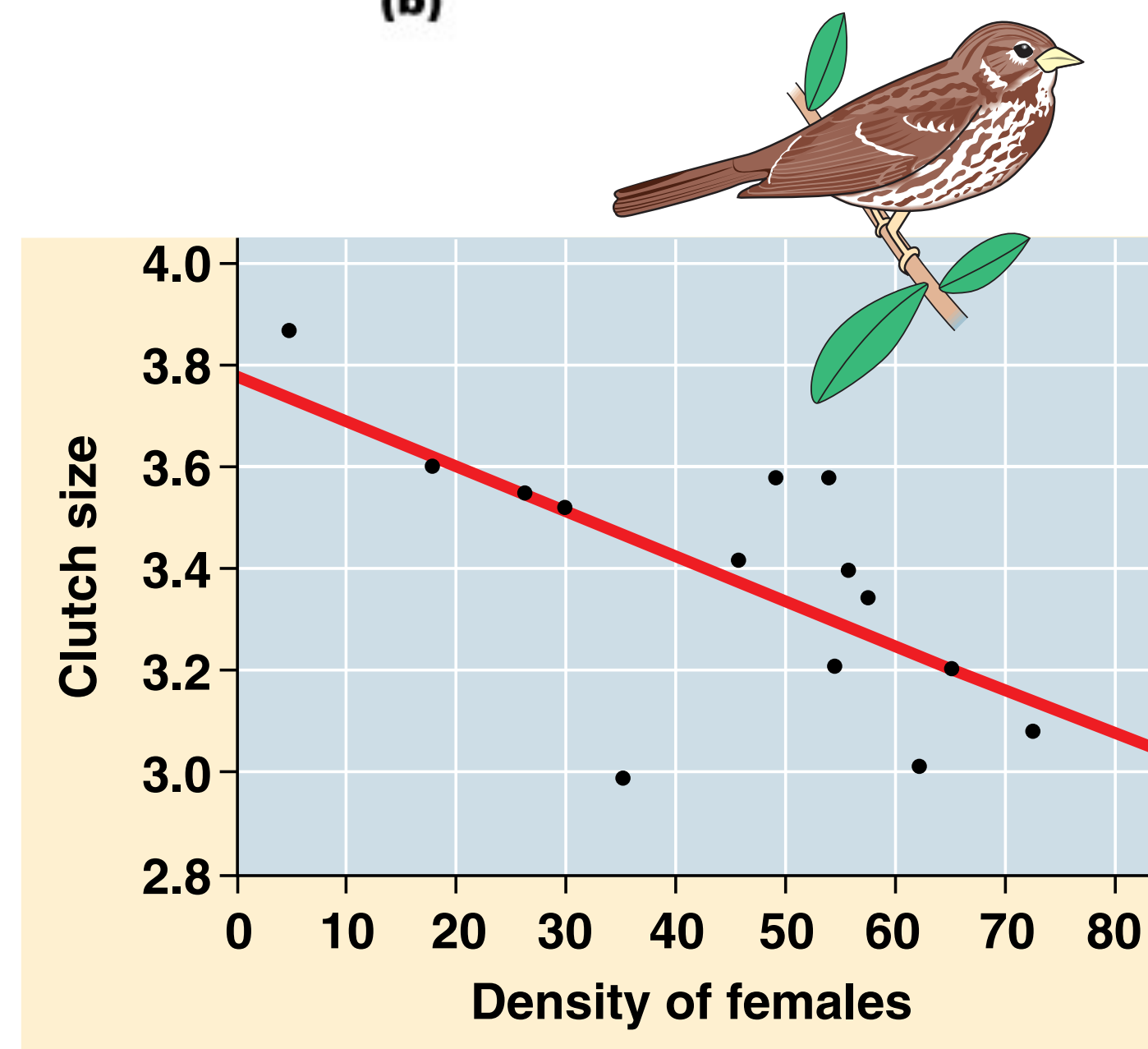
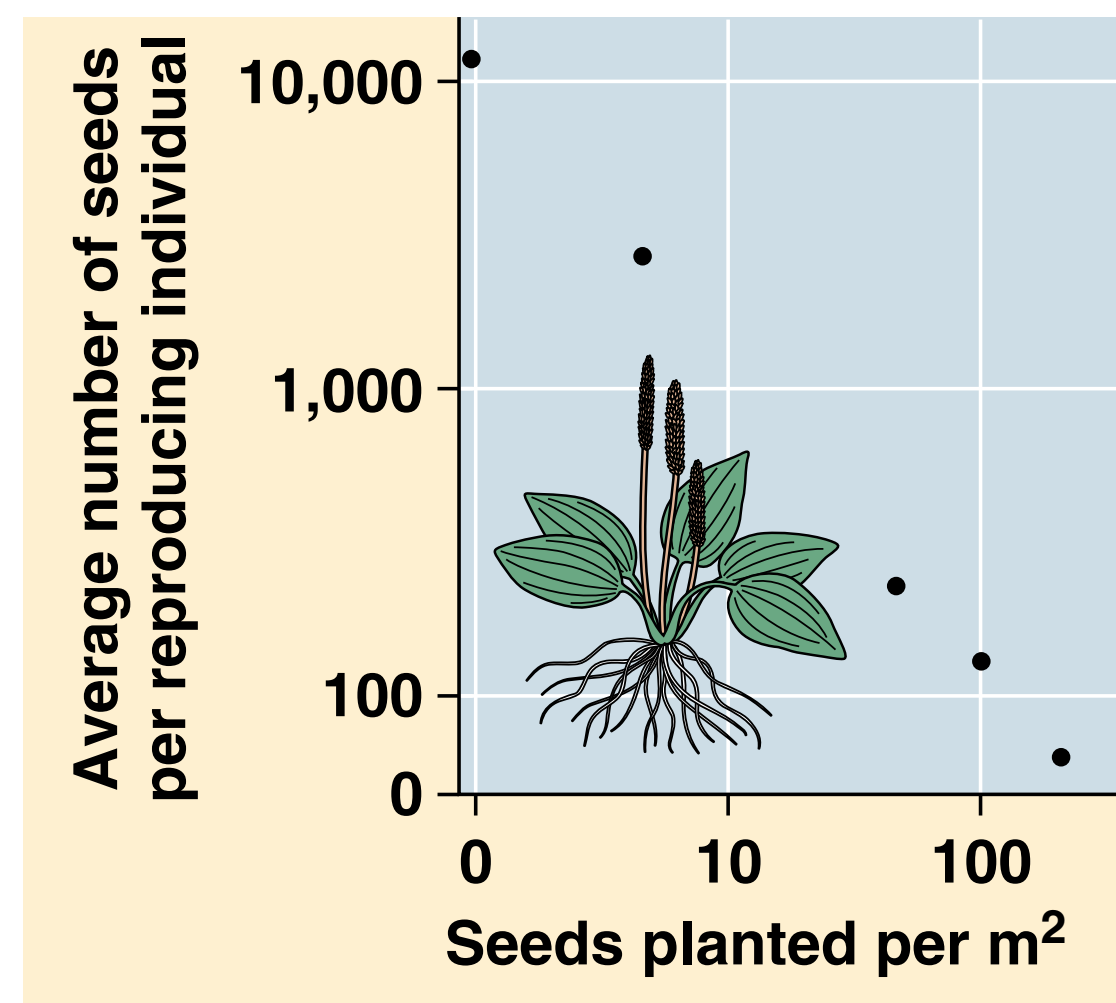
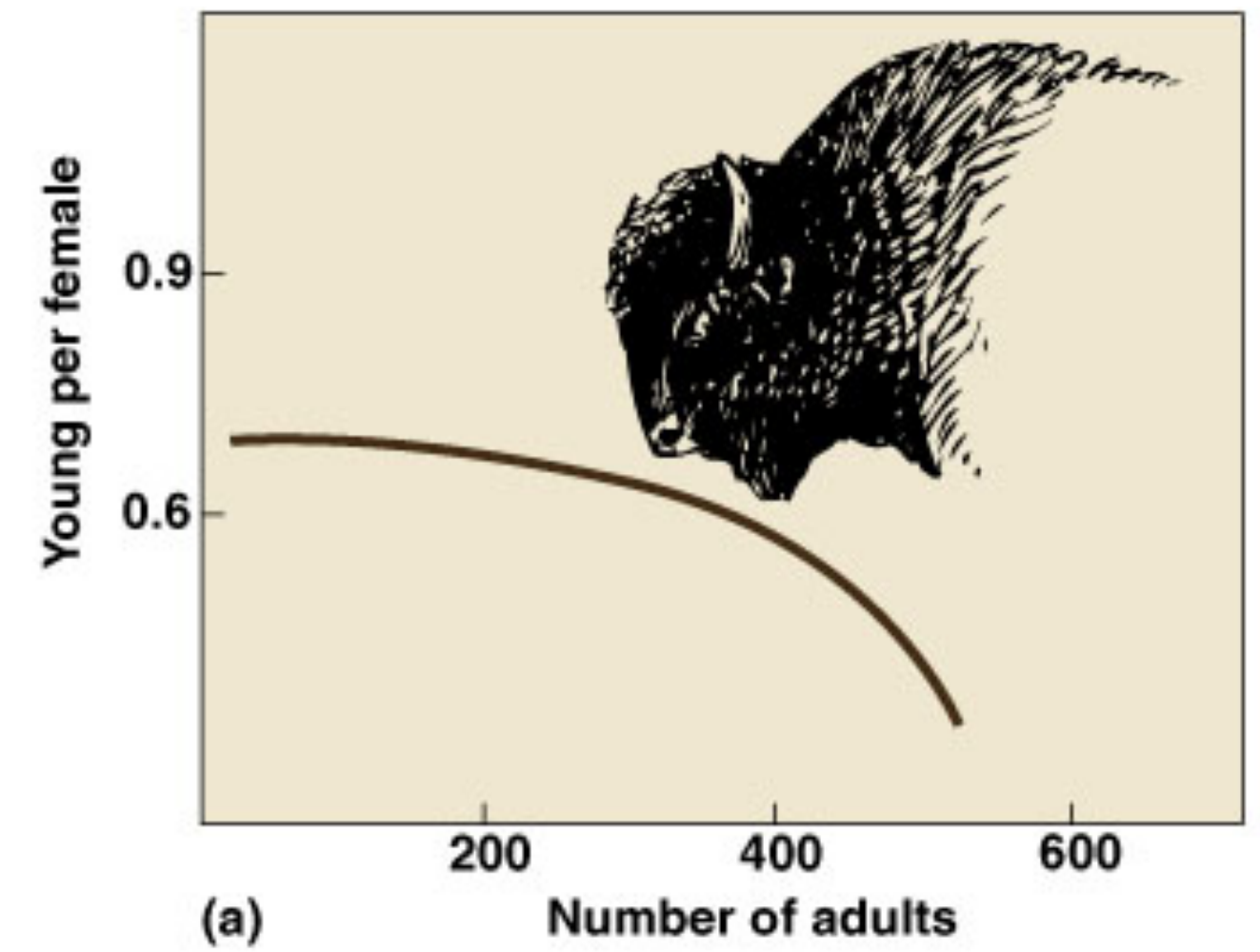
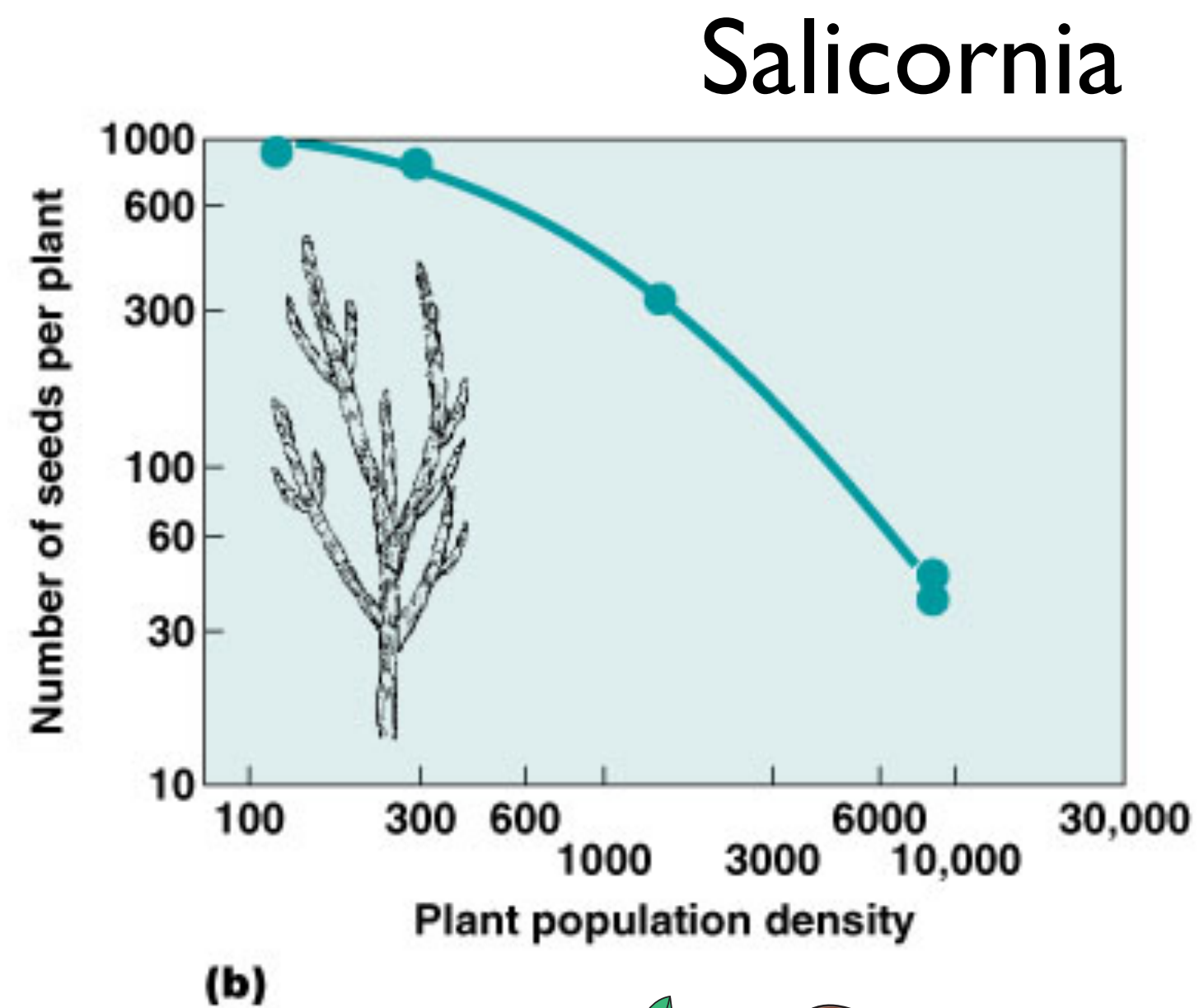
(a)



Density dependent birth is not always a linear function of N



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Grizzly bear

Non-linear density dependence

$$f(x) = \max(0, 1 - [x/k]^n)$$

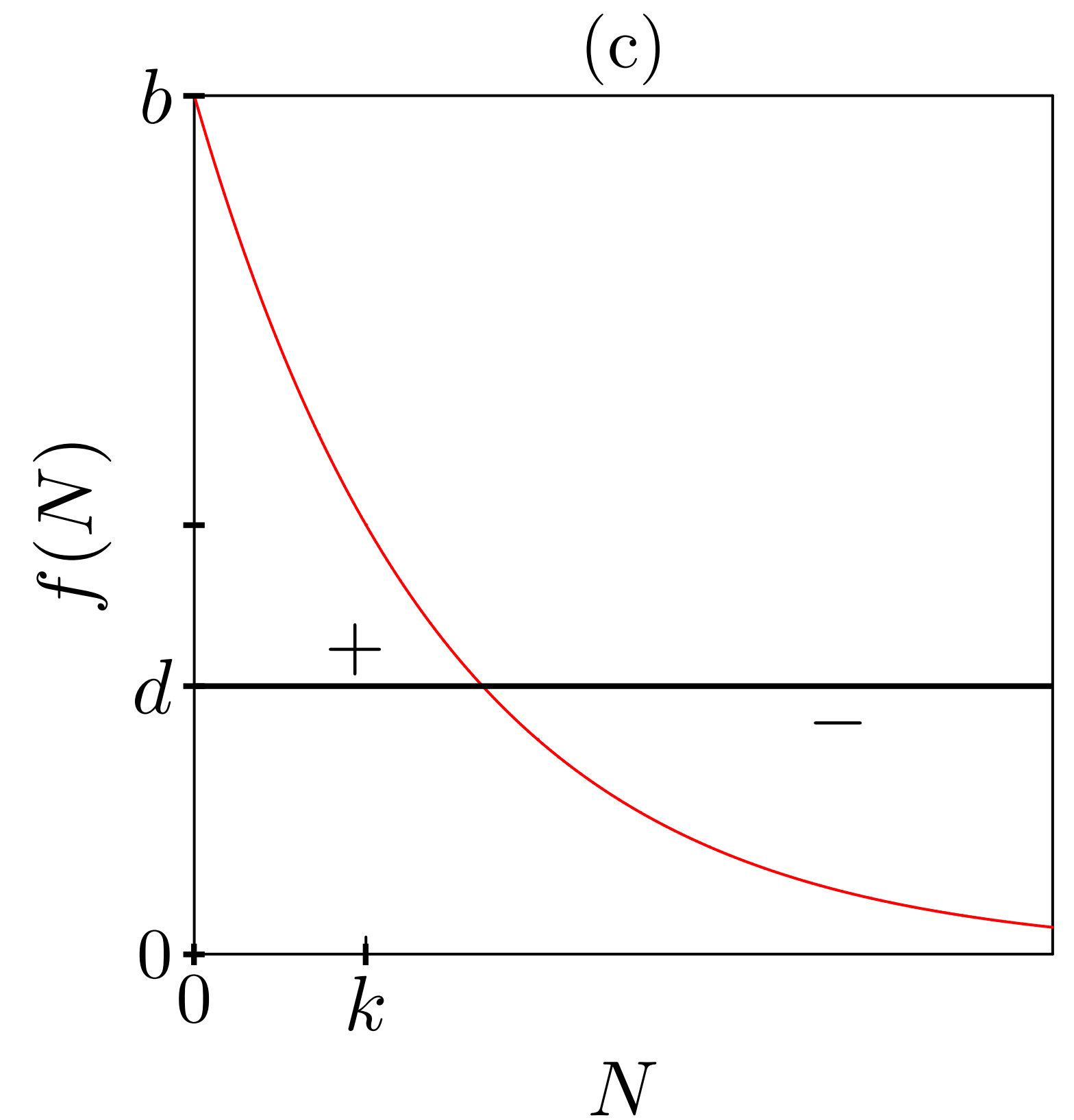
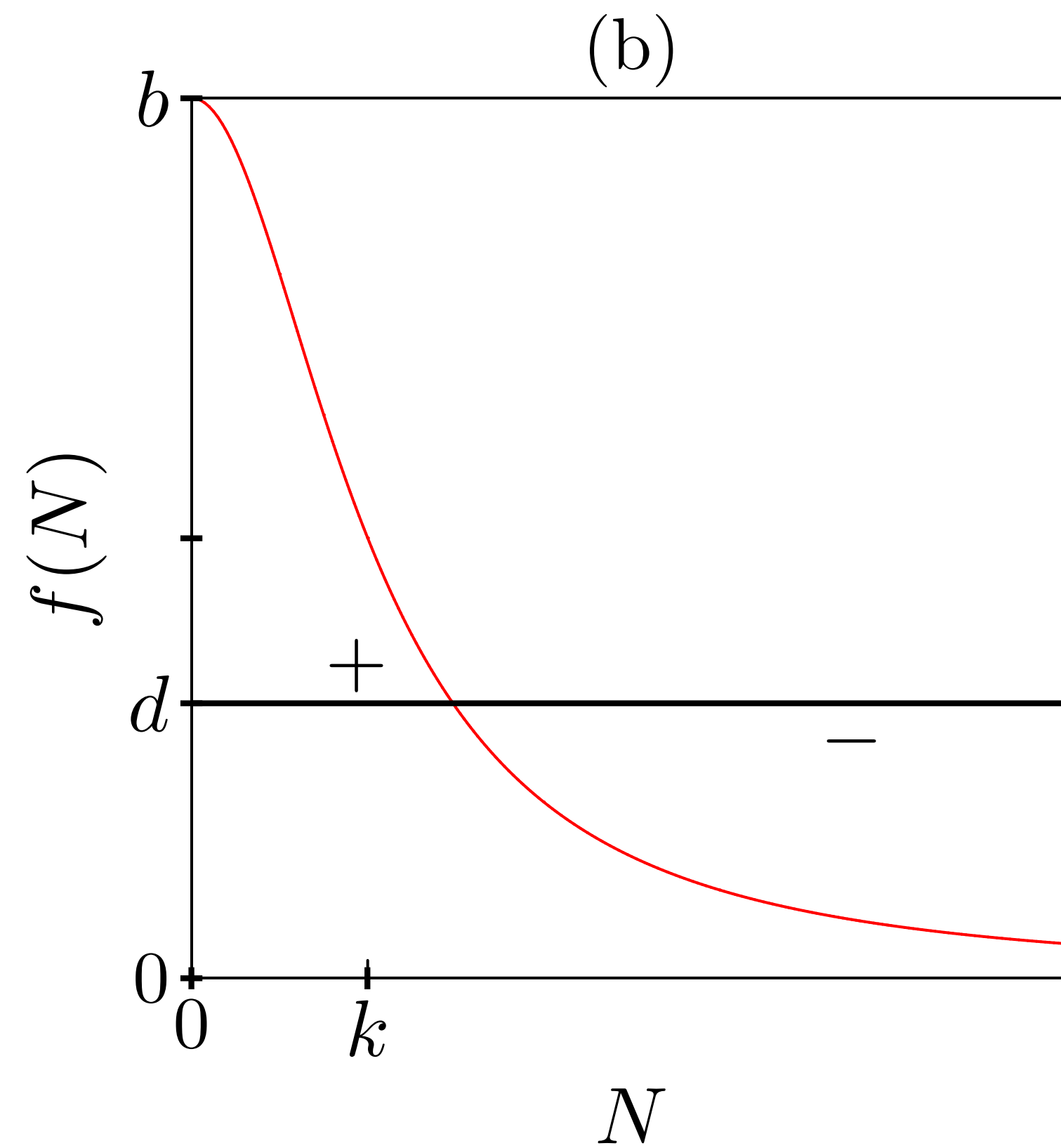
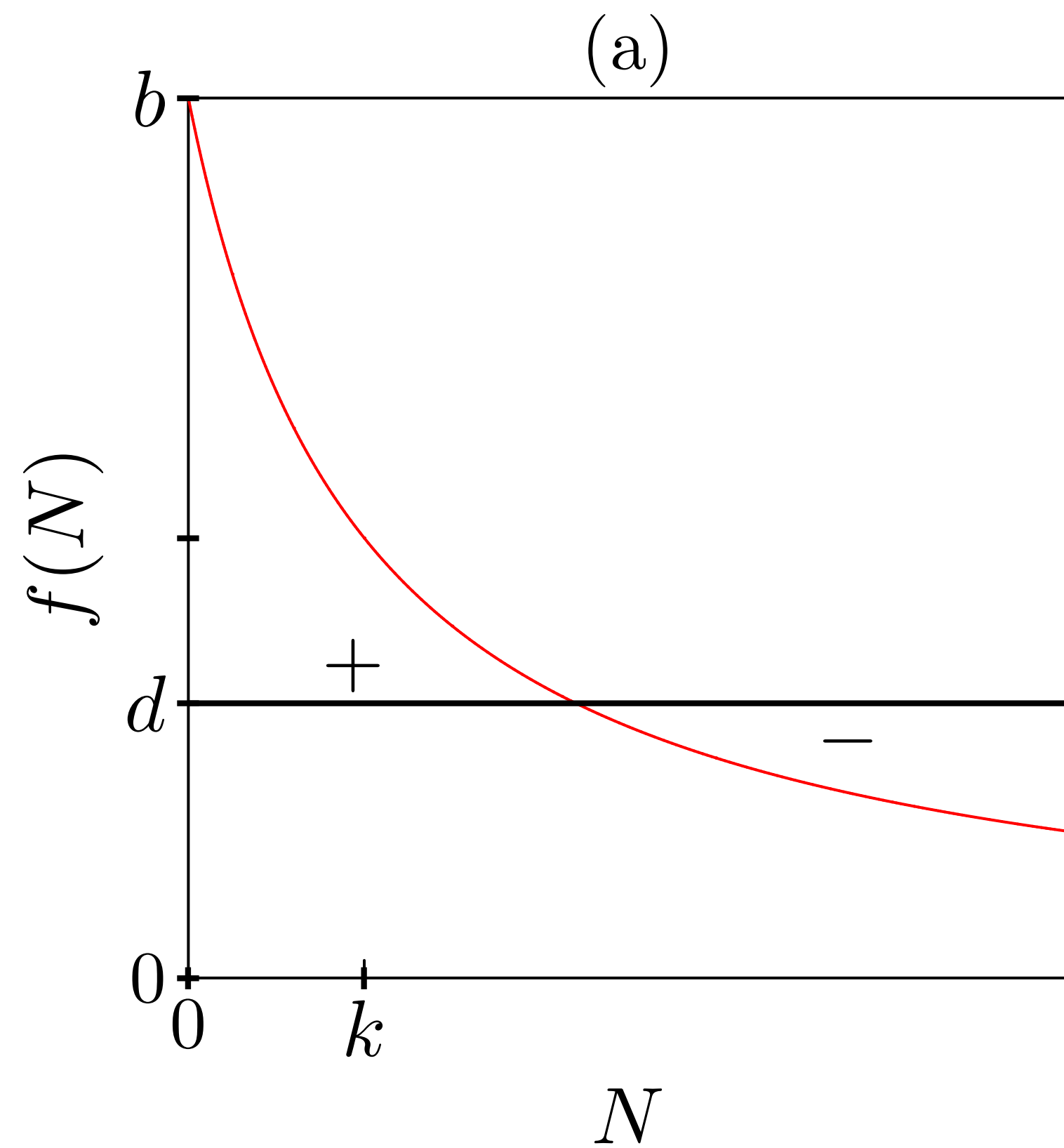
$$f(x) = \min(1, [x/k]^n)$$

$$f(x) = \frac{x^n}{h^n + x^n}$$

$$g(x) = \frac{1}{1 + (x/h)^n}$$

$$f(x) = 1 - e^{-\ln[2]x/h} \quad g(x) = e^{-\ln[2]x/h}$$

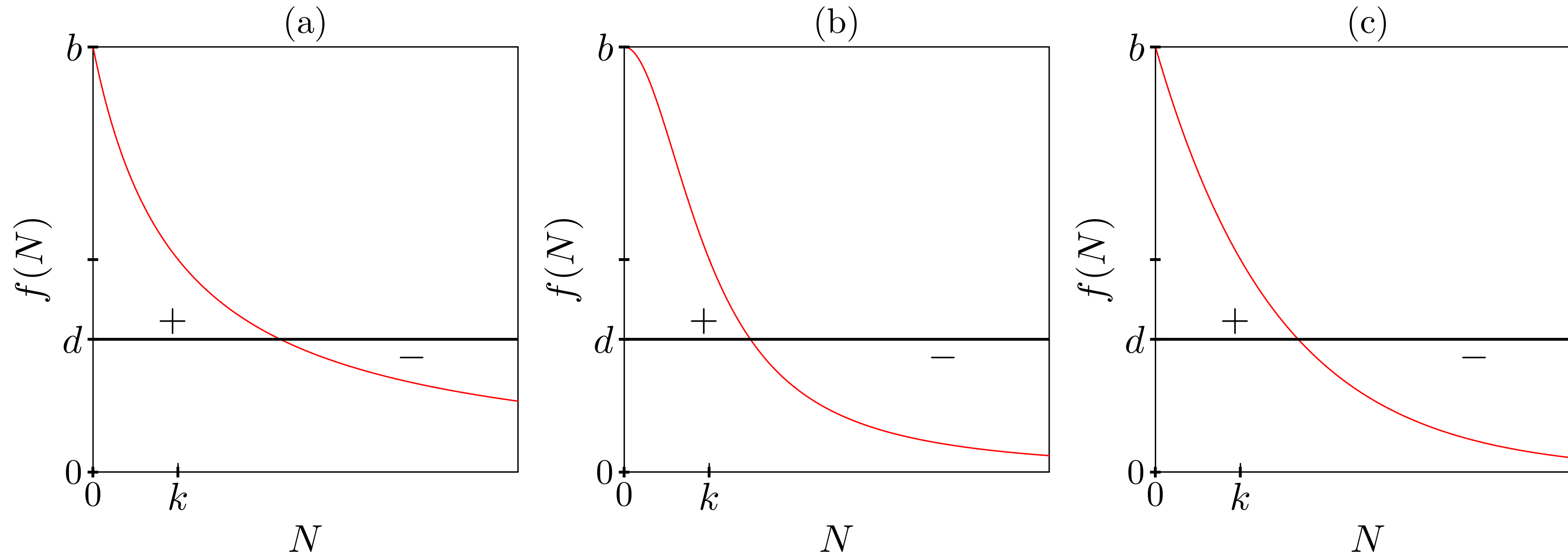
Non-linear density dependent birth rate



$$f(N) = \frac{1}{1 + N/k}, \quad f(N) = \frac{1}{1 + [N/k]^2} \quad \text{and} \quad f(N) = e^{-\ln[2]N/k}$$

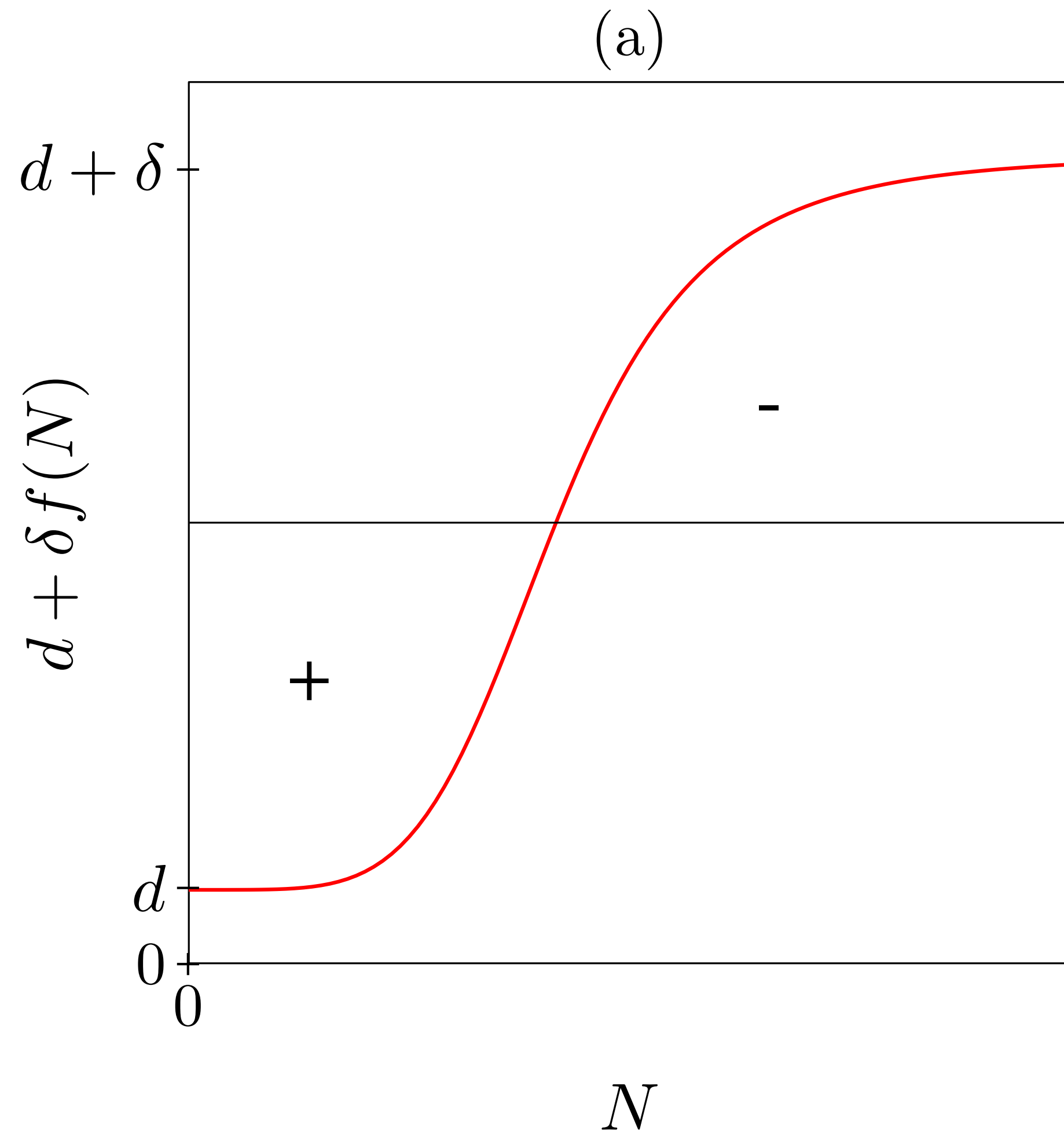
$$\frac{dN}{dt} = (bf(N) - d)N$$

$$\frac{dN}{dt} = (bf(N) - d)N \quad f(N) = \frac{1}{1 + N/k}, \quad f(N) = \frac{1}{1 + [N/k]^2} \quad \text{and} \quad f(N) = e^{-\ln[2]N/k}$$

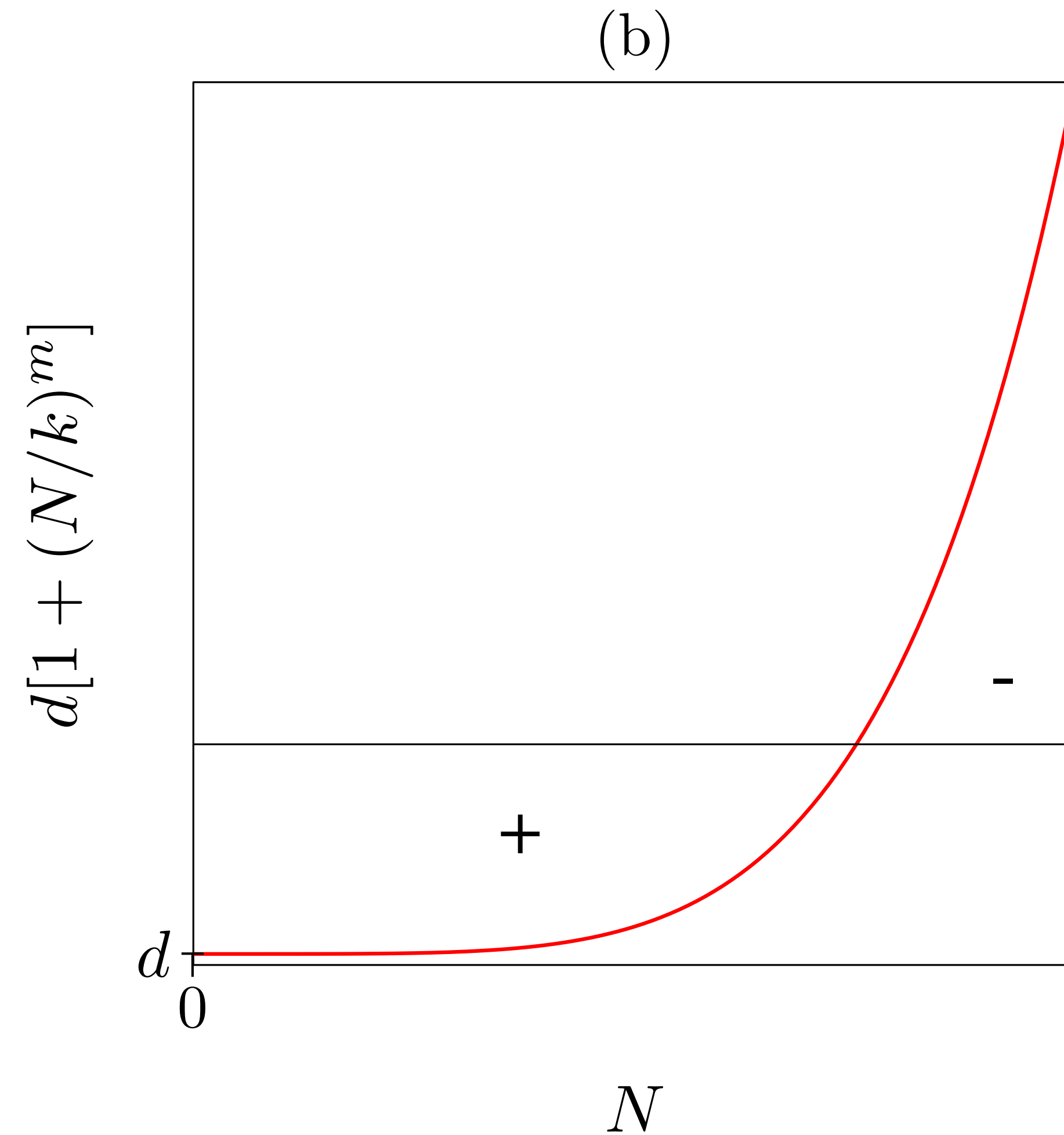


Function	$f(0)$	$f(k)$	$f(\infty)$	R_0	Carrying capacity	Eq.
$f(N) = \max(0, 1 - [N/k]^m)$	1	0	0	b/d	$\bar{N} = k \sqrt[m]{1 - 1/R_0}$	(3.12)
$f(N) = 1/(1 + N/k)$	1	0.5	0	b/d	$\bar{N} = k(R_0 - 1)$	(3.14)
$f(N) = 1/(1 + [N/k]^2)$	1	0.5	0	b/d	$\bar{N} = k\sqrt{R_0 - 1}$	(3.14)
$f(N) = e^{-\ln[2]N/k}$	1	0.5	0	b/d	$\bar{N} = (k/\ln[2]) \ln[R_0]$	(3.14)

Non-linear density dependent death rate

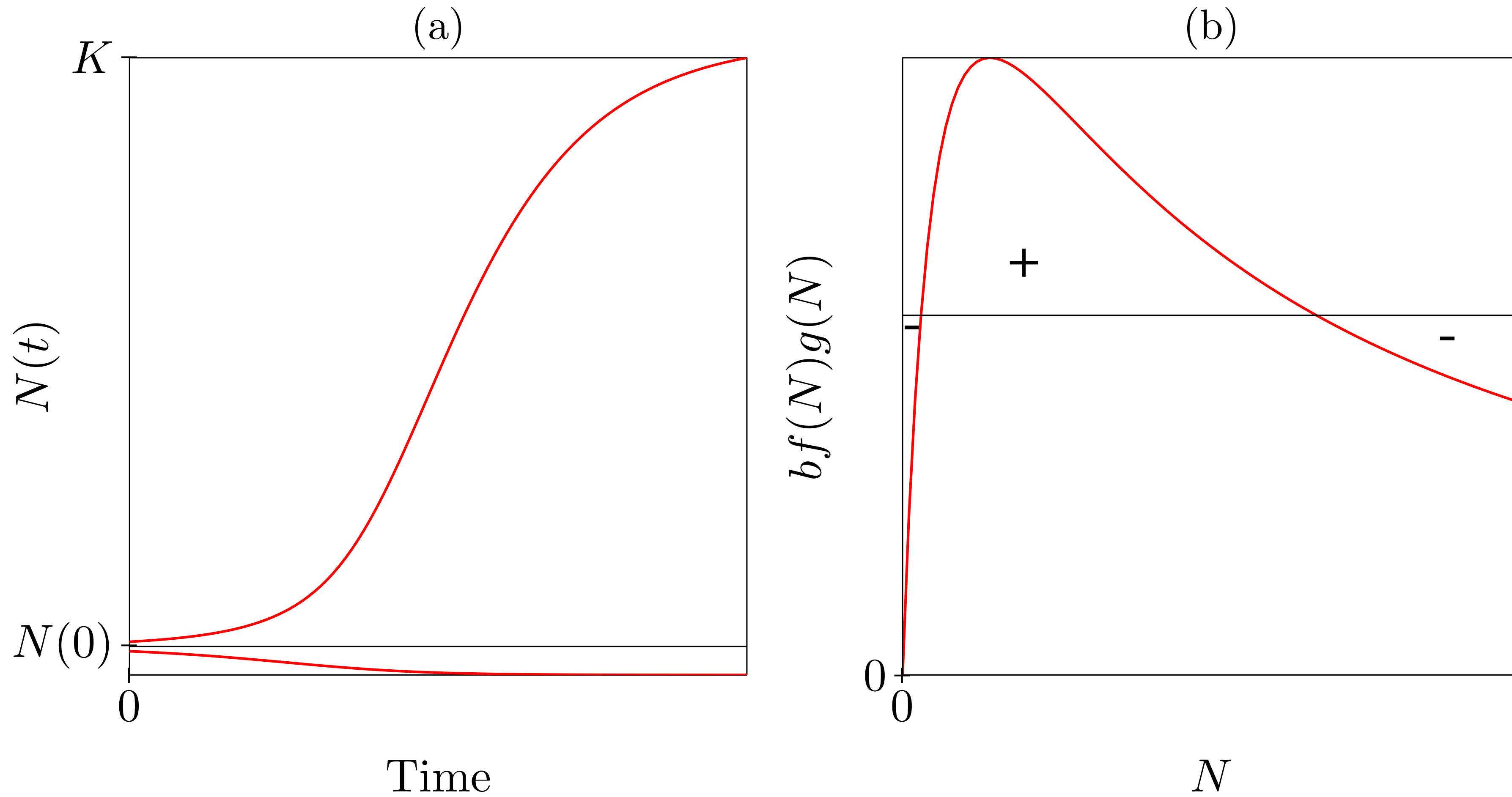


$$\frac{dN}{dt} = [b - d - \delta f(N)]N$$



$$\frac{dN}{dt} = (b - d[1 + (N/k)^m])N$$

Positive density dependence



$$\frac{dN}{dt} = (bf(N)g(N) - d)N \quad \text{or} \quad \frac{dN}{dt} = (bg(N) - d[1 + (N/k)^m])N ,$$

Regression to the mean

```
n <- 100; data <- rnorm(n, 1, 0.1); hist(data)
N <- data[1:(n-1)]; r <- (data[2:n] - N) / N
plot(N, r, type="p")
lm(r ~ N, as.data.frame(cbind(N, r)))
```


Cell division takes time

Conventional ODE: $dN/dt = (p - d)N$

Smith-Martin model (first ignoring death):

$$\frac{dA(t)}{dt} = 2pA_{t-\Delta} - pA(t) \quad \text{and} \quad \frac{dB(t)}{dt} = pA(t) - pA_{t-\Delta}$$

Smith-Martin model with death:

$$\frac{dA(t)}{dt} = 2pA_{t-\Delta}e^{-d\Delta} - (p+d)A(t) \quad \text{and} \quad \frac{dB(t)}{dt} = pA(t) - dB(t) - pA_{t-\Delta}e^{-d\Delta}$$

Time delays implemented as many small steps

Smith-Martin model with death:

$$\frac{dA(t)}{dt} = 2pA_{t-\Delta}e^{-d\Delta} - (p+d)A(t) \quad \text{and} \quad \frac{dB(t)}{dt} = pA(t) - dB(t) - pA_{t-\Delta}e^{-d\Delta}$$

Smooth the time delay by many (n) small steps:

$$\frac{dA}{dt} = \frac{2n}{\Delta}B_n - (p+d)A, \quad \frac{dB_1}{dt} = pA - \left(d + \frac{n}{\Delta}\right)B_1 \quad \text{and} \quad \frac{dB_i}{dt} = \frac{n}{\Delta}(B_{i-1} - B_i) - dB_i$$