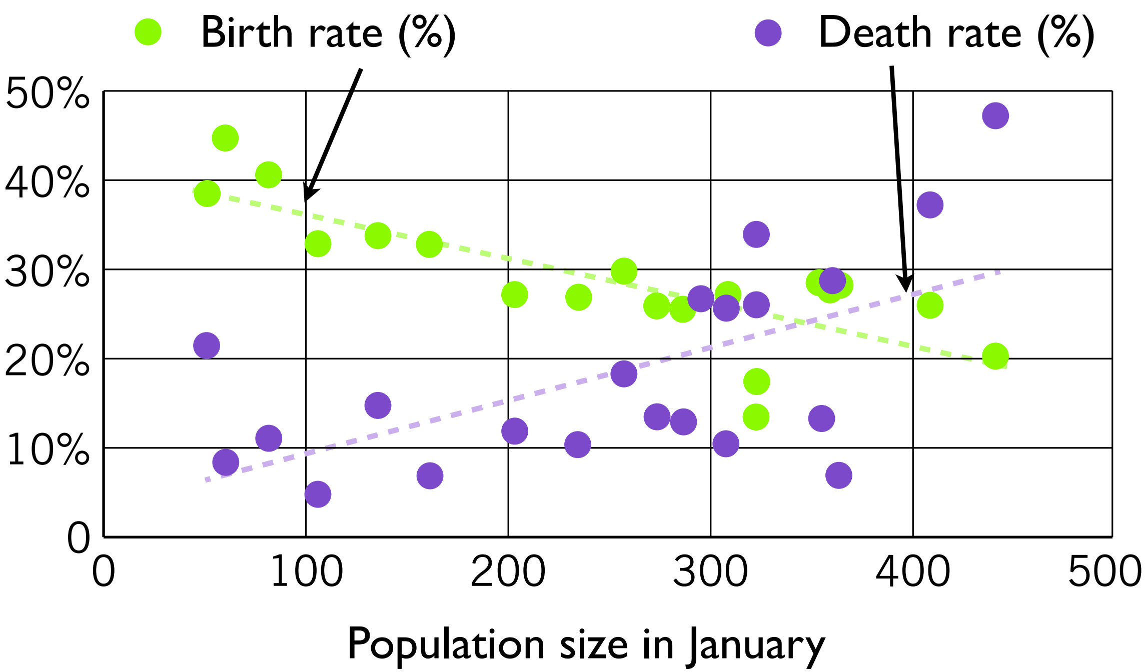
Last time

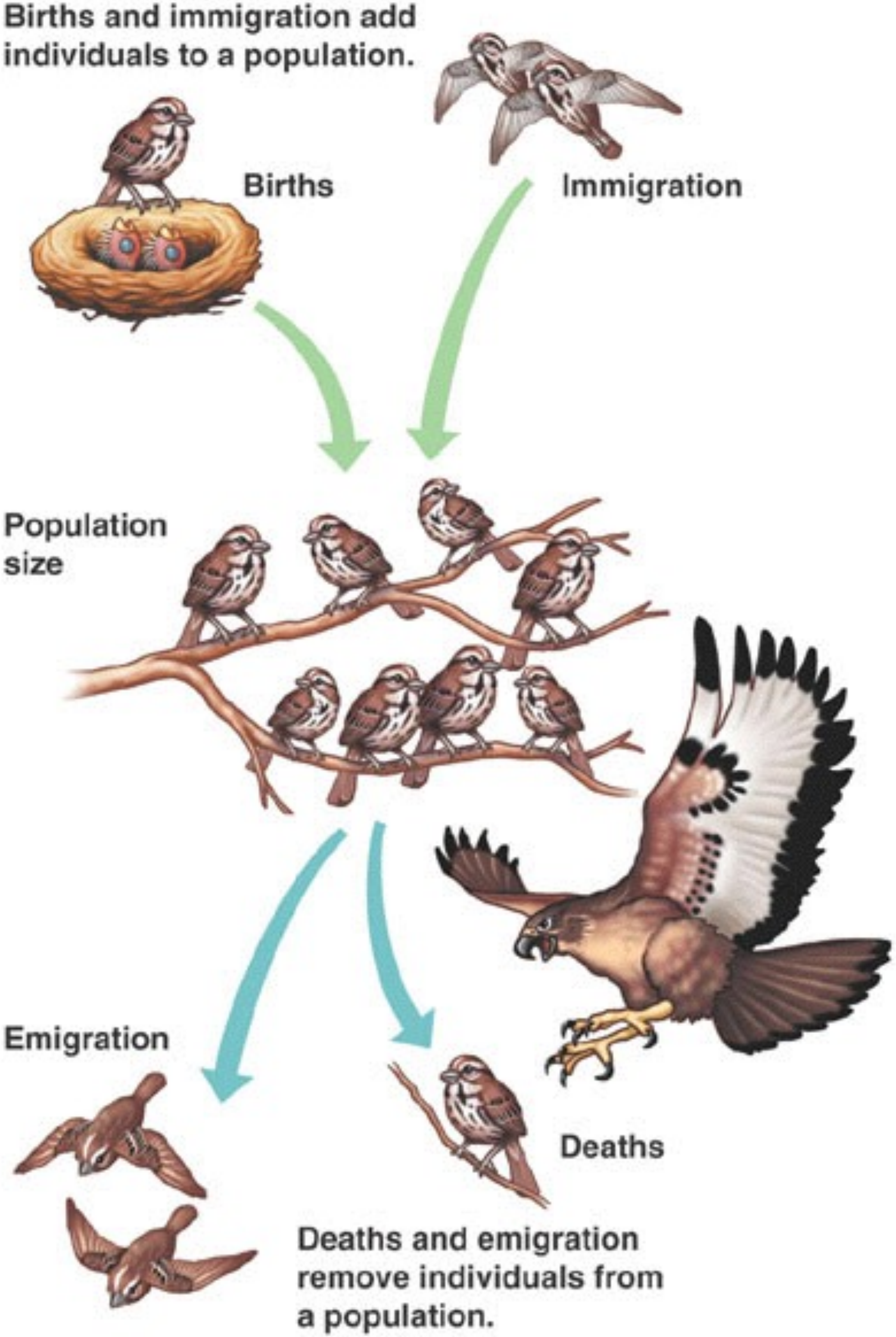
$$\frac{\mathrm{d}N}{\mathrm{d}t} = [b(1 - N/k) - d]N \qquad \bar{N} = 0 \quad \text{or} \quad \bar{N} = k(1 - d/b) = k(1 - 1/R_0)$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = [b - d(1 + N/k)]N \qquad \bar{N} = 0 \quad \text{or} \quad \bar{N} = k(b/d - 1) = k(R_0 - 1)$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(1 - N/K) \qquad \bar{N} = 0 \quad \text{or} \quad \bar{N} = K$$



Figures taken from NRC Handelsblad 11 Dec 2010 (left) and Wikipedia (right).

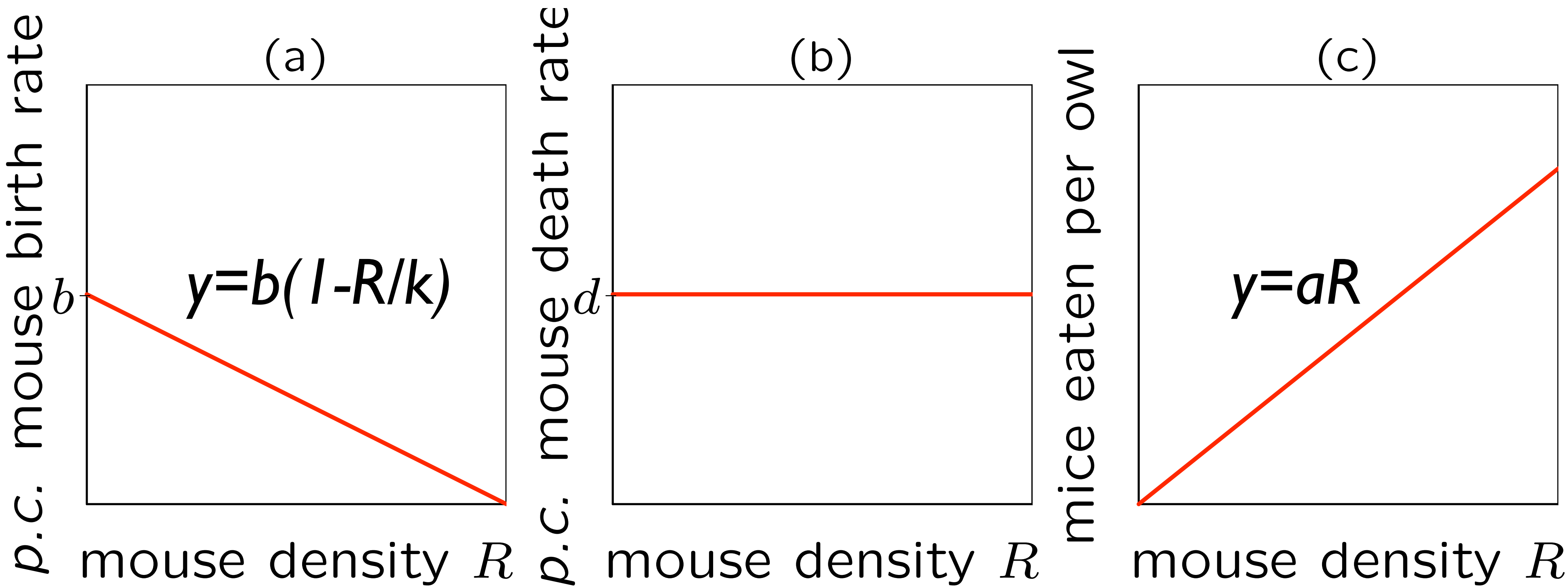


Chapter 3
Lotka Volterra model

Vito Volterra

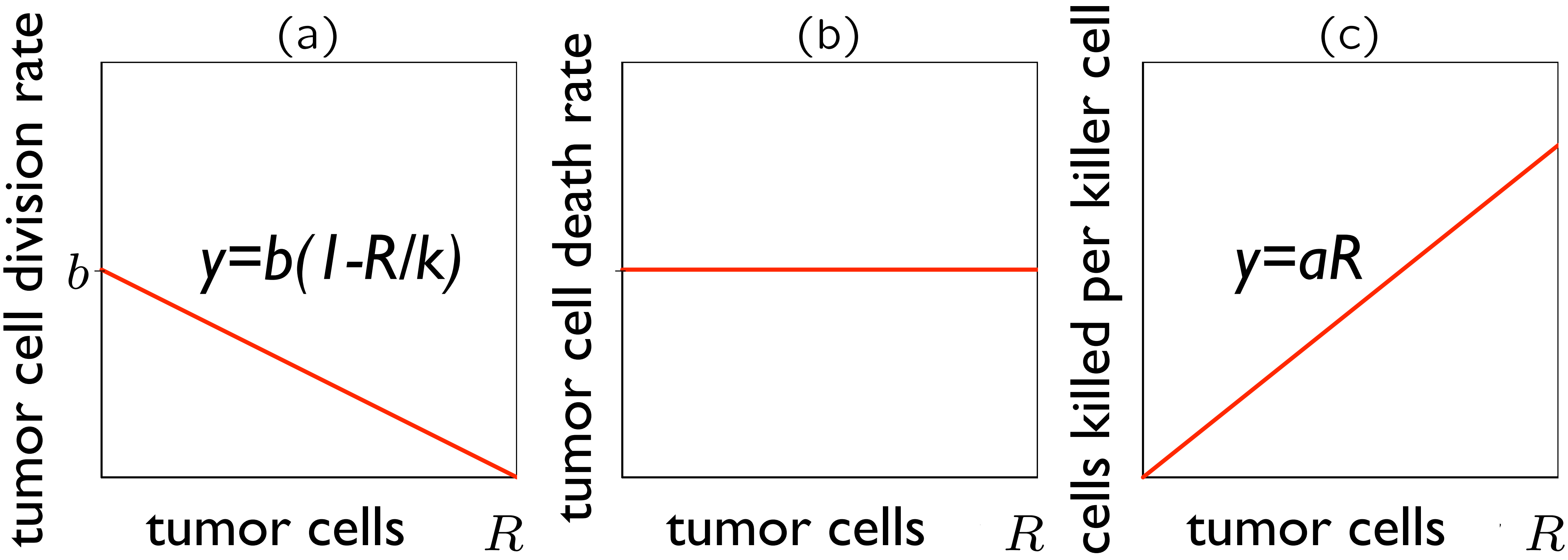
Theoretical Biology 2016

Suppose measurements for the prey



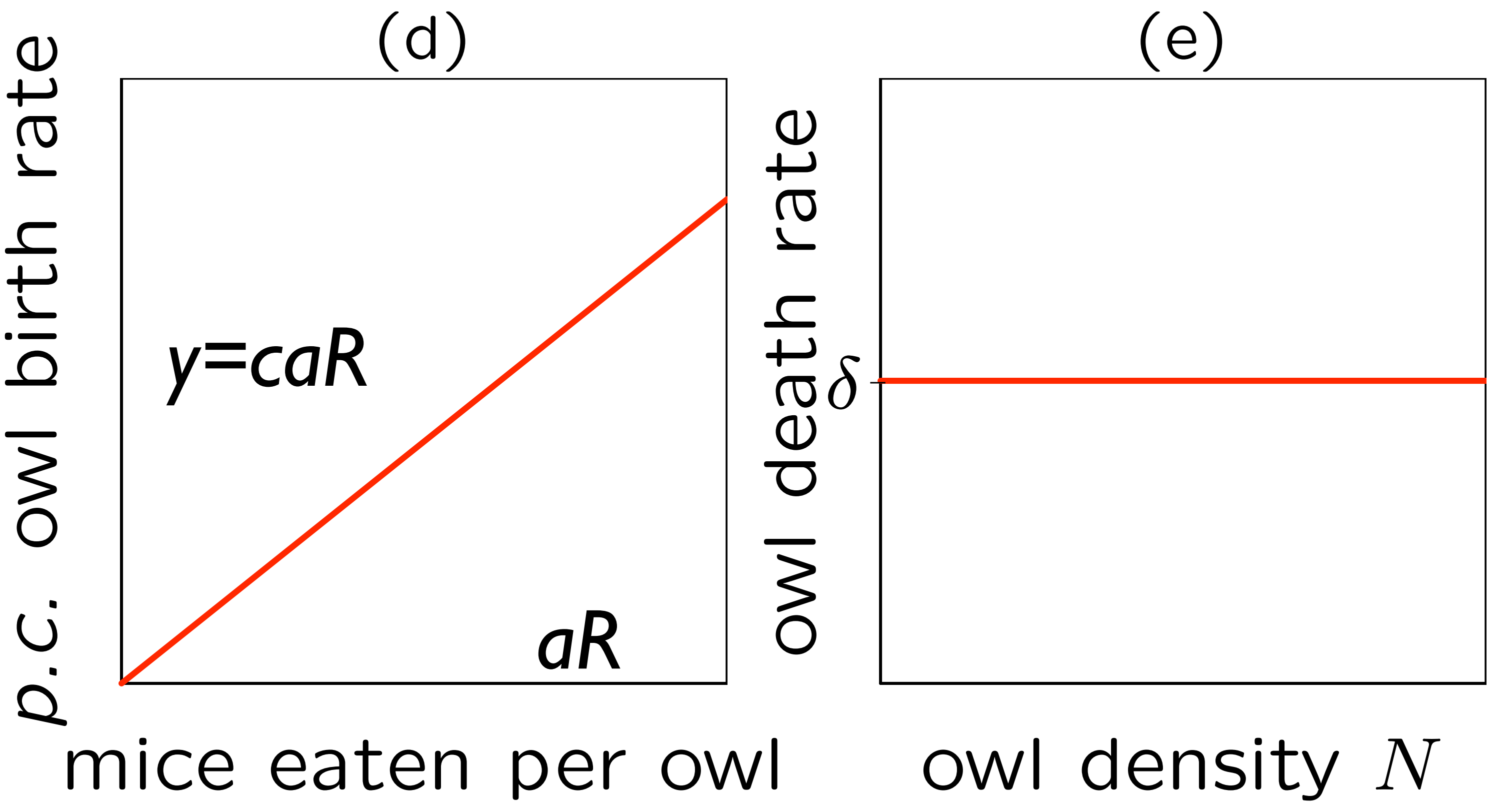
$$\frac{\mathrm{d}R}{\mathrm{d}t} = [bf(R) - d - aN]R \quad \text{where} \quad f(R) = 1 - R/k$$

Suppose measurements for the prey



$$\frac{\mathrm{d}R}{\mathrm{d}t} = [bf(R) - d - aN]R \quad \text{where} \quad f(R) = 1 - R/k$$

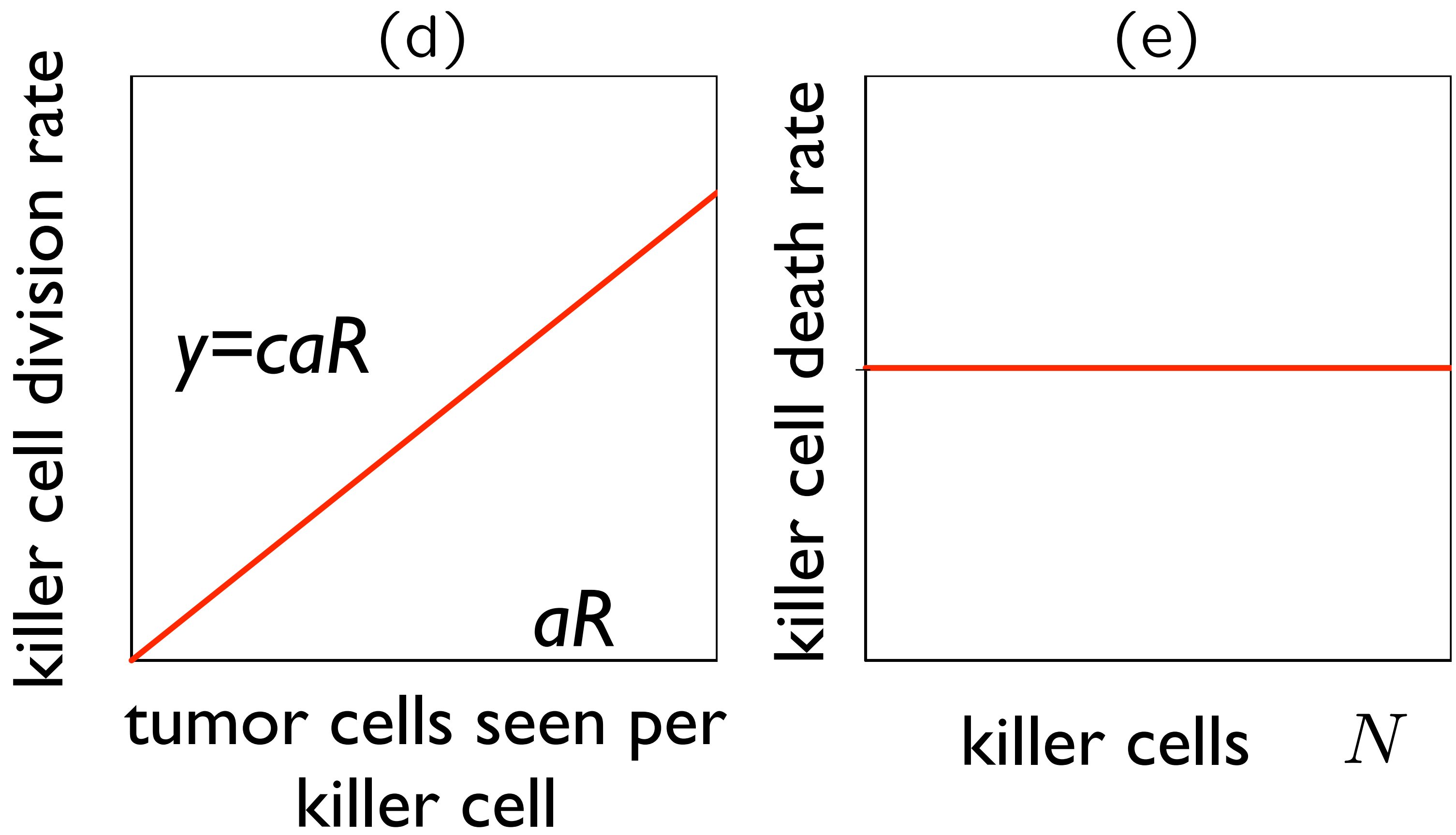
Measurements for the predator



$$\frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

where 1/δ is the expected owl life span

Measurements for the predator



$$\frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

where 1/δ is the expected killer cell life span

$$\frac{\mathrm{d}R}{\mathrm{d}t} = [bf(R) - d - aN]R \quad \text{where} \quad f(R) = 1 - R/k$$

In the abscence of predators the carrying capacity is:

$$\bar{R} = k(1 - d/b) = k(1 - 1/R_0) = K$$

Number of predators:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

where $1/\delta$ is the expected life-span.

Steady states

Setting $\mathrm{d}R/\mathrm{d}t = \mathrm{d}N/\mathrm{d}t = 0$ yields

$$R = 0 \quad \text{and} \quad N = \frac{1}{a}\left[b(1 - R/k) - d\right]$$

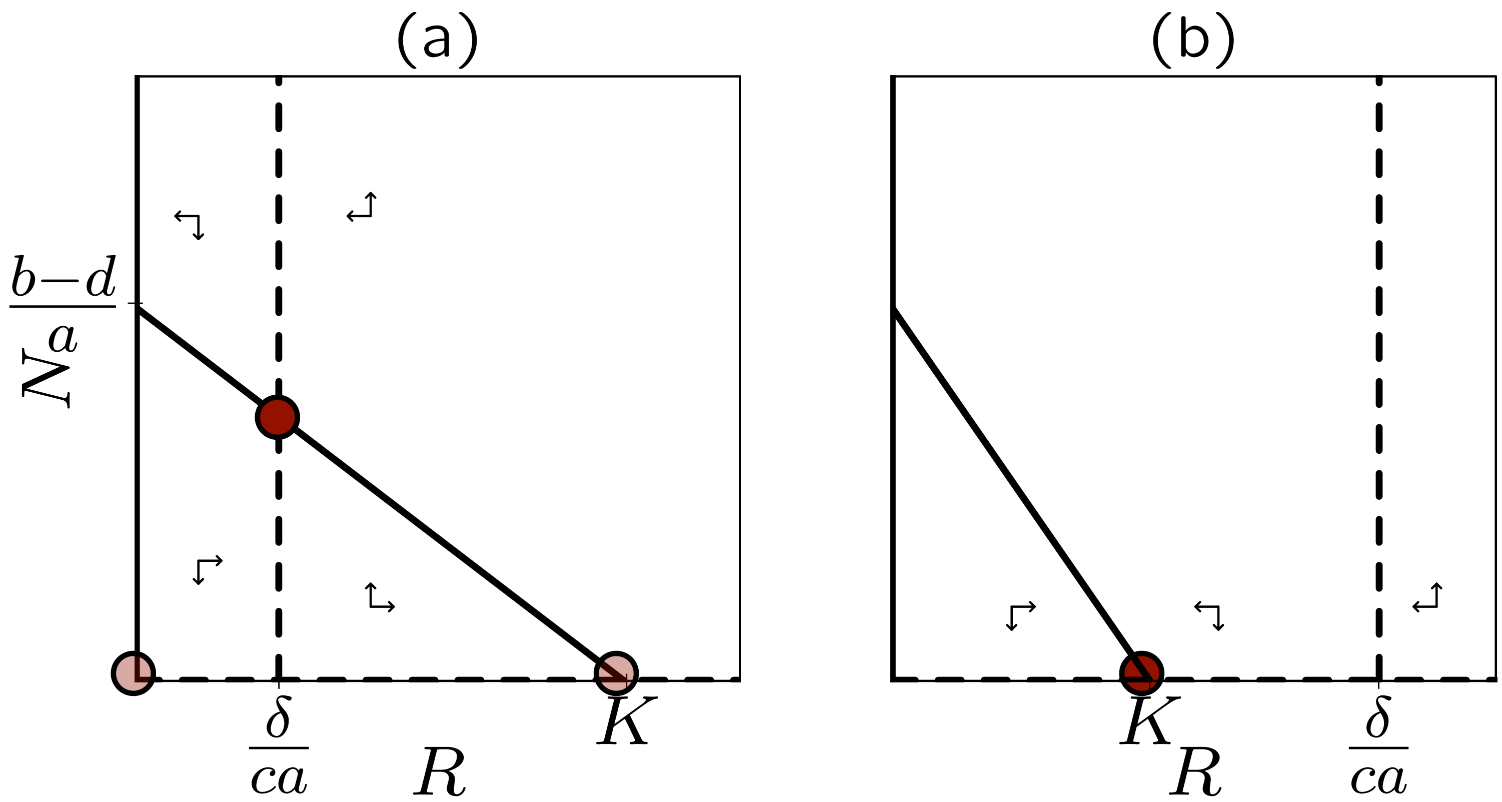
$$N = 0 \quad \text{and} \quad R = \frac{\delta}{ca}$$

Trivial: $(\bar{R}, \bar{N}) = (0, 0)$ and $(\bar{R}, \bar{N}) = (K, 0)$.

Non-trivial:

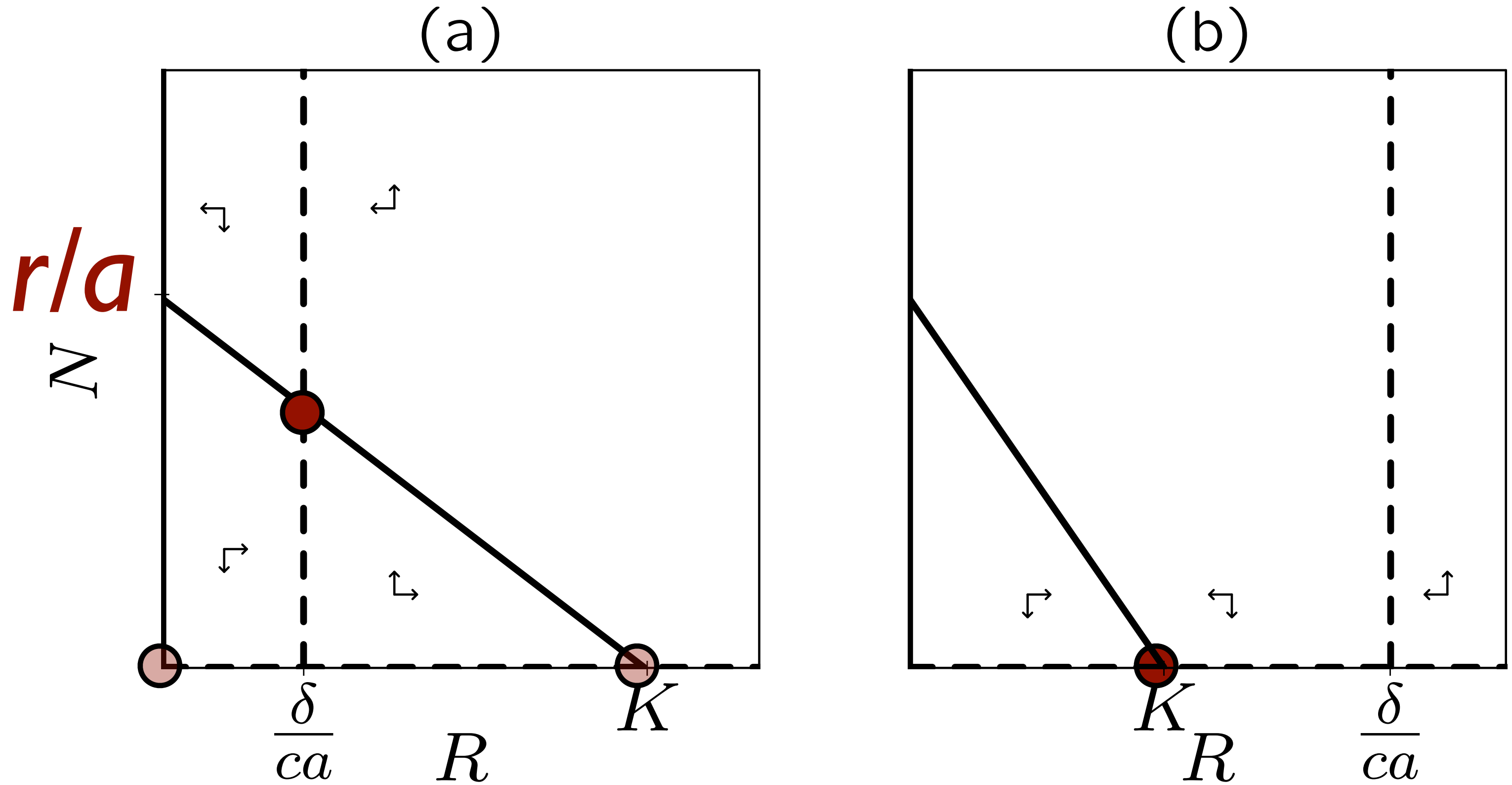
$$\bar{N} = \frac{1}{a}\left[b\left(1 - \frac{\delta}{cak}\right) - d\right]$$

Nullclines in phase space



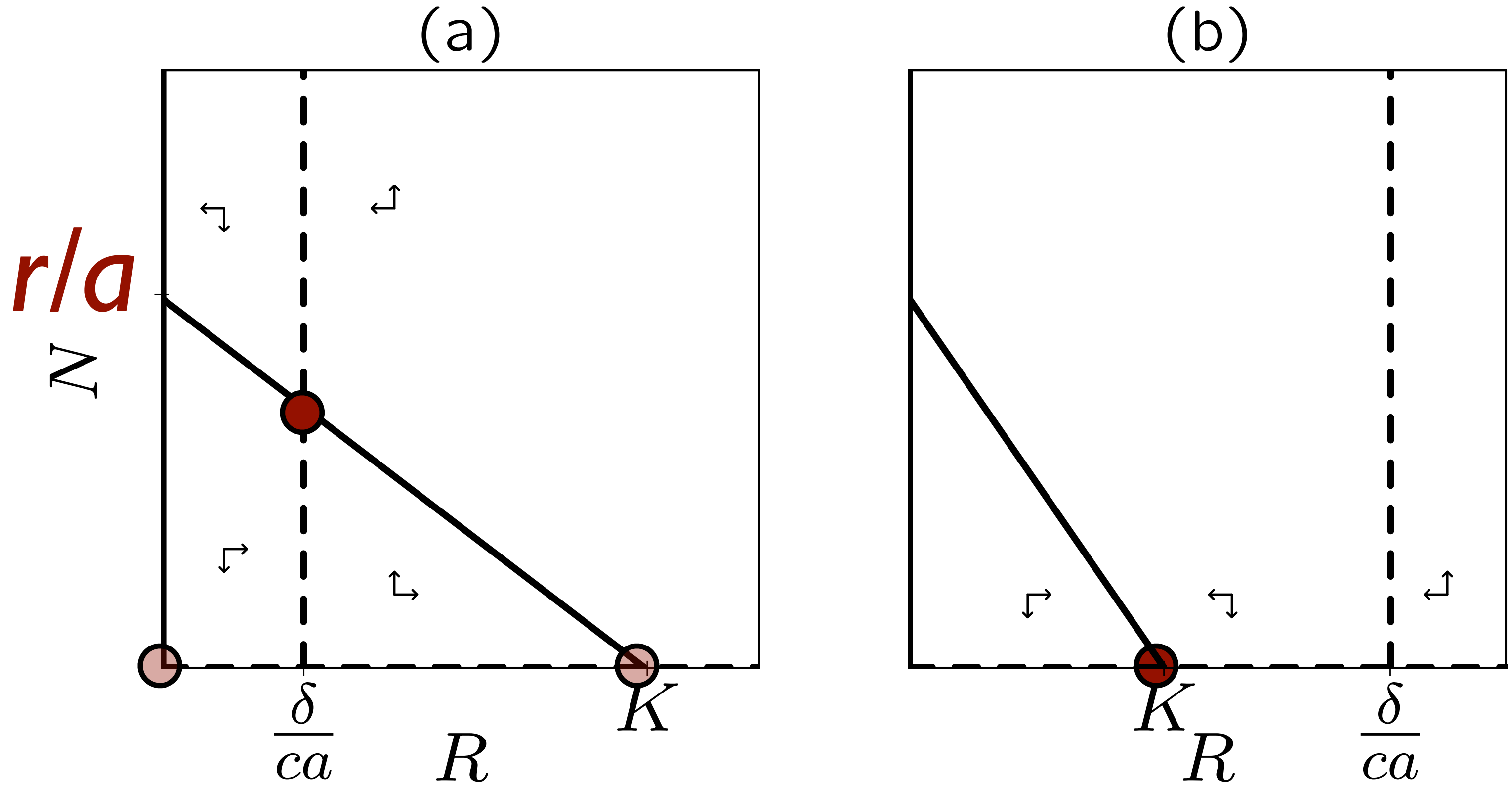
$$\frac{\mathrm{d}R}{\mathrm{d}t} = [b(1 - R/k) - d - aN]R \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

LV-model typically written with logistic growth



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

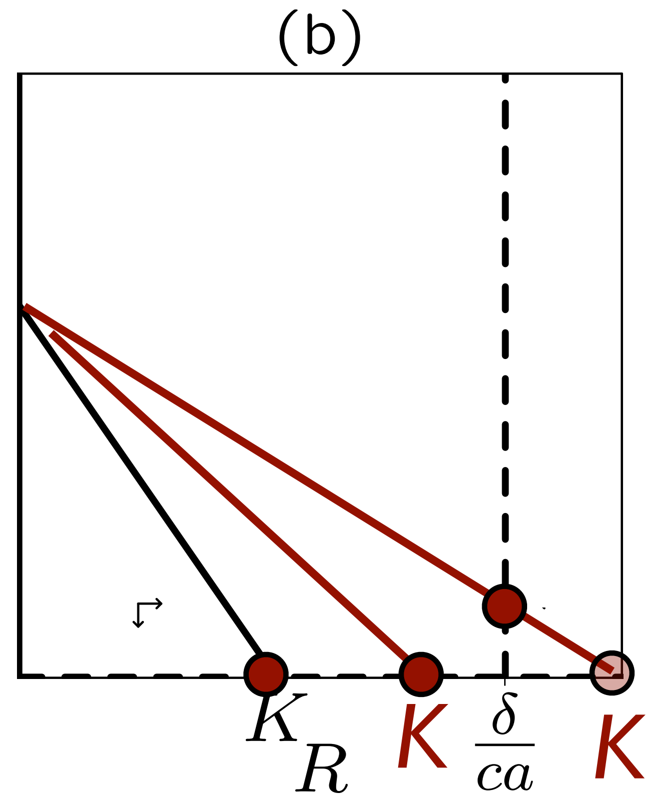
What happens if we feed the prey?



Increasing *K* in (b):

1. increases the prey density
2. increases the predator density
3. increases the prey density until predators can survive

What happens if we feed the prey?

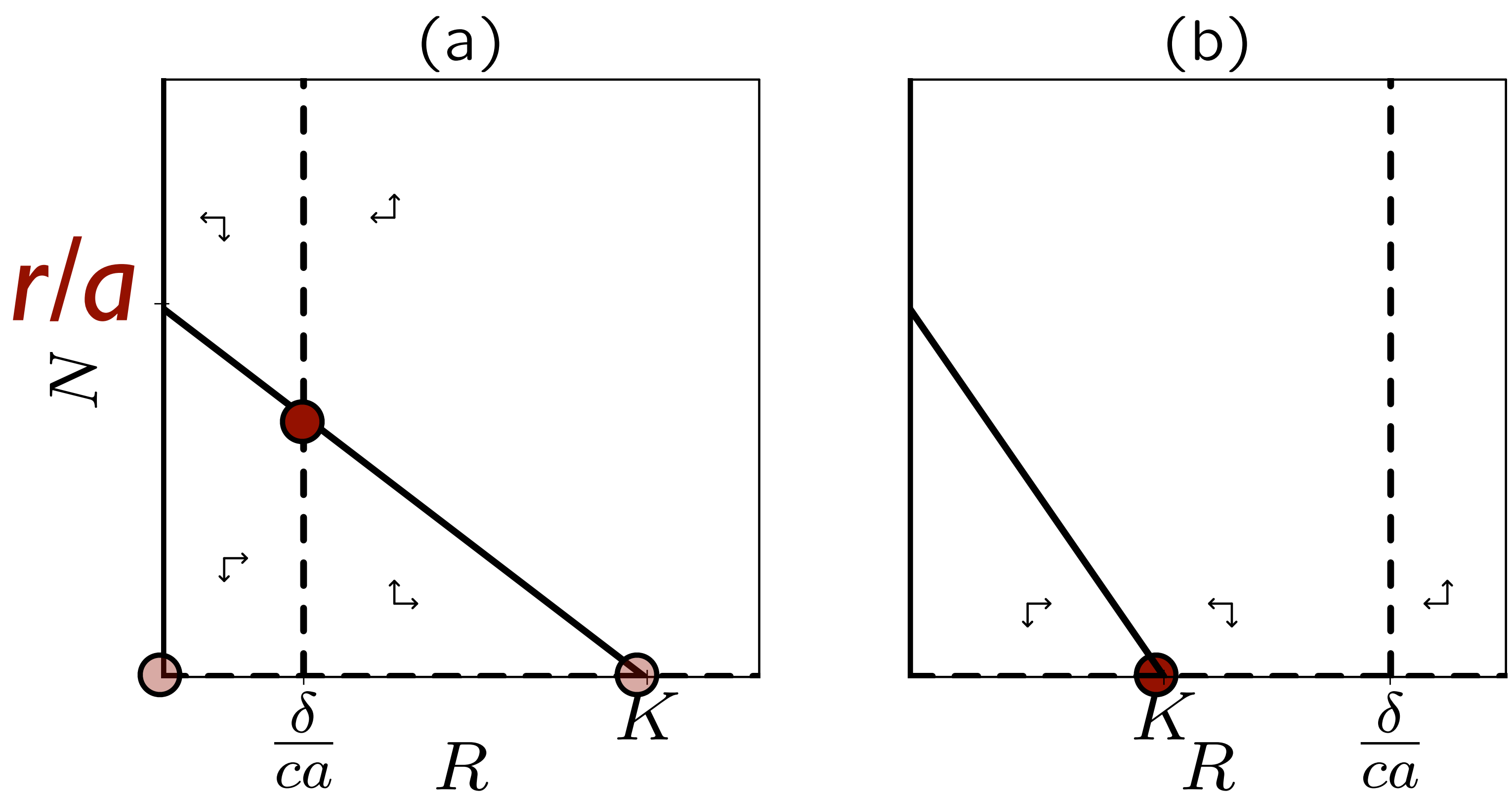


3. increases the prey density until predators can survive

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

By feeding the prey we get predators

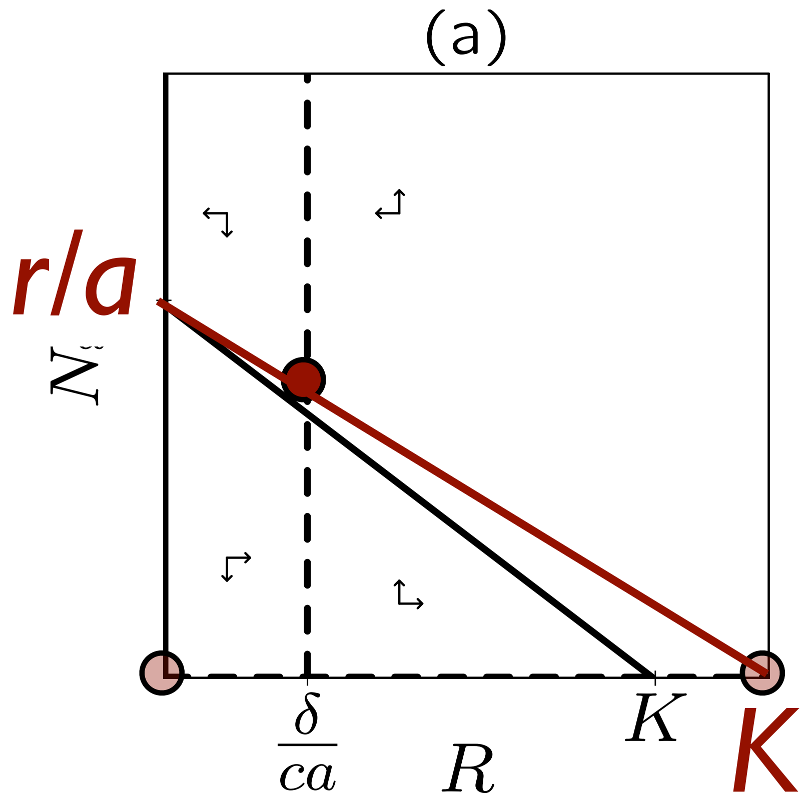
What happens if we feed the prey?



Increasing *K* in (a):

1. increases the prey density and keeps predators the same
2. increases the predator density and keeps prey the same
3. increases both populations

What happens if we feed the prey?

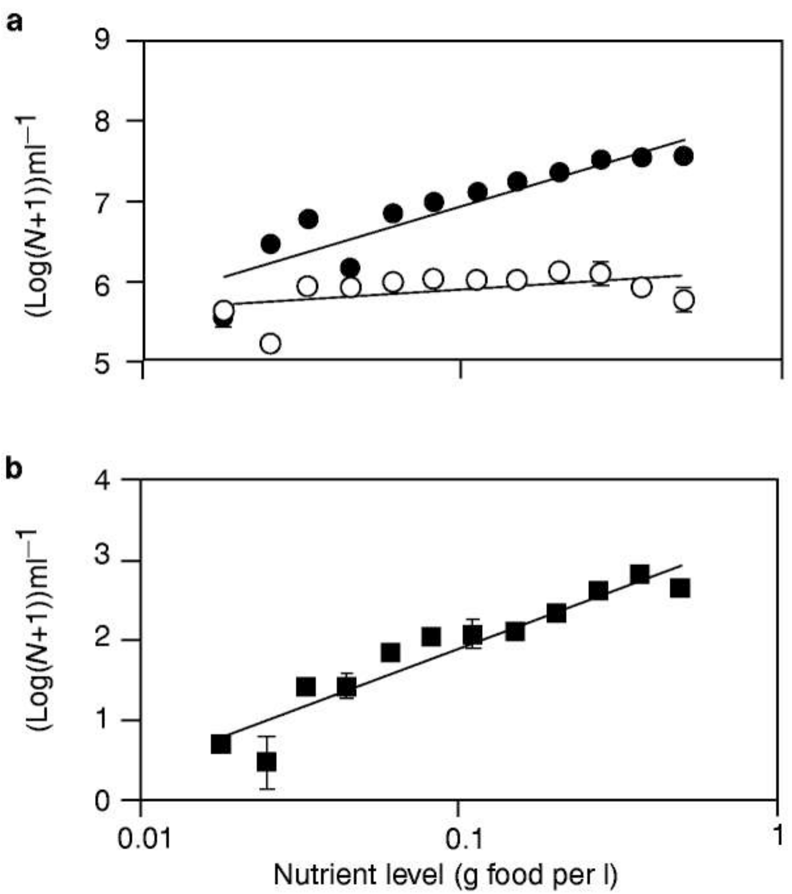


2. increases the predator density and keeps prey the same

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

By feeding the prey we get more predators

Example: bacterial food chain



← Predator

Colpidium striatium

← Prey with predator

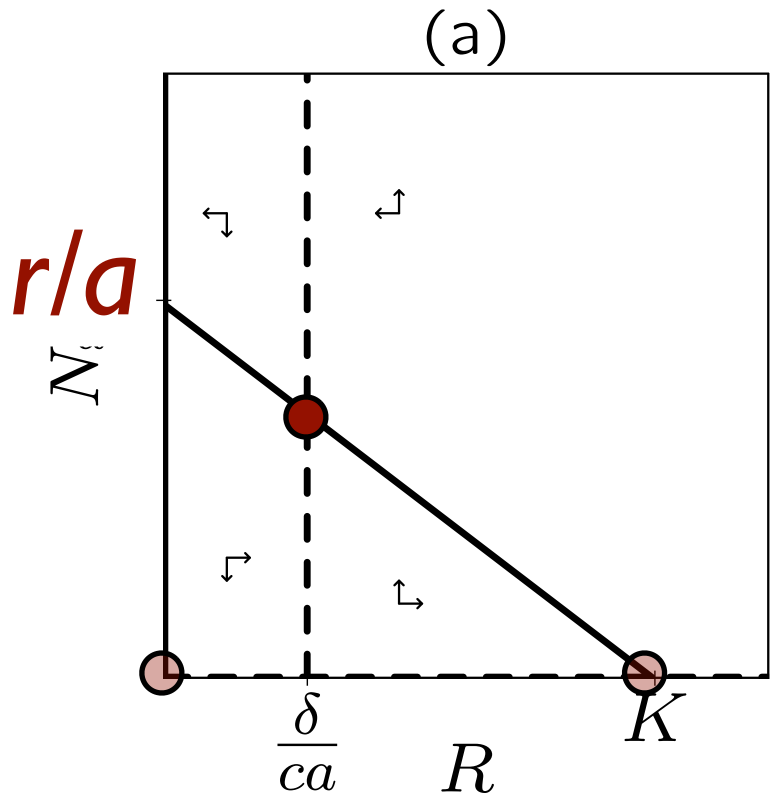
Serratia marcescens

← 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.

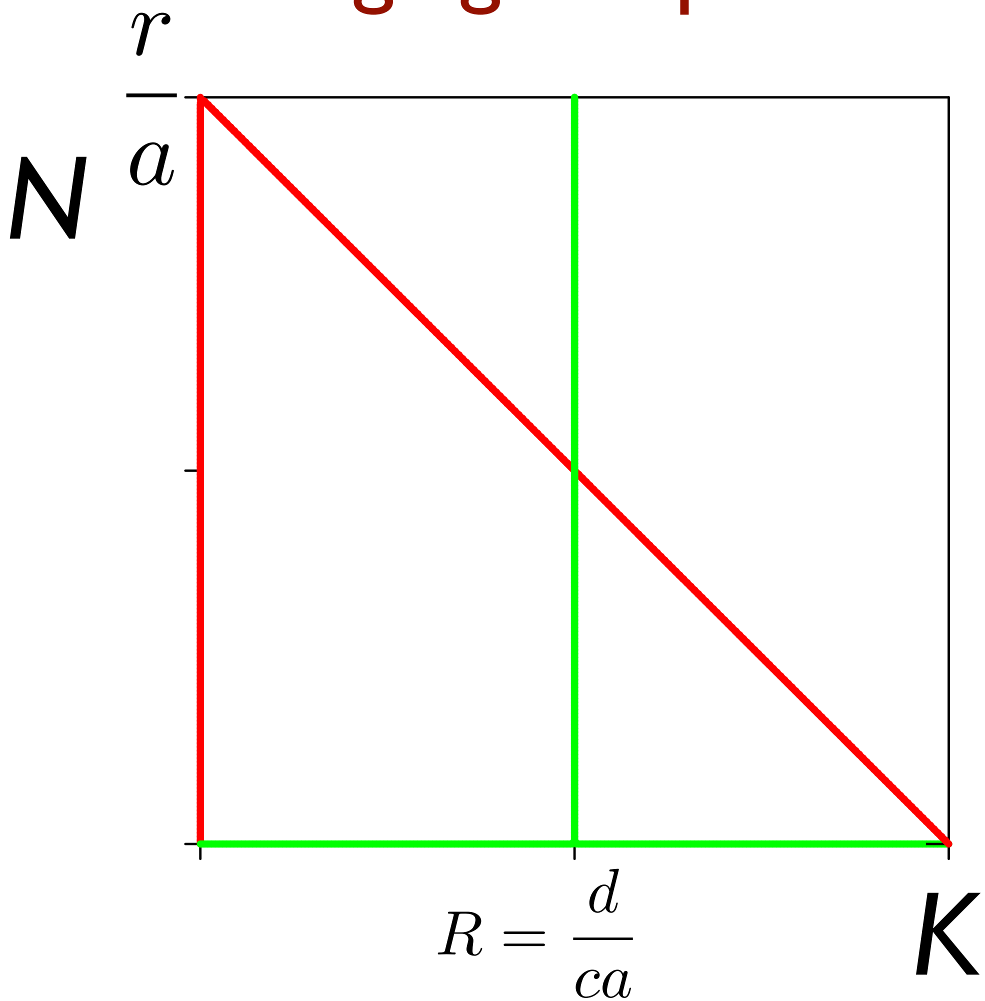
What happens if we change *a*?

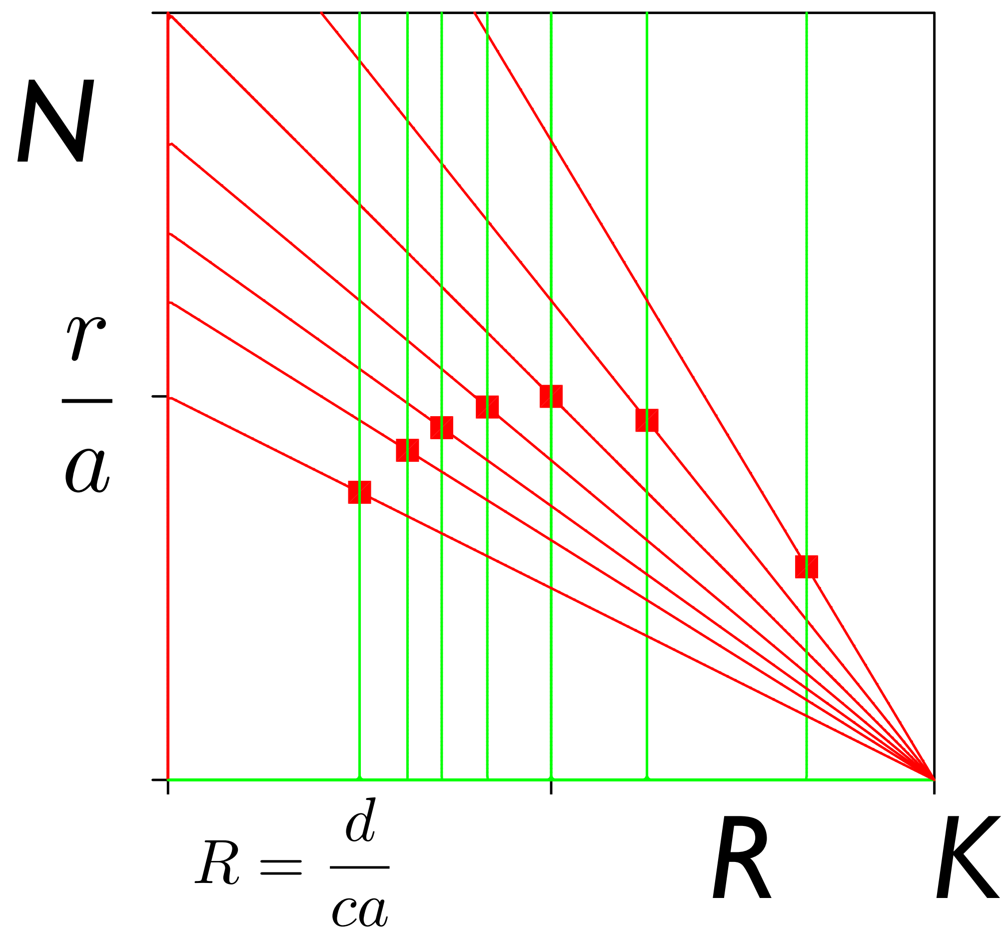


Prey: tumor cells
Predator: killer cells
a: drug changing the killing rate

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

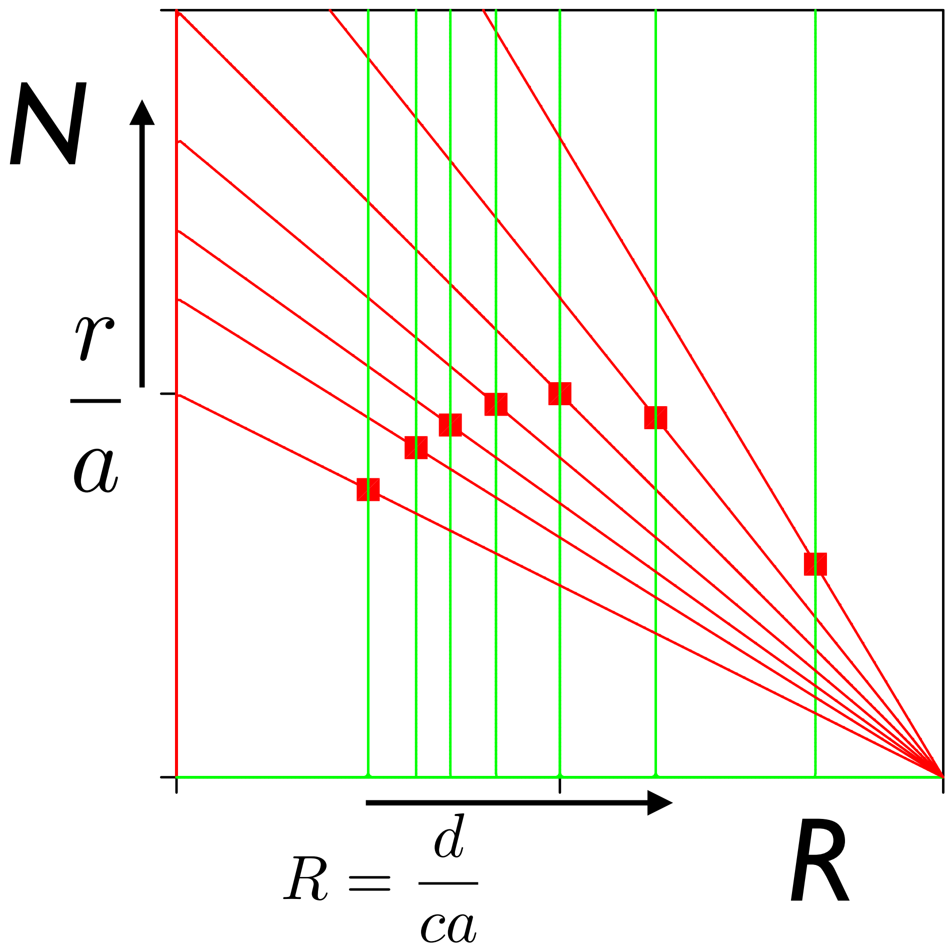
Changing the predation rate *a* changes both

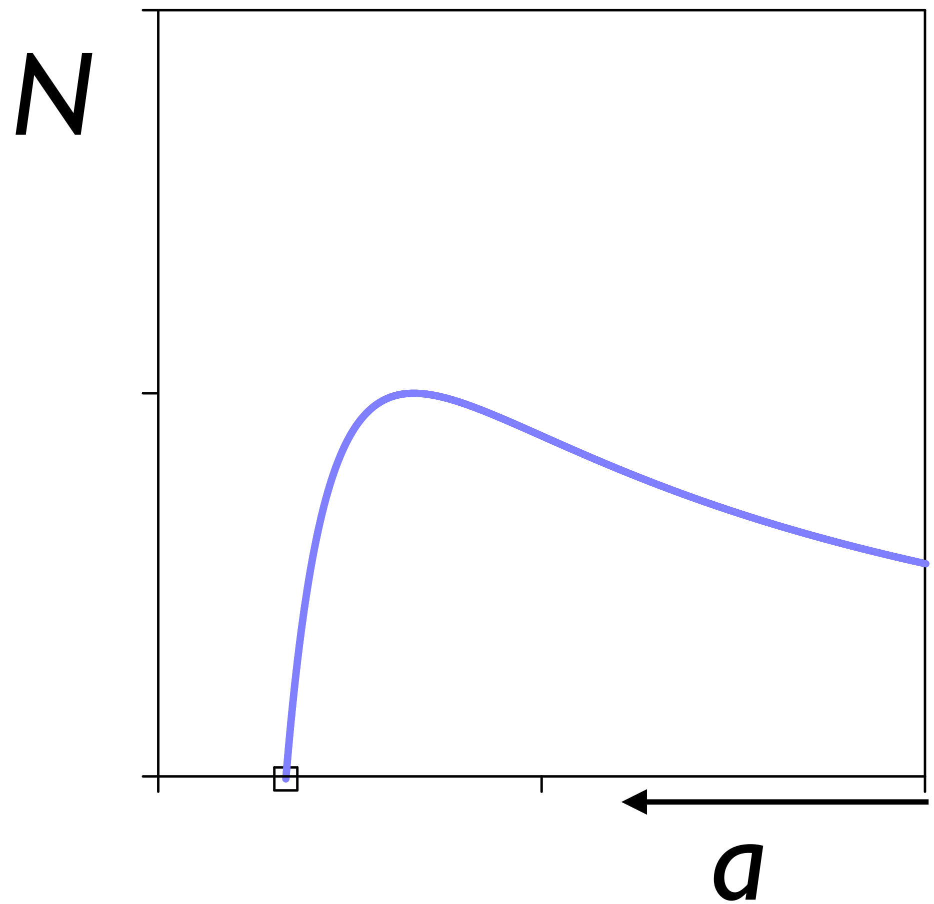




$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - aRN \ , \quad \frac{\mathrm{d}N}{\mathrm{d}t} = caRN - dN \ .$$

Decreasing the predation rate increases the predator





$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - aRN \ , \quad \frac{\mathrm{d}N}{\mathrm{d}t} = caRN - dN \ .$$

Predators with larger *a* have higher fitness R_0

Fitness R_0

For the prey $R_0 = b/d$

For the predator $R_0 = \frac{caR}{\delta}$ which is not a constant.

Take the best possible circumstances, i.e., $R = K$ and let $R_0 = \frac{caK}{\delta}$.

The prey equilibrium is at $R = \frac{\delta}{ca}$ or at $R = \frac{K}{R_0}$

This implies that a predator with an $R_0 = 2$ is expected to halve its prey population.

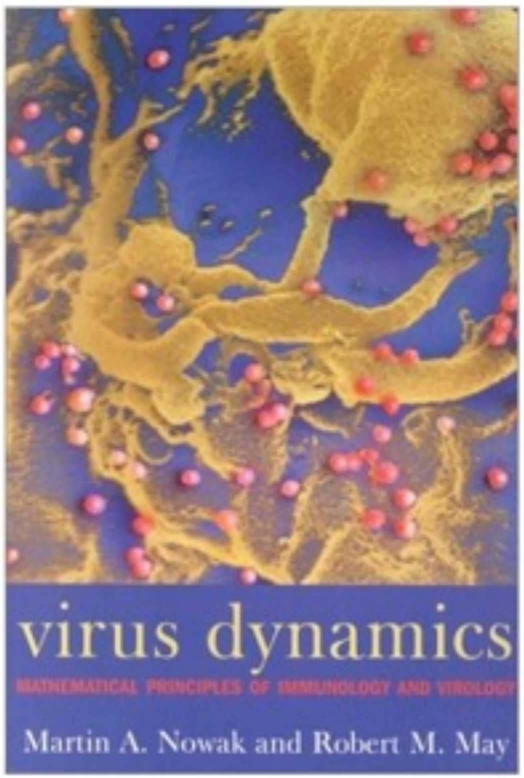
Lotka Volterra model is very general

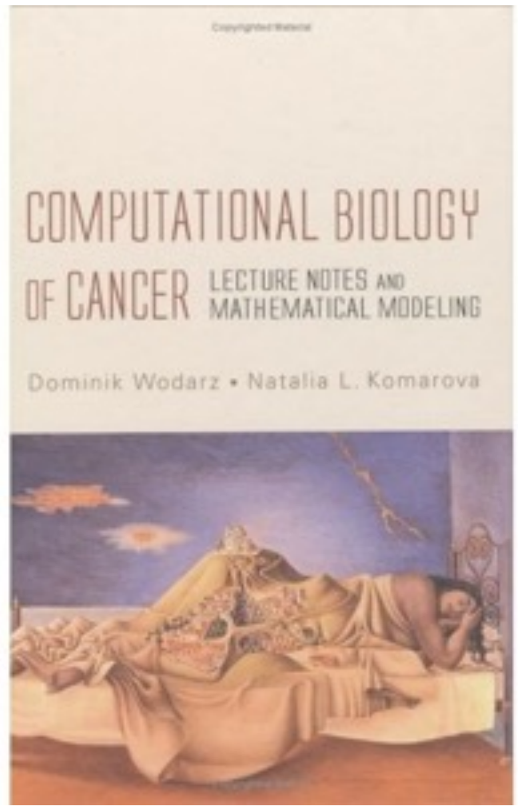
$$\frac{\mathrm{d}R}{\mathrm{d}t} = [r(1 - R/K) - aN]R \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

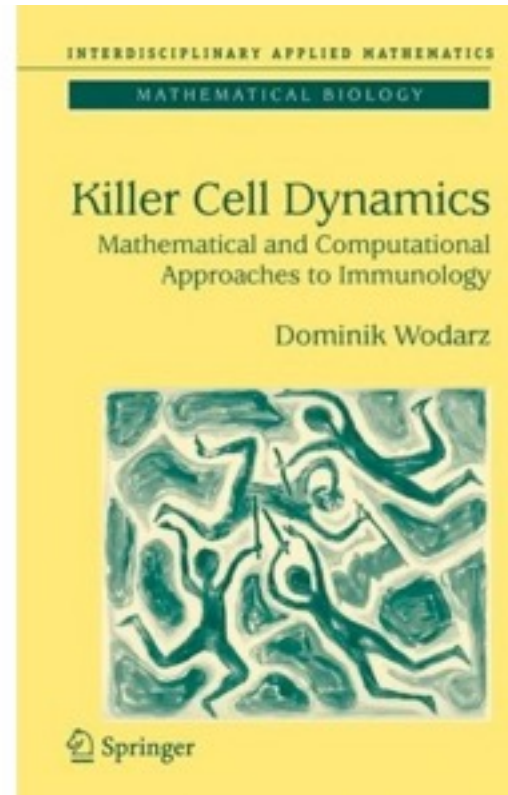
Predator-prey & host-parasite models

Seals in the Waddensea infected by virus
Hepatocytes infected by hepatitis
Cancer cells removed by killer cells
Economics: interactions industries

Lotka Volterra model is very general

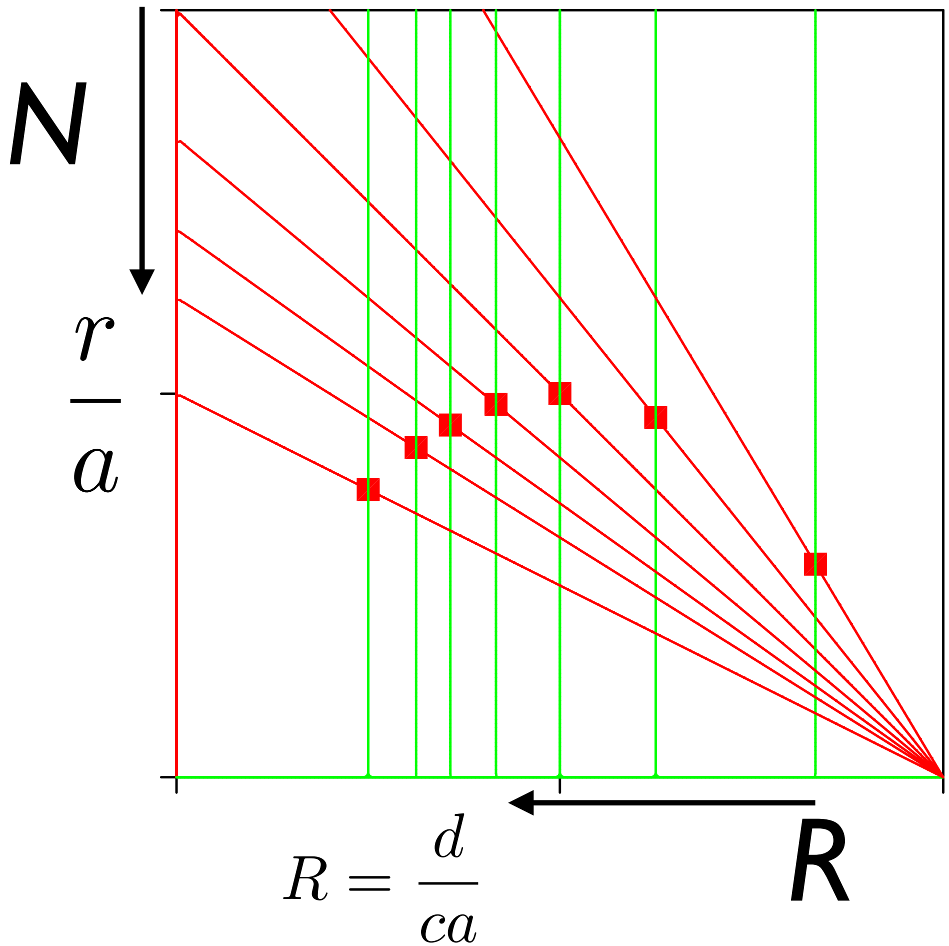


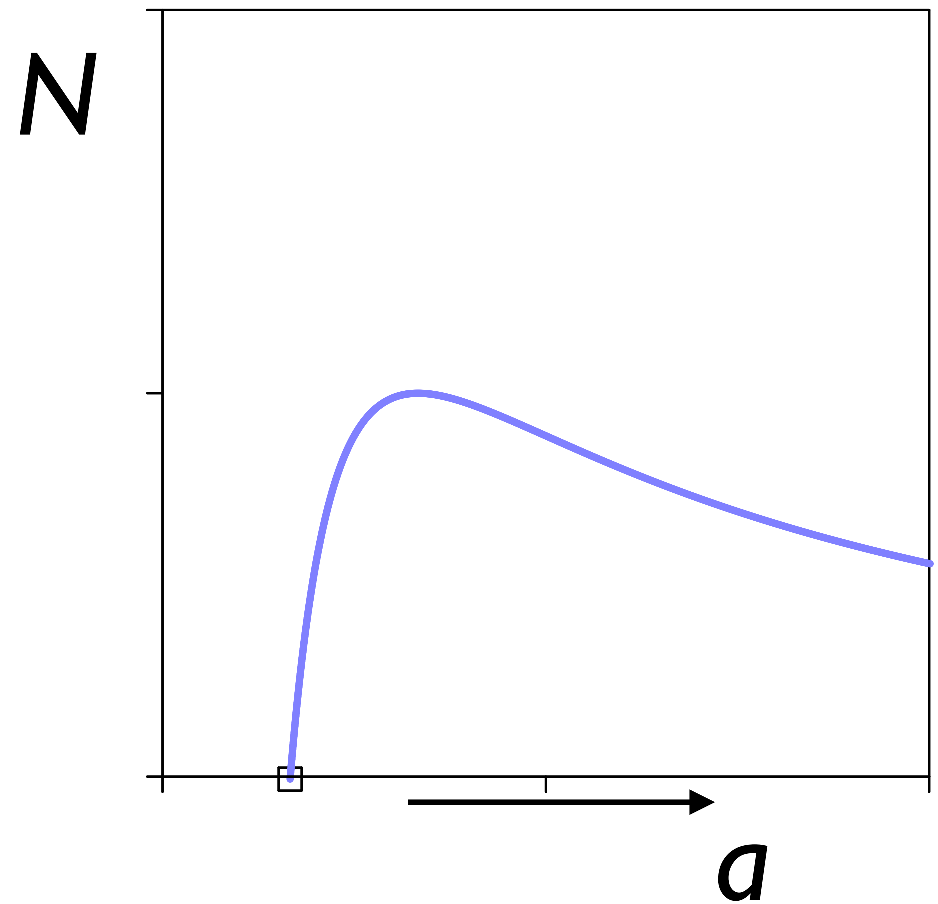




Many models use the Lotka Volterra equations

Increasing the killing rate decreases the killers



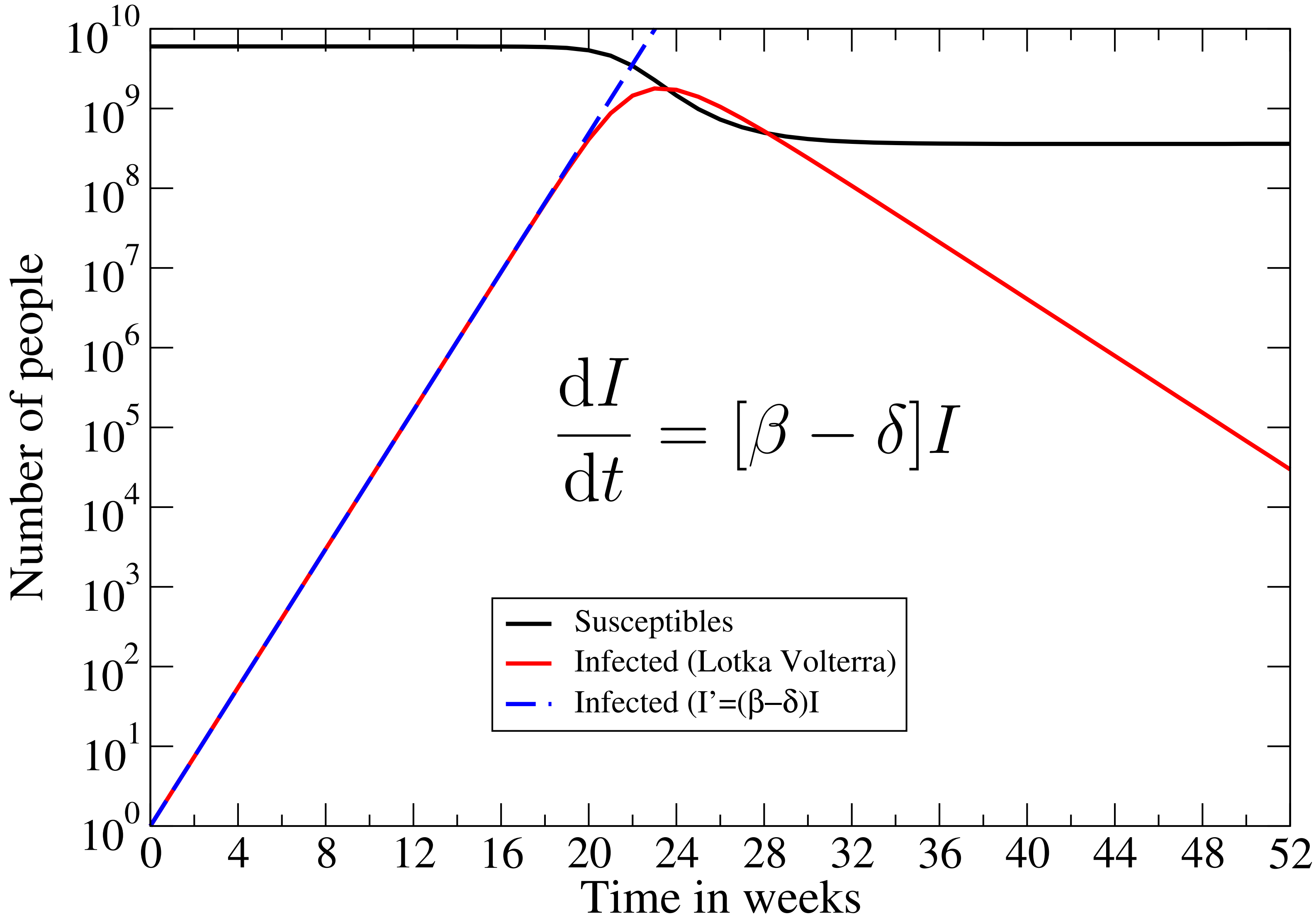


$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR(1 - R/K) - aRN \ , \qquad \frac{\mathrm{d}N}{\mathrm{d}t} = caRN - dN \ .$$

Tumor

Killer cells

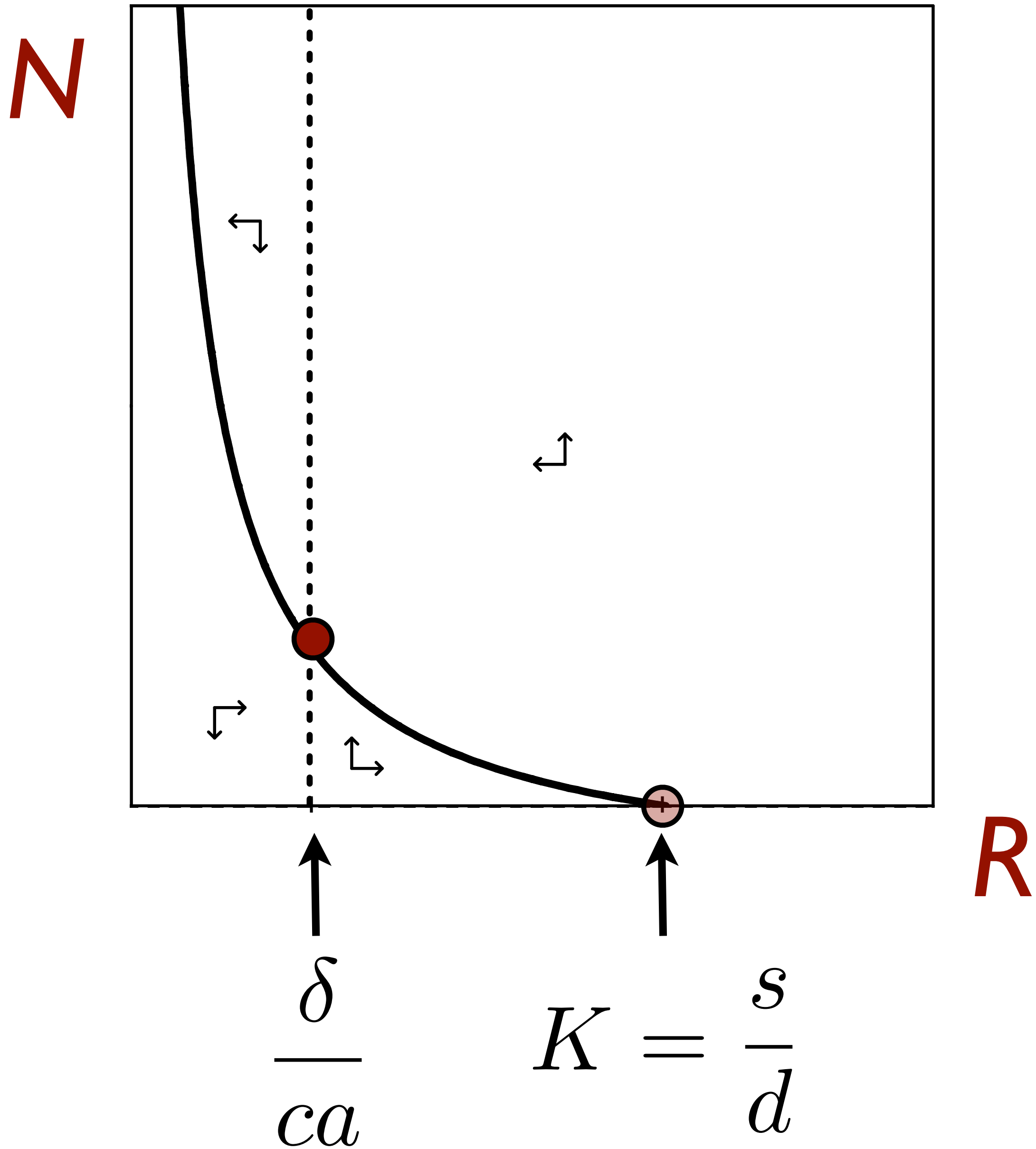
For example the SARS epidemic



$$\frac{\mathrm{d}S}{\mathrm{d}t} = rS(1 - S/K) - \beta SI \quad \text{and} \quad \frac{\mathrm{d}I}{\mathrm{d}t} = \beta SI - \delta I$$

with $R_0 = 3$, and $\beta = 1.5$ and $\delta = 0.5$ per week

Alternative: prey maintained by source



$$\frac{\mathrm{d}R}{\mathrm{d}t} = s - dN - aRN$$

predator remains:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

Several Lotka Volterra like models

Lotka-Volterra model (with birth and death rates):

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

Lotka-Volterra model (with logistic growth):

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

Resource maintained by a source:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = s - dR - aNR \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = [caR - \delta]N$$

Lotka-Volterra competition equations:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1(1 - N_1/K_1 - N_2/c_1) \quad \text{and} \quad \frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2(1 - N_2/K_2 - N_1/c_2)$$

History from Wikipedia

The Lotka–Volterra predator–prey model was proposed by Alfred J. Lotka “in the theory of autocatalytic chemical reactions” in 1910. This was effectively the logistic equation, originally derived by Pierre François Verhulst.

In 1920 Lotka extended the model to "organic systems" using a plant species and a herbivorous animal species as an example, and in 1925 he utilised it to analyse predator-prey interactions in his book on biomathematics arriving at the equations that we know today.

Vito Volterra, who made a statistical analysis of fish catches in the Adriatic independently investigated the equations in 1926.