Introduction to compartmental models

C. Jessica E. Metcalf
cmetcalf@princeton.edu

Population growth

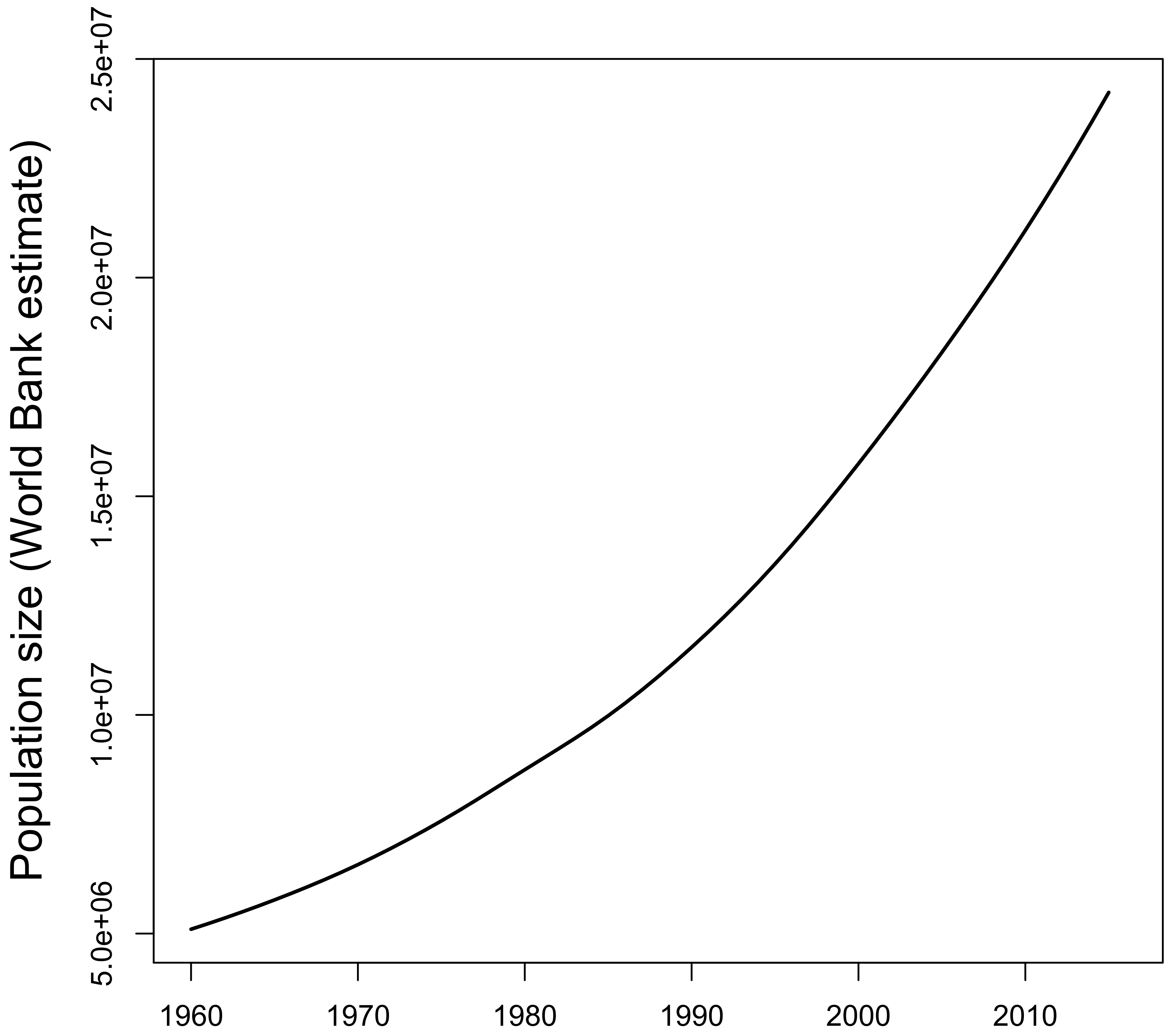
HEARTBEAT

ONE BIRTH

ONE DEATH

http://xkcd.com/1331/

Madagascar



http://databank.worldbank.org

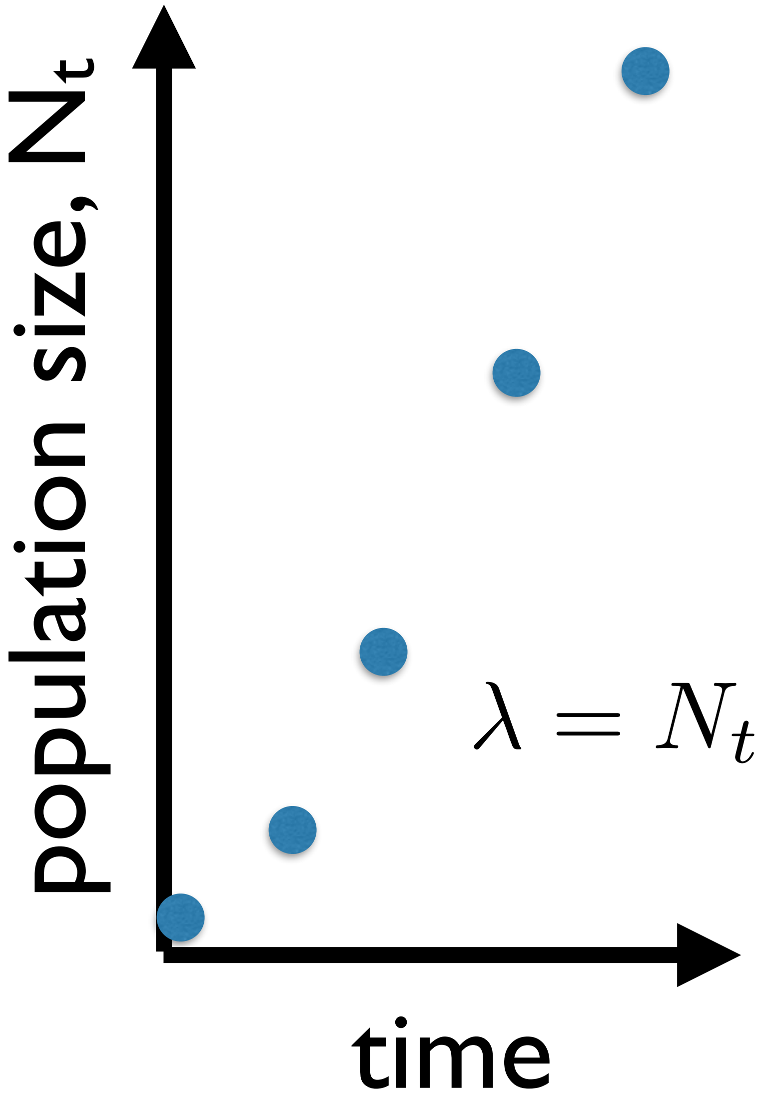
$$\lambda = N_{t+1}/N_t$$

Population rate of increase

pop size at t

pop size at t+1

Discrete time



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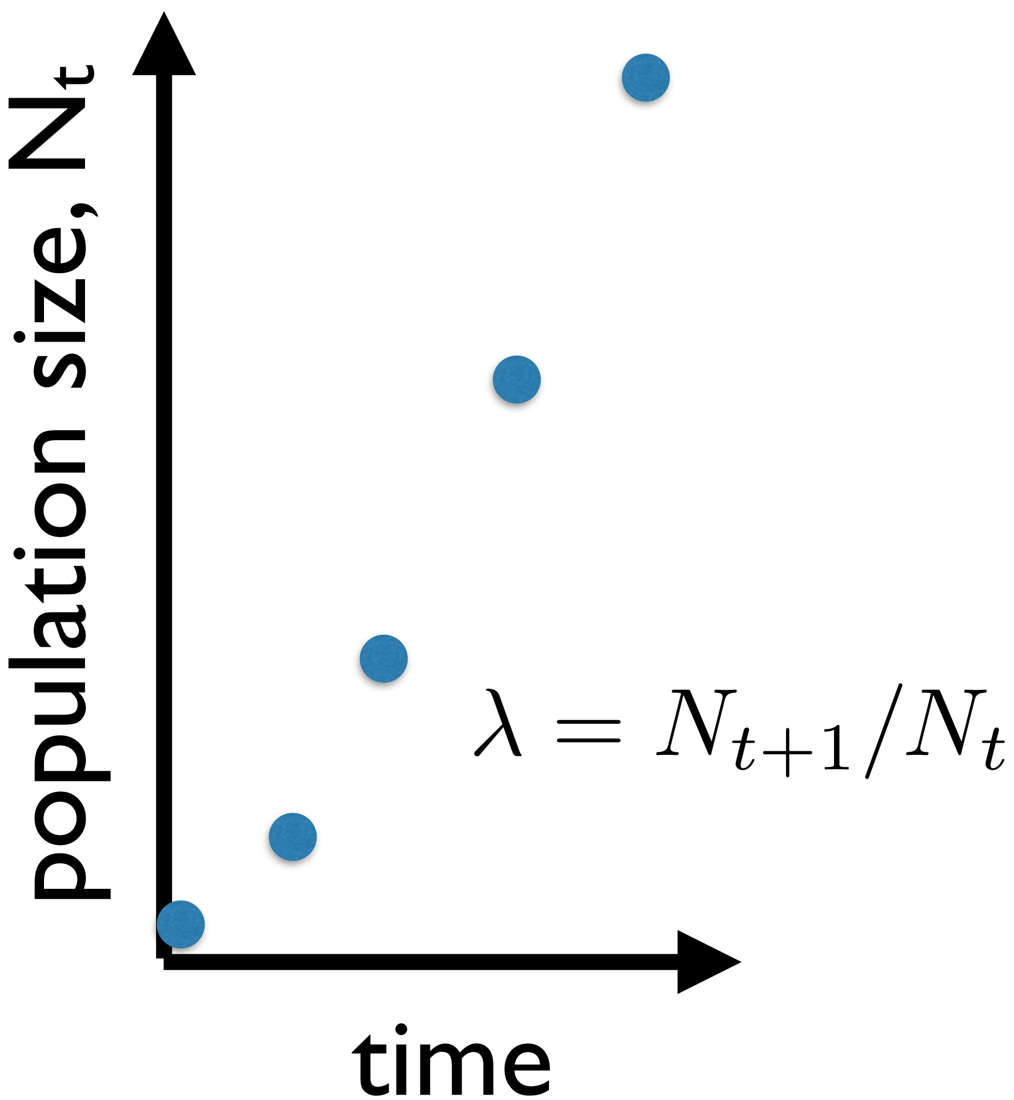
Discrete time



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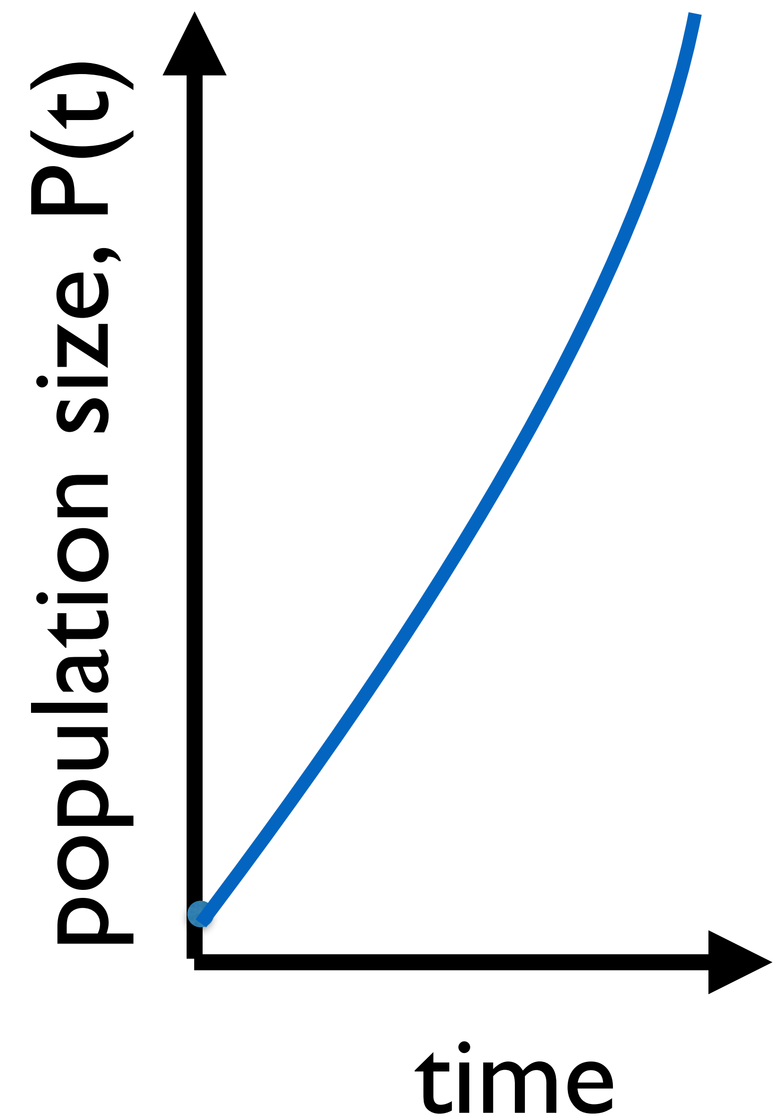
Continuous time

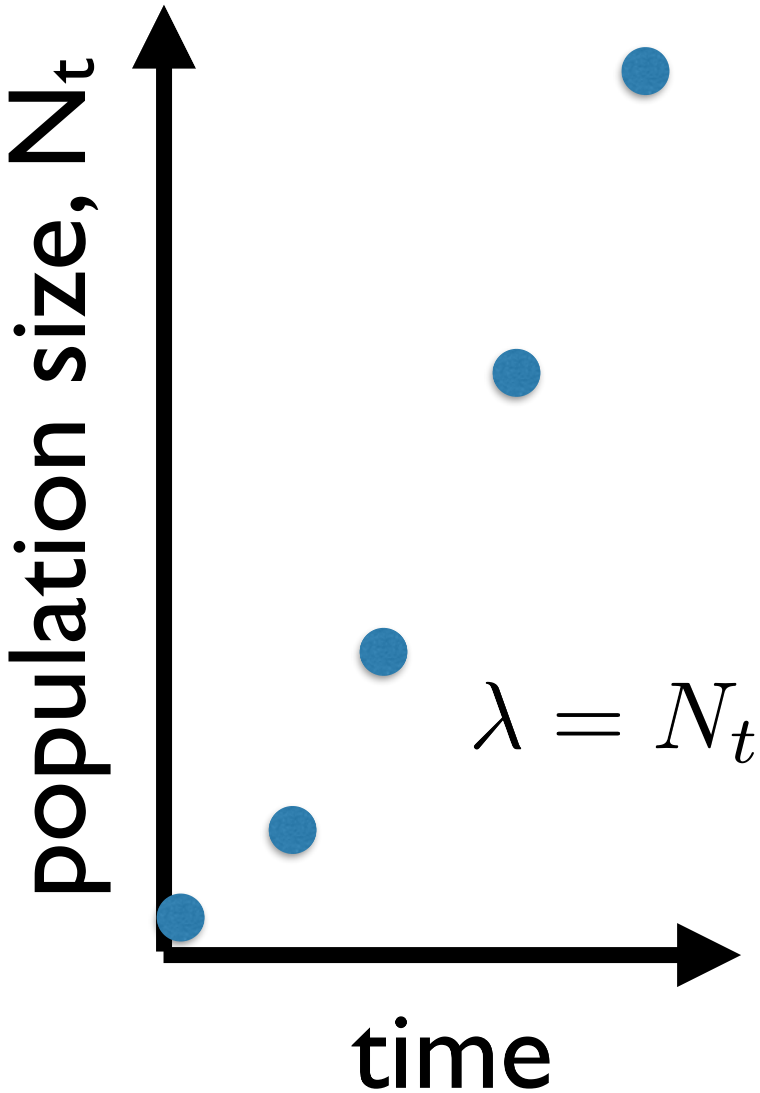


$dP/dt = rP$

!as $t \rightarrow 0$

$r = [P(t) - P(0)]/t$

Discrete time



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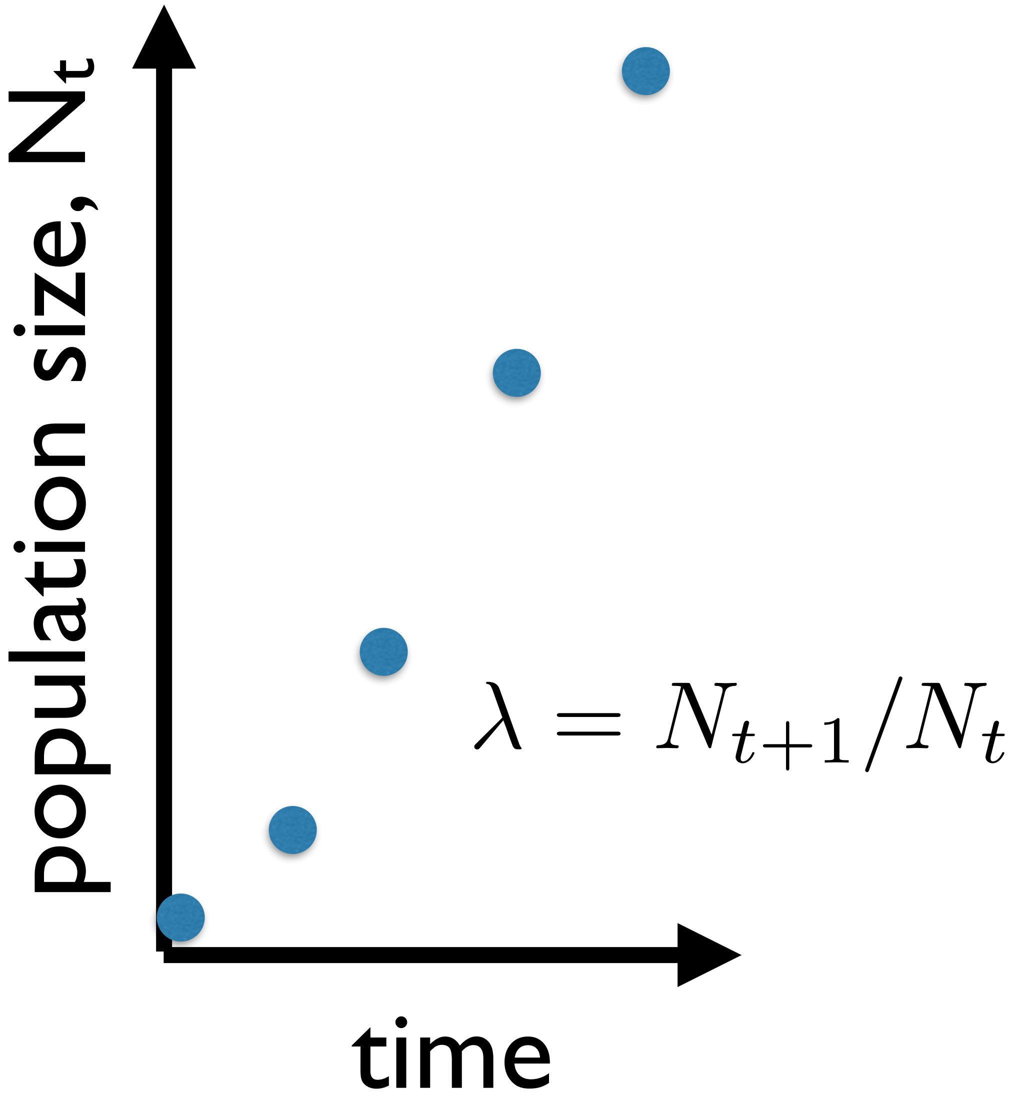
Continuous time

$dP(t)/dt = rP(t)$

Discrete time



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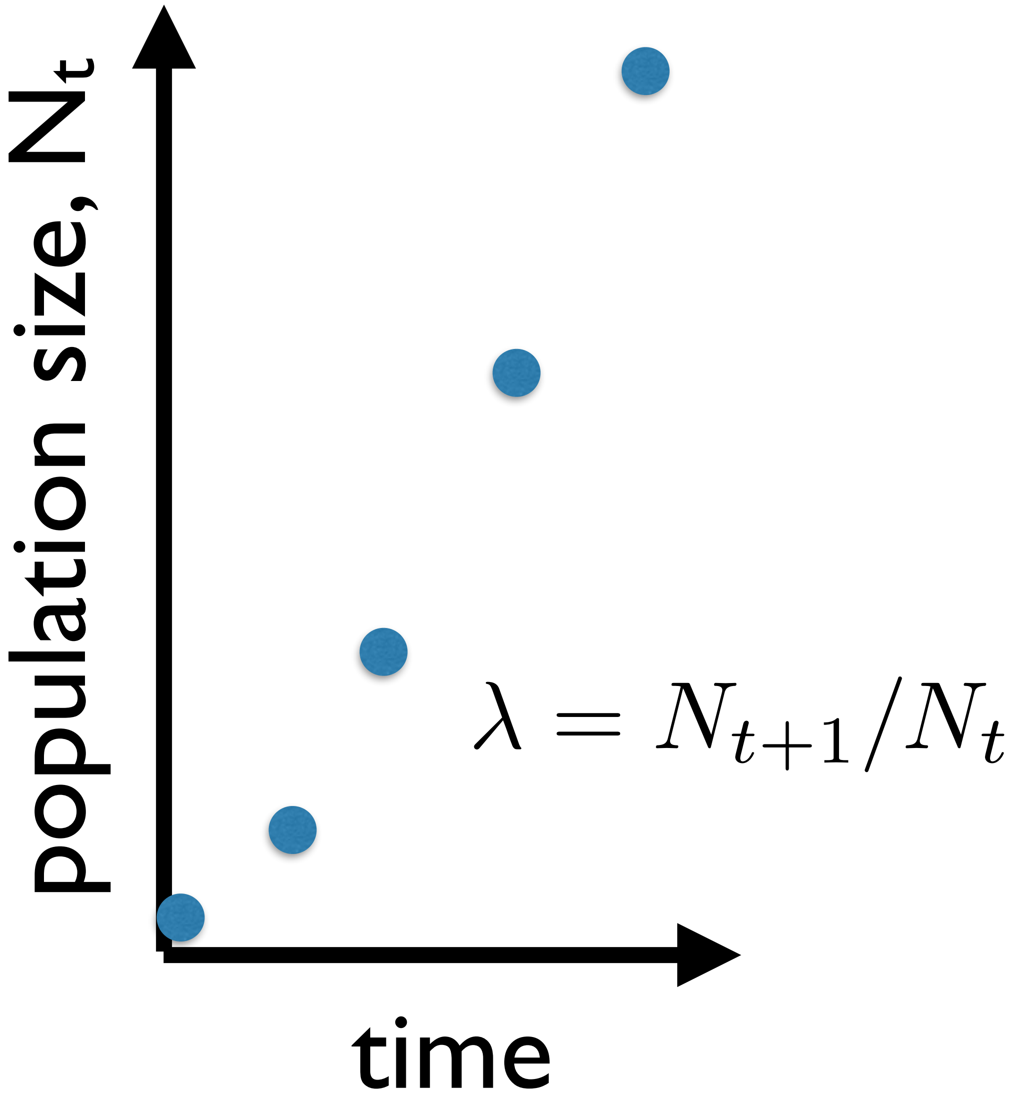
Continuous time

$dP(t)/dt = rP(t)$

Separation of variables:

$dP(t)/P(t) = r\, dt$

Discrete time



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Continuous time

$dP(t)/dt = rP(t)$

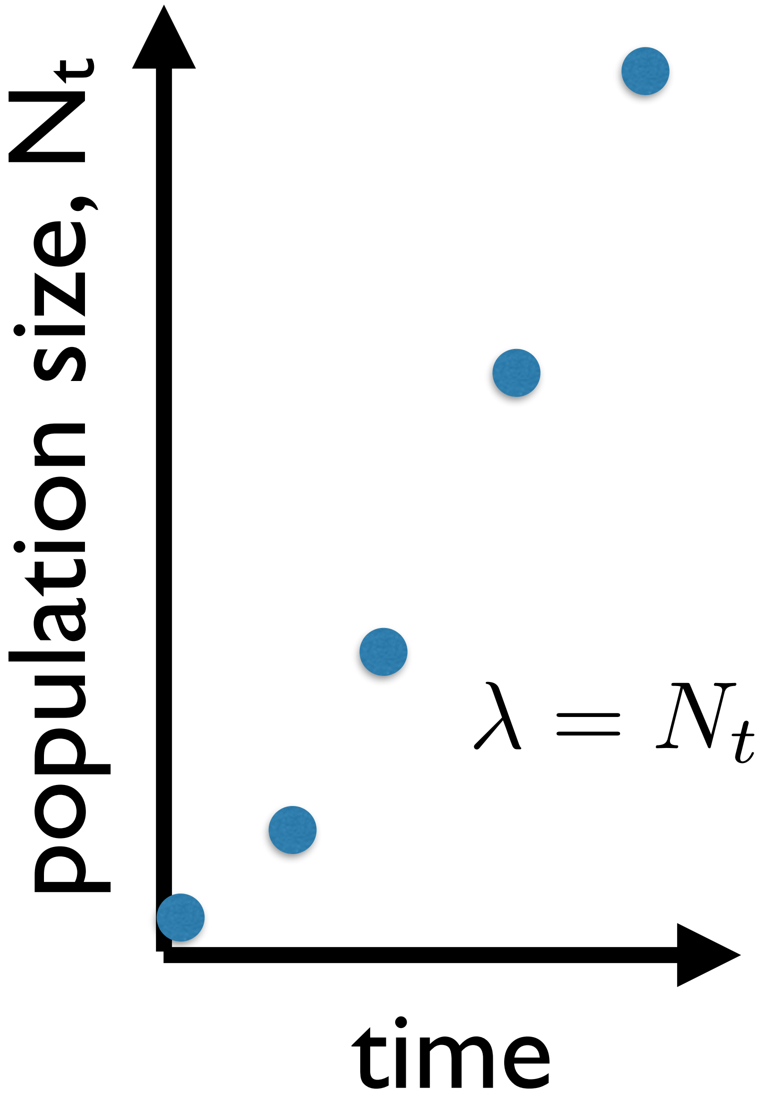
Separation of variables:

$dP(t)/P(t) = r\,dt$

Integrate both sides:

$\int dP(t)/P(t) = \int r\,dt$

Discrete time



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Continuous time

$dP(t)/dt = rP(t)$

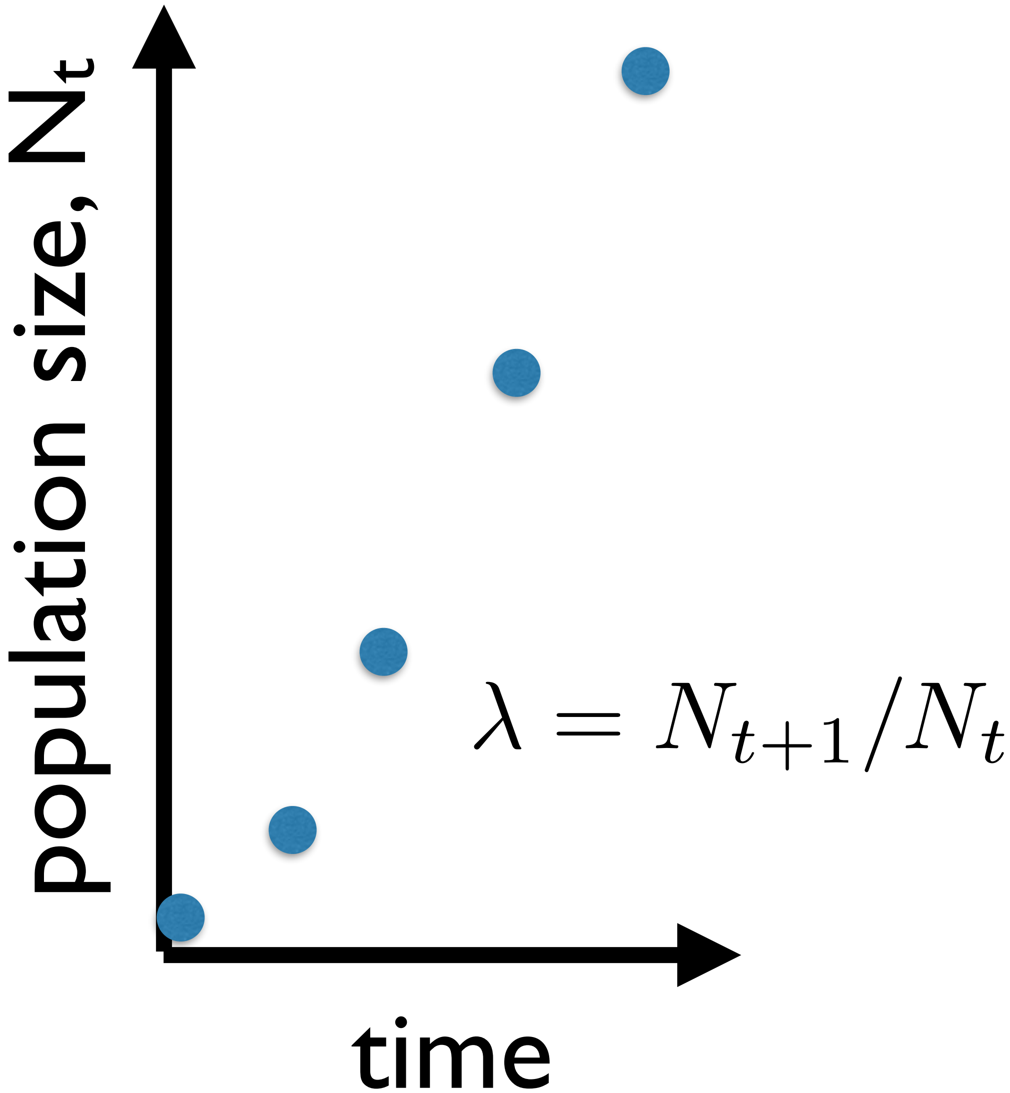
Separation of variables:
$dP(t)/P(t) = r\, dt$

Integrate both sides:
$\int dP(t)/P(t) = \int r\, dt$

By definition:
$\log(P(t)) = rt + c$

Take exponentials:
$P(t) = e^{rt + c} = Ce^{rt}$
$P(t) = P(0)e^{rt}$

Discrete time



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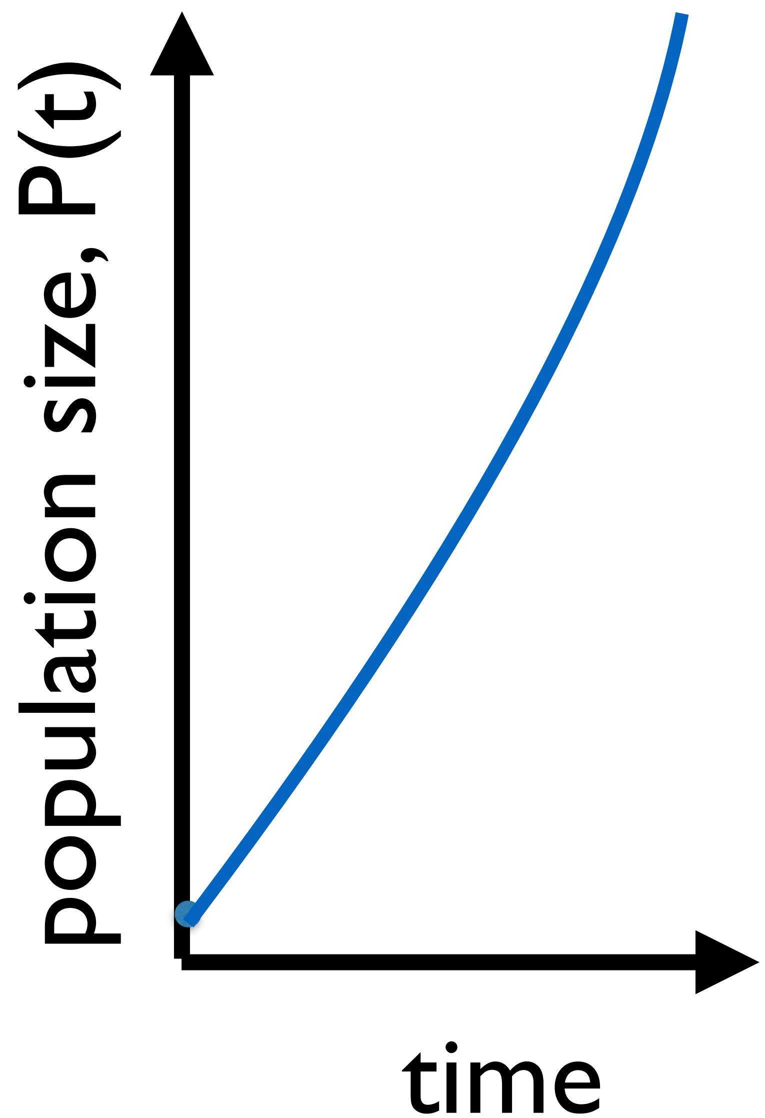
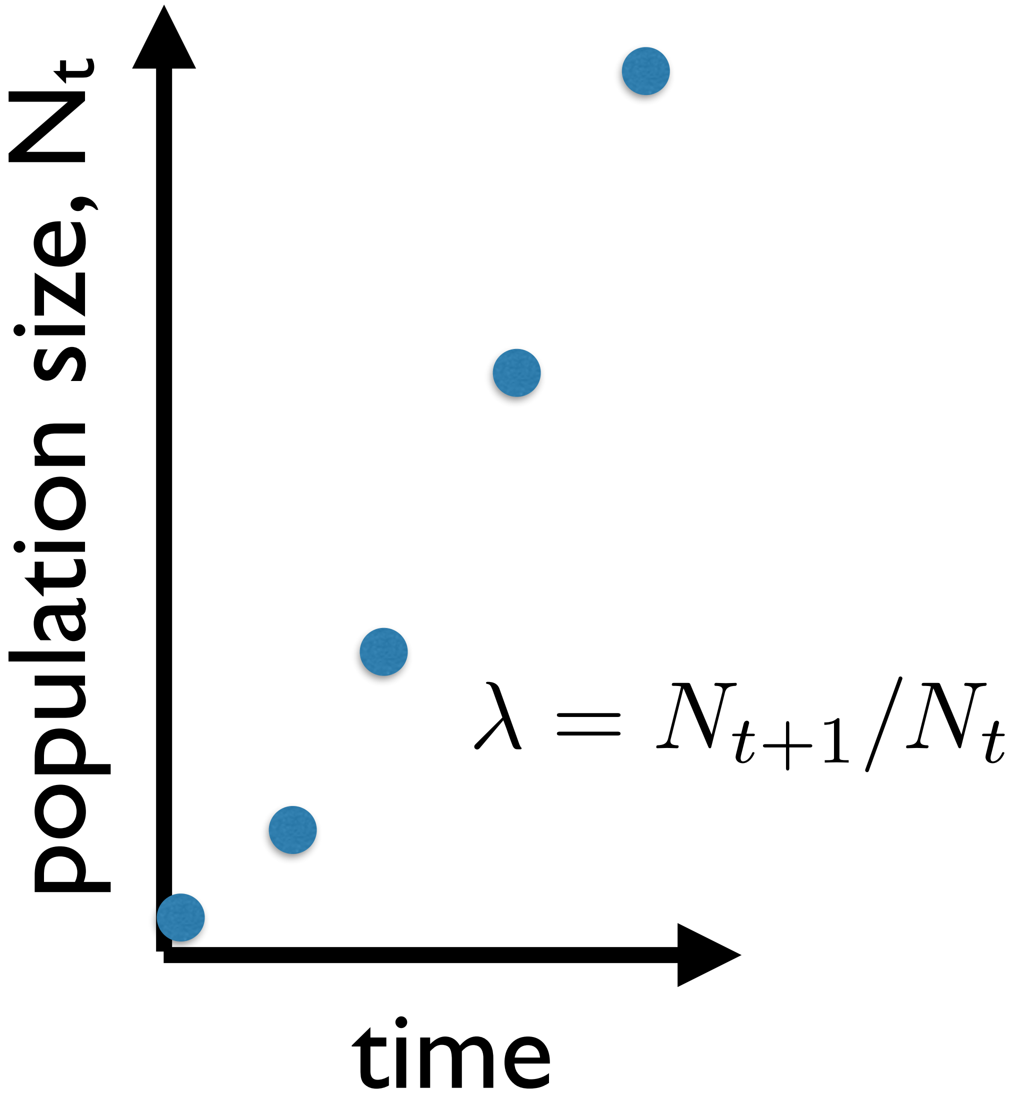


$dP/dt = rP$

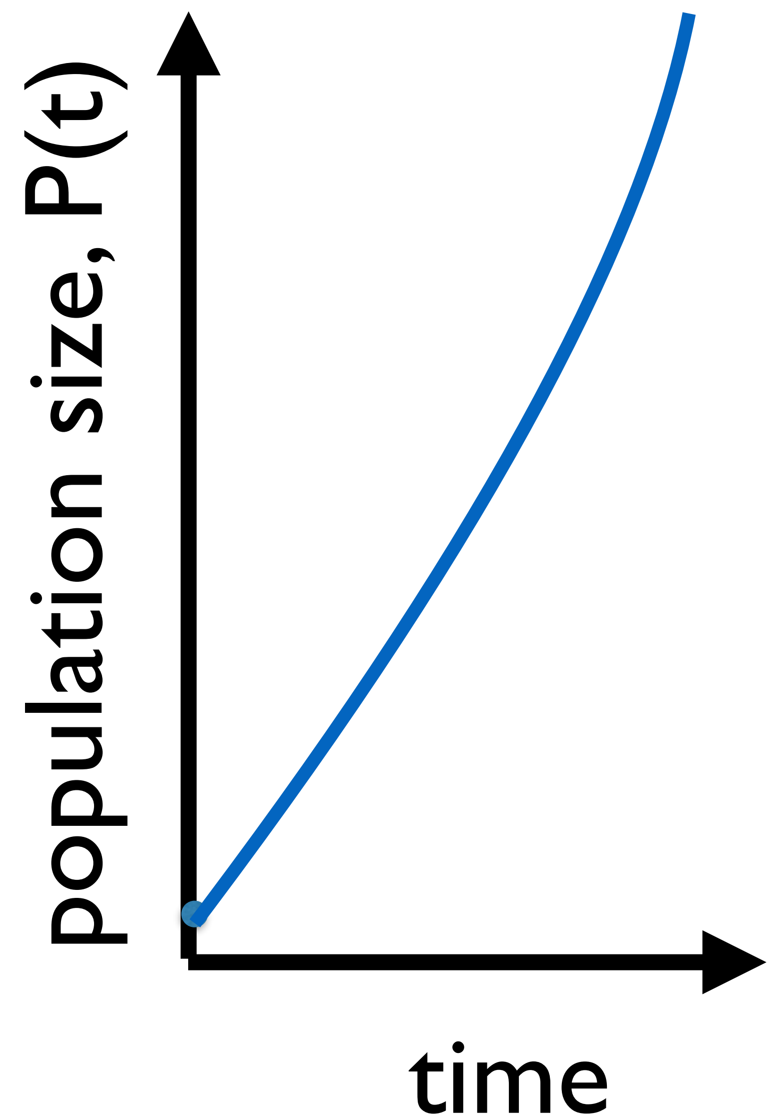
$r = [P(t) - P(0)]/t$!as $t \to 0$

$P(t) = P(0)e^{rt}$

Discrete time



Continuous time



Continuous models can be discretized; discrete models can be approximated by continuous ones. The appropriate framing may depend on the data / question.

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Population rate of increase

pop size at t

pop size at t+1

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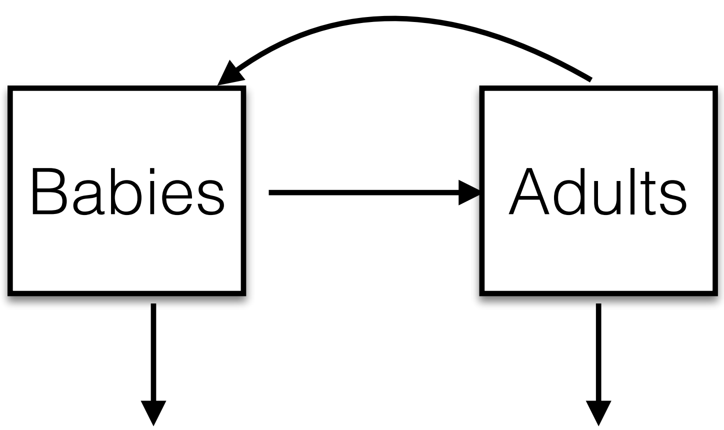

Structured population model

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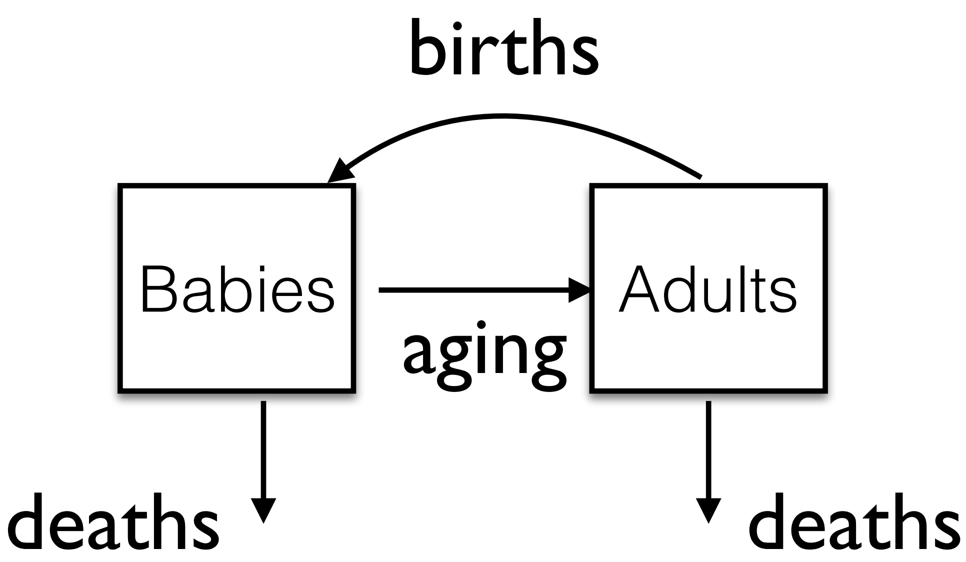
pop size at t+1



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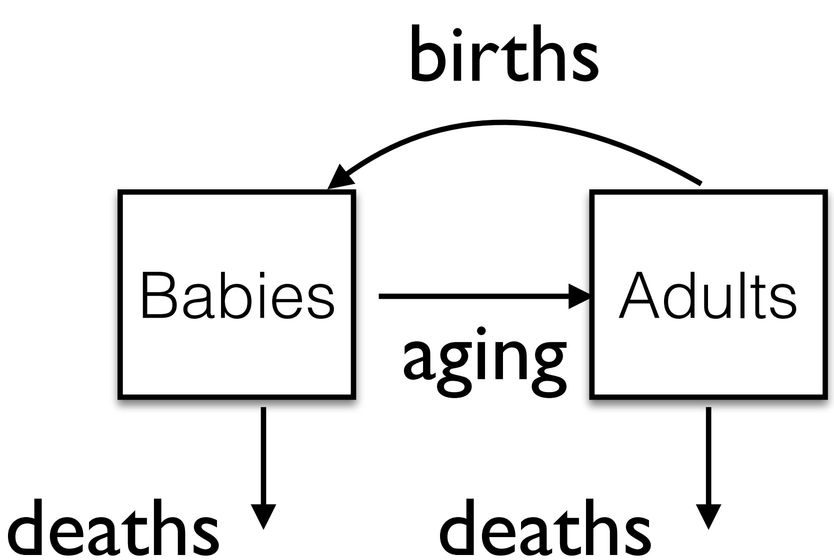


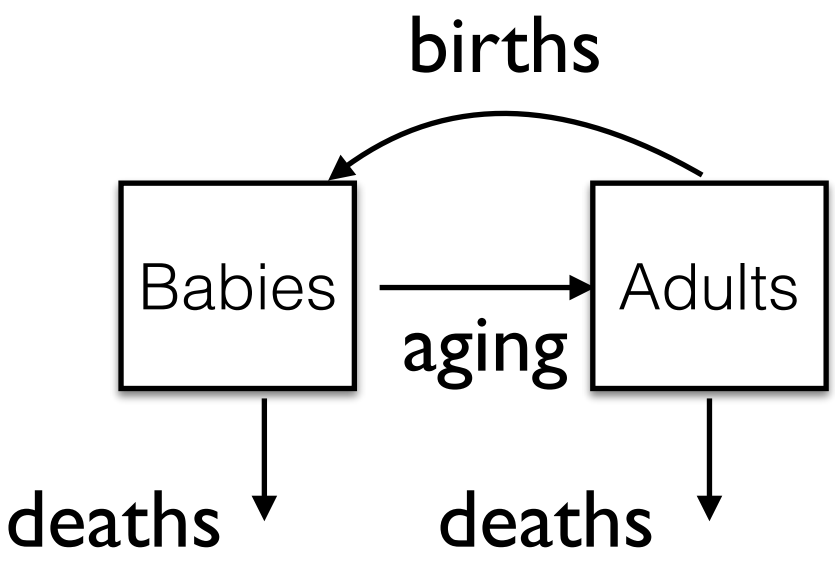
Structured population model

$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

vector of population sizes

$$\mathbf{A} = \begin{bmatrix} s_b(1-a) & b \\ s_b & s_a \end{bmatrix}$$

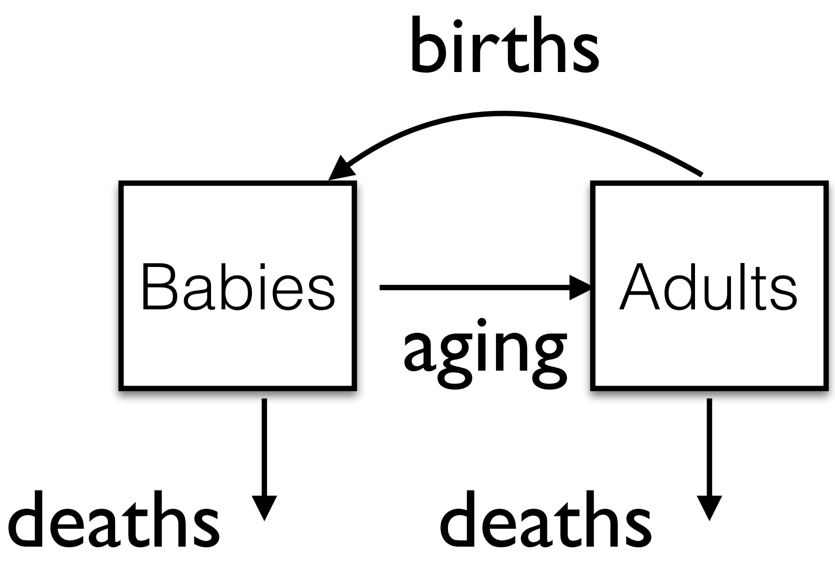
*discrete time



Structured population model

$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

$$\underset{\mathbf{A}}{\begin{bmatrix} s_b(1-a) & b \\ s_b a & s_a \end{bmatrix}} \times \underset{\mathbf{n_t}}{\begin{bmatrix} n_b \\ n_a \end{bmatrix}} = \underset{\mathbf{n_{t+1}}}{\begin{bmatrix} s_b(1-a)n_b + bn_a \\ s_b\, a\, n_b + s_a\, n_a \end{bmatrix}}$$



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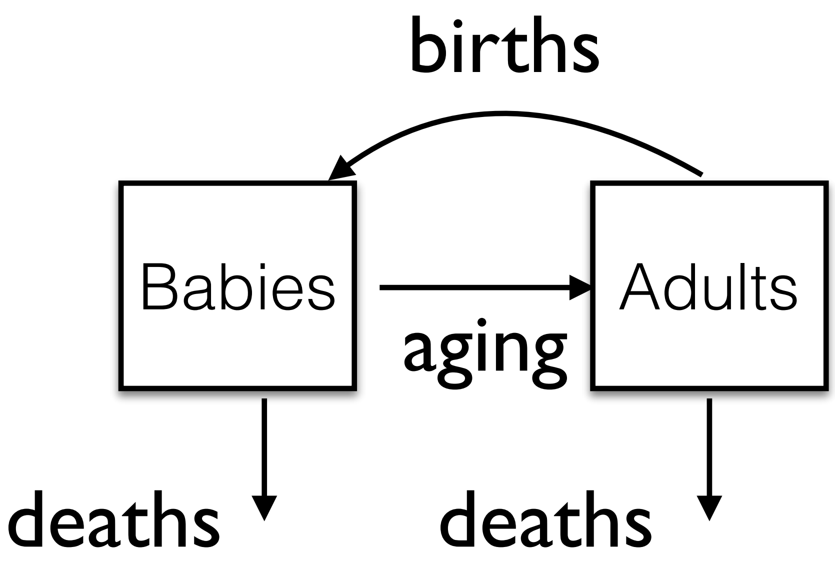
$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

$$\underbrace{\begin{bmatrix} s_b(1-a) & b \\ s_b a & s_a \end{bmatrix}}_{\mathbf{A}} \times \underbrace{\begin{bmatrix} n_b \\ n_a \end{bmatrix}}_{\mathbf{n_t}} = \underbrace{\begin{bmatrix} s_b(1-a)n_b + b n_a \\ s_b\, a\, n_b + s_a\, n_a \end{bmatrix}}_{\mathbf{n_{t+1}}}$$

Population growth will depend on population structure



Structured population model

$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

Dominant eigenvalue provides growth rate at equilibrium

$$\underset{\mathbf{A}}{\begin{bmatrix} s_b(1-a) & b \\ s_b a & s_a \end{bmatrix}} \times \underset{\mathbf{n_t}}{\begin{bmatrix} n_b \\ n_a \end{bmatrix}} = \underset{\mathbf{n_{t+1}}}{\begin{bmatrix} s_b(1-a)n_b + b n_a \\ s_b\, a\, n_b + s_a\, n_a \end{bmatrix}}$$

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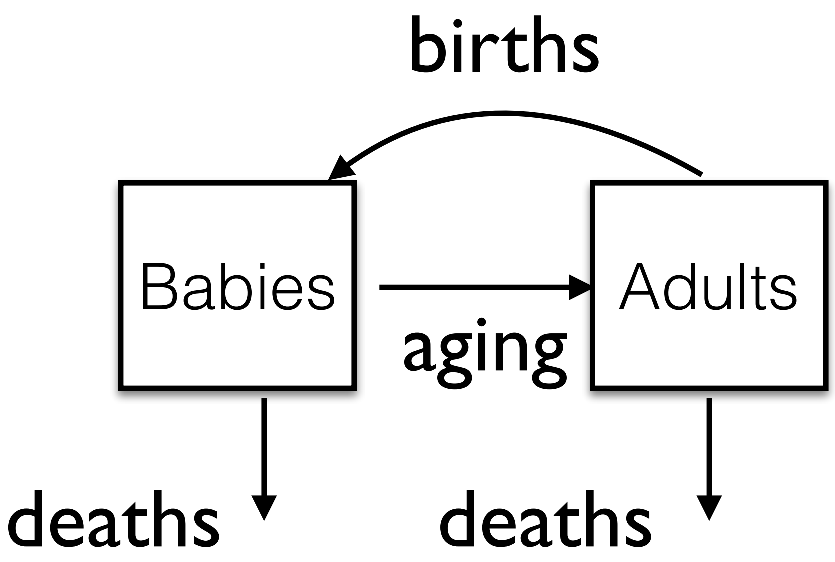

Structured population model

$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

Conservation and Management of a Threatened Madagascar Palm Species, *Neodypsis decaryi*, Jumelle

JOELISOA RATSIRARSON,*‡ JOHN A. SILANDER, JR.,* AND ALISON F. RICHARD†

*Department of Ecology and Evolutionary Biology, 75 N. Eagleville Road, The University of Connecticut, Storrs, CT 06269, U.S.A.

†Yale School of Forestry and Environmental Studies, 205 Prospect Street, New Haven, CT 06520, U.S.A.

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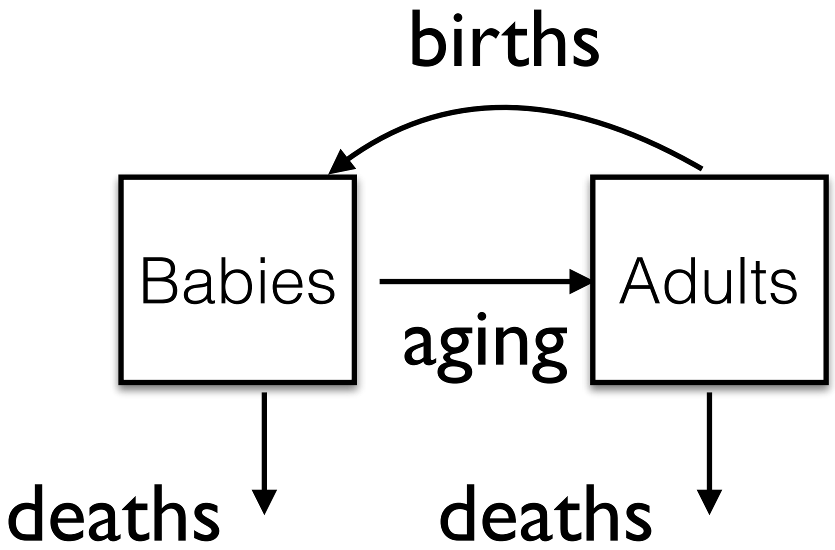
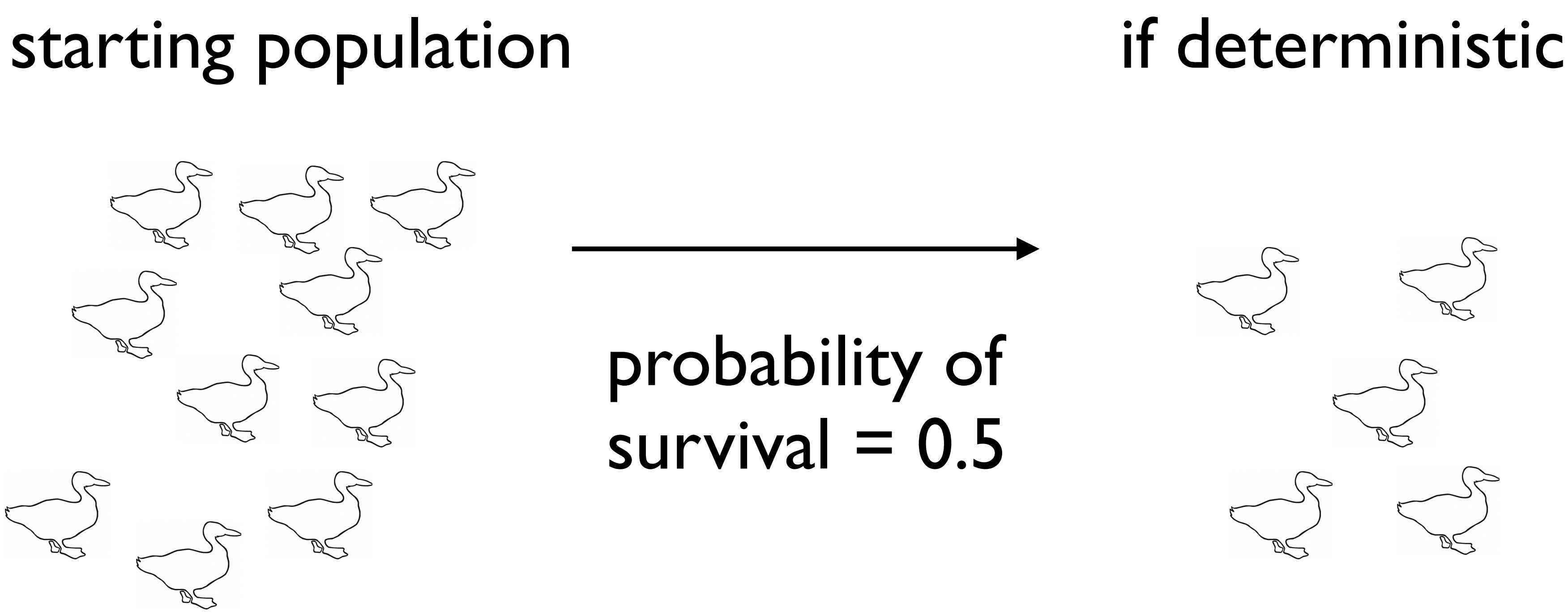


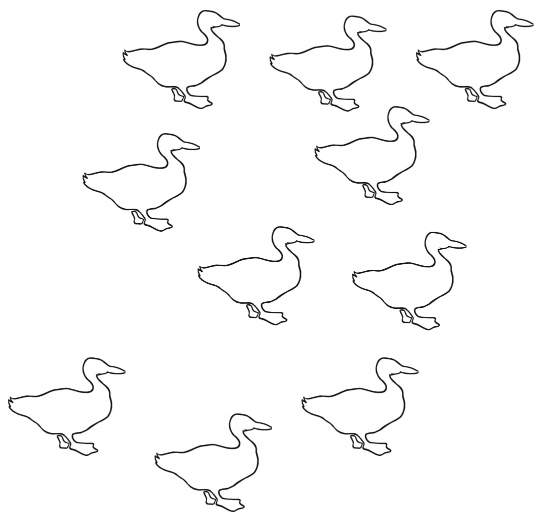
Structured population model

$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

Assumes no role of chance

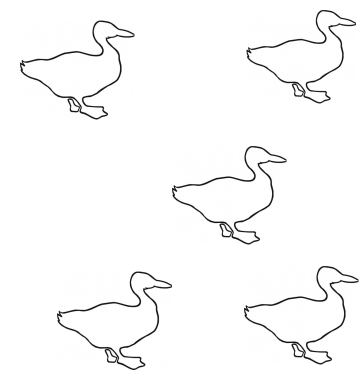


starting population



probability of
survival = 0.5

if deterministic



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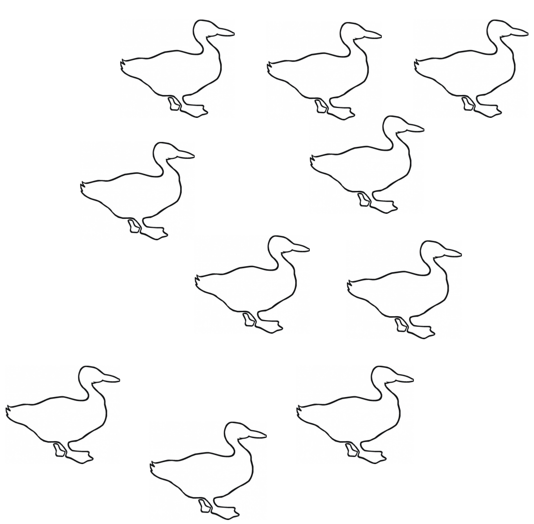
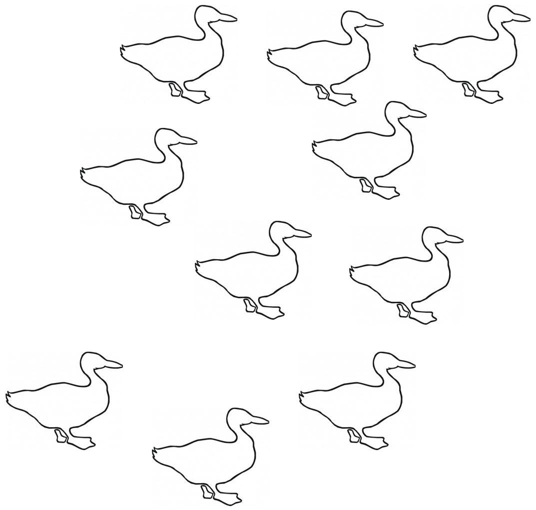


probability of
survival = 0.5

if stochastic?

starting population



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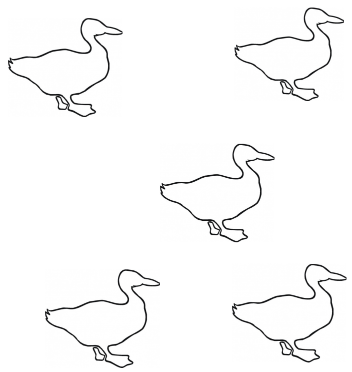

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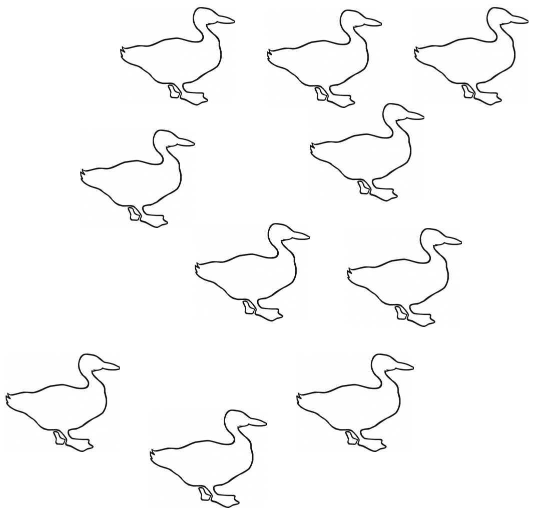

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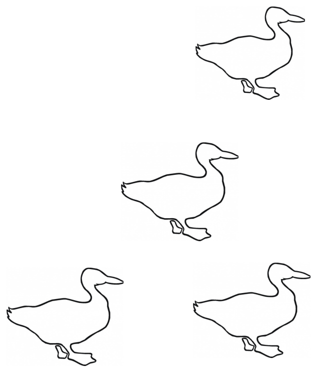
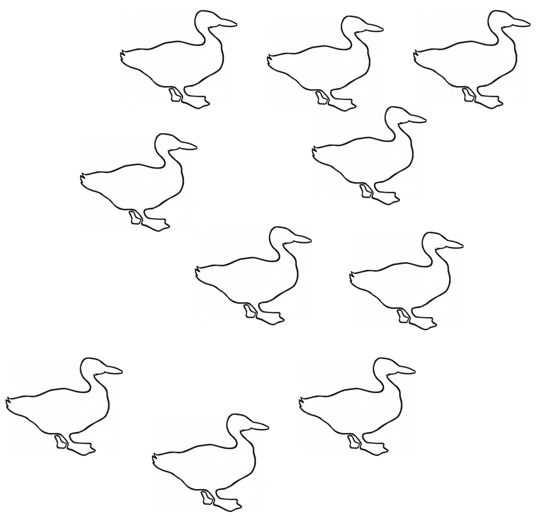


Flip a coin for every duck;

starting population



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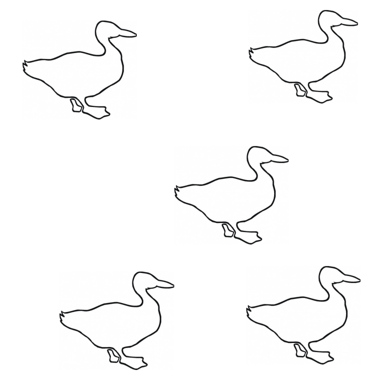
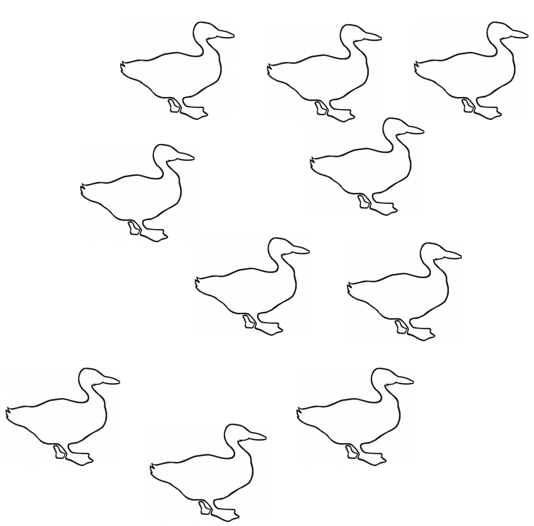


starting population



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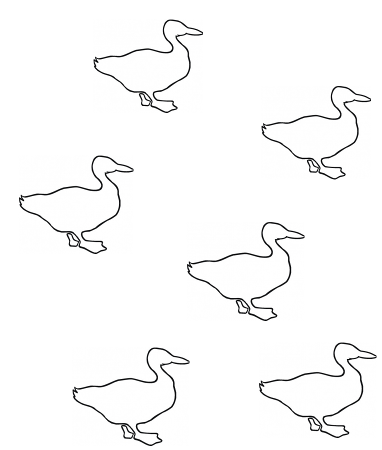

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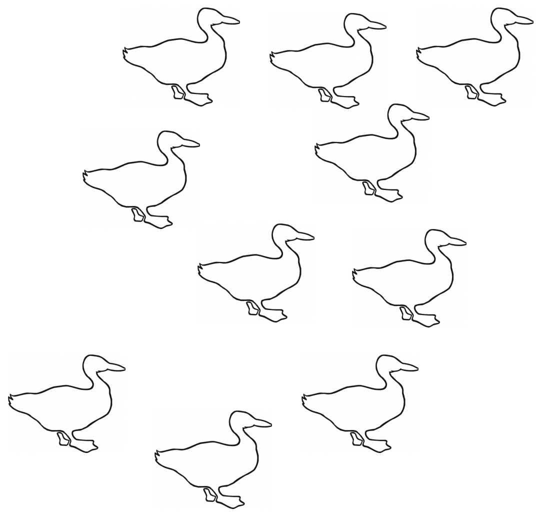

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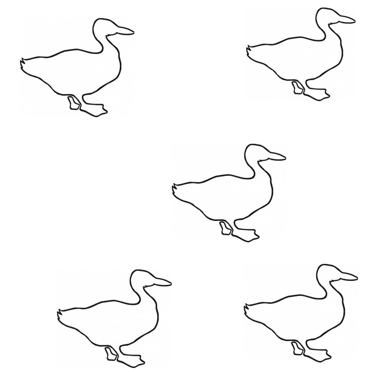

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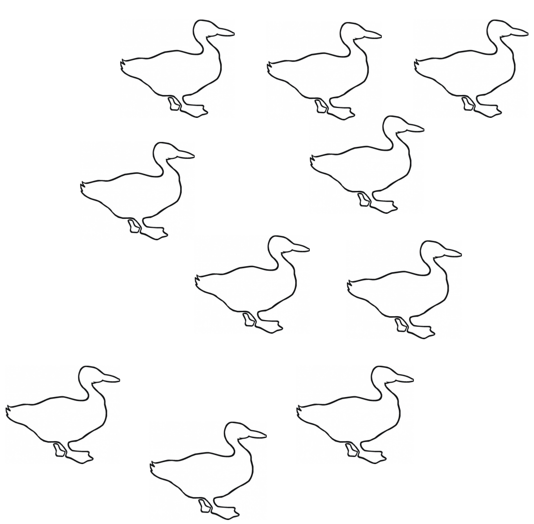

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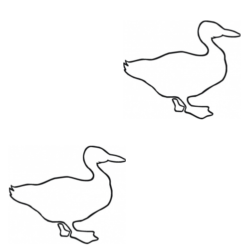

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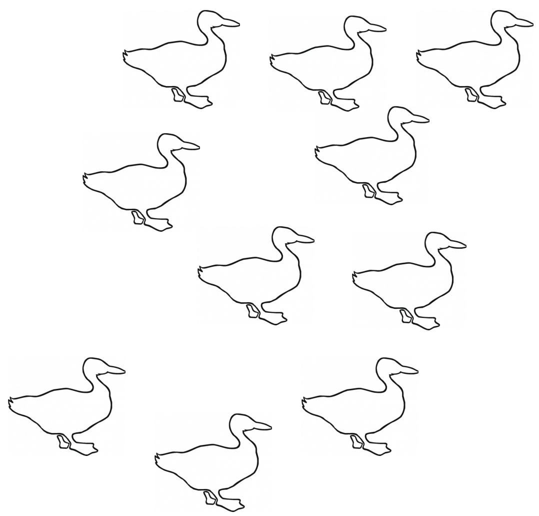

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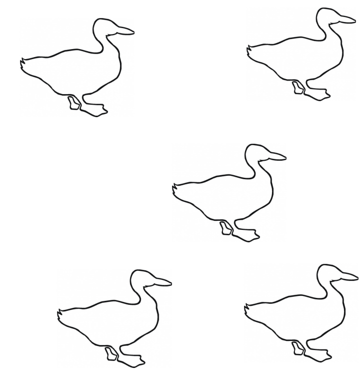

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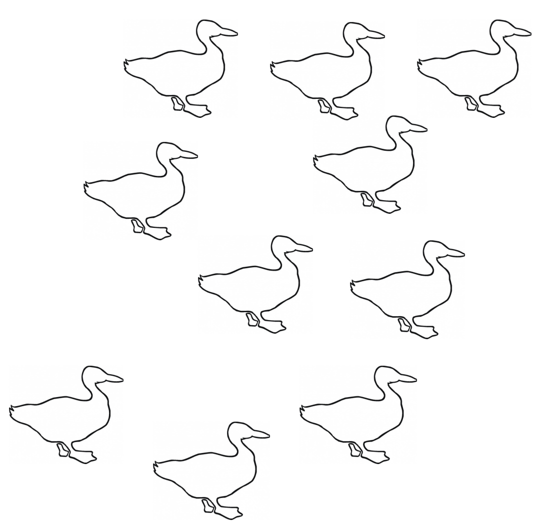

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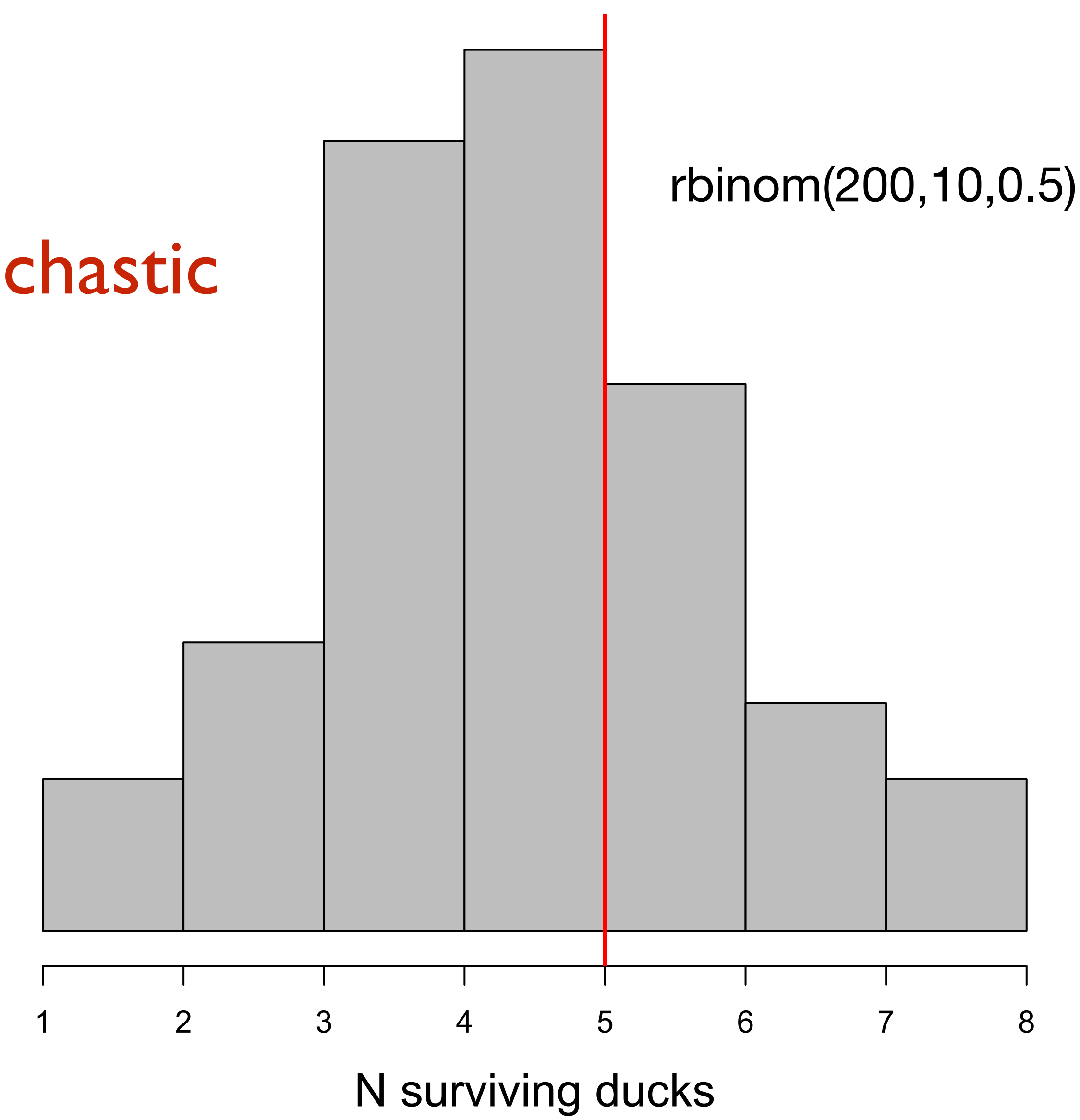

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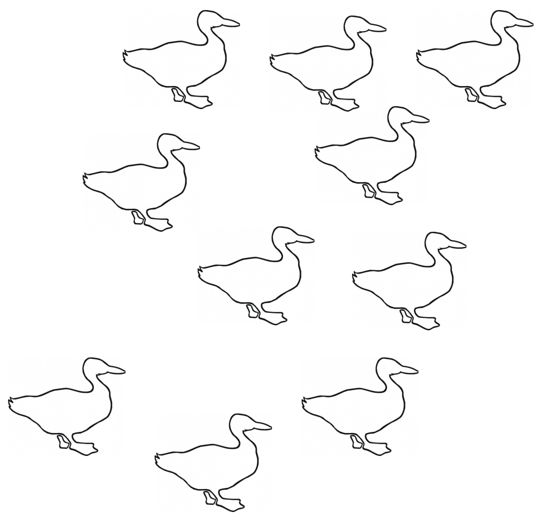

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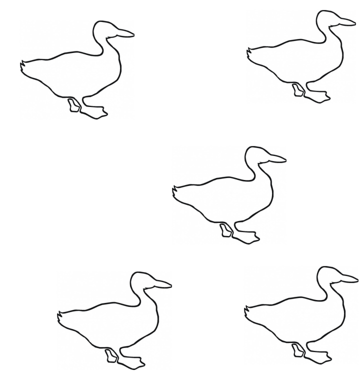
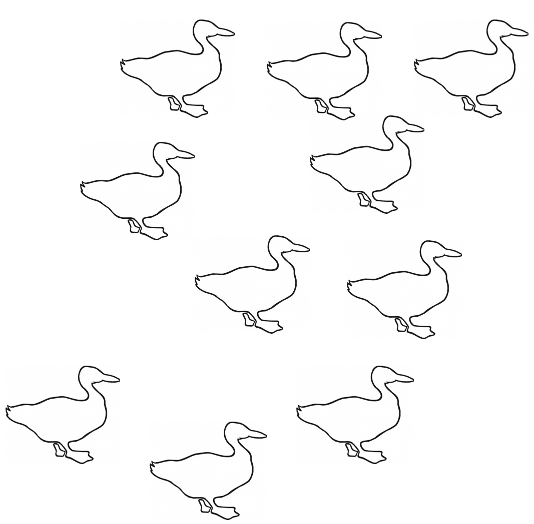


If you test your 10 ducks
many times, on average
you get 5

starting population



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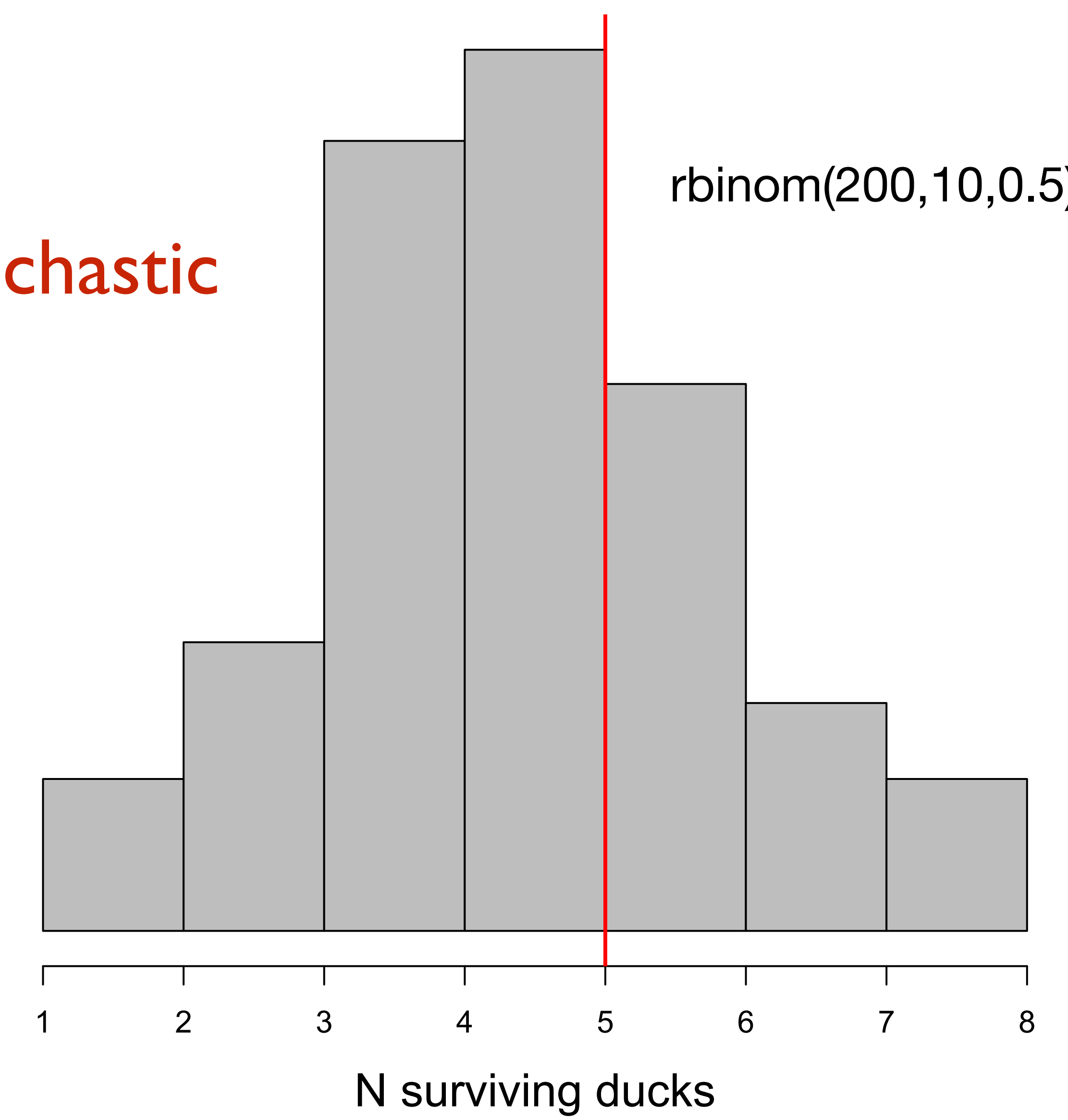

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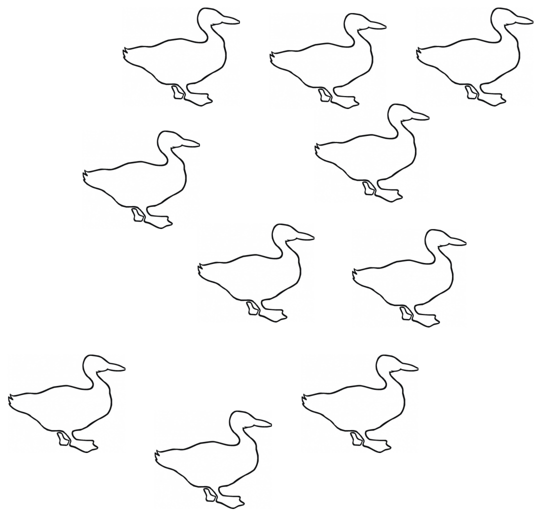

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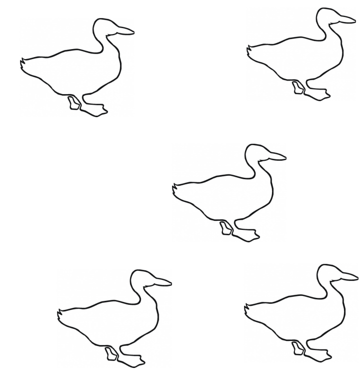

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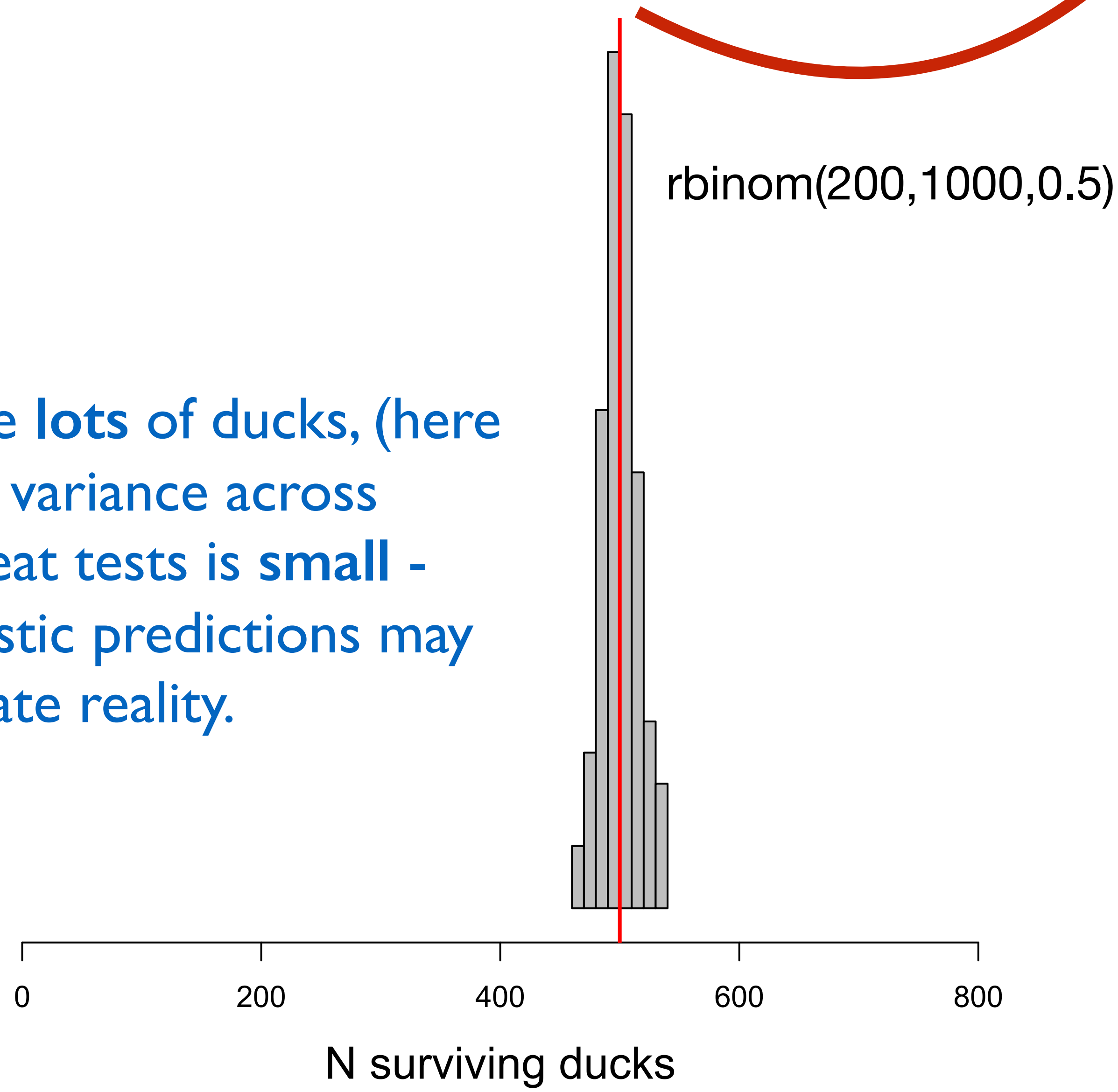
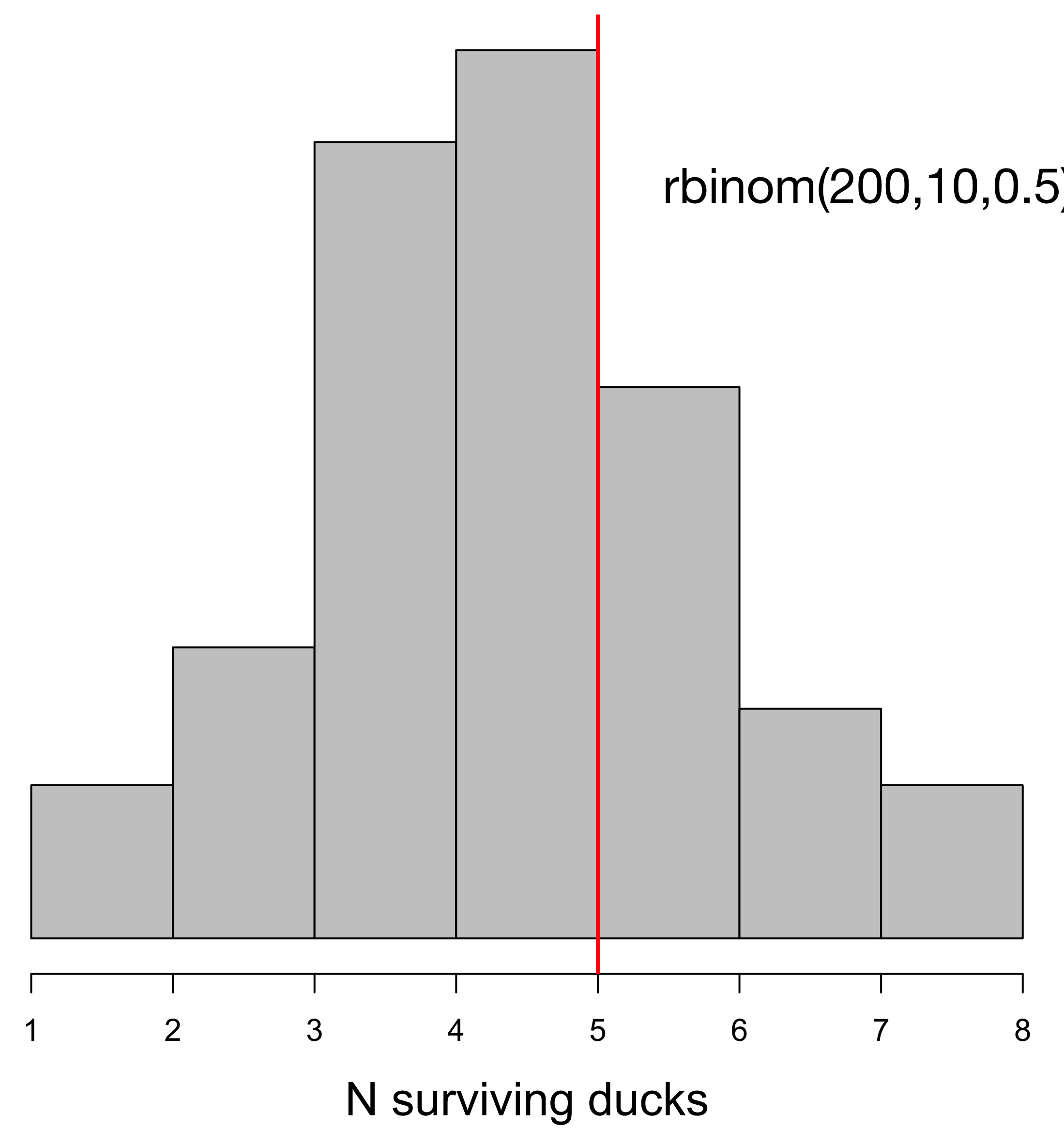




If you have **lots** of ducks, (here 1000) the variance across many repeat tests is **small** - deterministic predictions may approximate reality.

Stochasticity matters for ***statistical design***, and ***projecting future population growth***….

It has been suggested that it might also have been a key element in the ***evolution of the unique fauna and flora of Madagascar.***

PNAS

Evolution in the hypervariable environment of Madagascar

Robert E. Dewar*† and Alison F. Richard‡

*McDonald Institute of Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, England; and ‡
Vice-Chancellor, University of Cambridge, Cambridge CB2 1TN, England

Communicated by Henry T. Wright, University of Michigan, Ann Arbor, MI, June 29, 2007 (received for review August 26, 2005)

We show that the diverse ecoregions of Madagascar share one distinctive climatic feature: unpredictable intra- or interannual precipitation compared with other regions with comparable rain-fall. Climatic unpredictability is associated with unpredictable pat-terns of fruiting and flowering. It is argued that these features

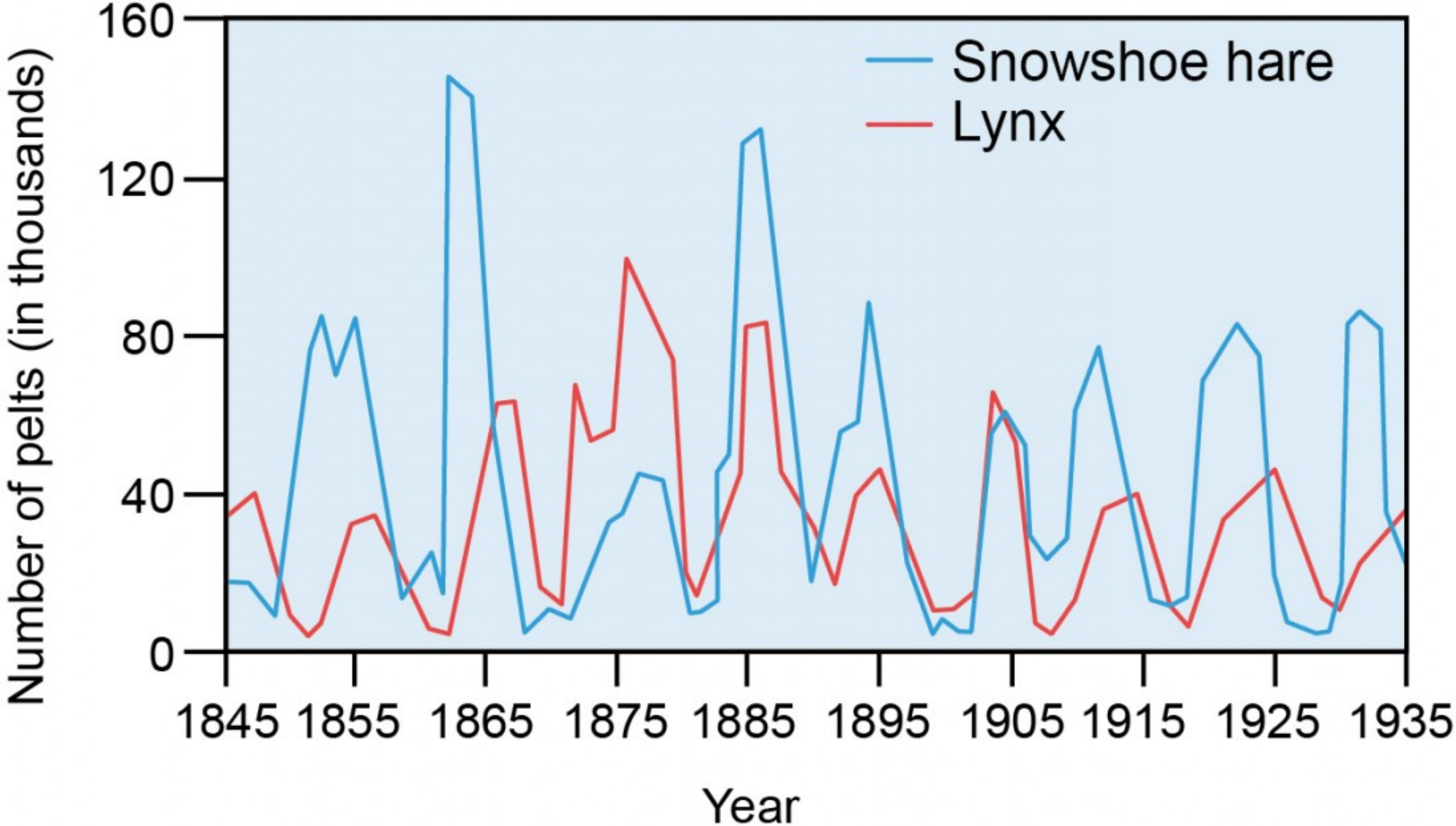
Key concepts

-Continuous vs. discrete models

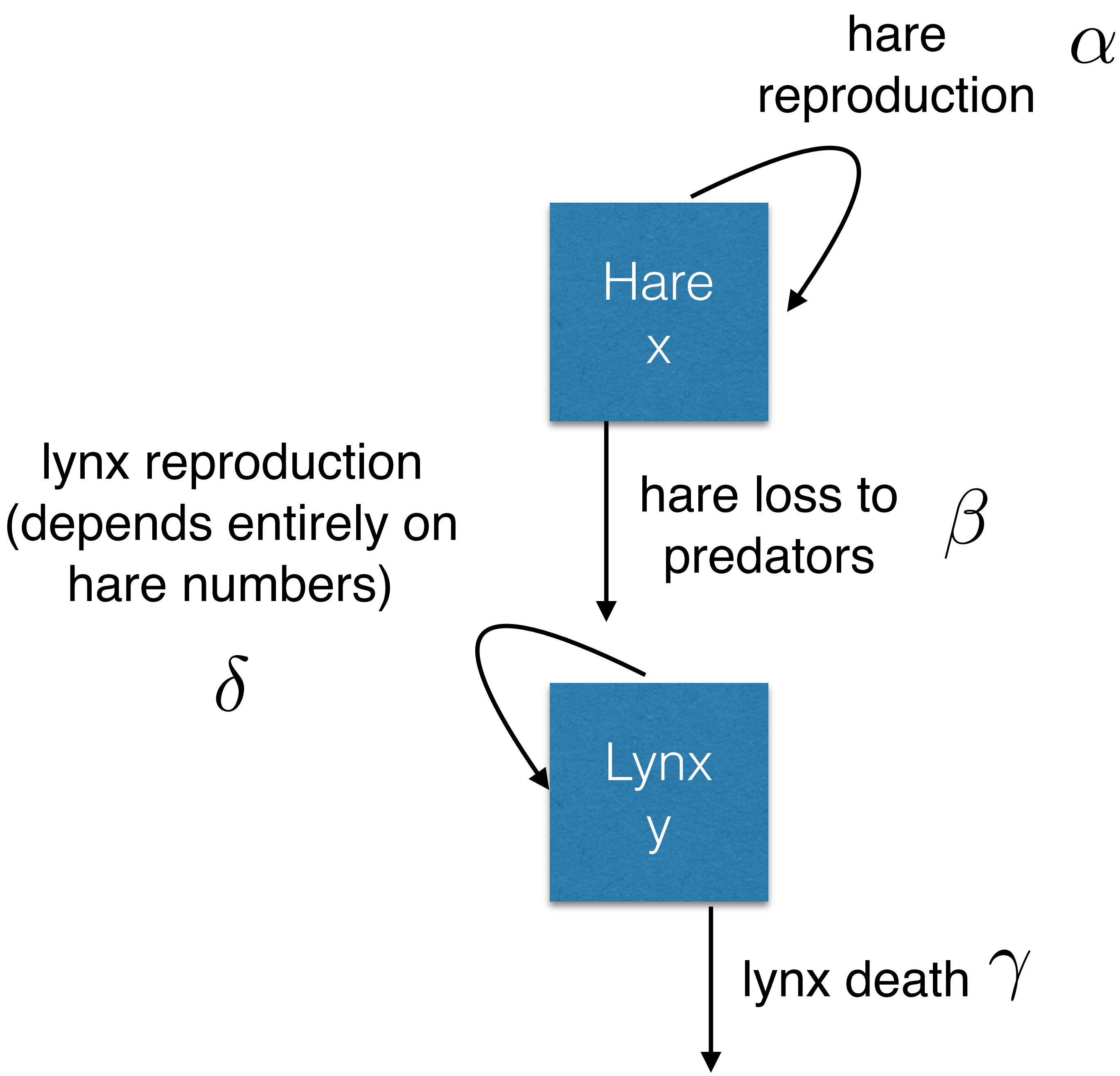
-Deterministic vs. stochastic models

-Structured models


Predator-prey

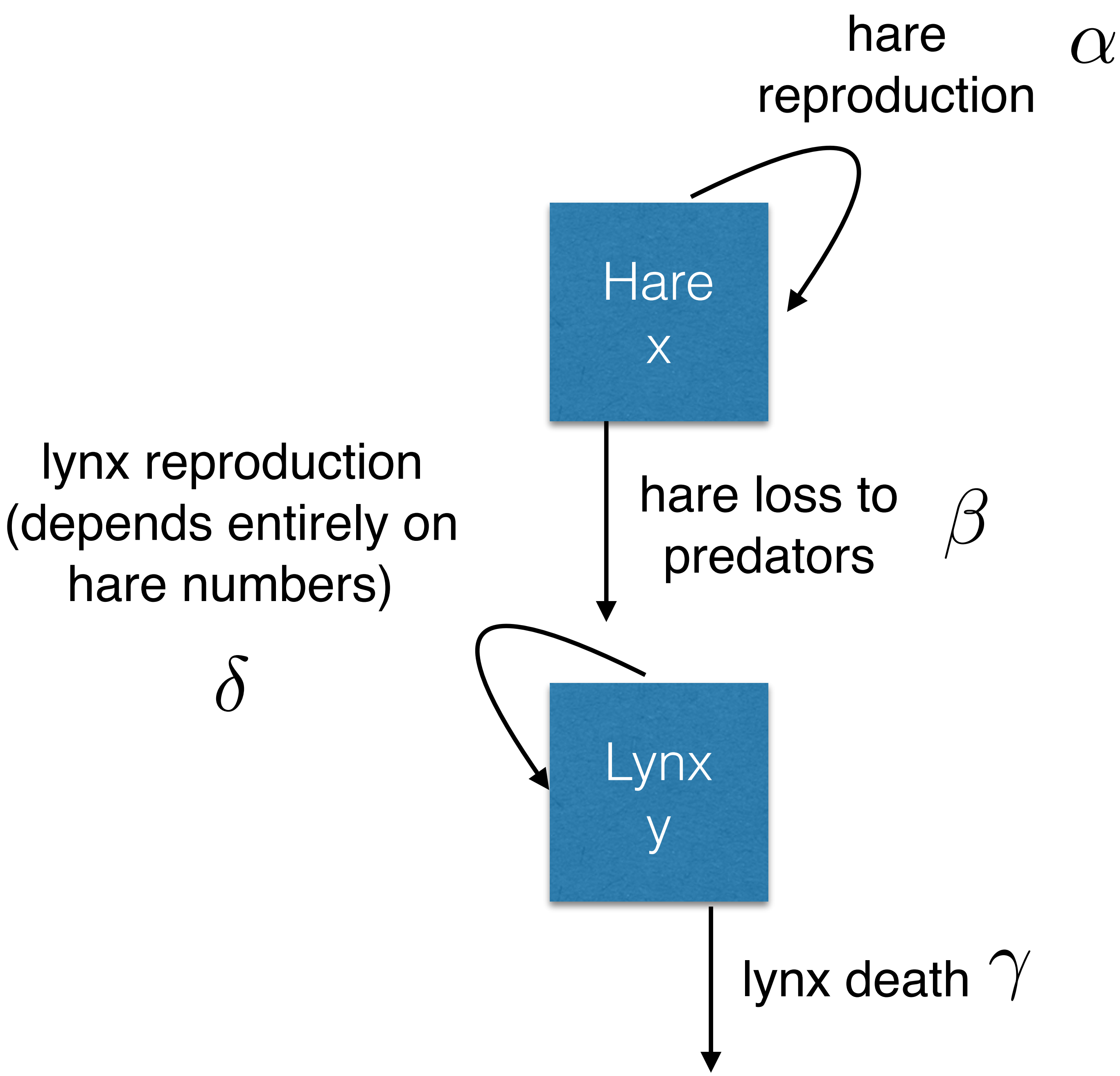


Snowshoe hare
Lynx
Number of pelts (in thousands)
160
120
80
40
0
1845
1855
1865
1875
1885
1895
1905
1915
1925
1935
Year



$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

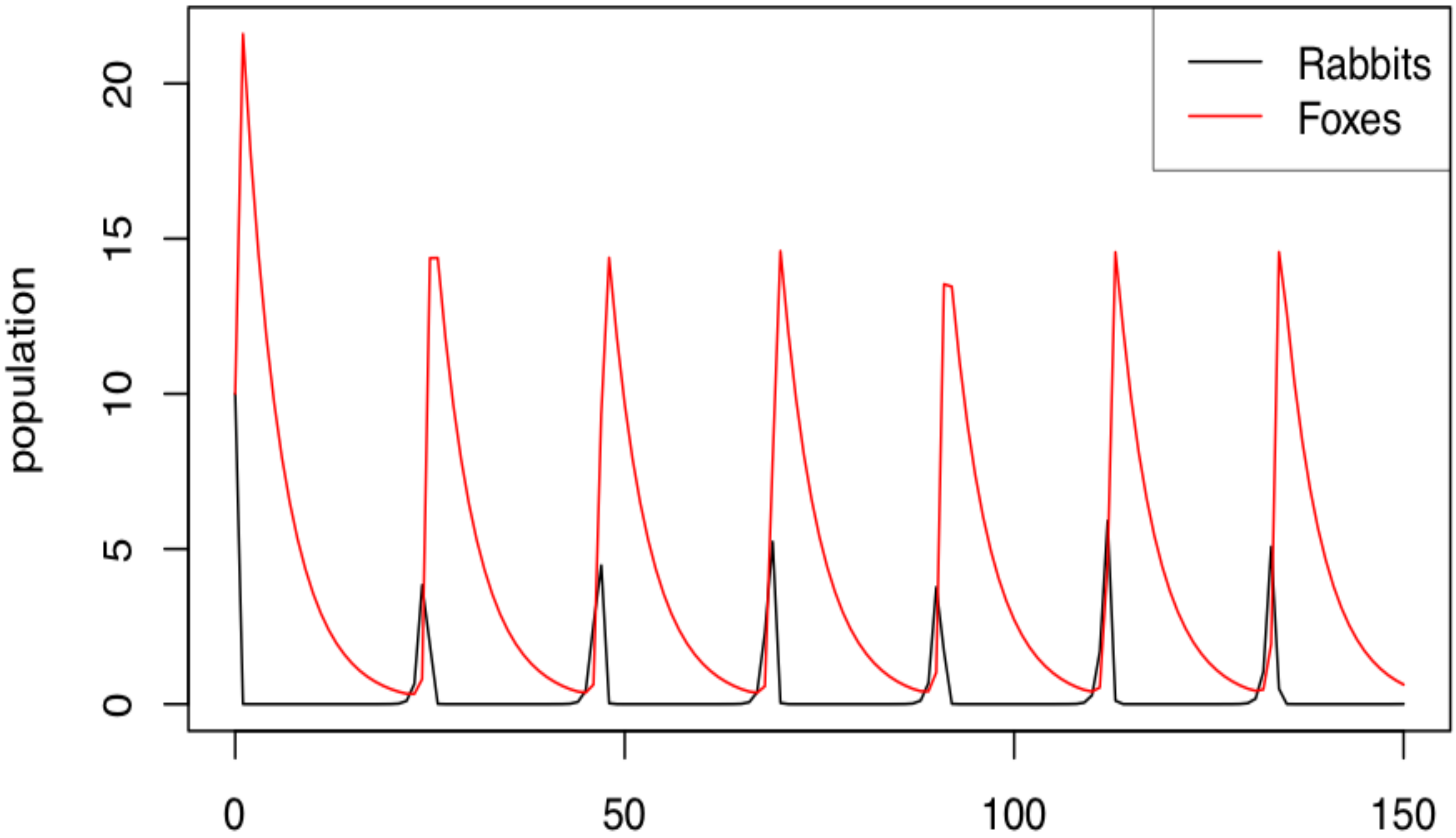


$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

SOME ASSUMPTIONS

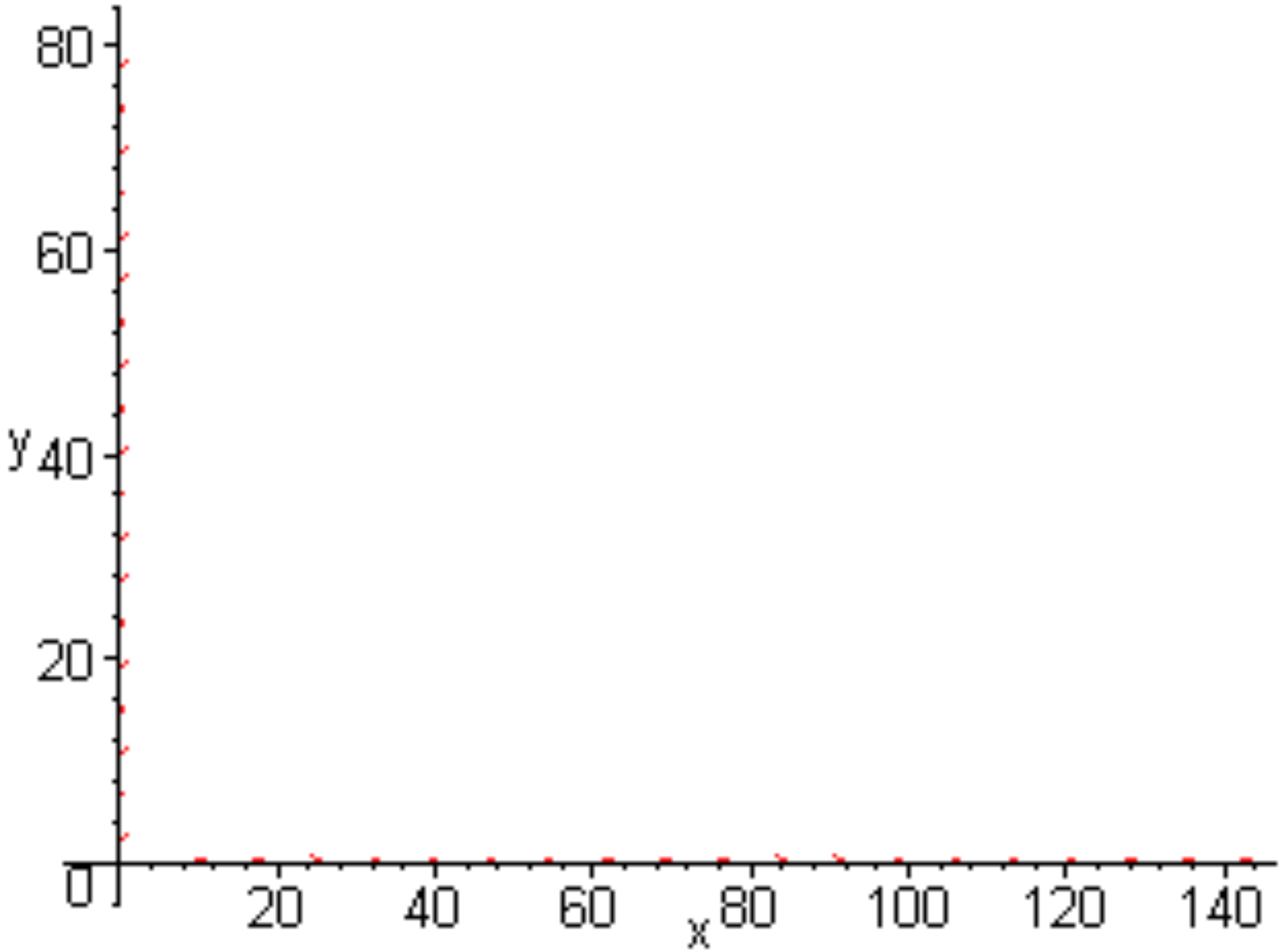
- the ***lynx*** is totally dependent on a single prey species (**the *hare***) as its only food supply,
- the ***hare*** has an unlimited food supply,
- there is no threat to the ***hare*** other than the specific predator.



Rabbits
Foxes
population
0
5
10
15
20
0
50
100
150

Phase plane plot: Lotka-Volterra model

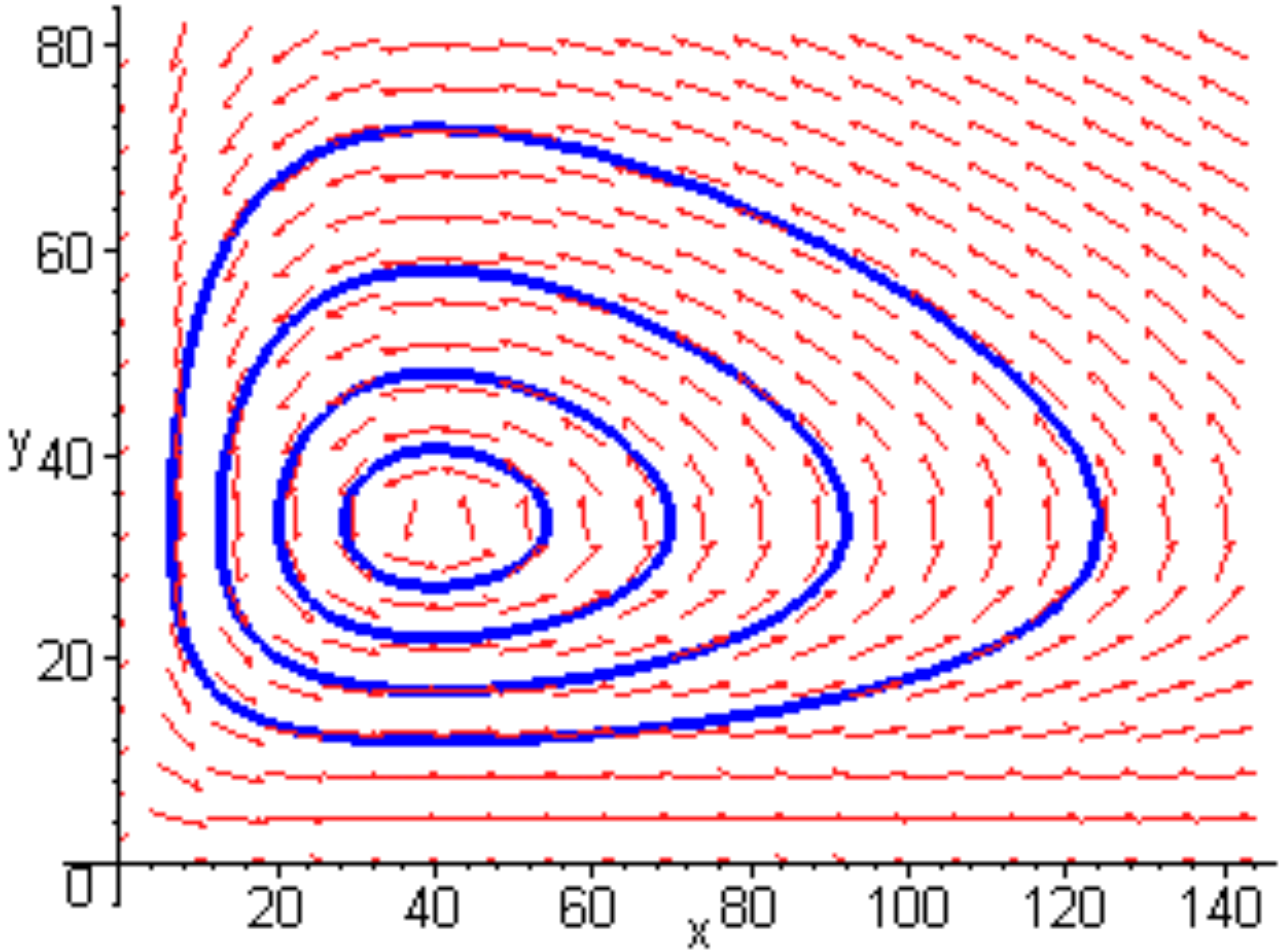
‘Lynx’



‘Rabbits’

Phase plane plot: Lotka-Volterra model

‘Lynx’



‘Rabbits’

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

What happens if no change in rabbit (prey) population?

$$\frac{dx}{dt} = 0$$

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

What happens if no change in rabbit (prey) population?

$x = 0$ or:

$\frac{dx}{dt} = 0$ means that either: $\alpha - \beta y = 0$

$$\boxed{y = \alpha/\beta}$$

Constant predators

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

What happens if no change in rabbit (prey) population?

$\frac{dx}{dt} = 0$ means that either: $x = 0$ or: $\alpha - \beta y = 0$

$$\boxed{y = \alpha/\beta}$$

Constant predators

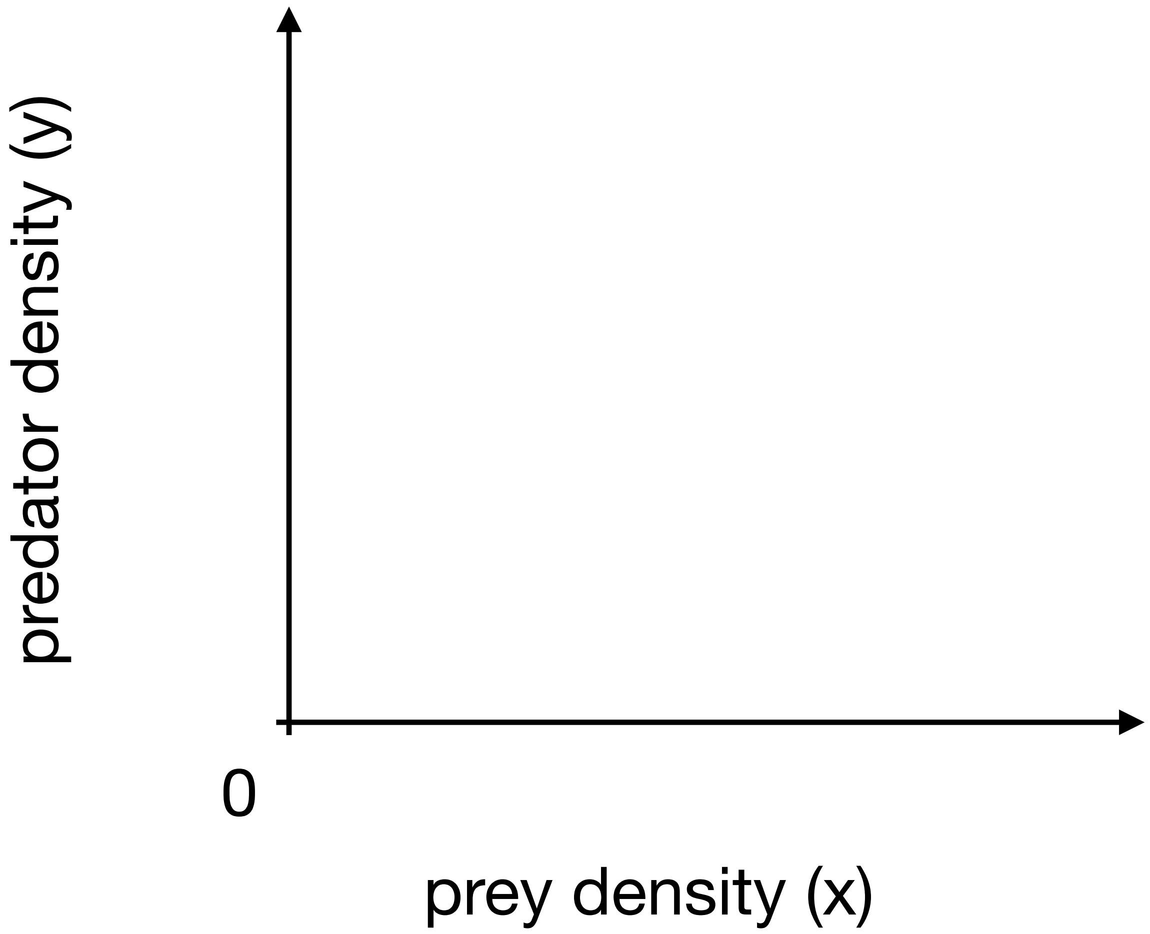
What happens if no change in lynx (predator) population?

$\frac{dy}{dt} = 0$ means that either: $y = 0$ or: $\gamma - \delta x = 0$

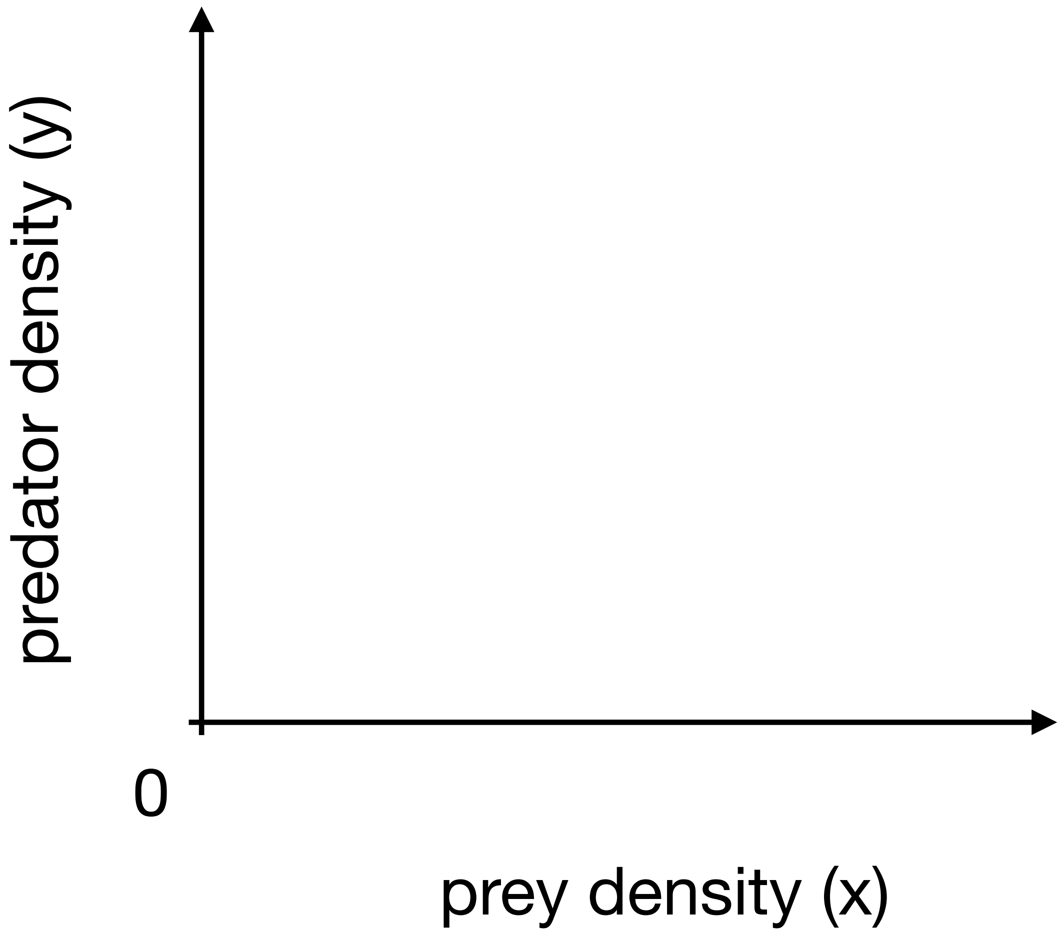
$$\boxed{x = \gamma/\delta}$$

Constant prey

What happens to the prey?

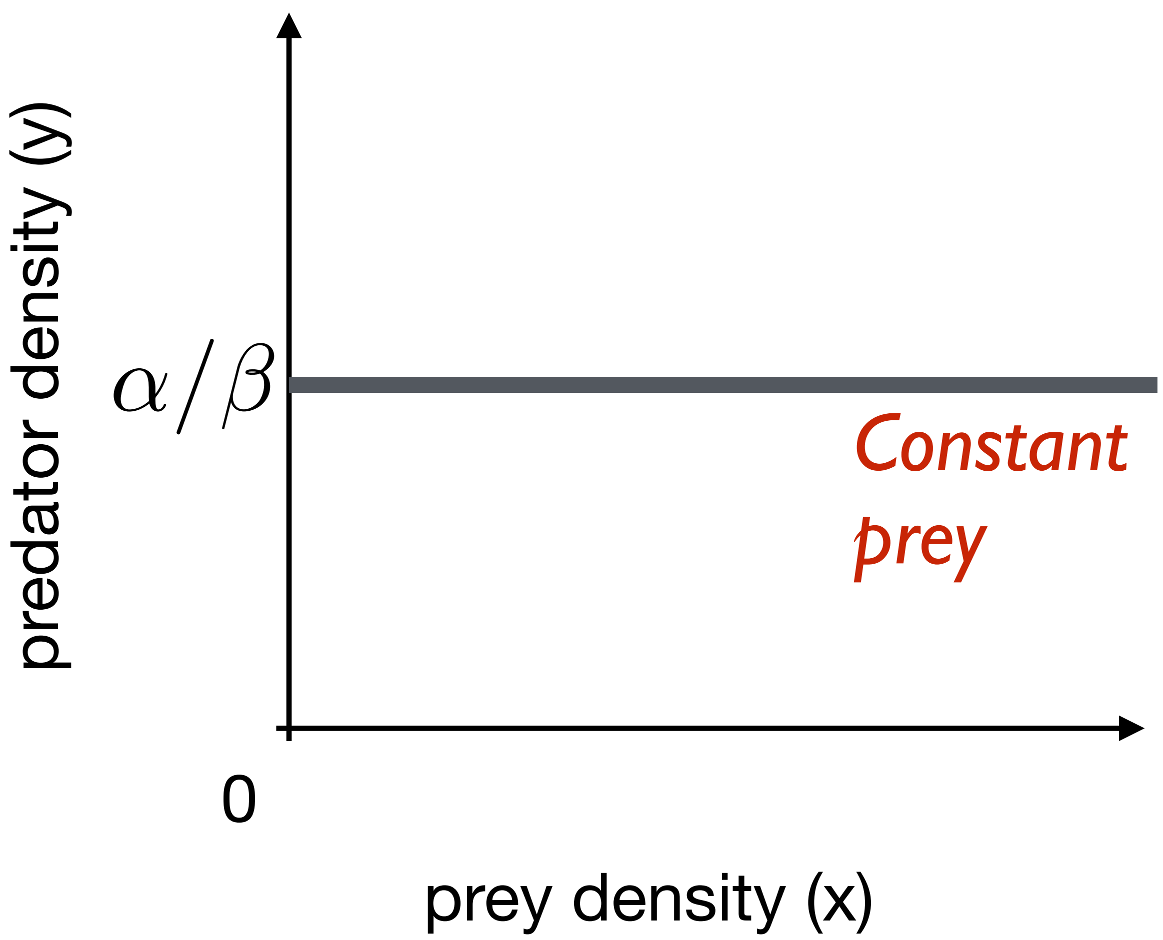


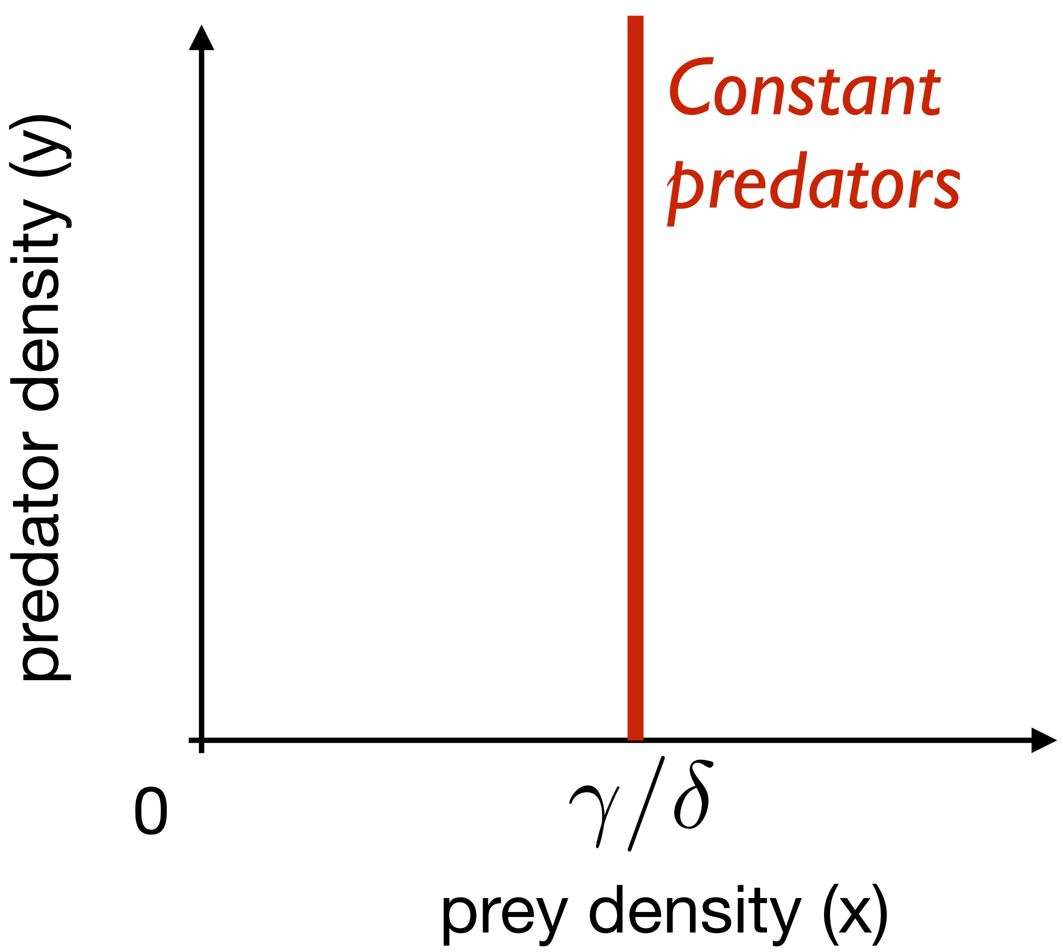
What happens to the predators?



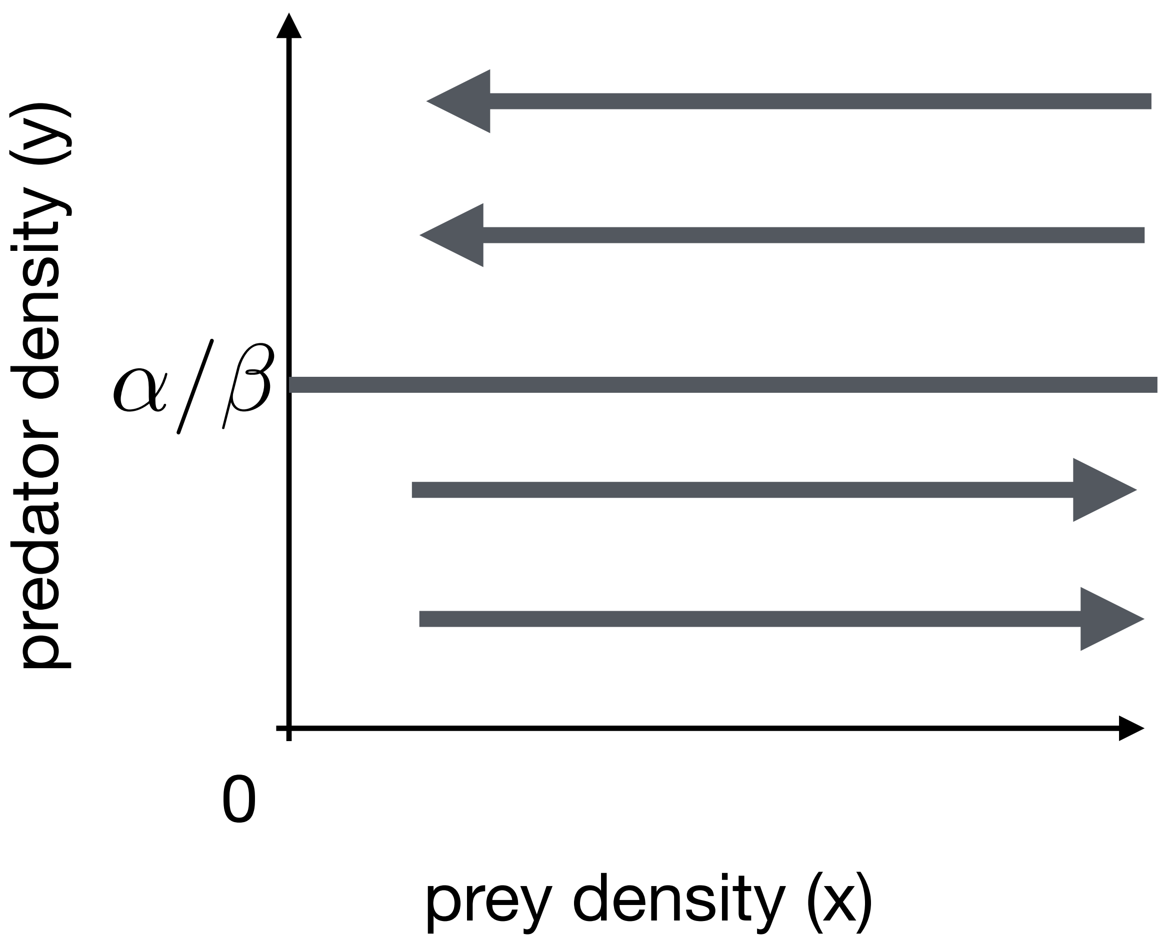
What happens to the prey?

What happens to the predators?

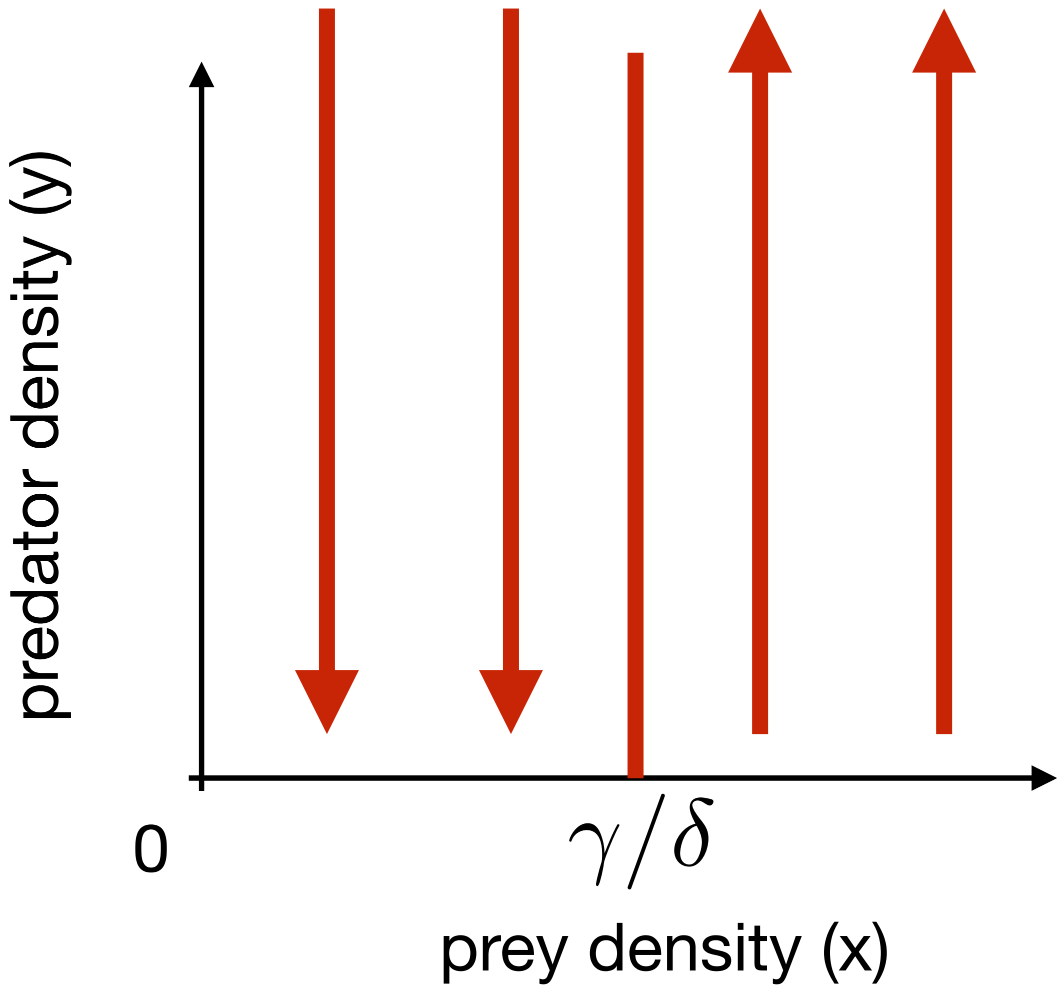


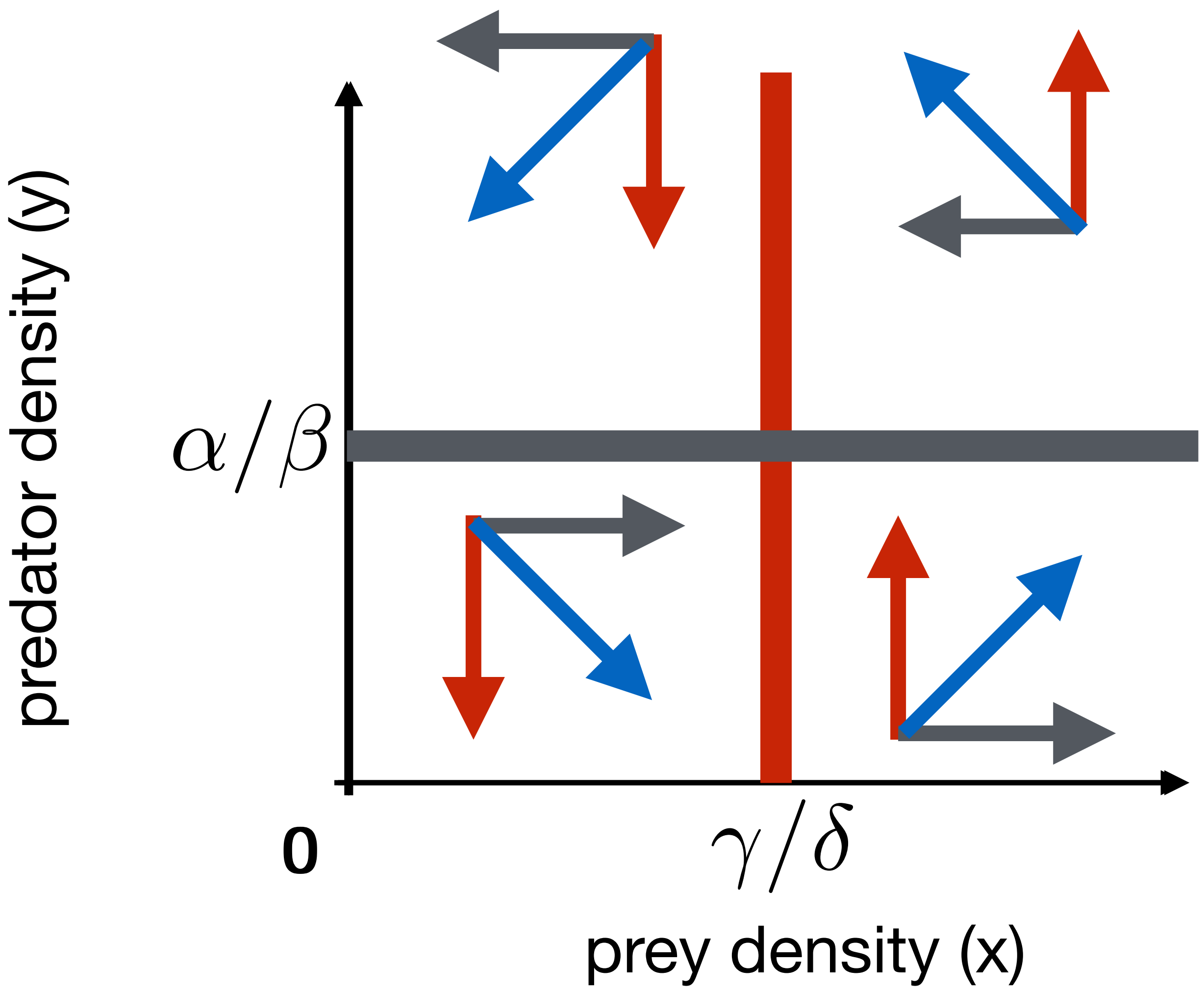


What happens to the prey?



What happens to the predators?




predator density (y)
α/β
0
γ/δ
prey density (x)

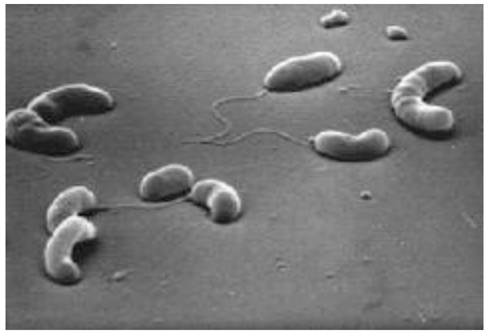
Key concepts

-Inter-dependence of species' demography (here, we considered ***predation***, but ***competition*** *is also possible*)

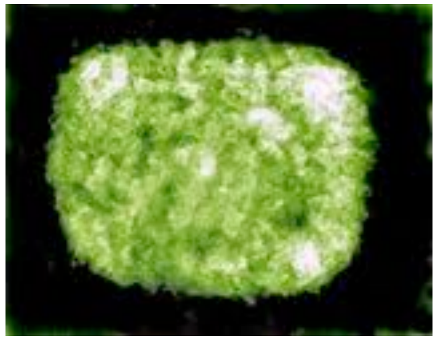
-Internal cycles can be driven ***endogenously***

-Finding the **null-clines** (where there is no change) can be helpful for predicting or understanding dynamics.

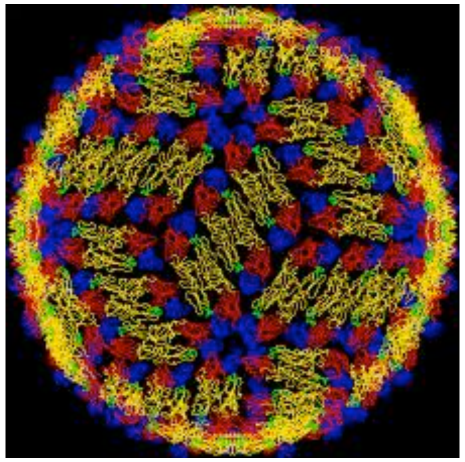
-Many assumptions in this simple framework! And a number of aspects can be added to map this closer to real systems.



cholera



pox virus



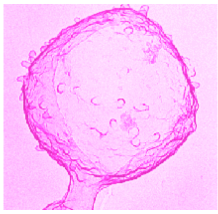
dengue

E. coli

SIR models

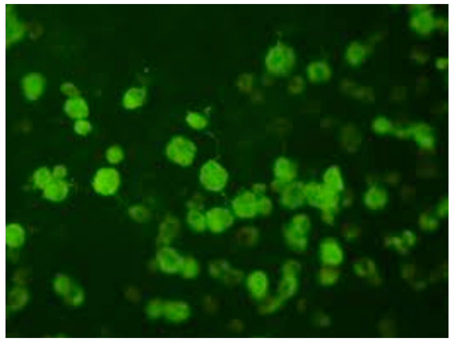
brucella

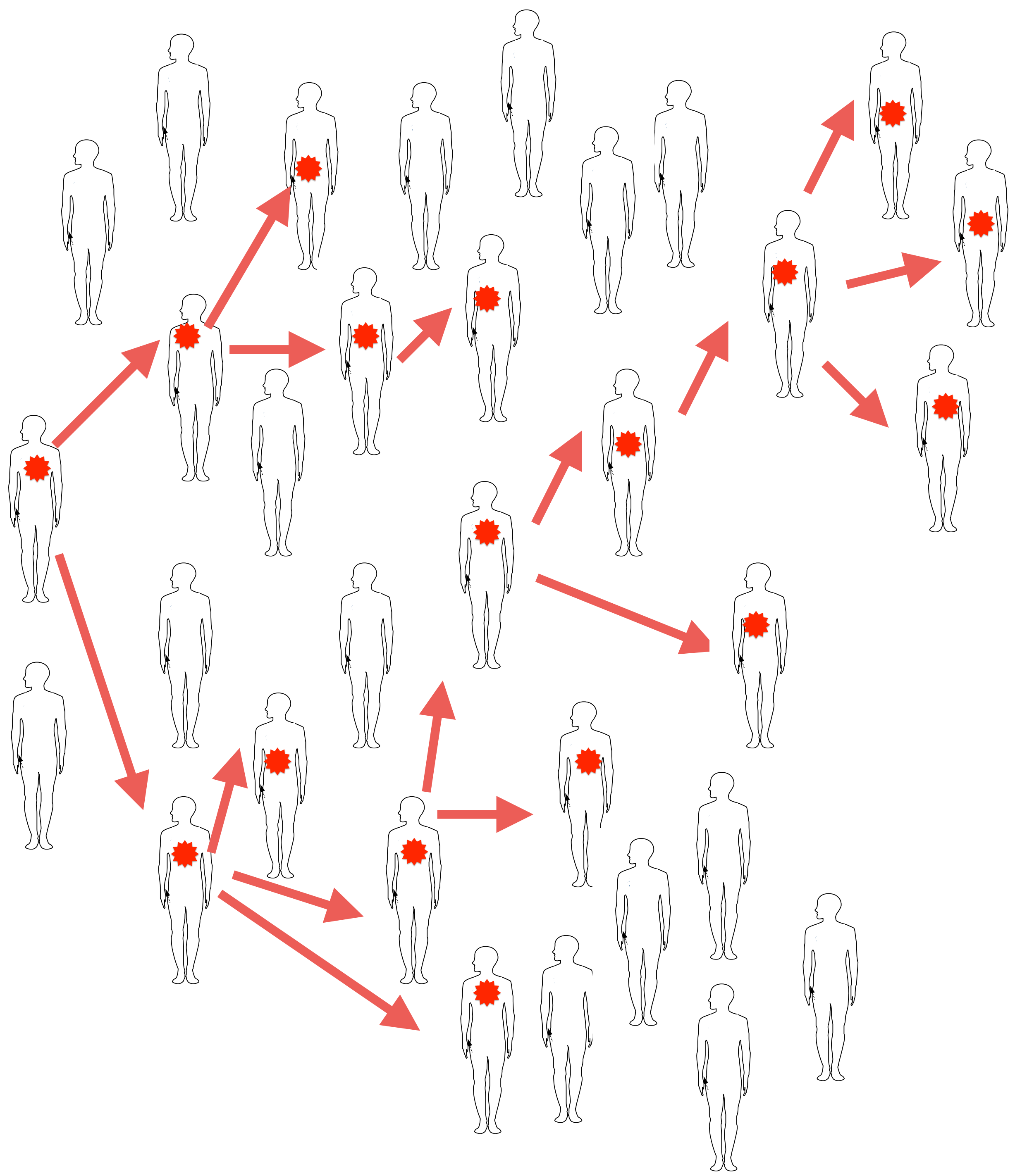
strep



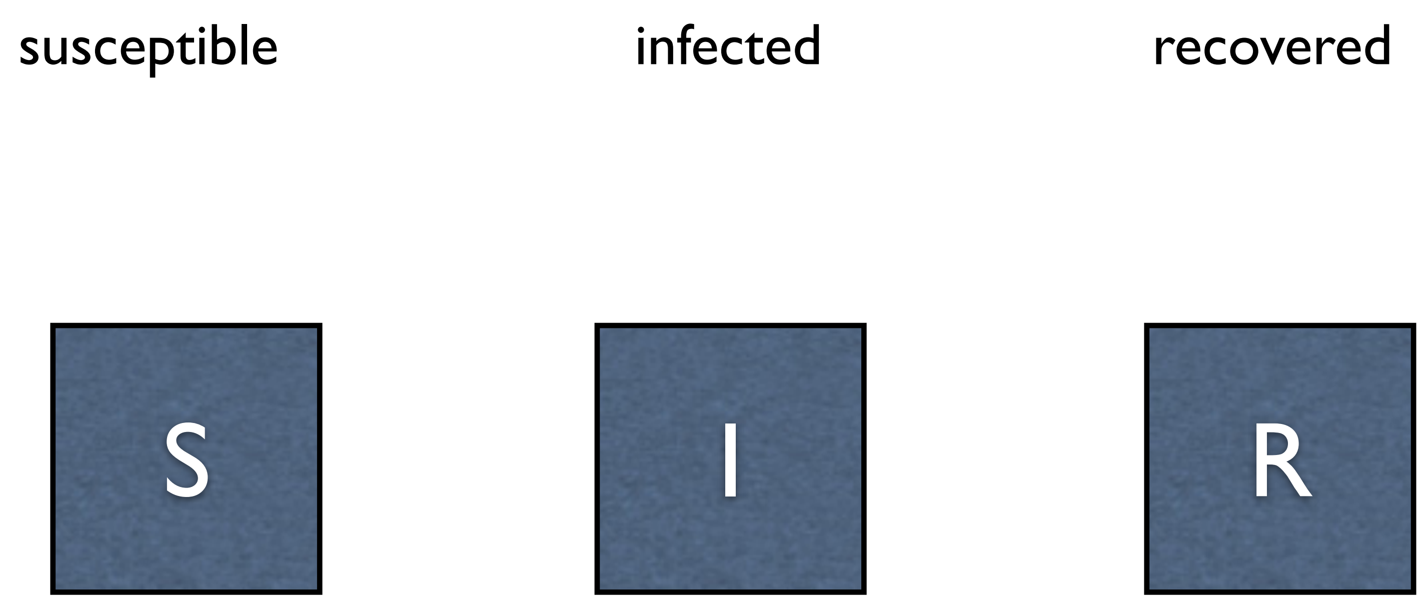
Tb

trichomonas





The SIR model



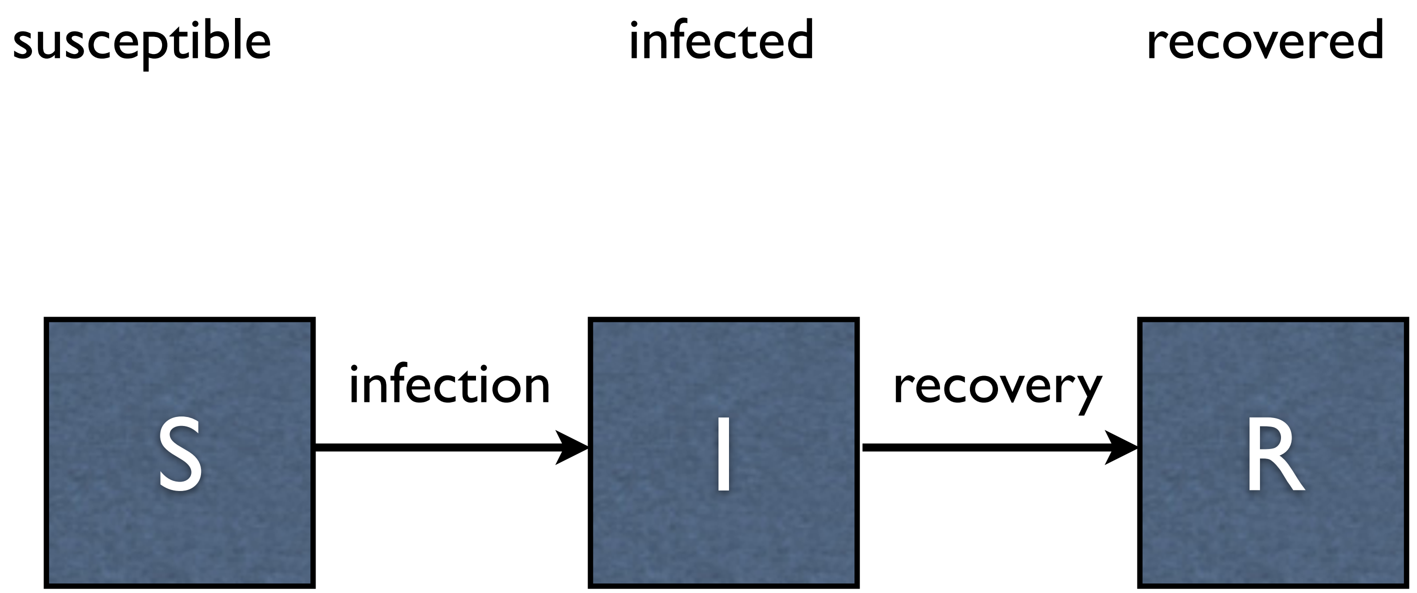
Easiest infections to stylize… completely immunizing viruses.

Replicate inside the host = no dose dependence

Immunizing = once you recover, recovered forever.

Measles, mumps, rubella

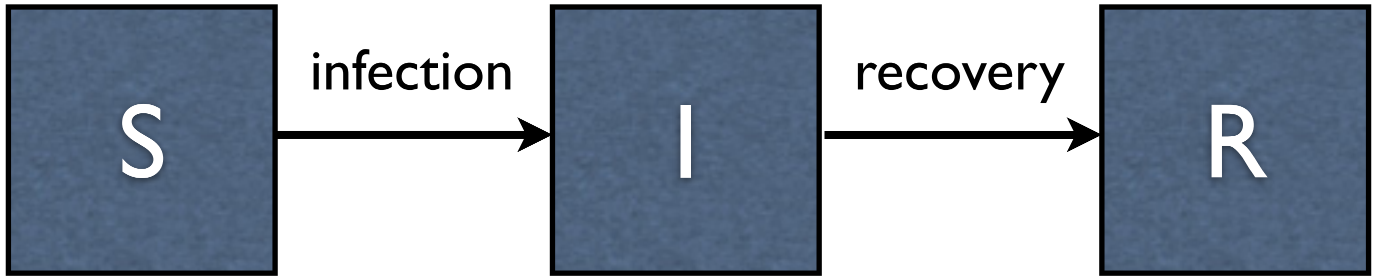
The SIR model



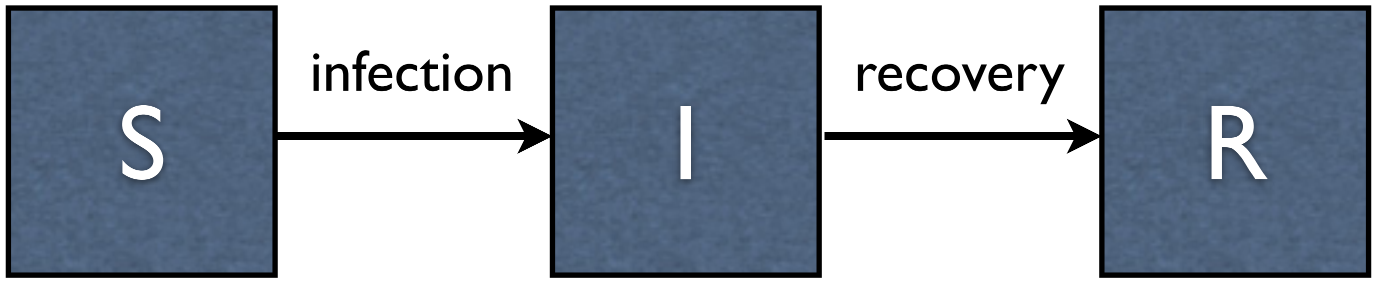
What are the big assumptions here?

The SIR model

everyone is either:



The SIR model

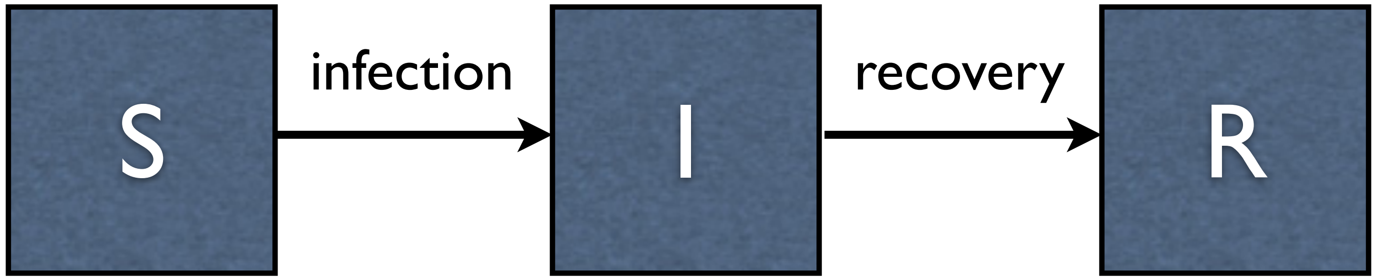


people **mix uniformly**
(mass action)

The SIR model

no latent period
(infectious when infected)

everyone is either:



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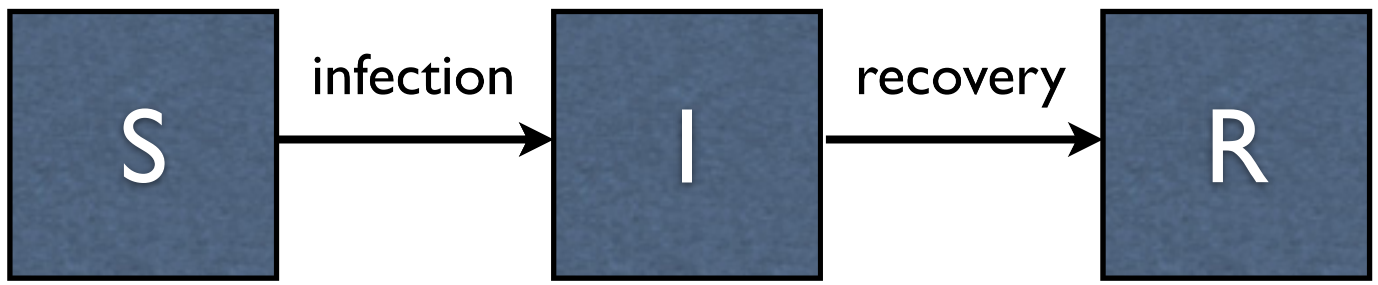


people **mix uniformly** **(mass action)**

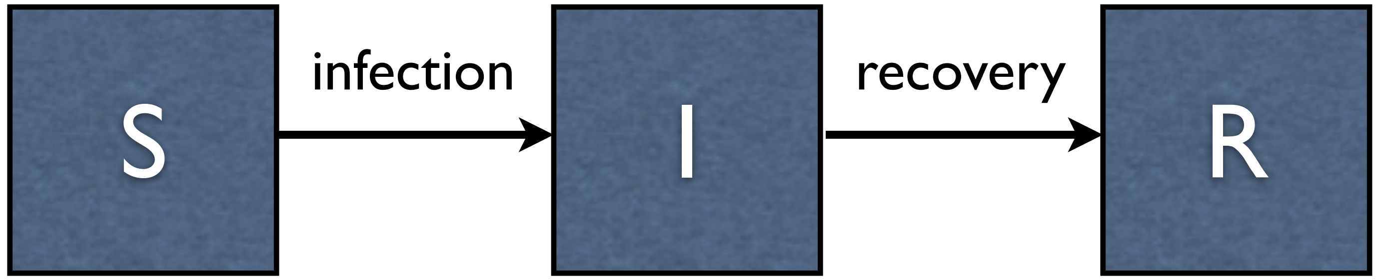
recovery is **permanent**

The SIR model

no latent period
(infectious when infected)

population size
constant - no births
or deaths, migration

everyone is either:



people **mix**
uniformly
(mass action)

recovery is
permanent

The SIR model

Parameters

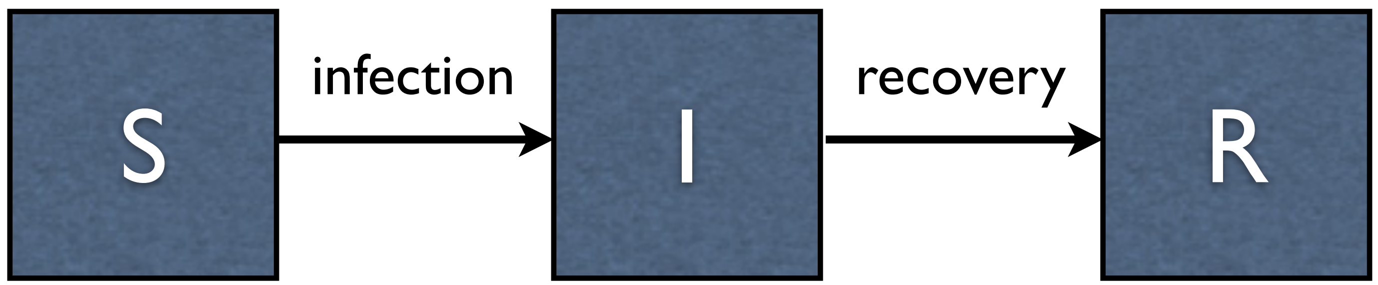
β : infection or transmission rate per contact

γ : rate of recovery

no latent period
(infectious when infected)

population size **constant** - no births or deaths, migration

everyone is either:



people **mix uniformly (mass action)**

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The SIR model

Parameters

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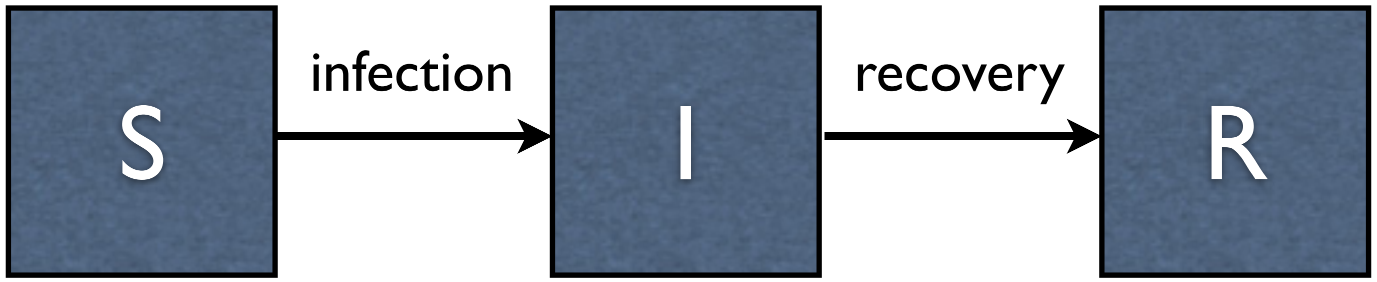


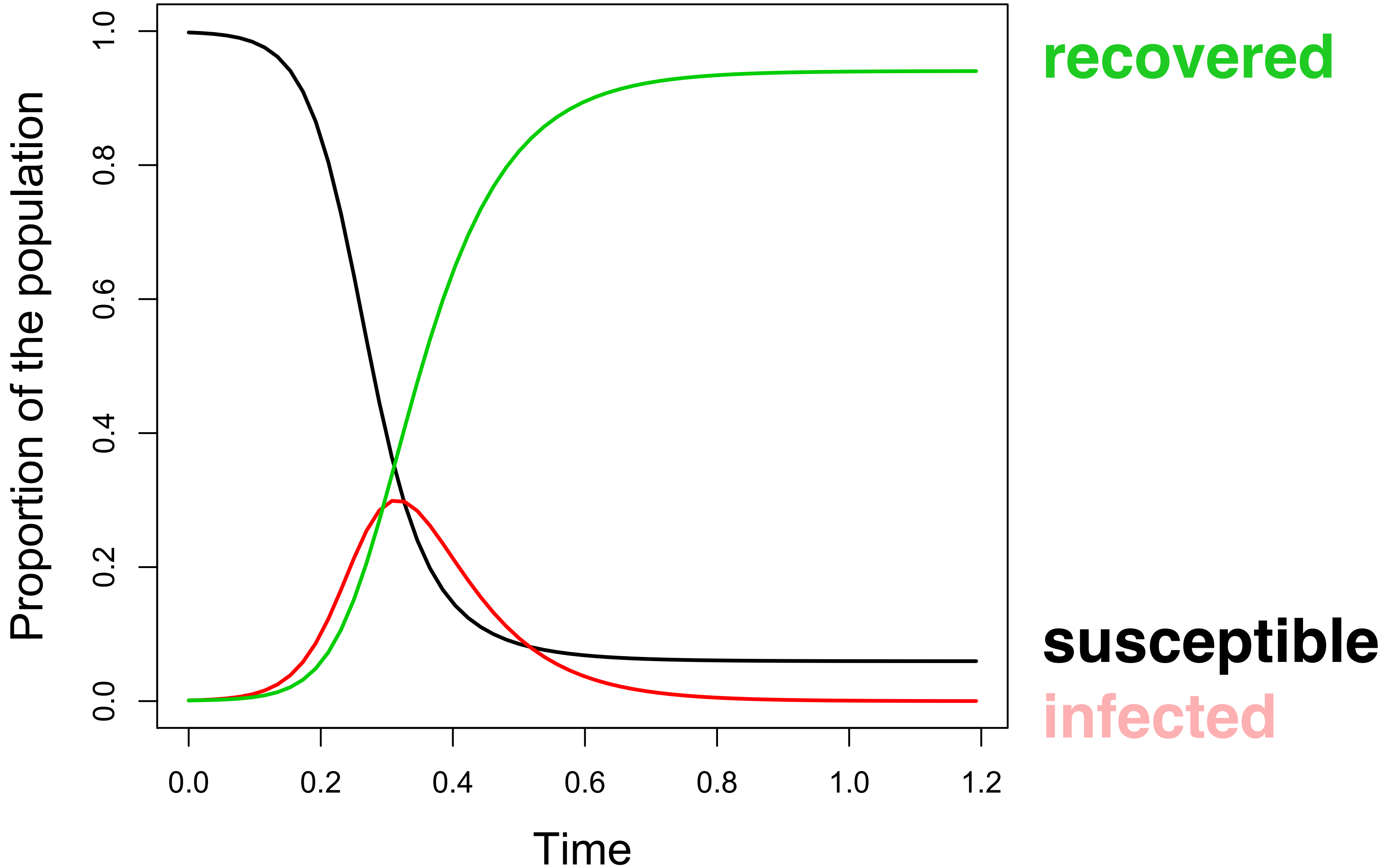
$$\frac{dS(t)}{dt} = -\beta S(t)I(t)$$

$$\frac{dI(t)}{dt} = \beta S(t)I(t) - \gamma I(t)$$

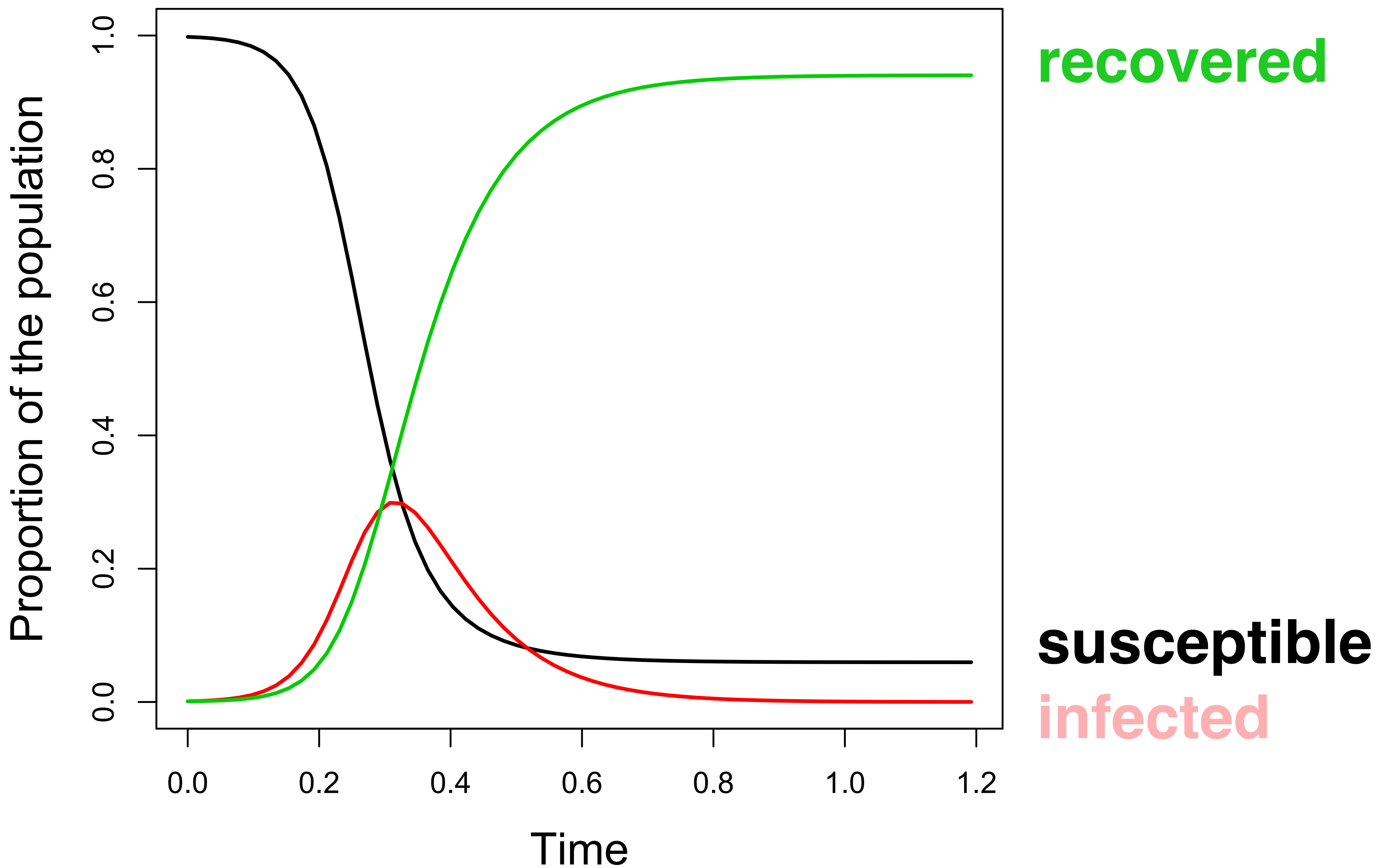
$$\frac{dR(t)}{dt} = \gamma I(t)$$

What will the dynamics look like?

The SIR model: dynamics



The SIR model: dynamics



??Epidemic ends even though there are still some susceptibles….

The SIR model: insights

A magic number: the average number of persons infected by an infectious individual when everyone is susceptible (start of an epidemic)

$$R_0 = \beta/\gamma$$

!has to be bigger than 1 for infection to spread!

Parameters

β : infection or transmission rate per contact

γ : rate of recovery

The SIR model: insights

A magic number: the average number of persons infected by an infectious individual when everyone is susceptible (start of an epidemic)

$$R_0 = \beta/\gamma$$

!has to be bigger than 1 for infection to spread!

A related value: what you get in a population where the infection is circulating.

$$R_E = R_0 S$$

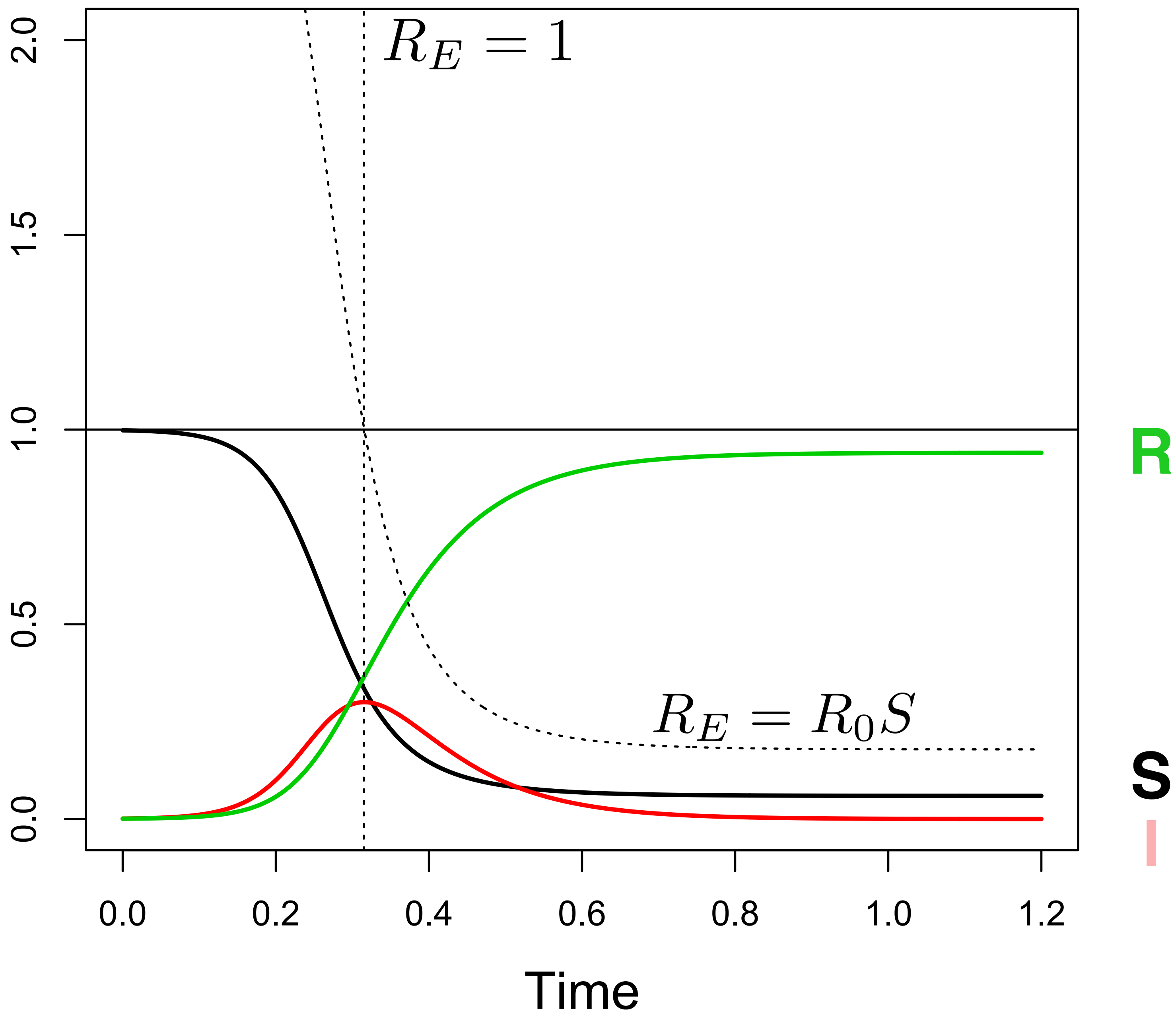
!has to be bigger than 1 for infection to be spreading

Parameters

β : infection or transmission rate per contact

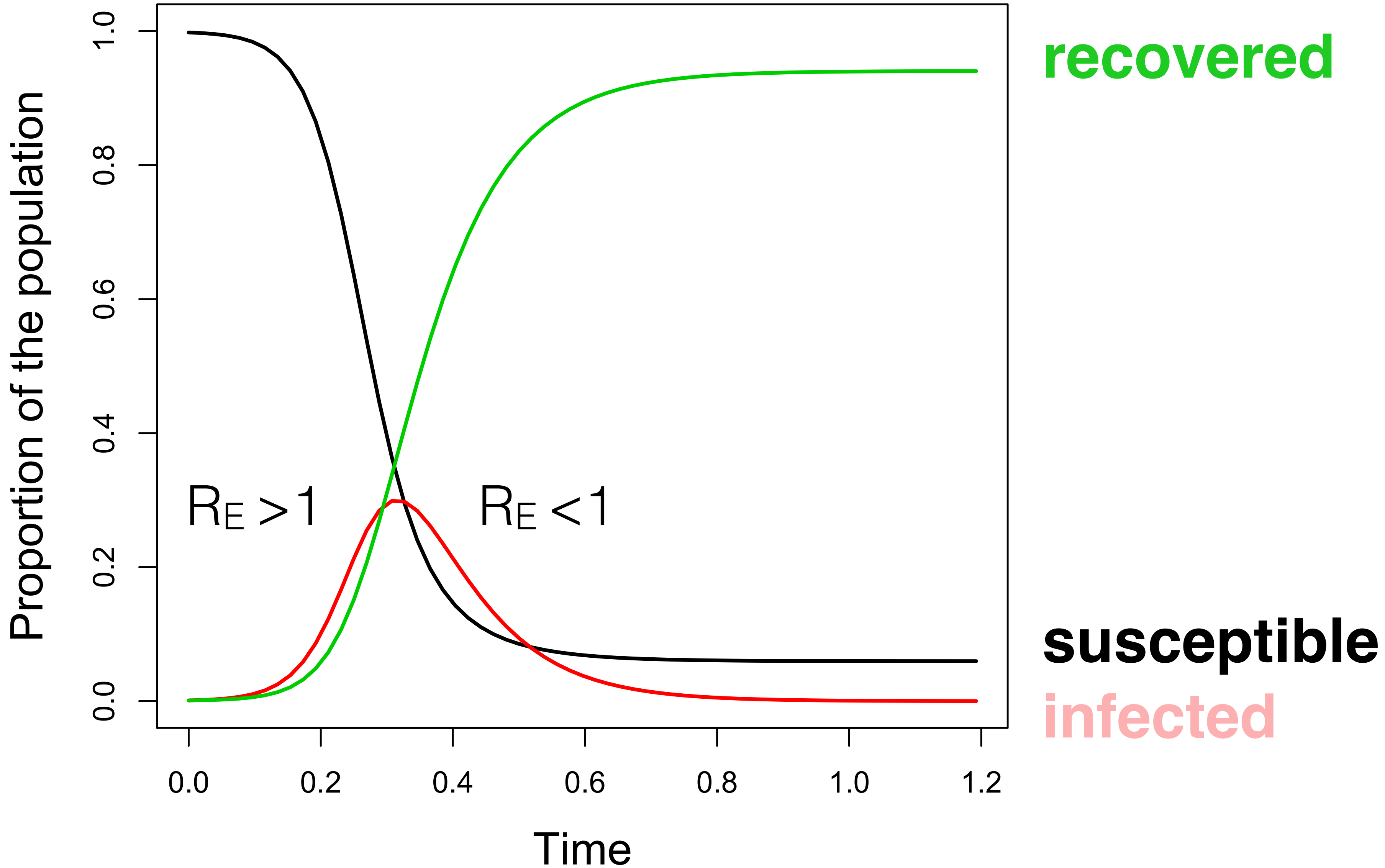
γ : rate of recovery

The SIR model: insights

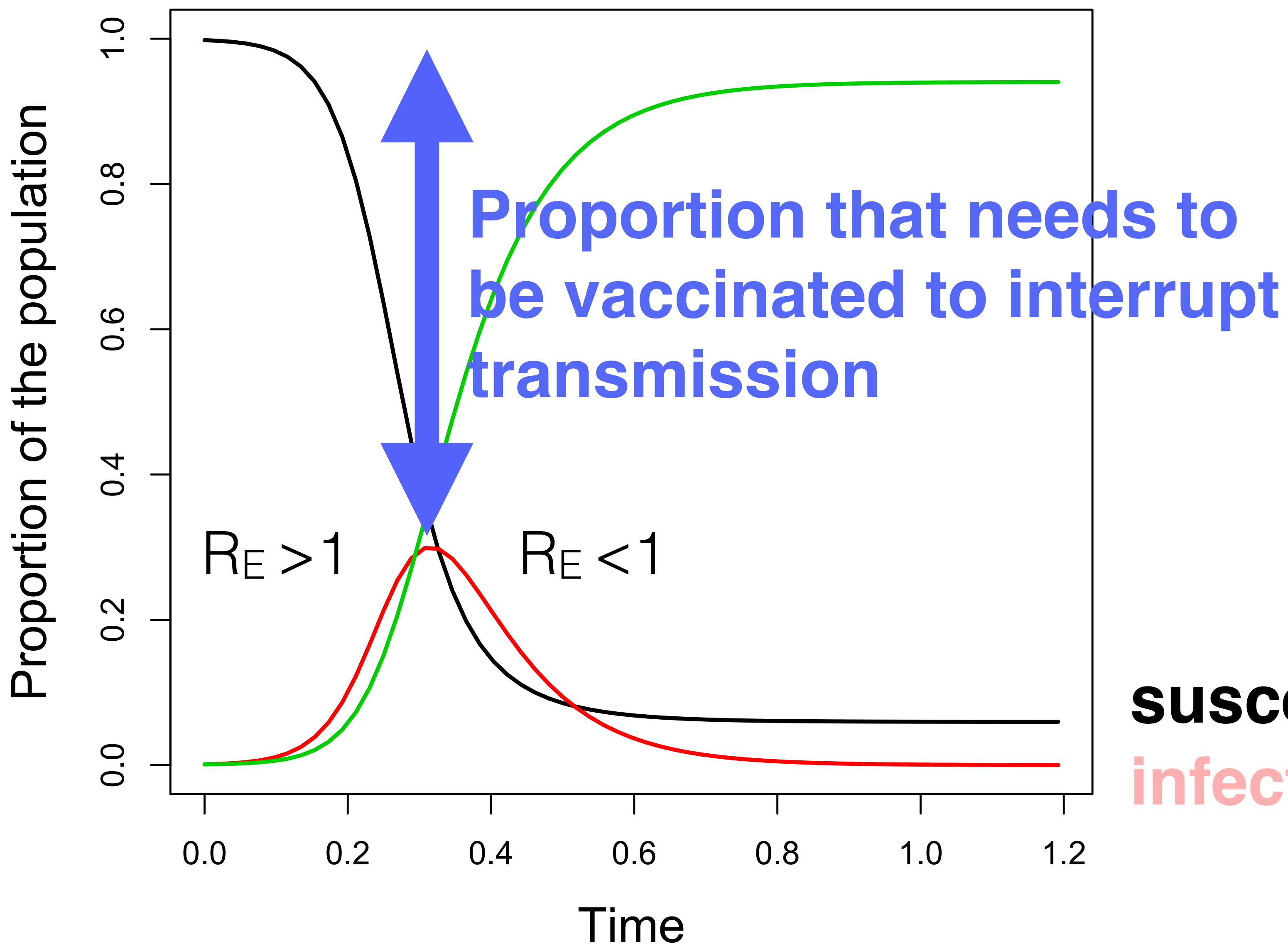


When $R_E<1$; the outbreak declines; infectious individuals are infecting less than 1 susceptible individual.

The SIR model: control



The SIR model: control



susceptible

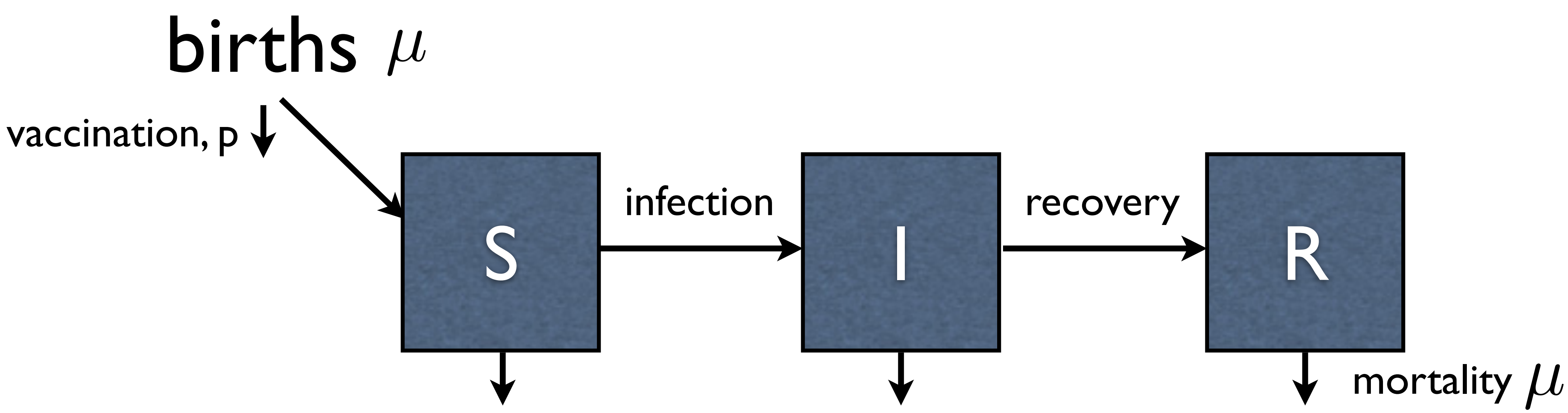
infected

$$R_E = R_0 S$$

$$p_c = 1 - \frac{1}{R_0}$$

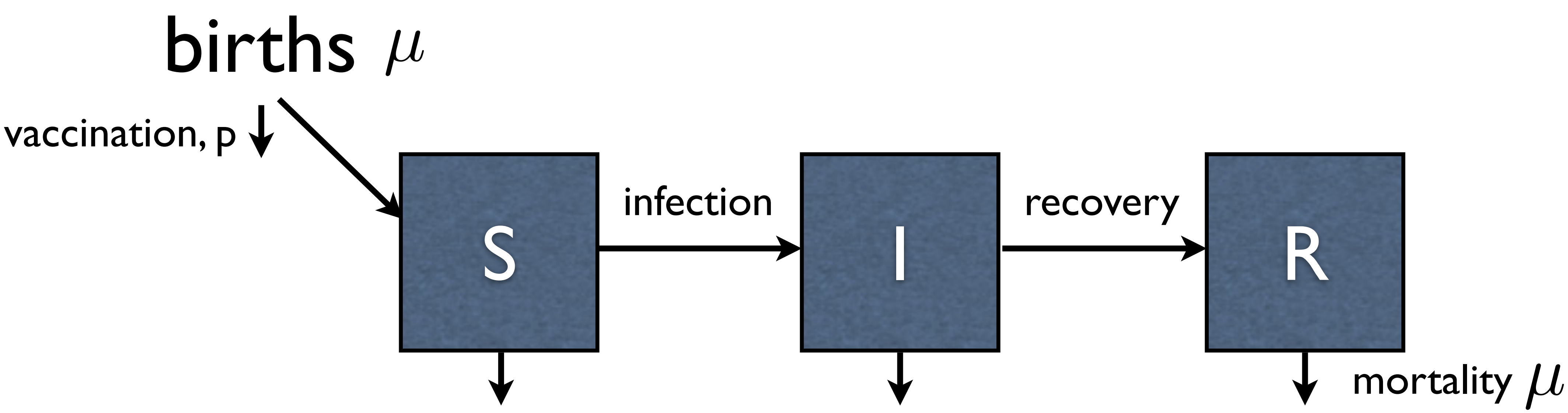
The SIR model: extensions

Moving beyond a 'closed' population



The SIR model: extensions

Moving beyond a 'closed' population



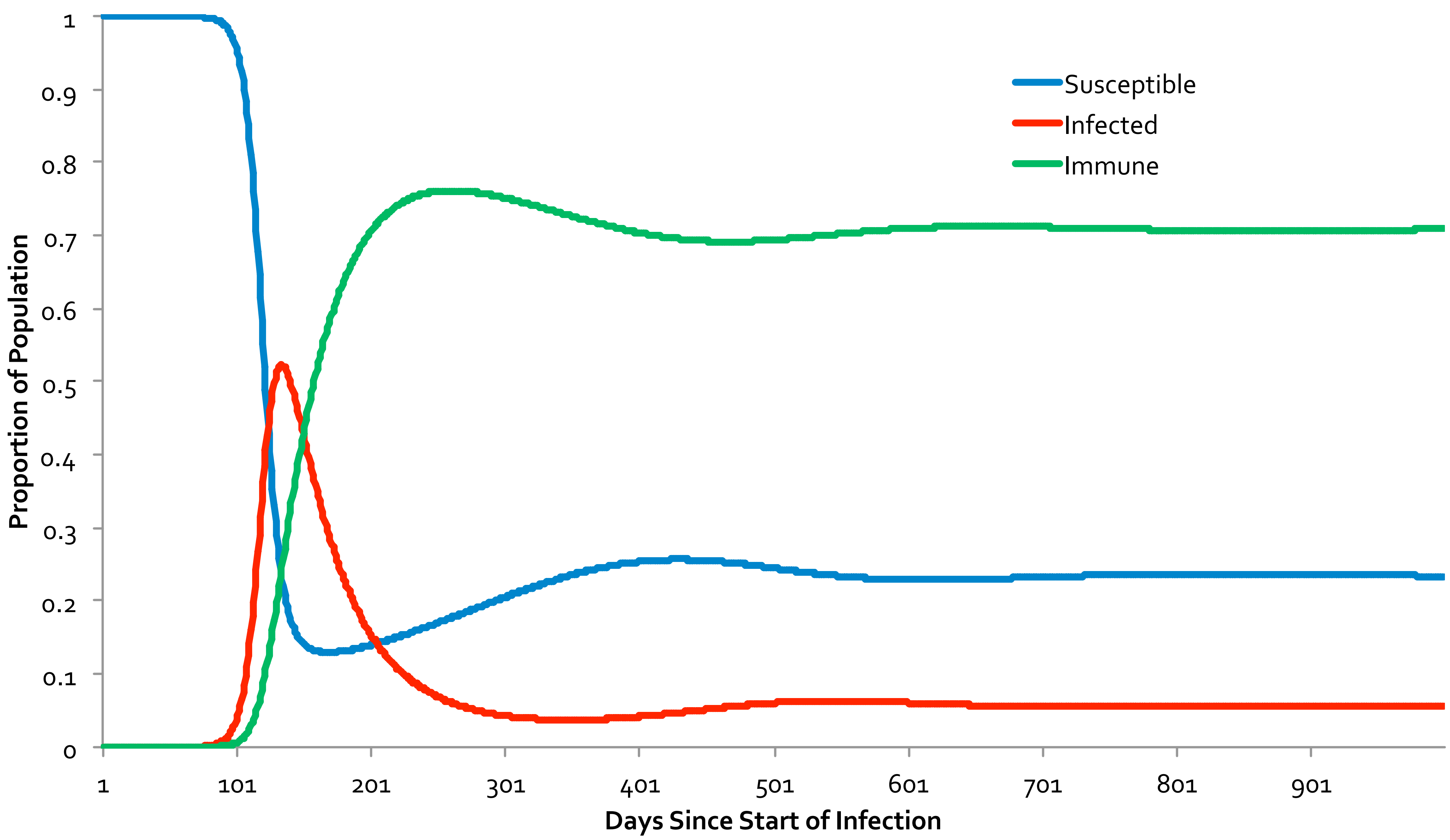
$$\frac{dS(t)}{dt} = \mu(1-p) - \beta S(t)I(t) - \mu S(t)$$

$$\frac{dI(t)}{dt} = \beta S(t)I(t) - \gamma I(t) - \mu I$$

What is likely to be the BIGGEST dynamical difference?

The SIR model: extensions

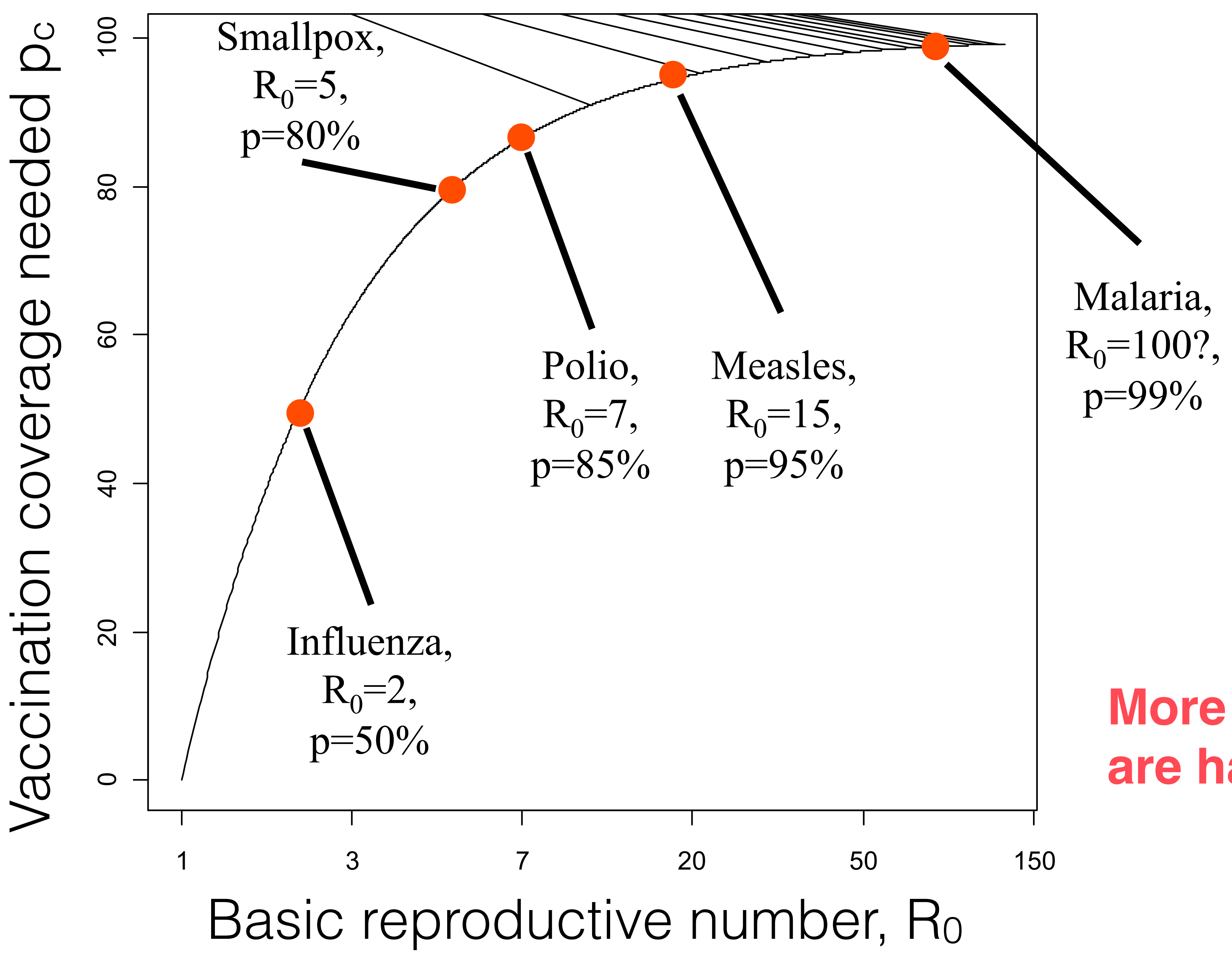
Moving beyond a 'closed' population



Can get persisting infection (doesn't just go extinct)

The SIR model: eradication

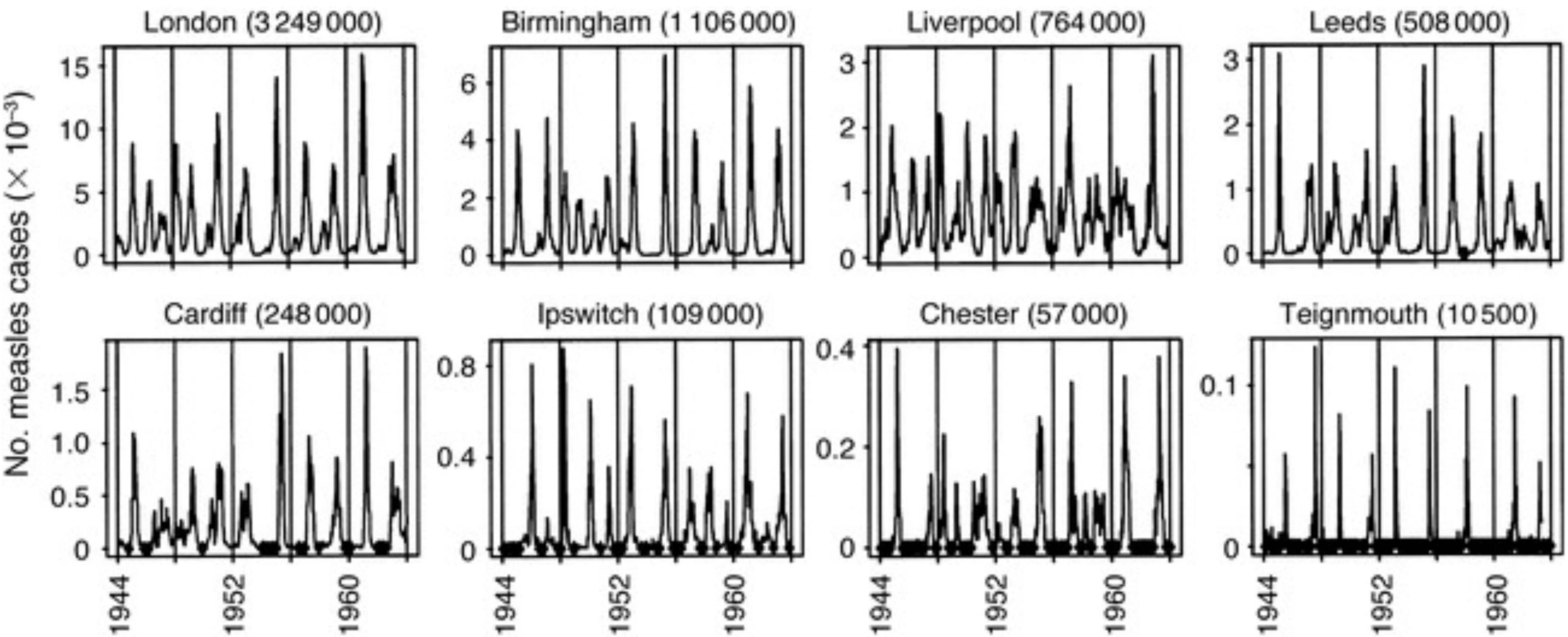
Same logic as without births: $p_c = 1 - \frac{1}{R_0}$



More transmissible diseases are harder to eradicate

The SIR model: data

Measles across various cities in the UK



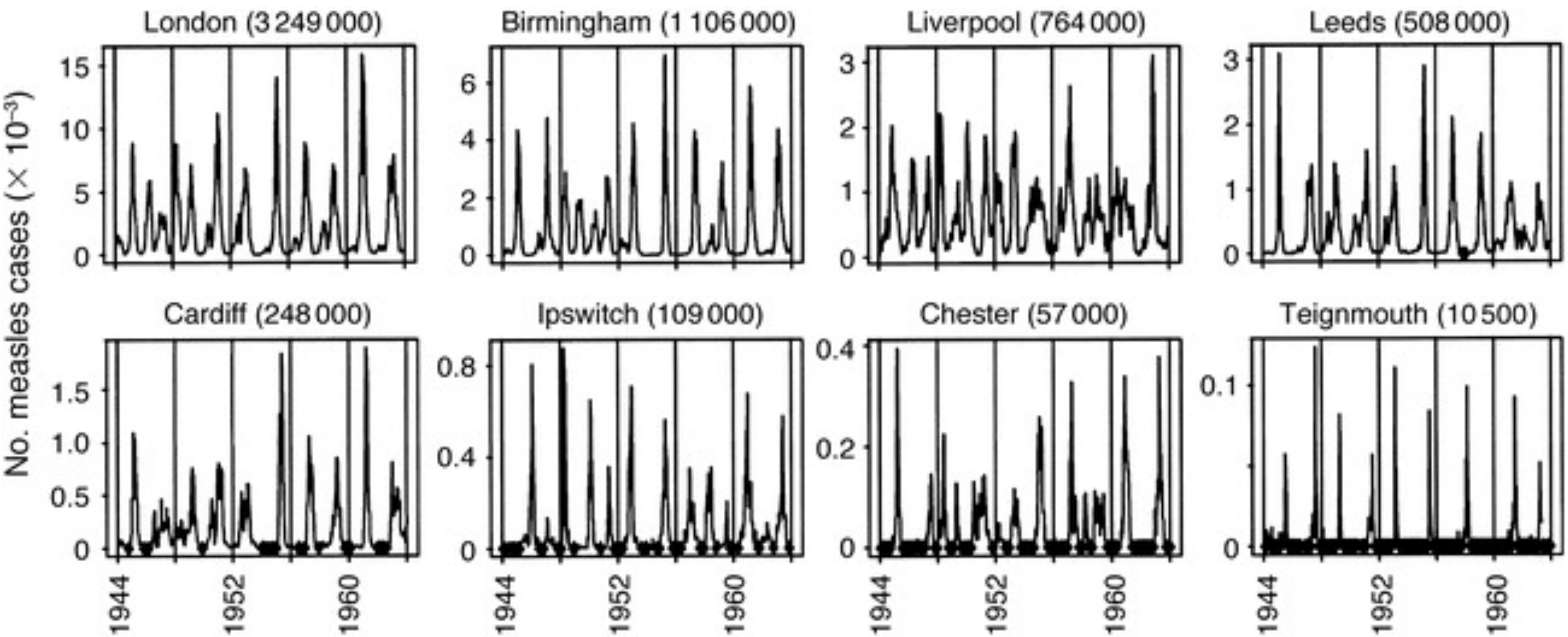
Peaks every year, or every other year; more erratic in smaller places.

NOTHING LIKE the SIR with births

Bjornstad, Finkenstadt Grenfell, 2002, *Ecological monographs*

The SIR model: data

Measles across various cities in the UK



Peaks every year, or every other year; more erratic in smaller places.

What else might be happening?

Bjornstad, Finkenstadt Grenfell, 2002, *Ecological monographs*

The SIR model: extensions to match data

1. Seasonal fluctuations in transmission.

Explore using regression techniques, based around the generation time of infection

$$E[I_{t+\delta}] = \beta_s \, I_t \, S_t$$

$$E[\ln(I_{t+\delta})] = \ln(\beta_s) + \ln(I_t) + \ln(S_t)$$

Bjornstad, Finkenstadt Grenfell, 2002, *Ecological monographs*
Ferrari et al., 2008 *Nature*

The SIR model: extensions to match data

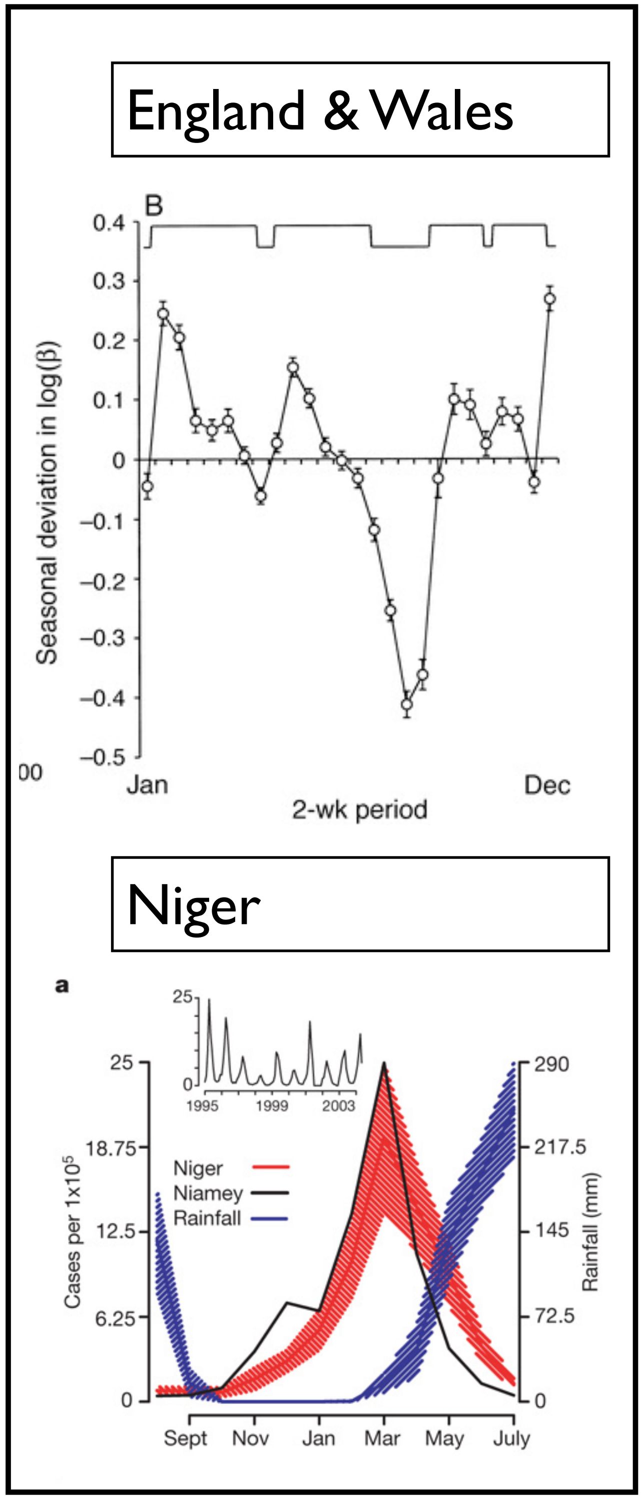
1. Seasonal fluctuations in transmission.

Explore using regression techniques, based around the generation time of infection

$$E[I_{t+\delta}] = \beta_s \, I_t \, S_t$$

$$E[\ln(I_{t+\delta})] = \ln(\beta_s) + \ln(I_t) + \ln(S_t)$$

Functionally, seasonal variation in transmission will actually be shaped by changes in social networks linked to school terms, or rainfall, rather than the drivers themselves.

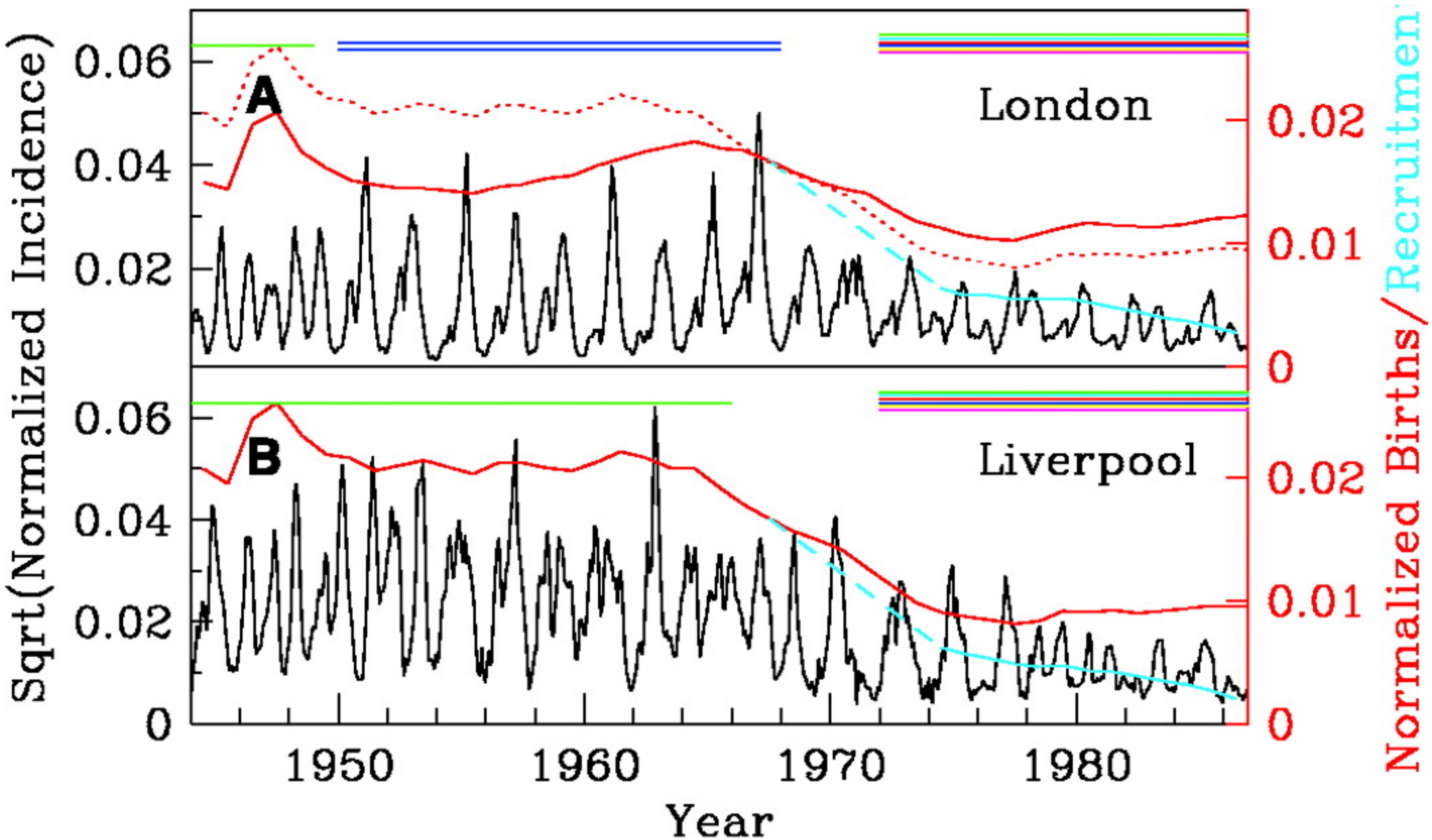


Bjornstad, Finkenstadt Grenfell, 2002, *Ecological monographs*
Ferrari et al., 2008 *Nature*

The SIR model: extensions to match data

2. Demographic changes

Lower birth rates drive biennial dynamics

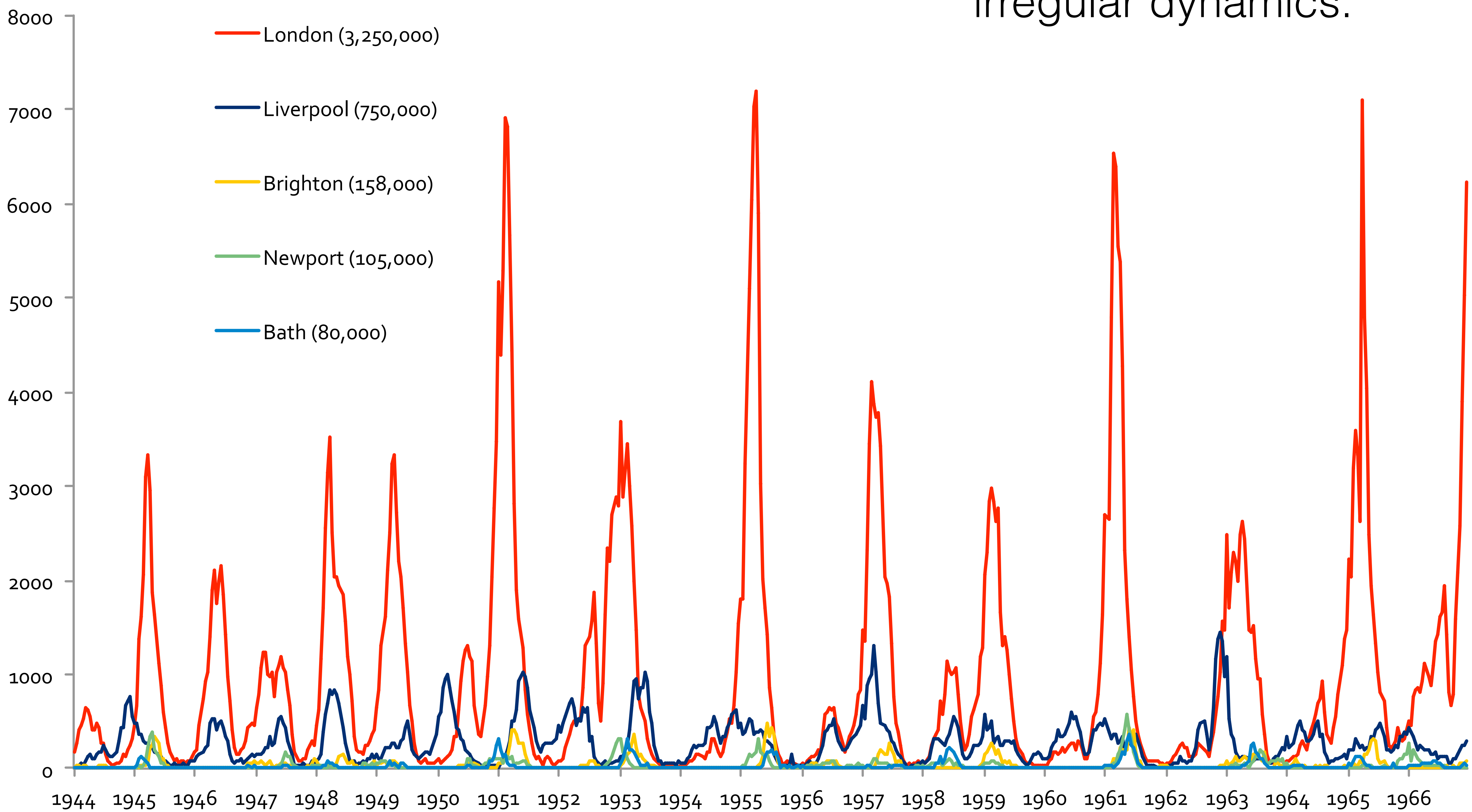


Earn et al. 2000, *Science*

The SIR model: extensions to match data

3. Demographic "noise"

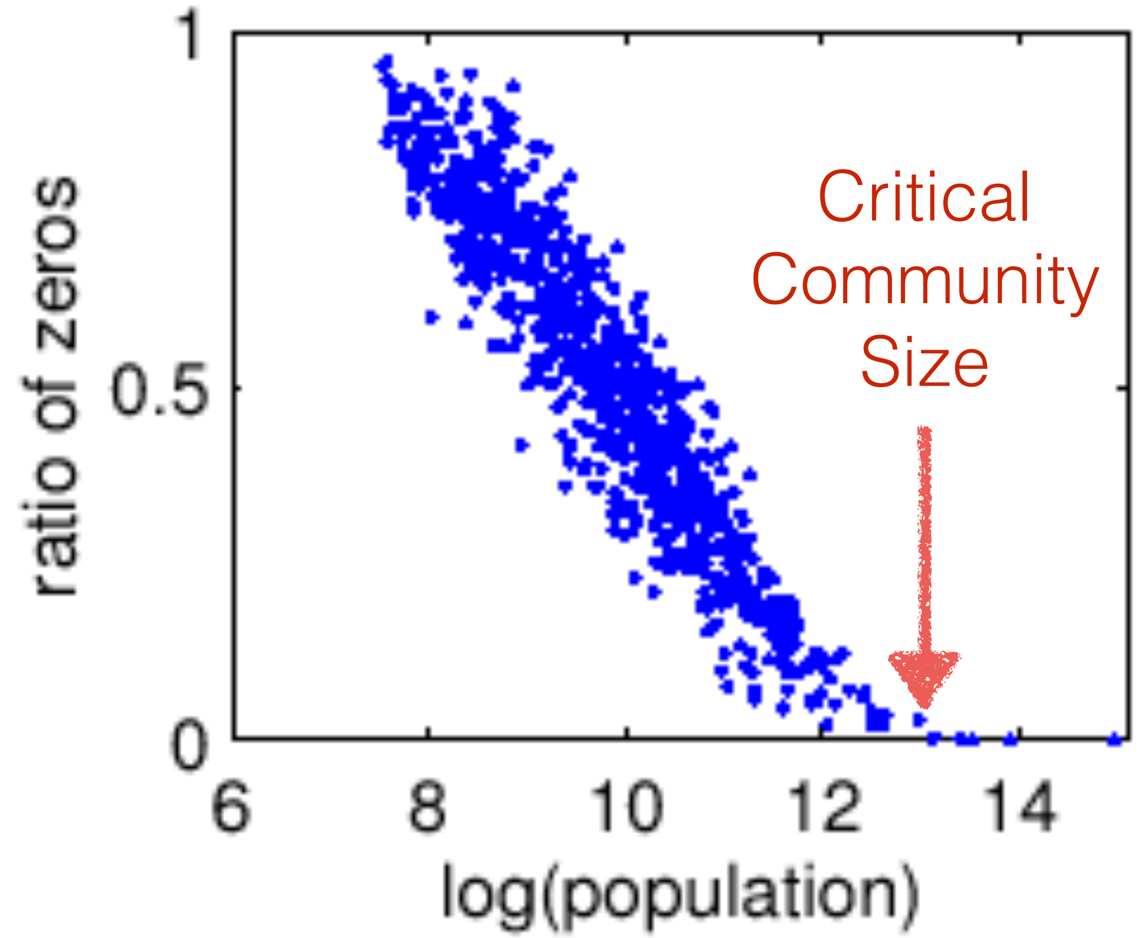
Smaller cities have more irregular dynamics.



The SIR model: extensions to match data

3. Demographic "noise"

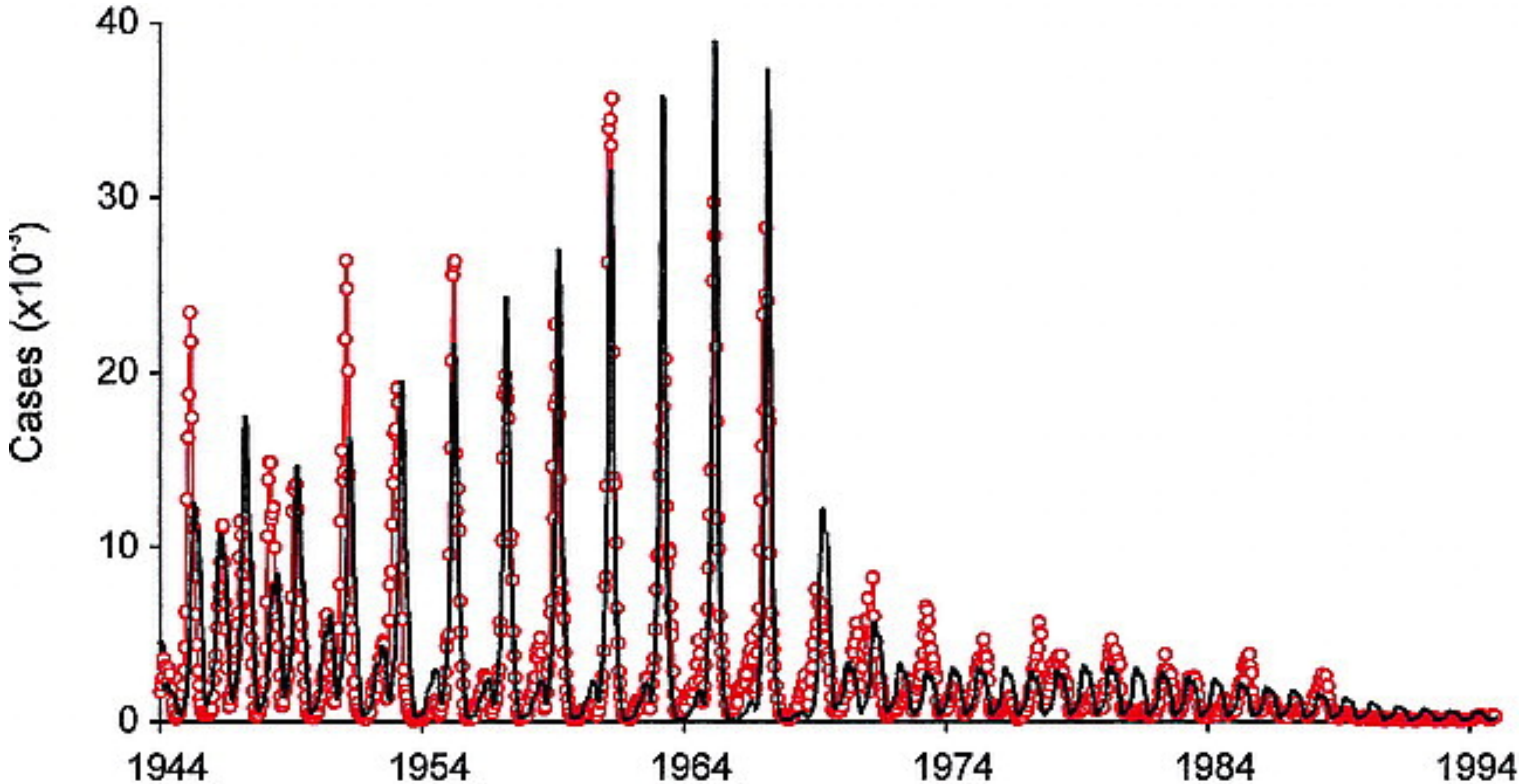
Smaller cities go extinct more often



Smaller cities tend to be "stochastically forced" by larger cities (like London) where the infection persists.

Grenfell et al., 2001, *Nature*

The SIR model: extensions to match data



Grenfell et al., 2002, *Ecological Monographs*

Key concepts

-SIR models essentially resemble predator-prey dynamics

-For simple infections that fit the SIR template, adding demography and seasonality can allow development of models that closely resemble observed systems.