Introduction to Compartmental Models and Differential Equations

Amy Wesolowski
Department of Epidemiology
Slides and tutorial from Jess Metcalf
(Princeton University)

JOHNS HOPKINS
BLOOMBERG SCHOOL
of PUBLIC HEALTH

Learning objectives

- Understand the difference between statistical and mechanistic models
  Comprendre la différence entre les modèles statistiques et mécanistes.

- Understand how to formalize and conceptualize compartmental models
  Comprendre comment formuler et conceptualiser les modèles compartimentés

- Example: population growth, predator prey, SIR models

Compartmental models (Mechanistic Models)

Compartmental models (Mechanistic Models)

Populations are divided into compartments

Les populations sont subdivisées en compartiments

Compartmental models (Mechanistic Models)

Populations are divided into compartments

Les populations sont subdivisées en compartiments

Compartments and transition rates are determined by biological systems

Les compartiments et les taux de transition sont déterminés par les systèmes biologiques

Compartmental models (Mechanistic Models)

Populations are divided into compartments

Les populations sont subdivisées en compartiments

Compartments and transition rates are determined by biological systems

Les compartiments et les taux de transition sont déterminés par les systèmes biologiques

Rates of transferring between compartments are expressed mathematically

Taux de transition entre les compartiments sont exprimés mathématiquement

Compartmental models (Mechanistic Models)

Populations are divided into compartments
Les populations sont subdivisées en compartiments

Compartments and transition rates are determined by biological systems
Les compartiments et les taux de transition sont déterminés par les systèmes biologiques

Rates of transferring between compartments are expressed mathematically
Taux de transition entre les compartiments sont exprimés mathématiquement

Individuals within a compartment are homogeneously mixed
Les individus d'un compartiment sont mélangés de manière homogène

How are these different from statistical models?

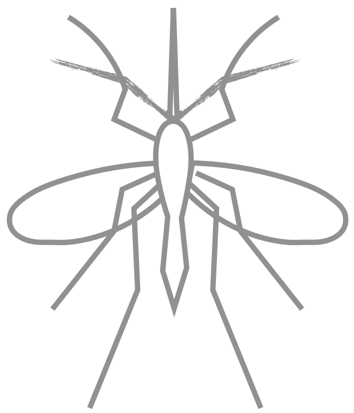
En quoi sont-ils différents des modèles statistiques?

How are these different from statistical models?

En quoi sont-ils différents des modèles statistiques?

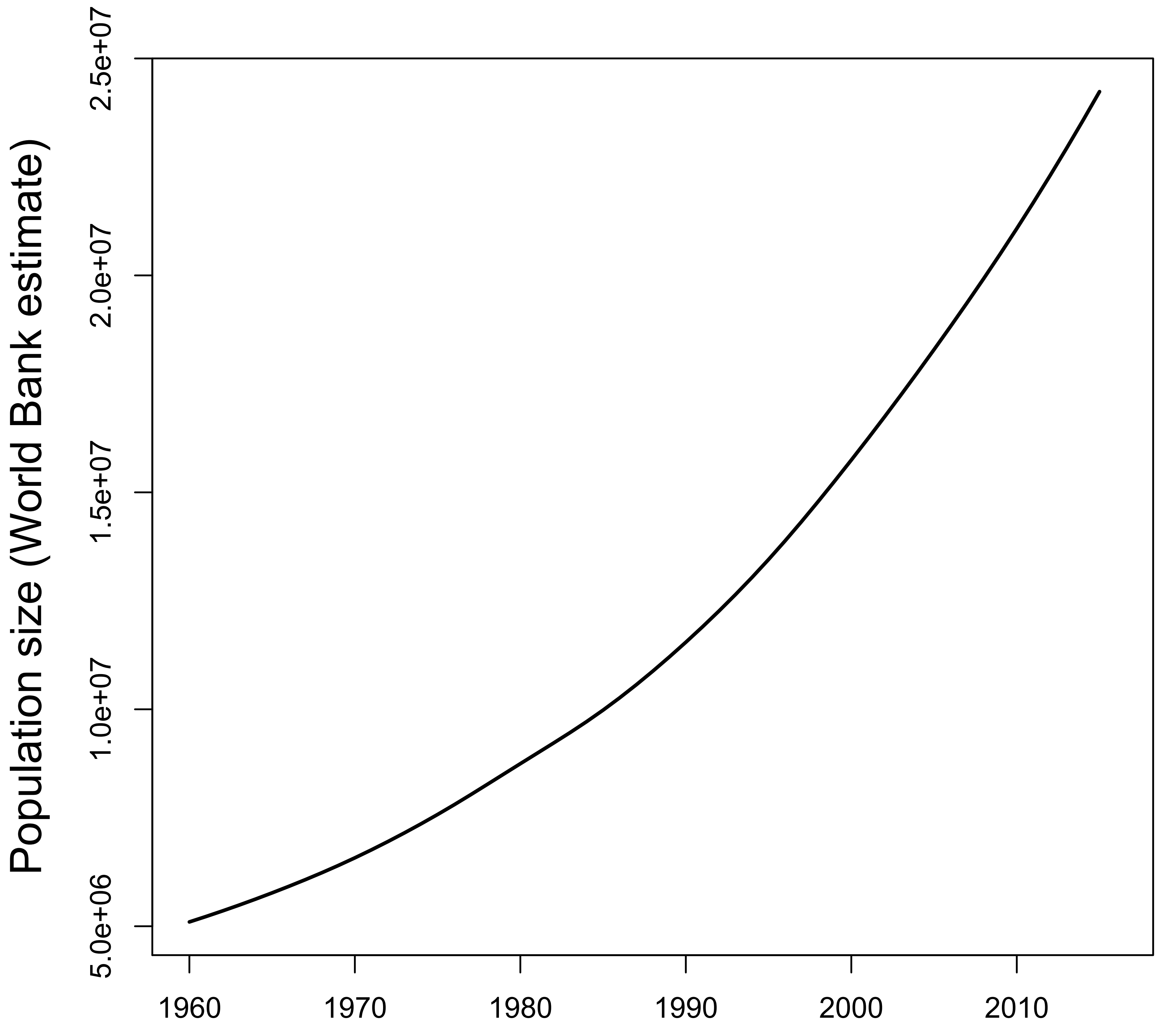
Make explicit hypotheses about biological mechanisms that drive dynamics (may not be realistic, but still explicit)

Faire des hypothèses explicites sur les mécanismes biologiques qui régissent la dynamique (peut ne pas être réaliste, mais toujours explicite)



1. Population Models
1. modèles de population

Madagascar



http://databank.worldbank.org

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

Compartmental models (Mechanistic Models)

1. Les populations sont subdivisées en compartiments
2. Les compartiments et les taux de transition sont déterminés par les systèmes biologiques
3. Taux de transition entre les compartiments sont exprimés mathématiquement

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

How could we build a compartmental model of population growth?

Comment pourrions-nous construire un modèle fragmentaire de croissance démographique?

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

Madagascar
(N)

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

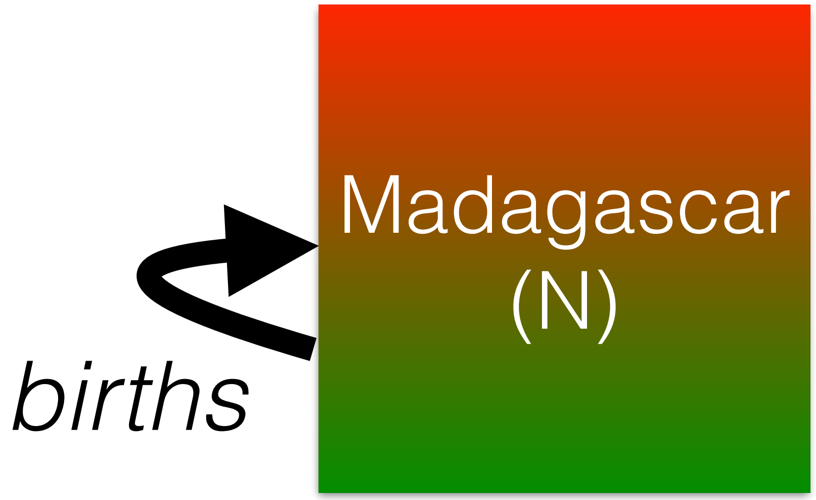
Madagascar
(N)

How does the population increase?

The basic population model

<u>Compartmental models (Mechanistic Models)</u>

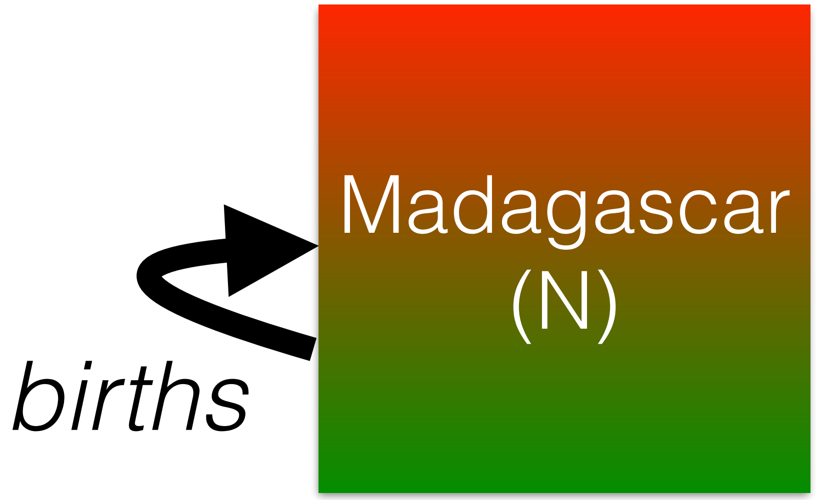
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The basic population model

<u>Compartmental models (Mechanistic Models)</u>

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

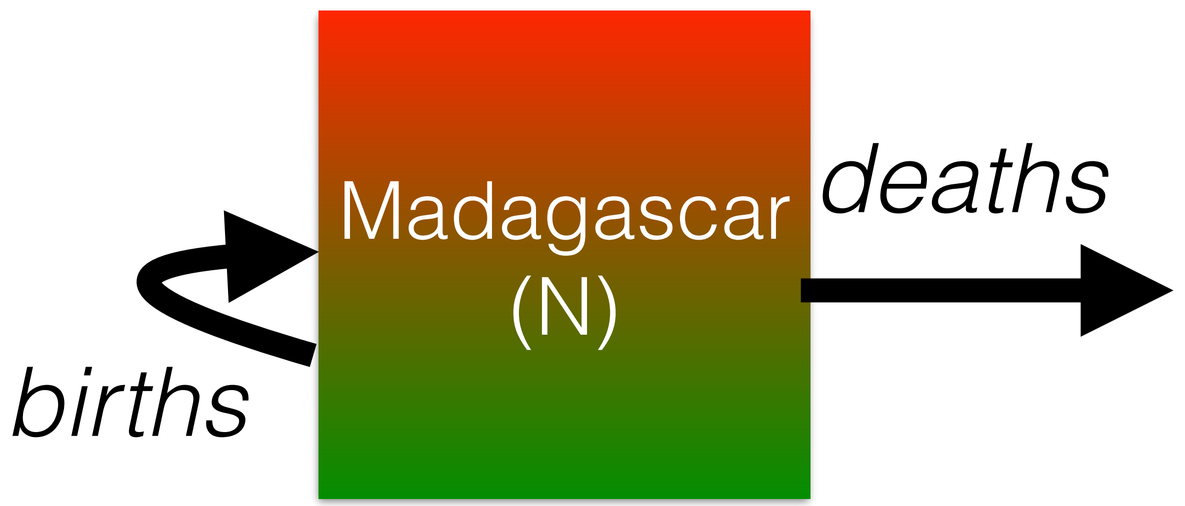


How does the population decrease?

The basic population model

Compartmental models (Mechanistic Models)

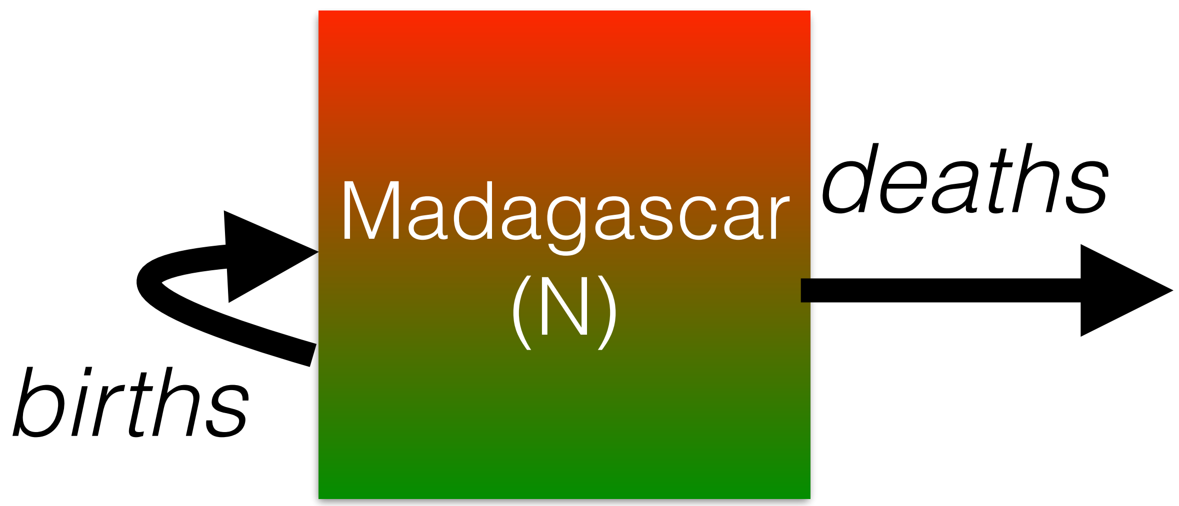
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

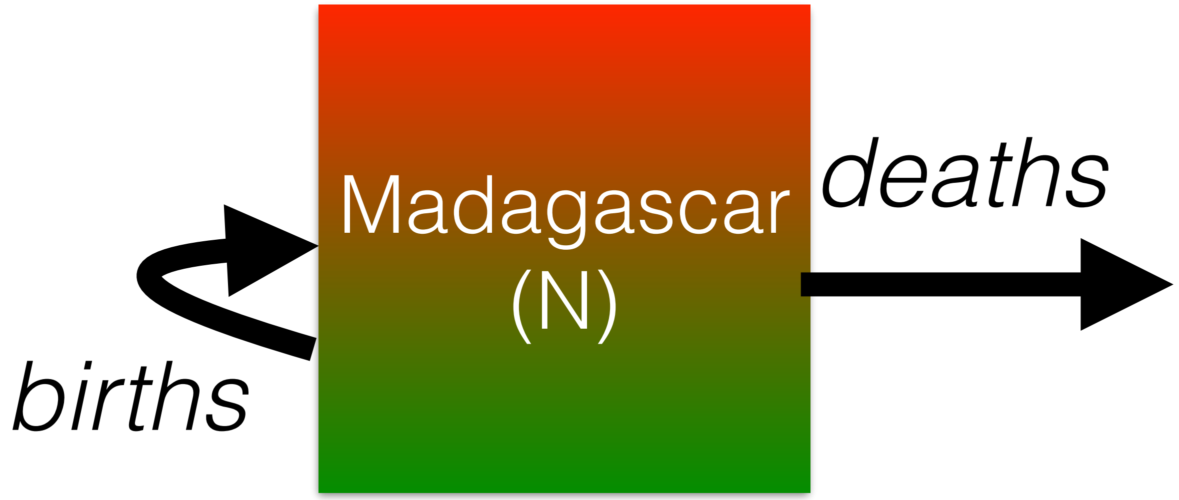


$$N_{t+1} =$$

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

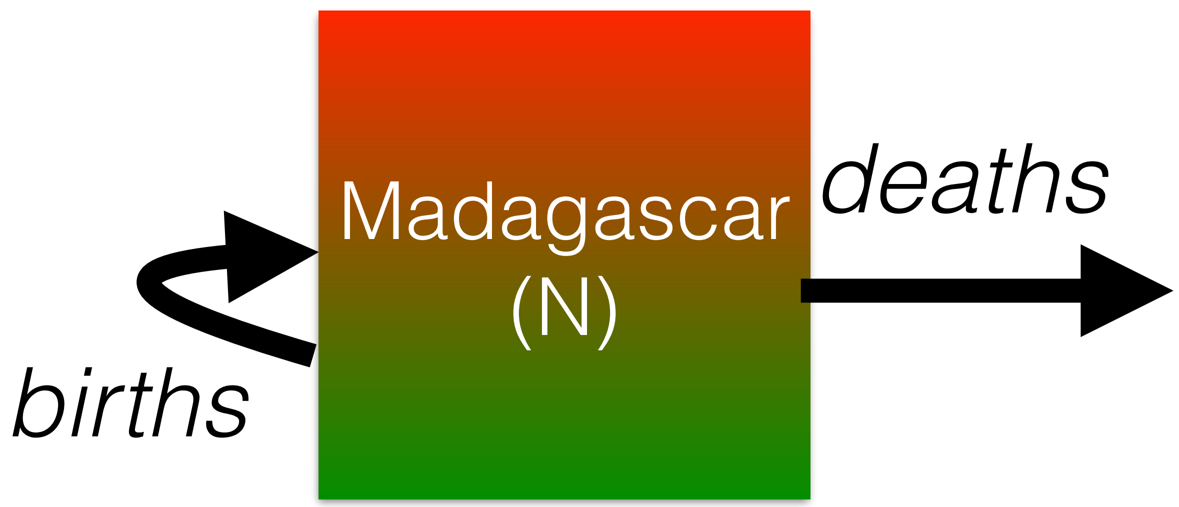


N_{t+1}=births*N_t.

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

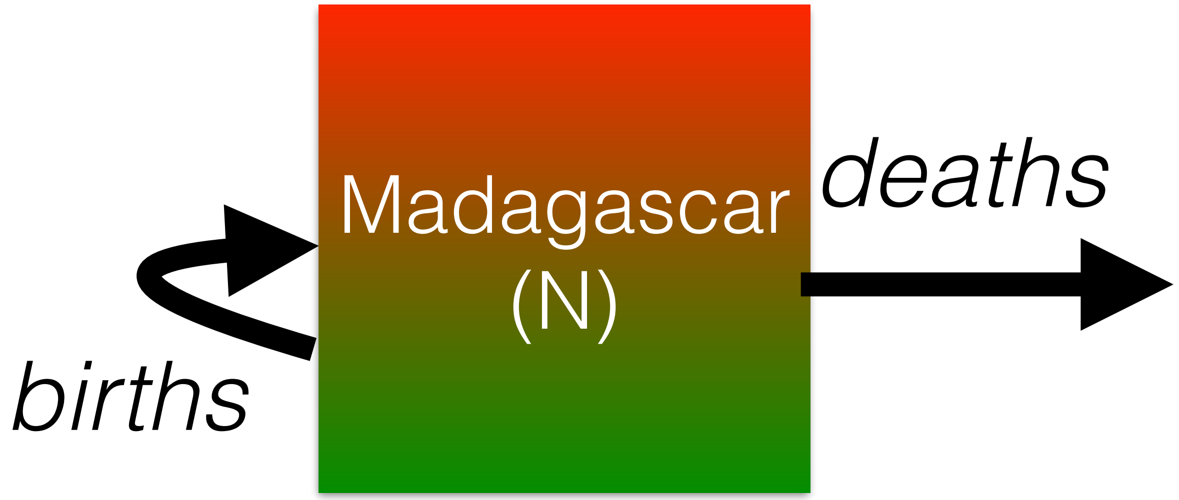


$$N_{t+1}=\text{births}*N_t-\text{deaths}*N_t$$

The basic population model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

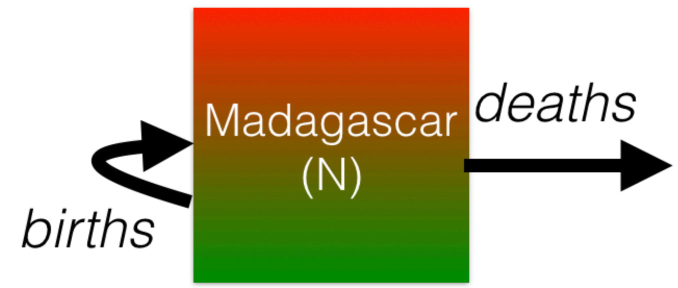


$$N_{t+1}=births*N_t-deaths*N_t$$

$$N_{t+1}=(births-deaths)*N_t$$

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

The basic population model



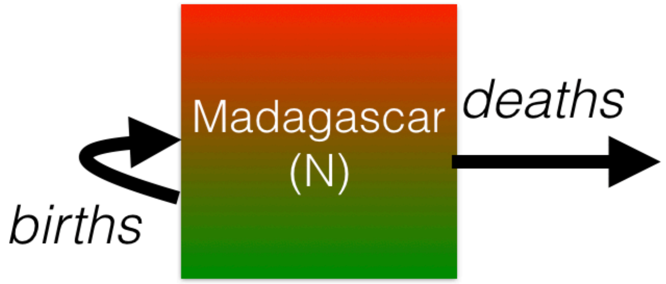
$$\lambda = N_{t+1}/N_t$$

Population rate of increase

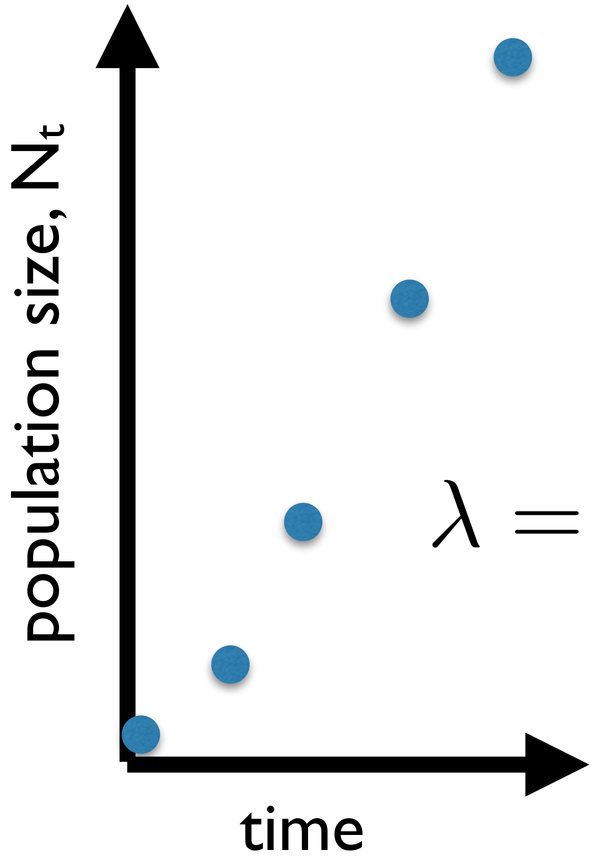
pop size at t

pop size at t+1

The basic population model



Discrete time



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

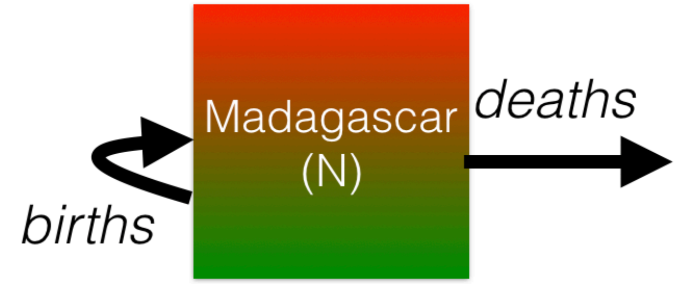
$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

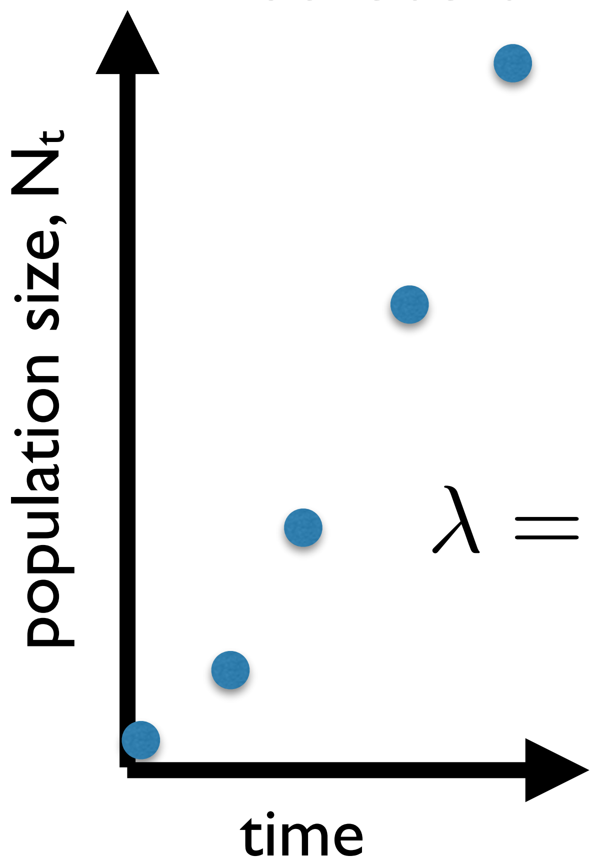
$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

The basic population model



Discrete time



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

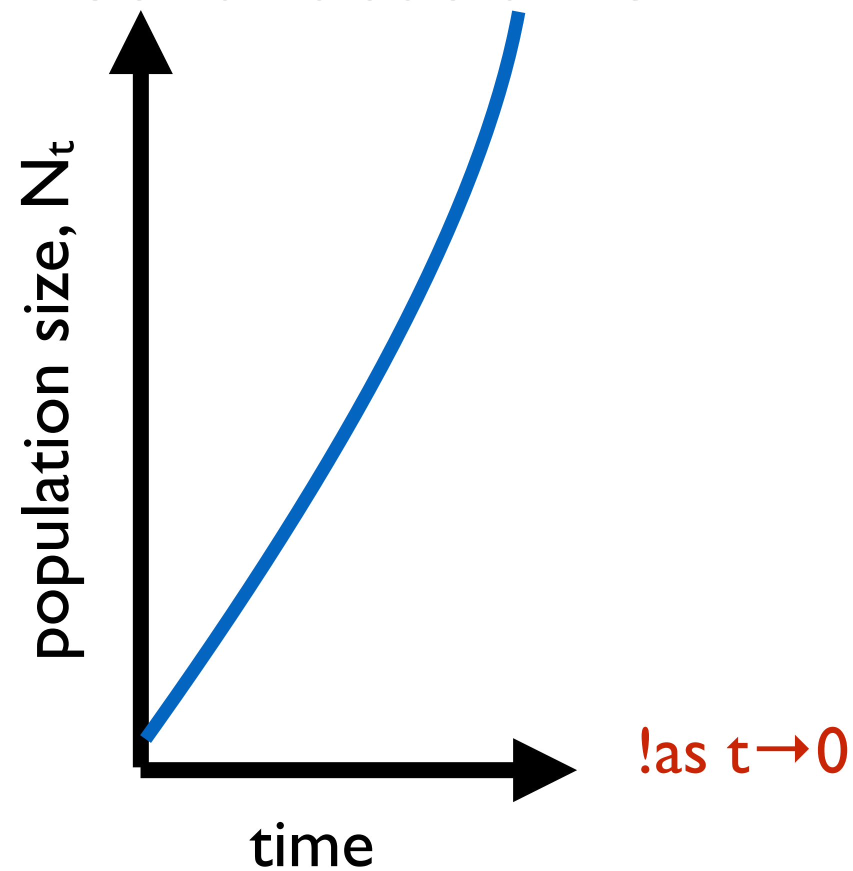
$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

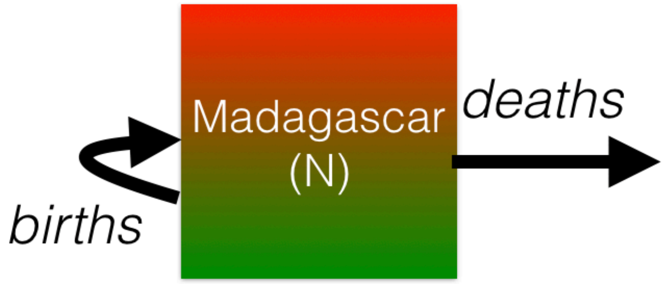
Continuous time



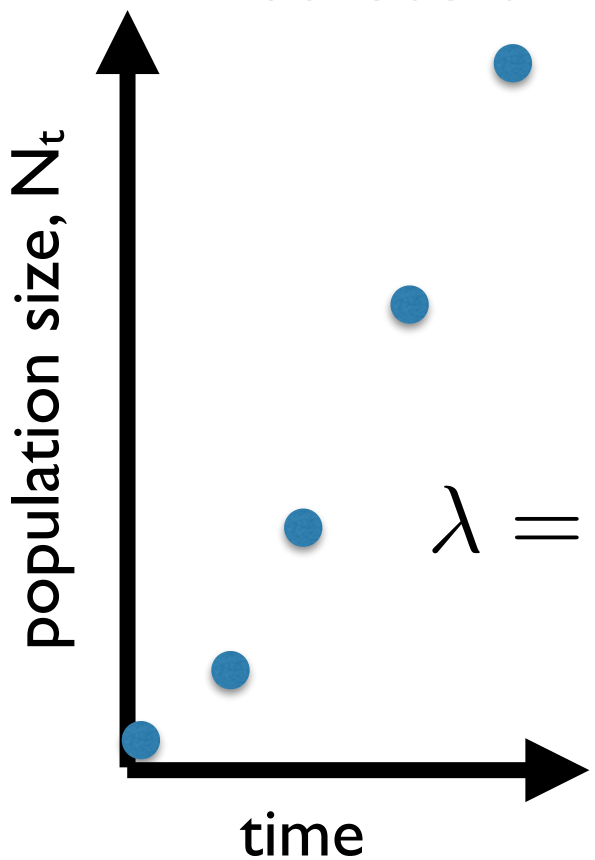
$dP/dt = rP$

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

The basic population model



Discrete time



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

$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

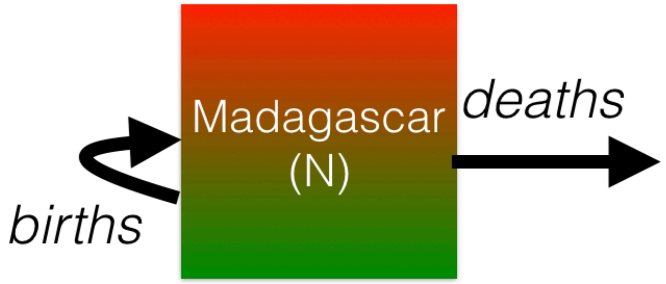
$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

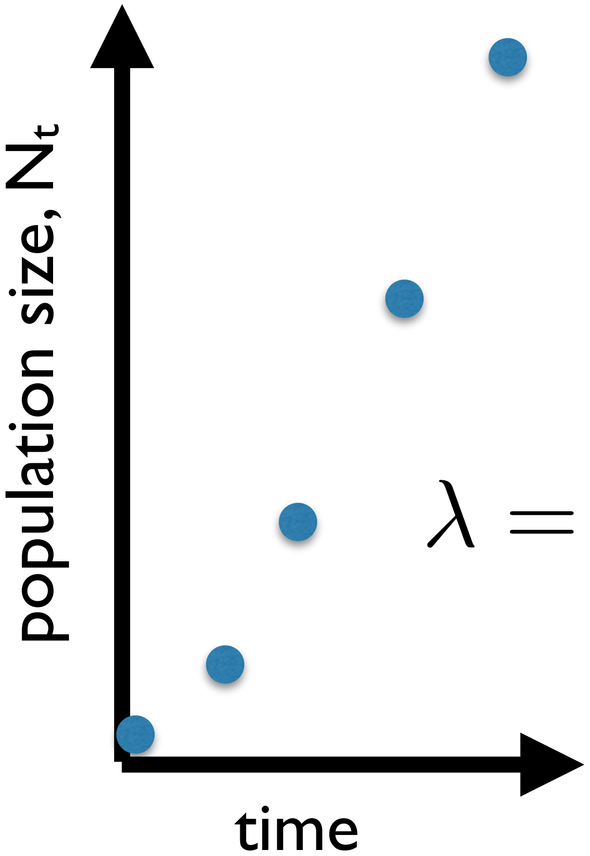
Continuous time

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

The basic population model



Discrete time



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

$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

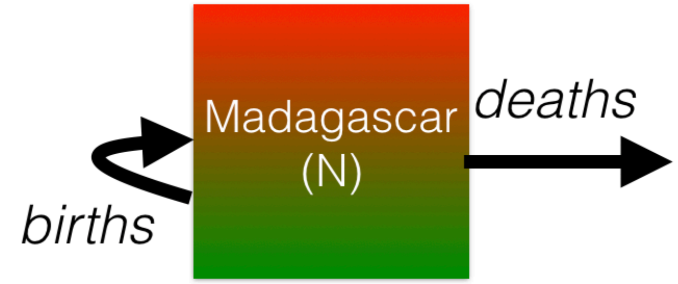
Continuous time

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

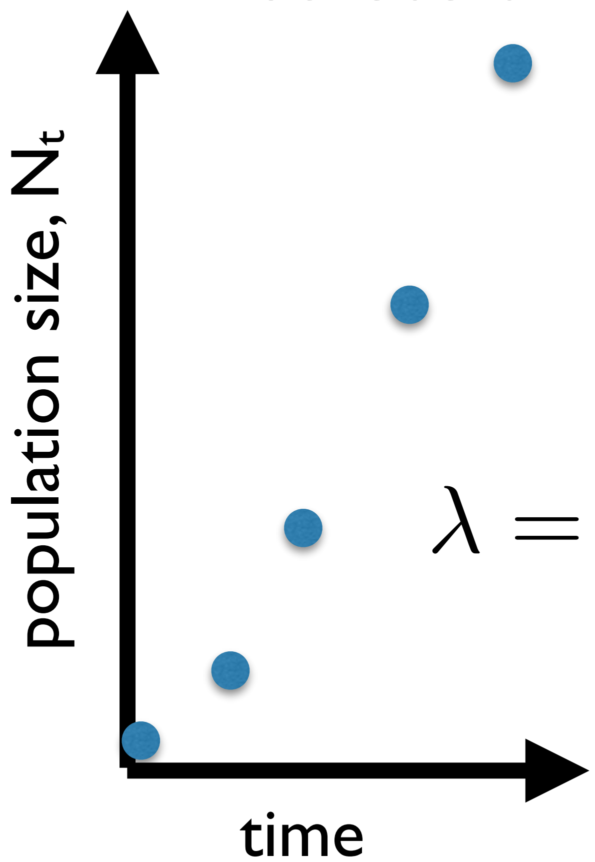
Separation of variables:

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

The basic population model



Discrete time



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

$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

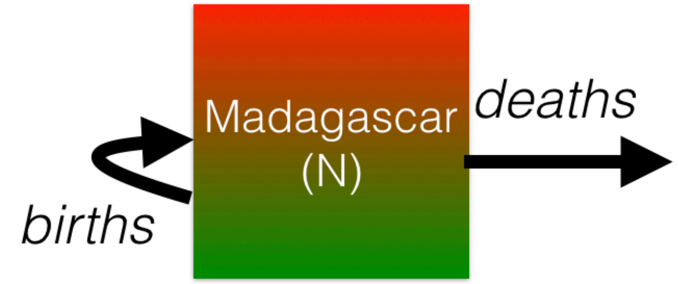
Continuous time

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

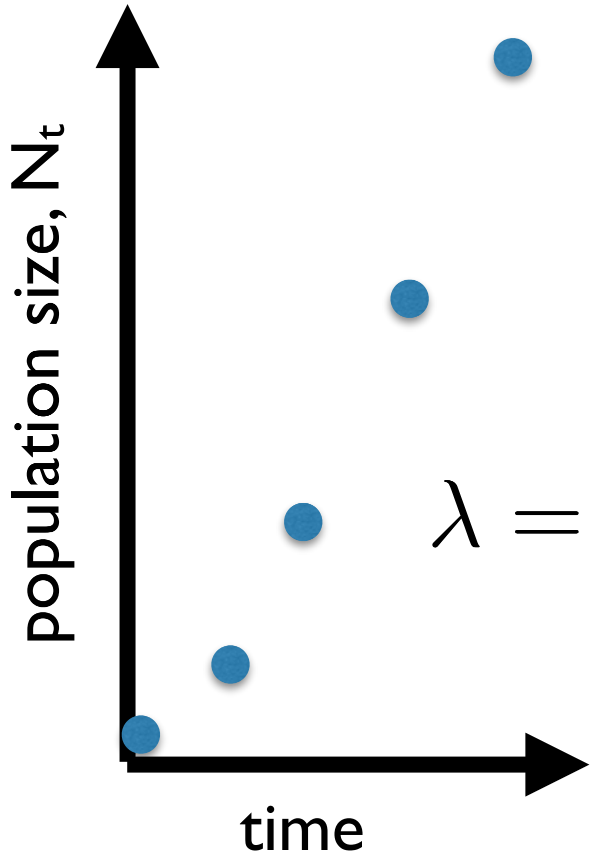
Separation of variables:
$dP(t)/P(t) = r\ dt$

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

The basic population model



Discrete time



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

$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

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:

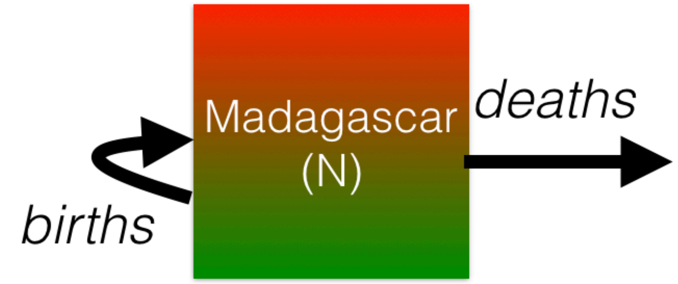
$\log(P(t)) = rt + c$

Take exponentials:

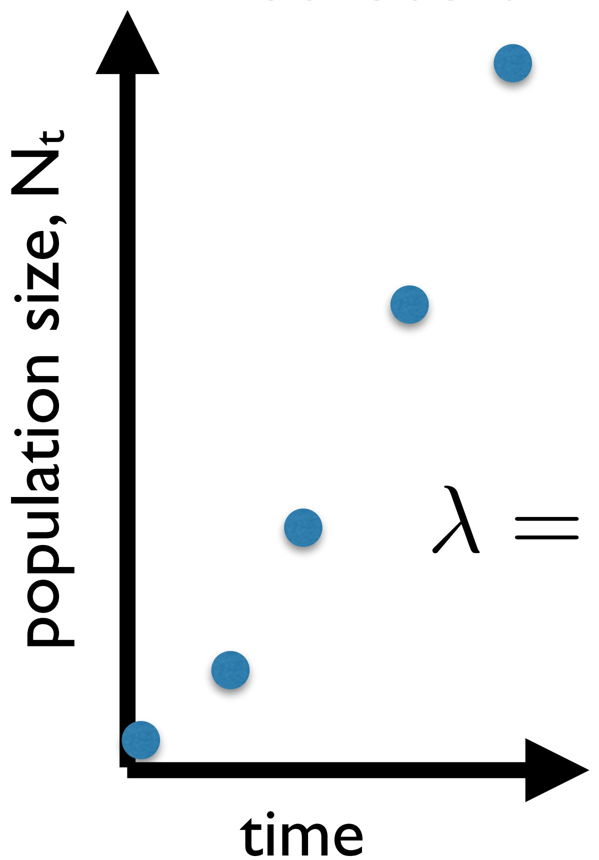
$P(t) = e^{rt + c} = Ce^{rt}$

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

The basic population model



Discrete time



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

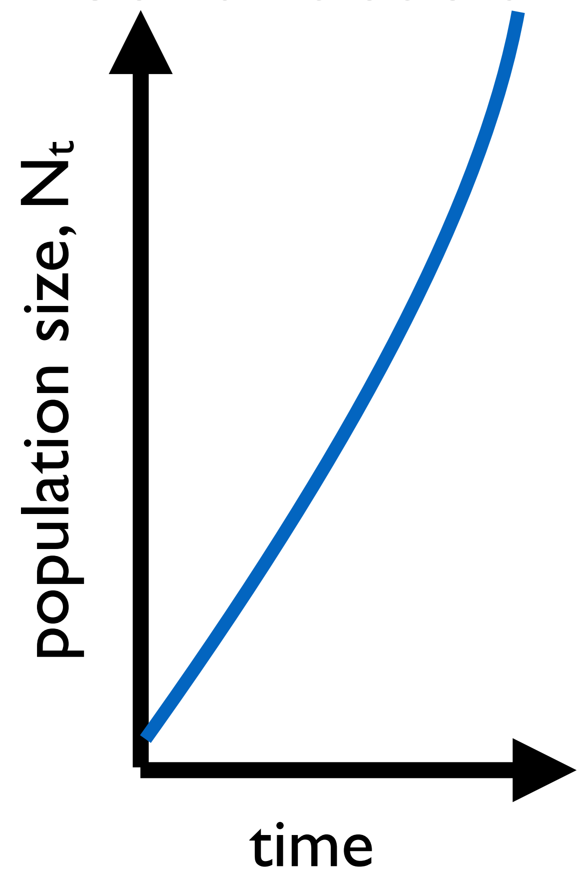
$N_1 = \lambda N_0$

$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$

$N_3 = \lambda^3 N_0$

$\boxed{N_t = \lambda^t N_0}$

Continuous time

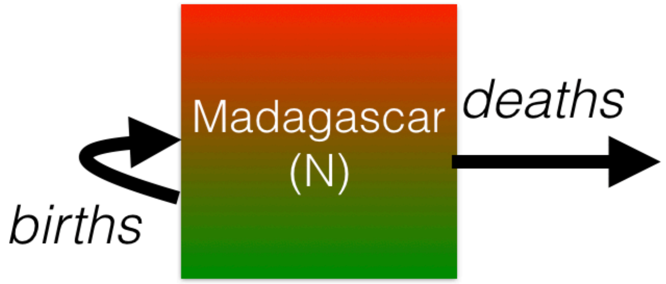


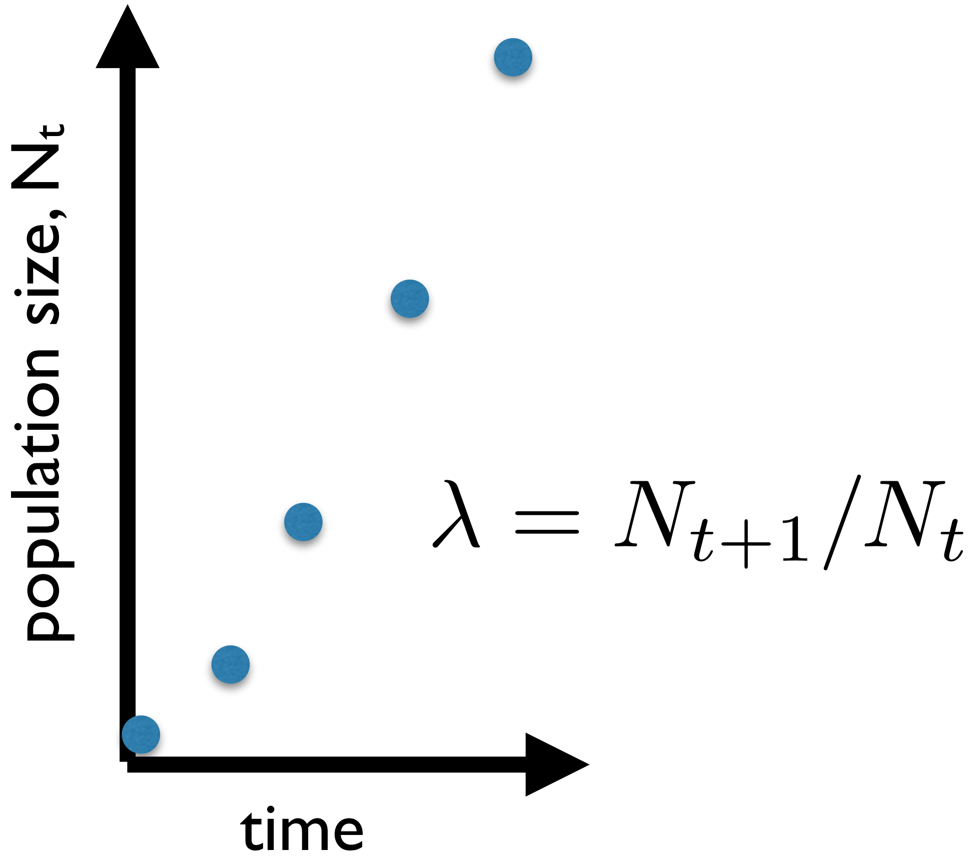
!as t→0

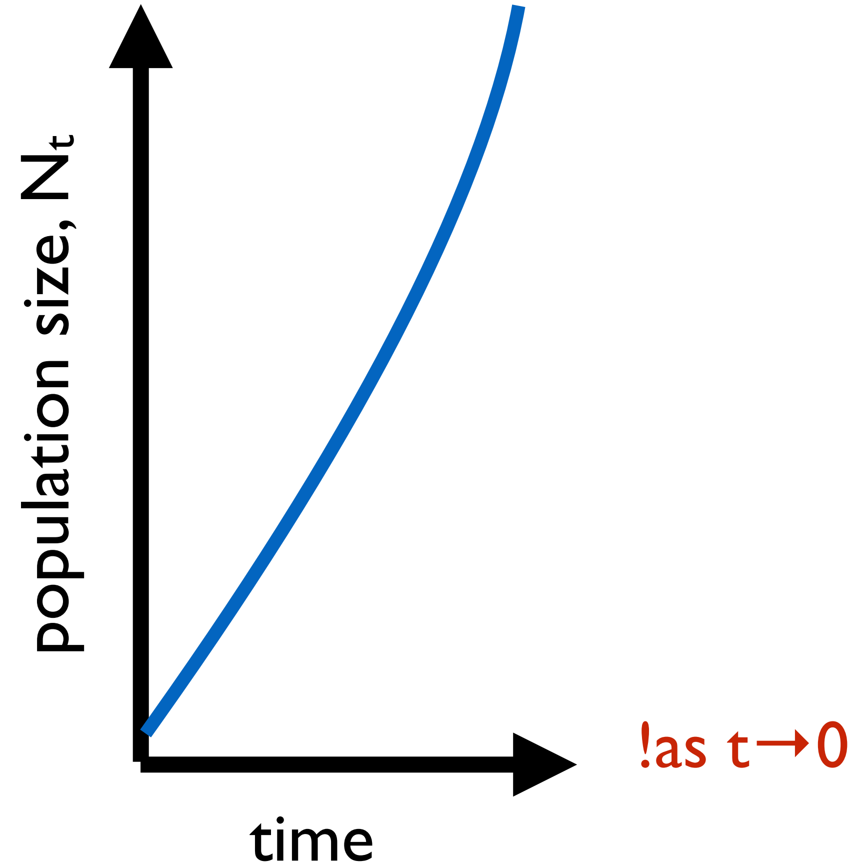
$dP(t)/dt = rP(t)$

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

The basic population model







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

The basic population model

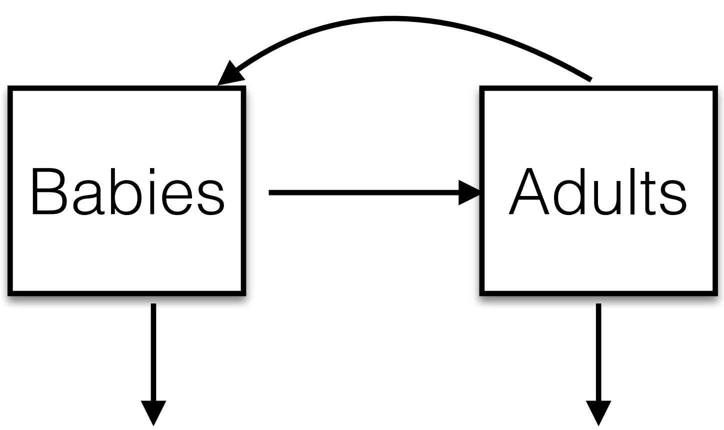
$$\lambda = N_{t+1}/N_t$$

Population rate of increase

pop size at t

pop size at t+1

Structured population model



The basic population model

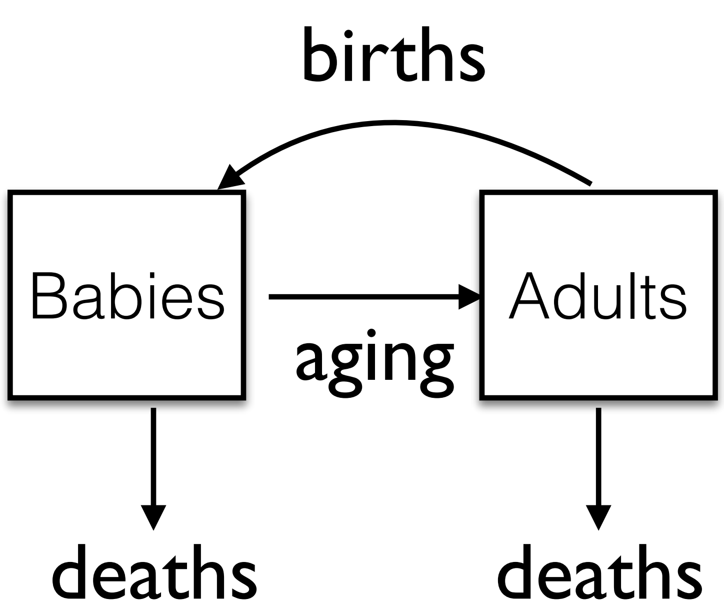
$$\lambda = N_{t+1}/N_t$$

Population rate of increase

pop size at t

pop size at t+1

Structured population model



The basic population model

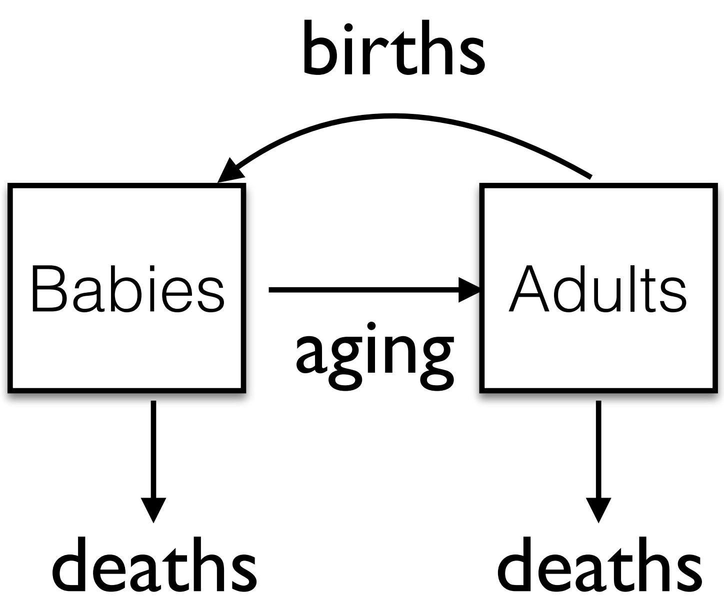
$$\lambda = N_{t+1}/N_t$$

Population rate of increase

pop size at t

pop size at t+1

Structured population model



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

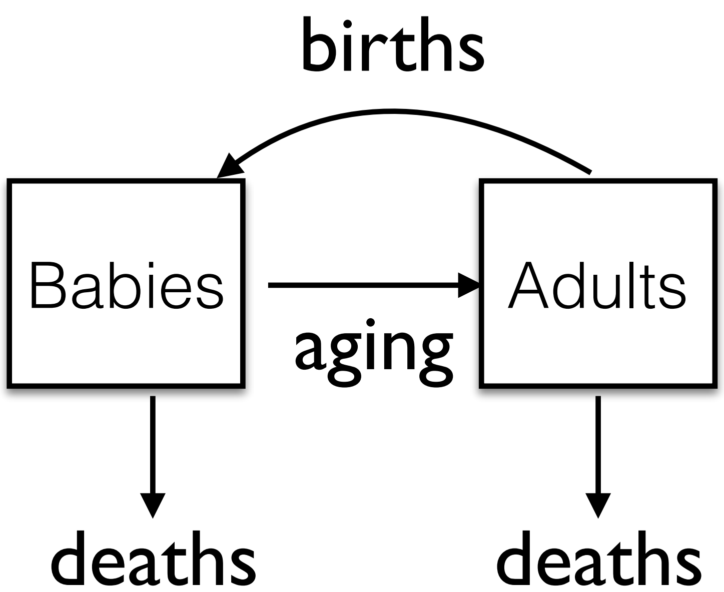
vector of population sizes

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

*discrete time

The basic population model

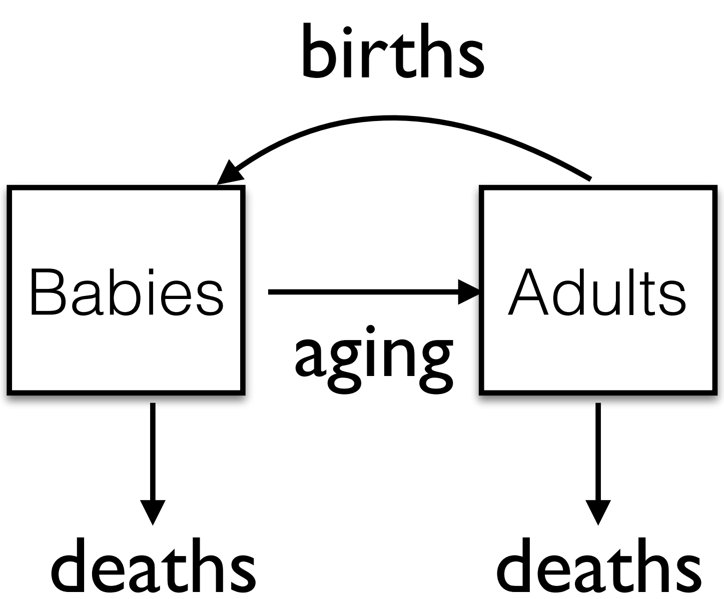
Structured population model



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

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

The basic population model



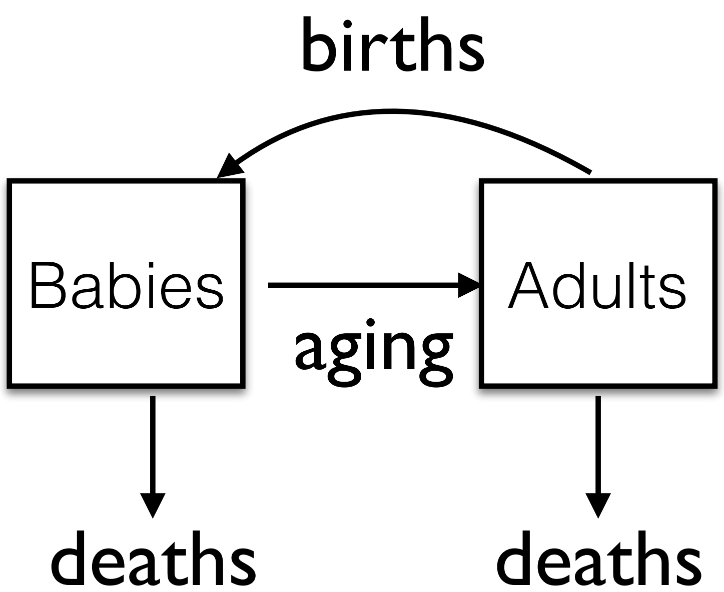
Structured population model

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

Population growth will depend on population structure

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

The basic population model



Structured population model

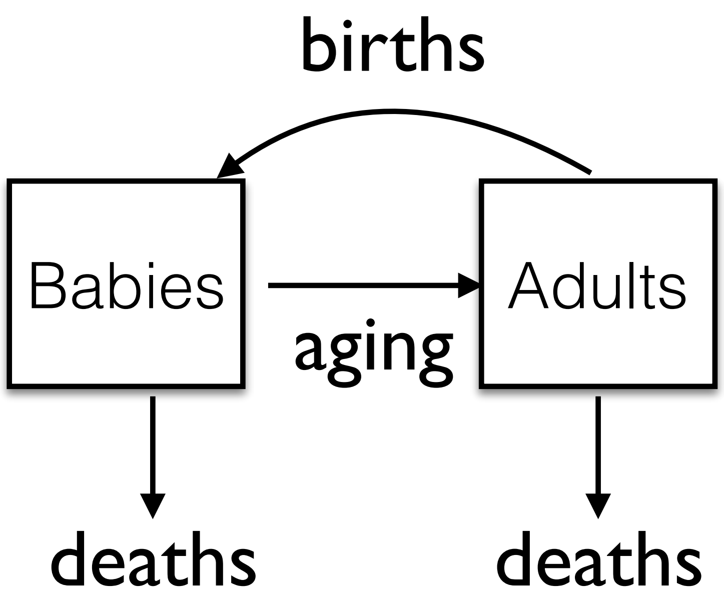
$$\mathbf{n_{t+1}} = \mathbf{A}\,\mathbf{n_t}$$

Dominant eigenvalue provides growth rate at equilibrium

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

The basic population model

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.

‡Current Address: Yale School of Forestry and Environmental Studies, 205 Prospect Street, New Haven, CT 06520, U.S.A.

Key concepts

-Continuous vs. discrete models

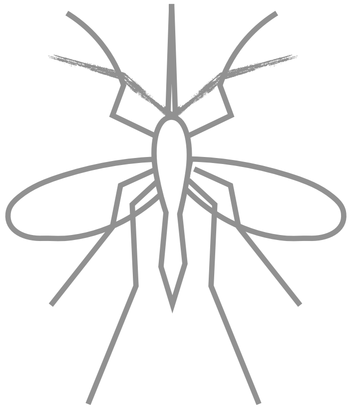
Modèles en temps continue vs. modèles en temps discret

-Deterministic vs. stochastic models

Modèles détérministique vs. stochastique

-Structured models

Modèles structurés .



2. Predator-Prey Models

The predator prey model

Compartmental models (Mechanistic Models)

1. Les populations sont subdivisées en compartiments
2. Les compartiments et les taux de transition sont déterminés par les systèmes biologiques
3. Taux de transition entre les compartiments sont exprimés mathématiquement

How could we build a compartmental model of two animals: a predator (fosa) and prey (rabbit)?

Comment pourrions-nous construire un modèle compartimenté de deux animaux: un prédateur (fosa) et une proie (lapin)?

The predator prey model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

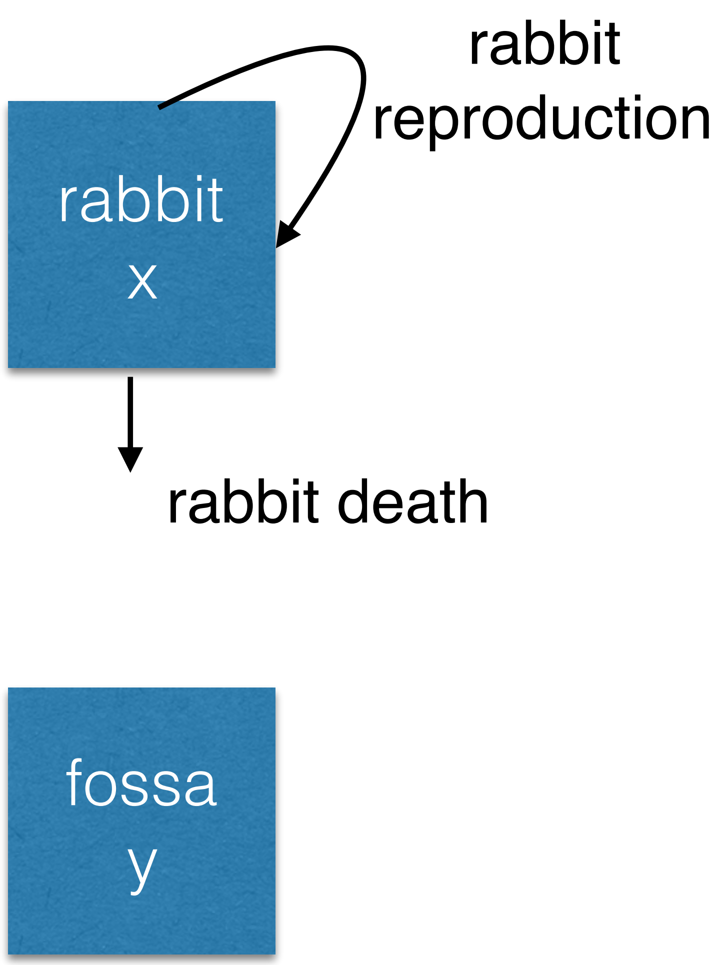
rabbit
x

fossa
y

The predator prey model

Compartmental models (Mechanistic Models)

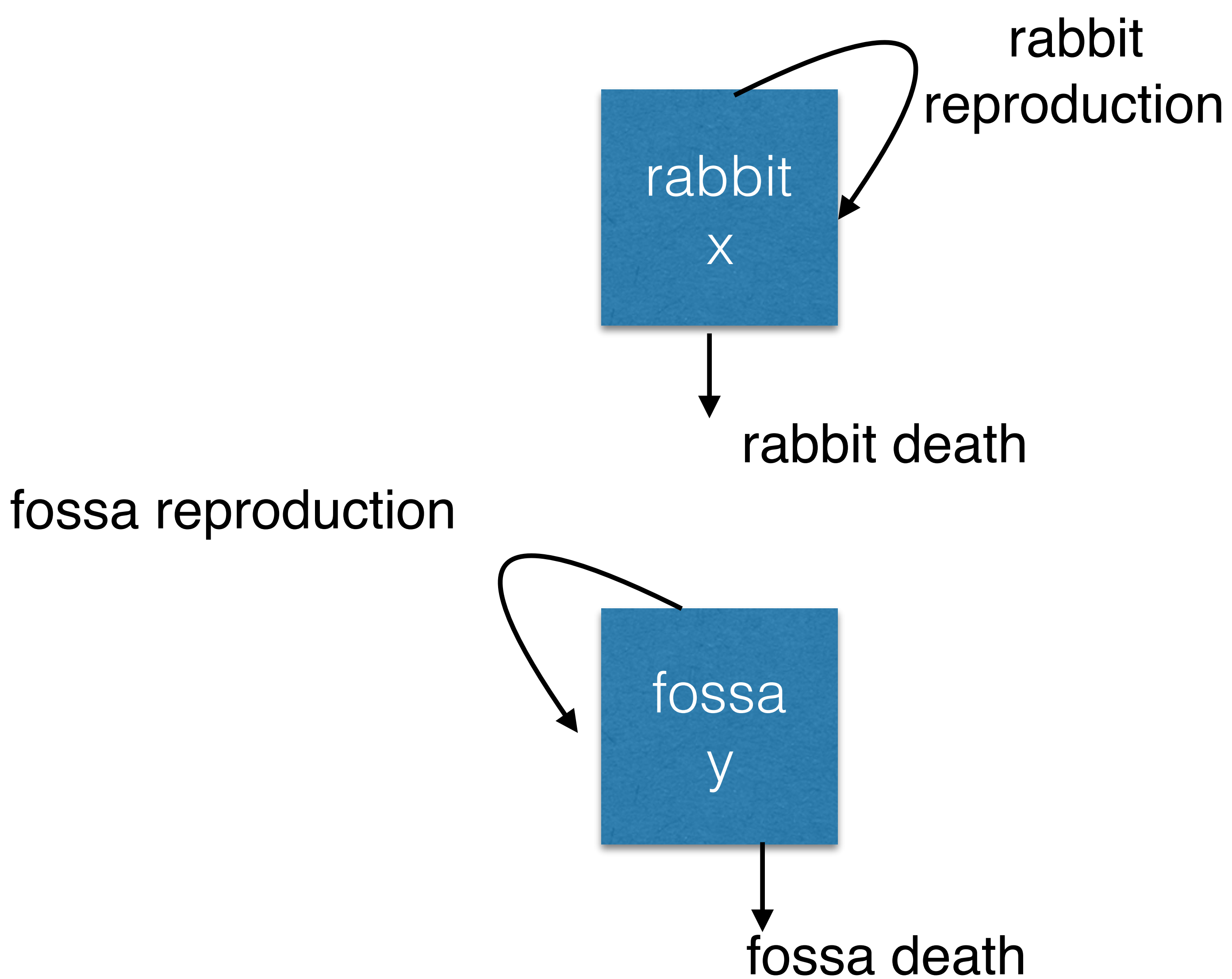
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The predator prey model

Compartmental models (Mechanistic Models)

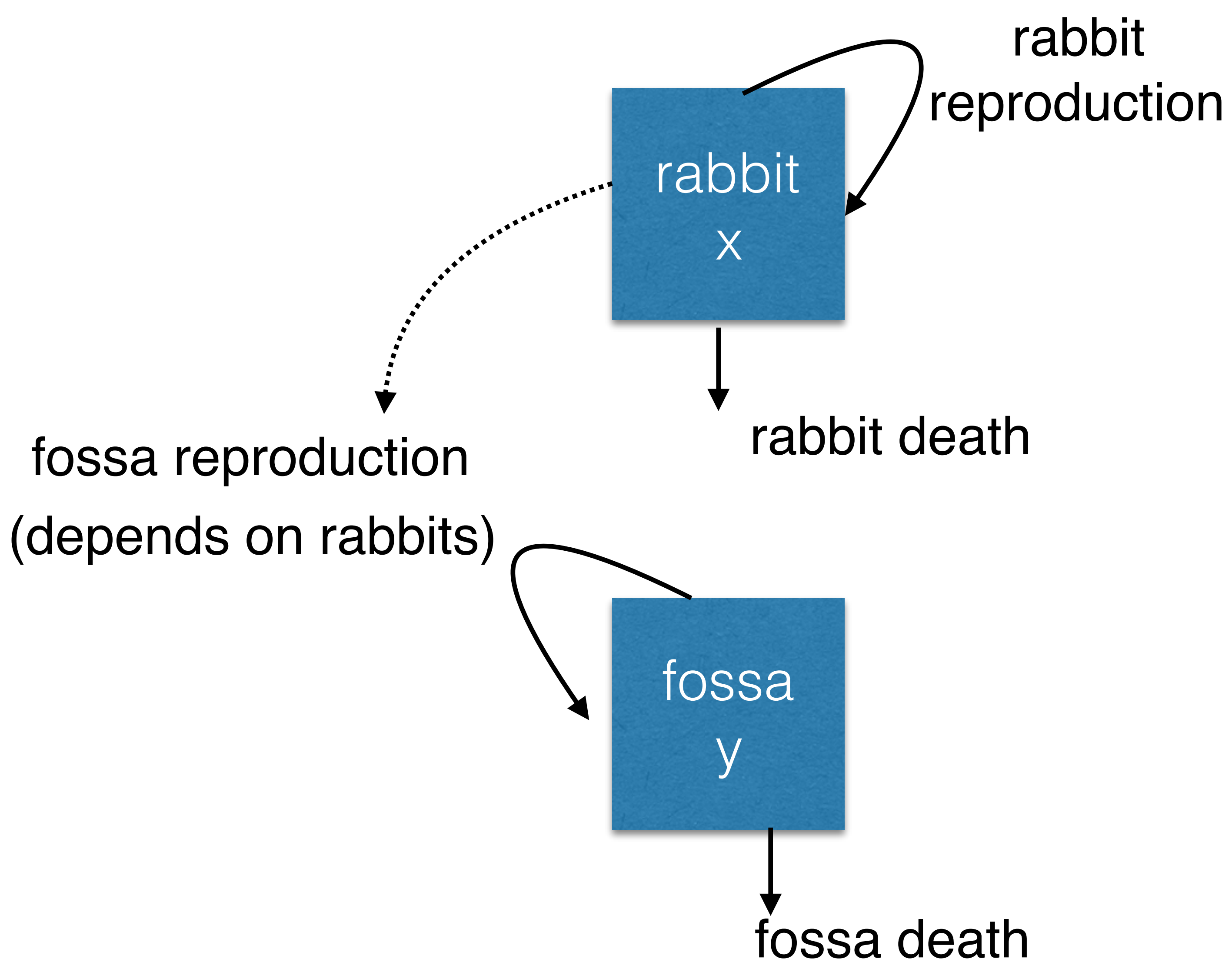
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The predator prey model

Compartmental models (Mechanistic Models)

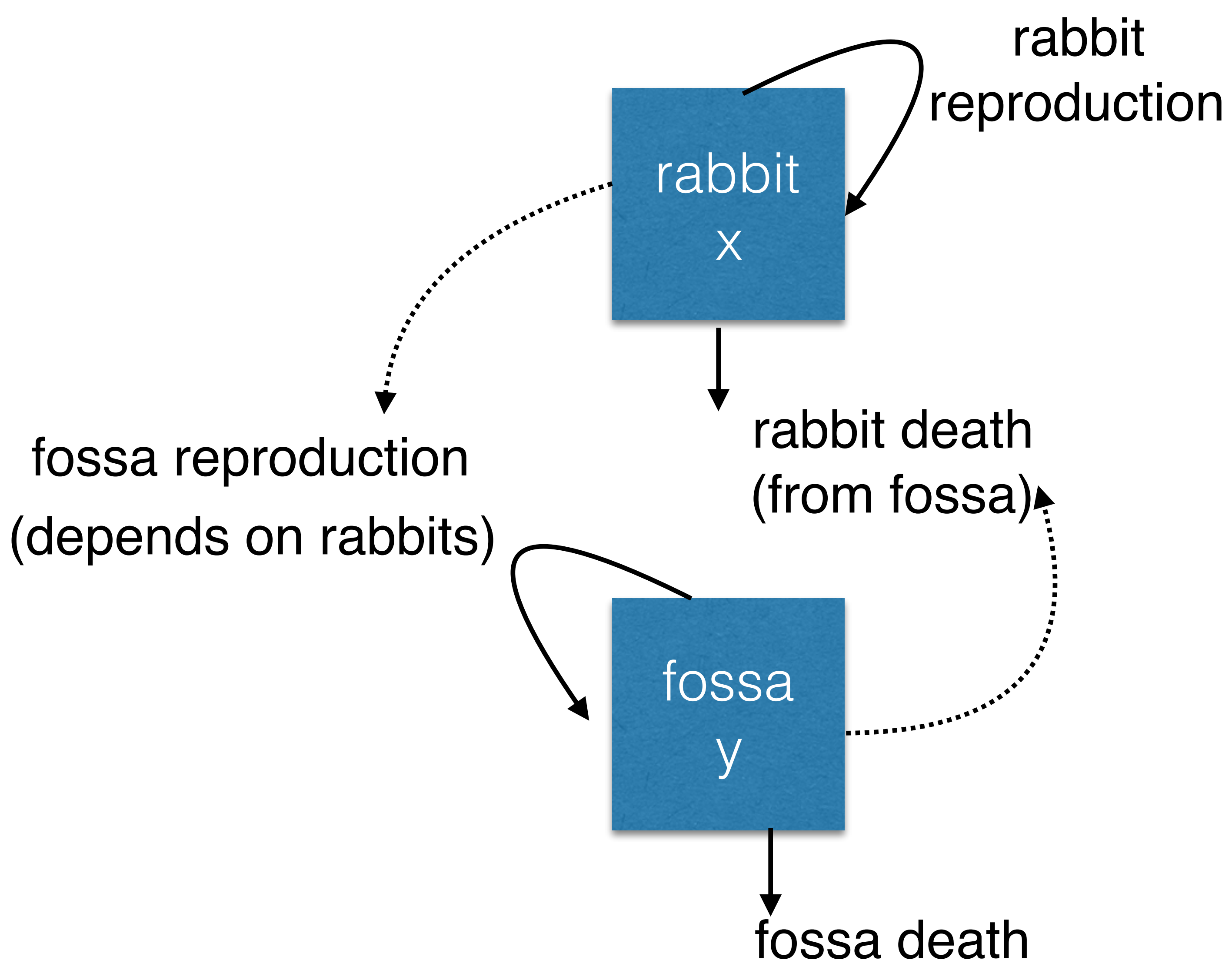
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The predator prey model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The predator prey model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

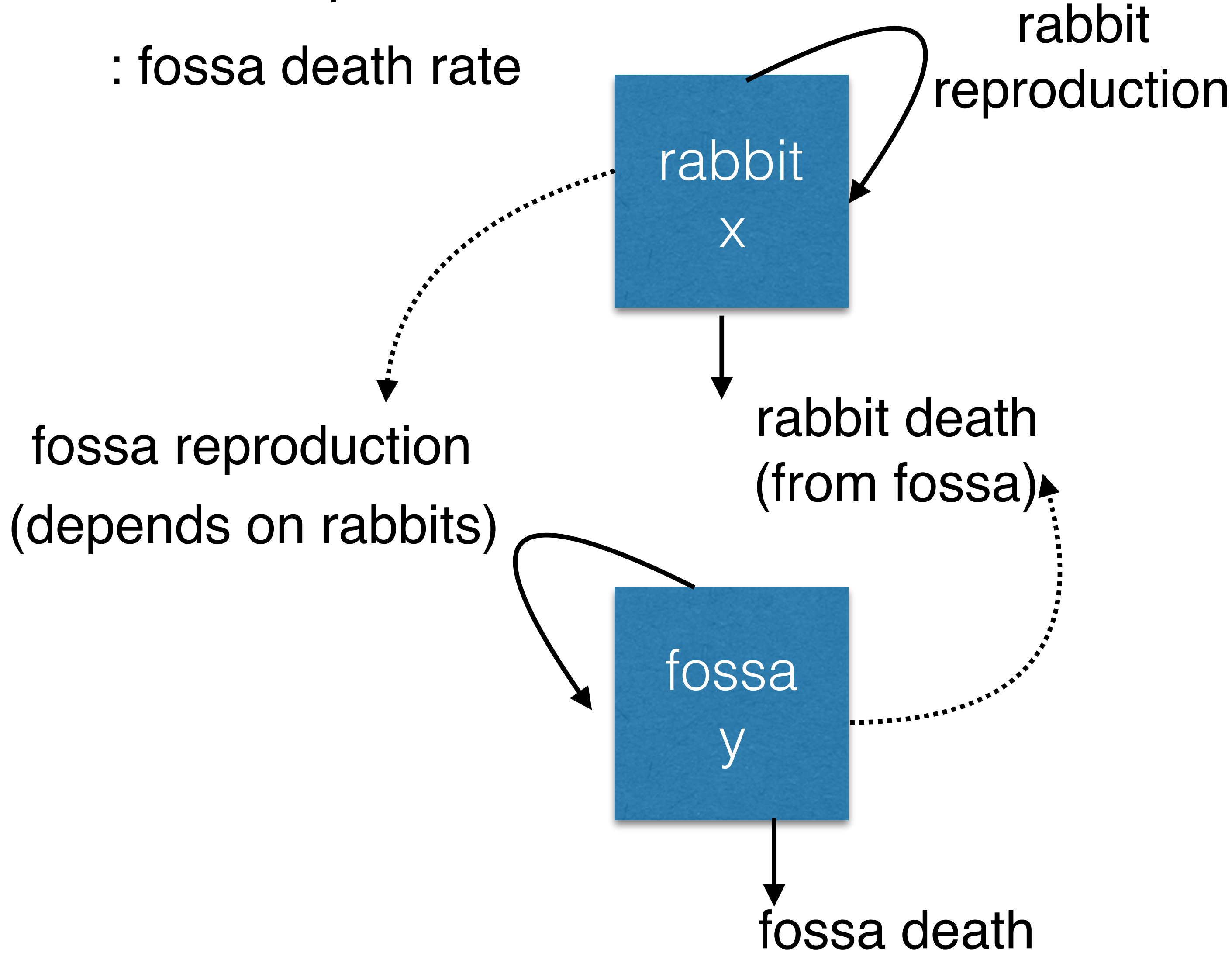
Parameters

: rabbit rep. rate

: rabbit death rate

: fossa rep. rate

: fossa death rate



The predator prey model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

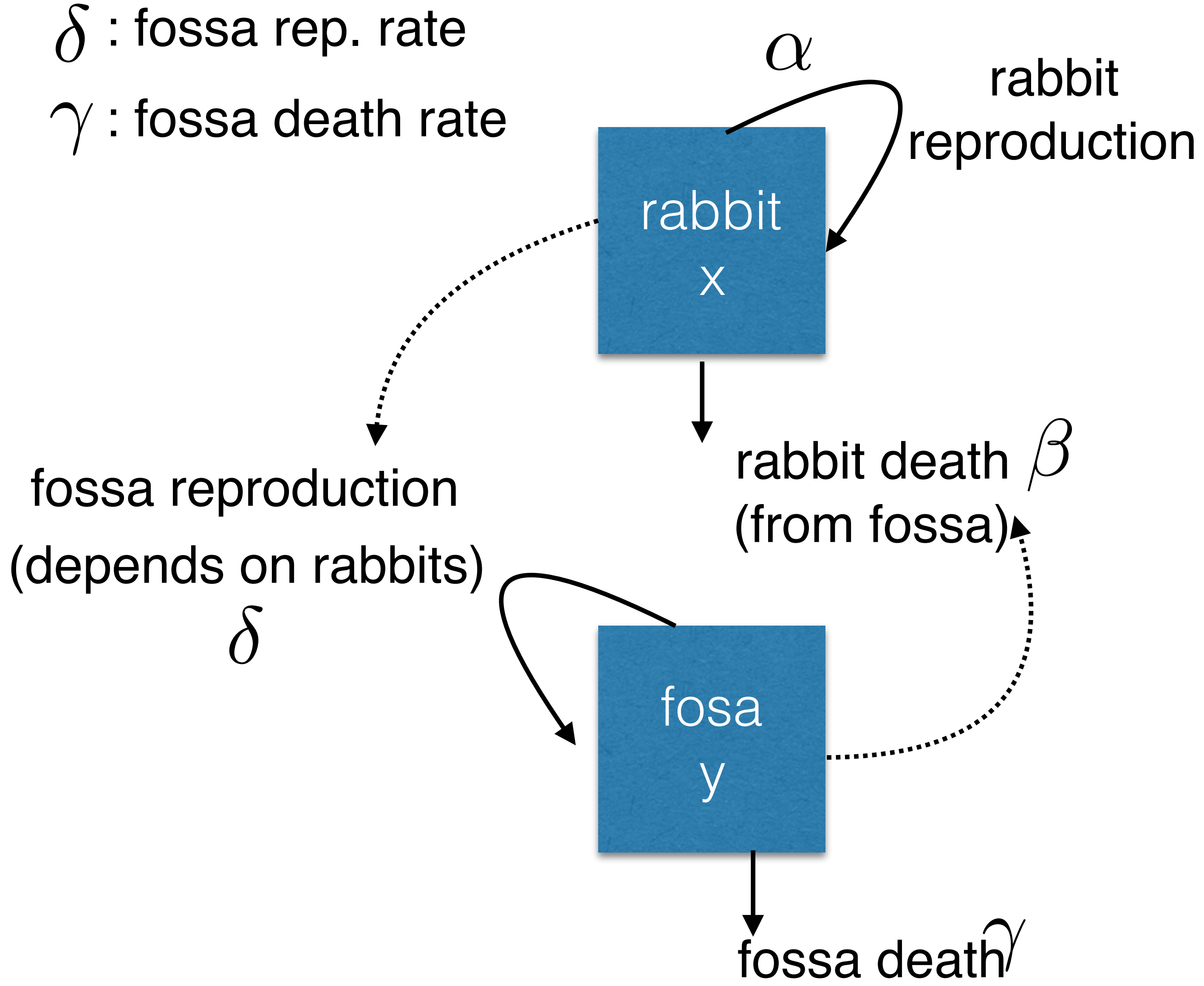
Parameters

α : rabbit rep. rate

β : rabbit death rate

δ : fossa rep. rate

γ : fossa death rate



The predator prey model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

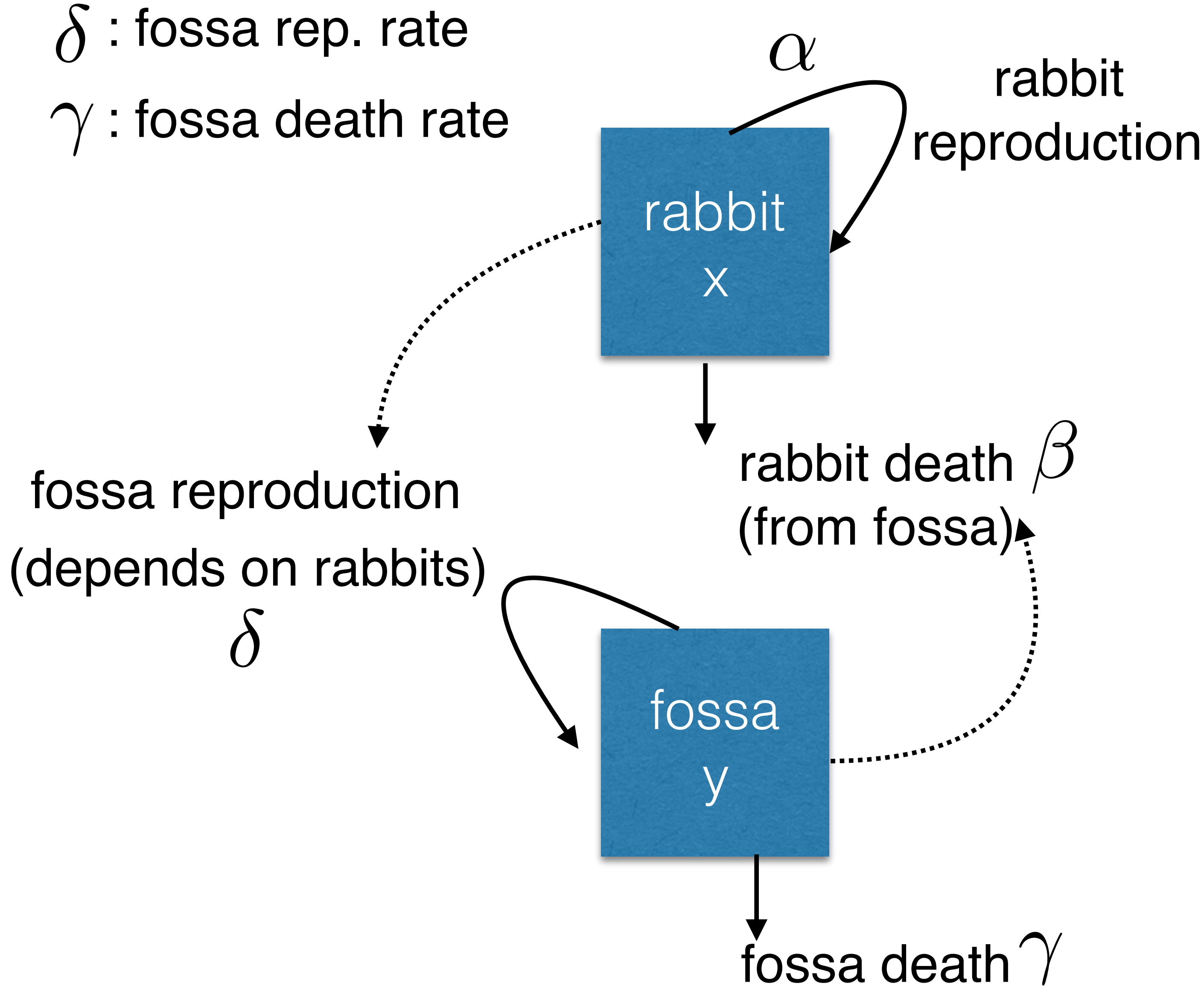
Parameters

α : rabbit rep. rate

β : rabbit death rate

δ : fossa rep. rate

γ : fossa death rate



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

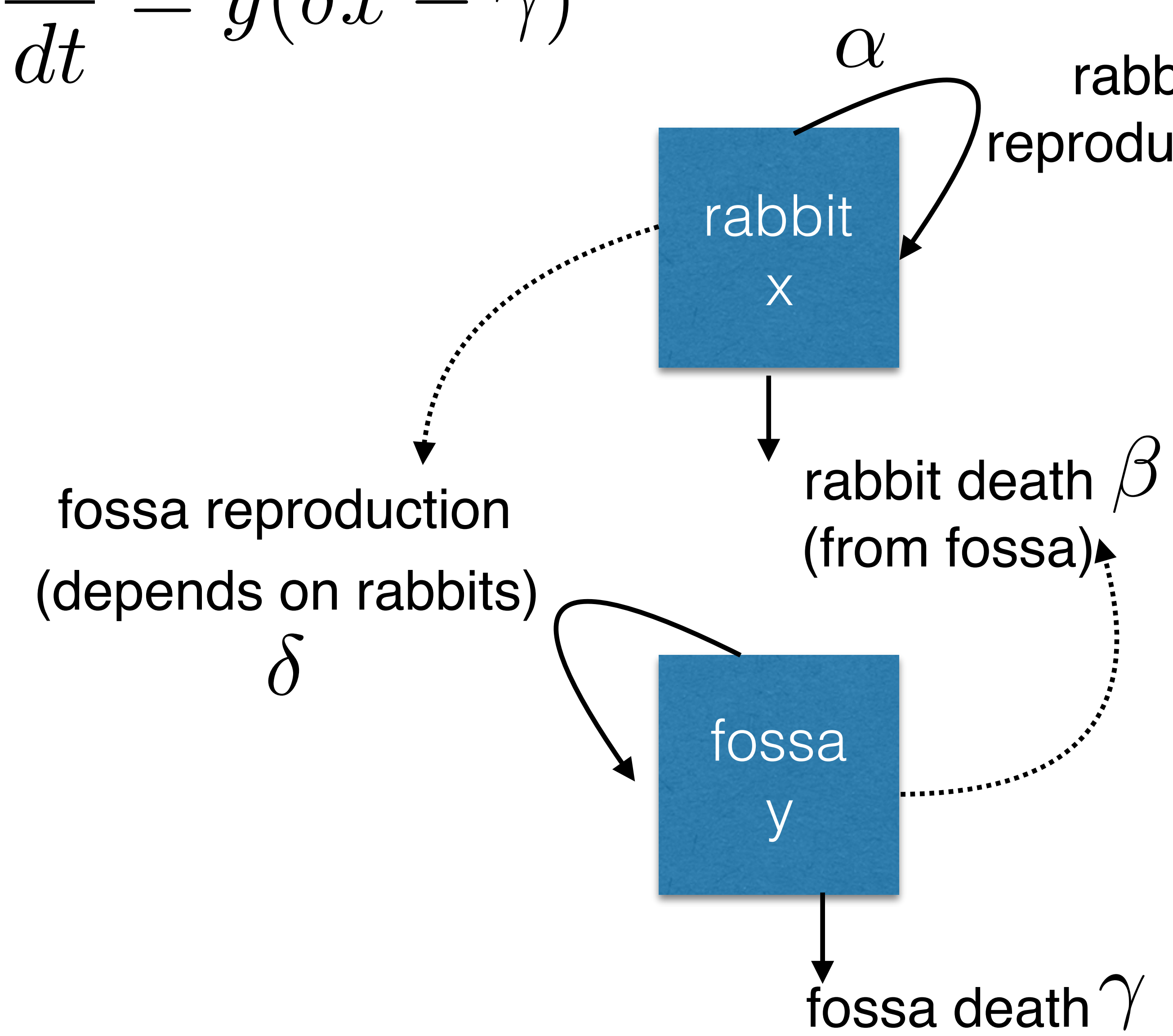
$$\frac{dy}{dt} = y(\delta x - \gamma)$$

The predator prey model

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

Compartmental models (Mechanistic Models)

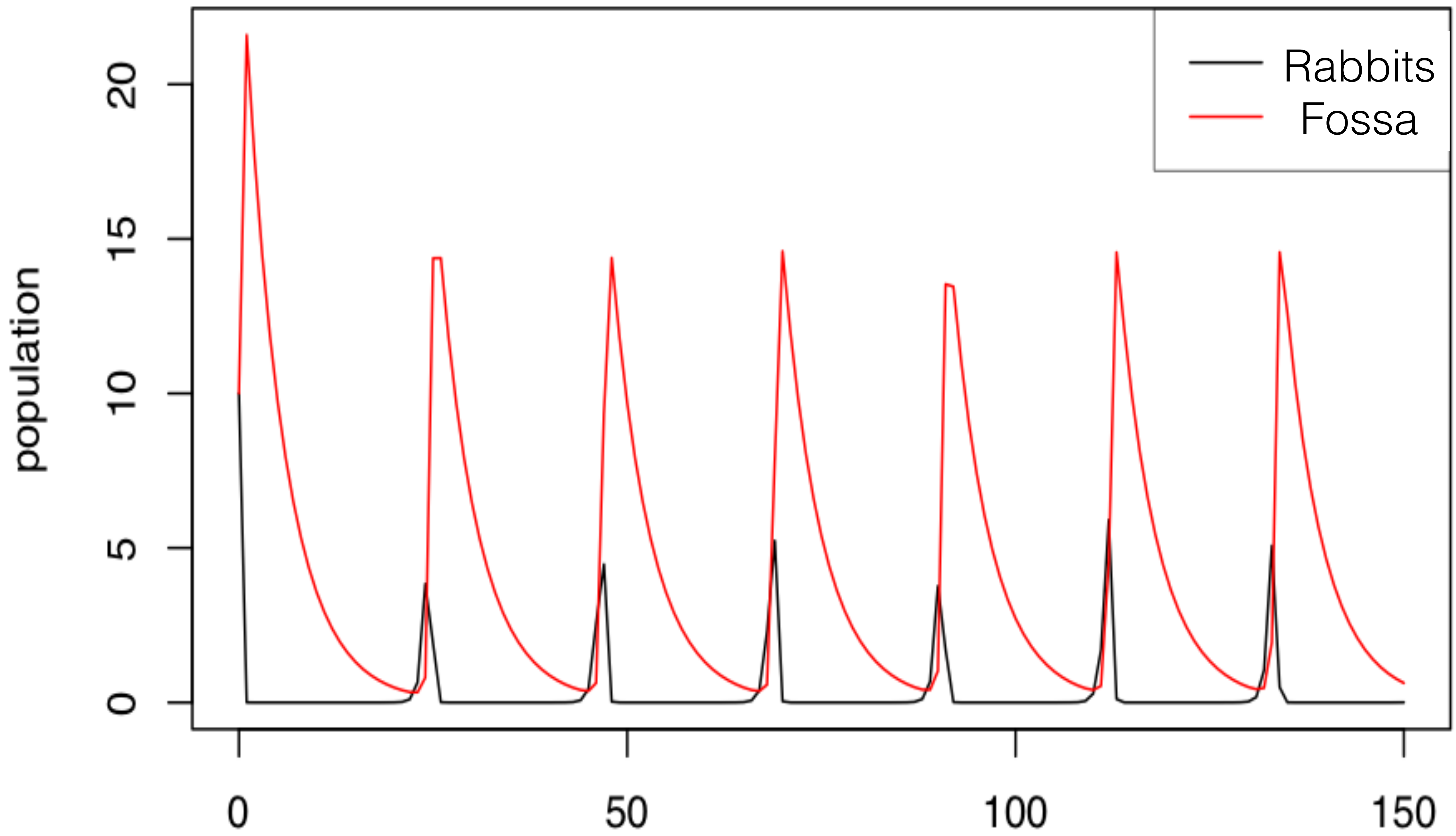
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



SOME ASSUMPTIONS

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

The predator prey model



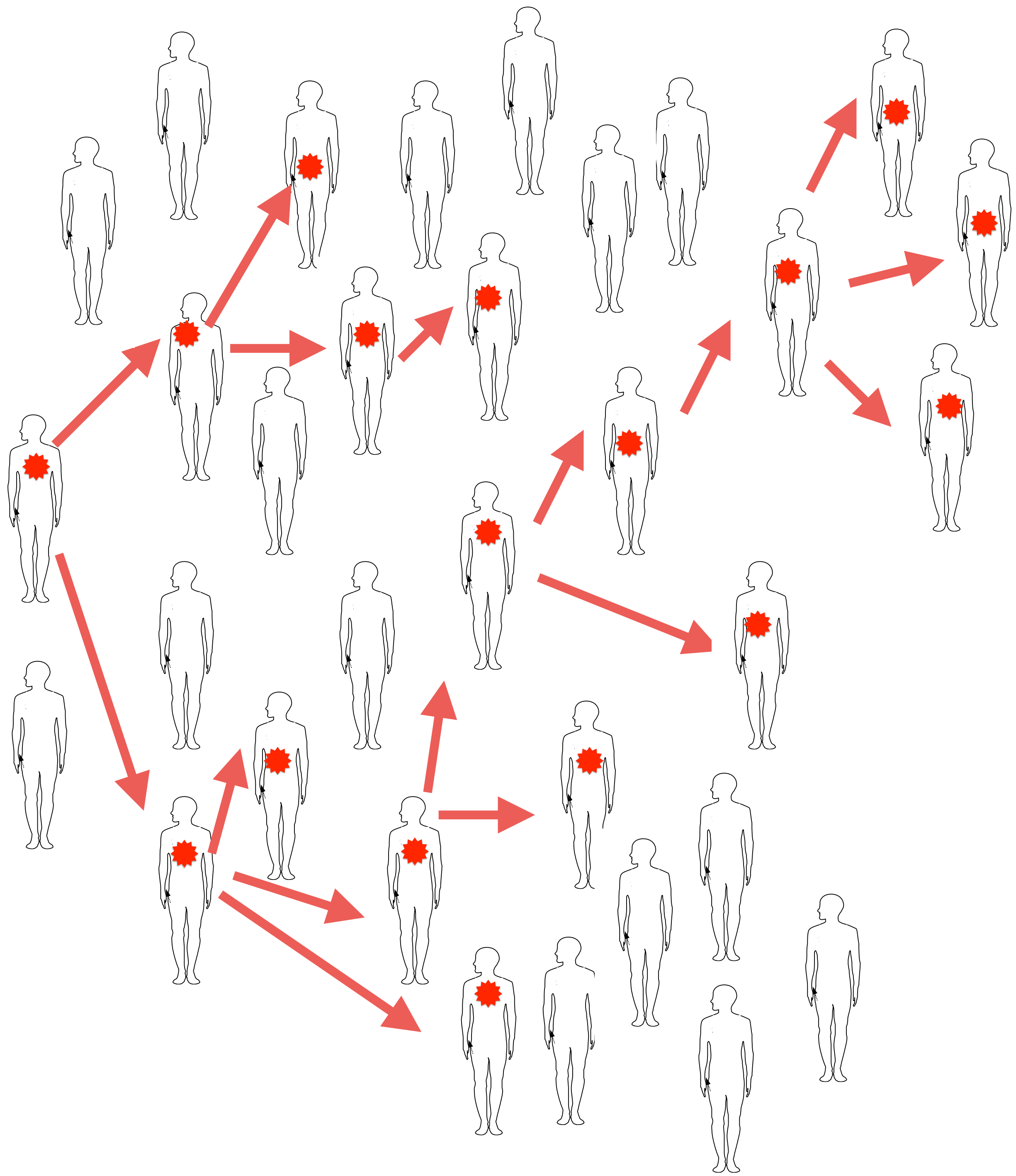
Key concepts

-Inter-dependence de la démographie des espèces (nous avons parlé de ***predation***, mais la ***competition*** *est aussi possible*)

-Les cycles peuvent émerger de forces internes, sans un role d'environnement, saisonnalité, etc.

-Beaucoup d'assumptions dans ce modèle simple! On pourrait ajouter des détails pour se rapprocher de vraies systèmes.

3. SIR models



The SIR model

Compartmental models (Mechanistic Models)

1. Les populations sont subdivisées en compartiments
2. Les compartiments et les taux de transition sont déterminés par les systèmes biologiques
3. Taux de transition entre les compartiments sont exprimés mathématiquement

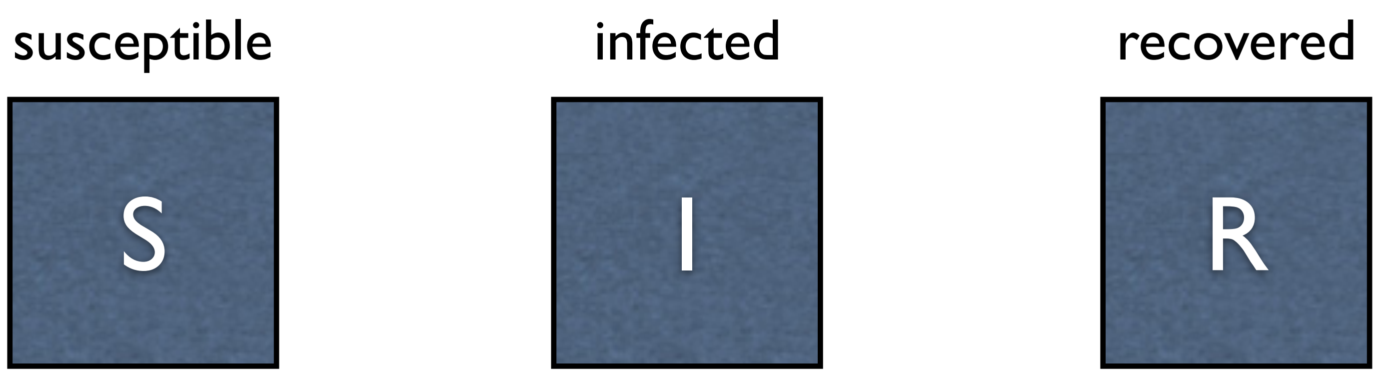
How could we build a mechanistic model of disease transmission where individuals are susceptible, become infected, and then recover?

Comment pourrions-nous construire un modèle mécaniste de transmission de maladies où les individus sont susceptibles, deviennent infectés, puis guérissent?

The SIR model

<u>Compartmental models (Mechanistic Models)</u>

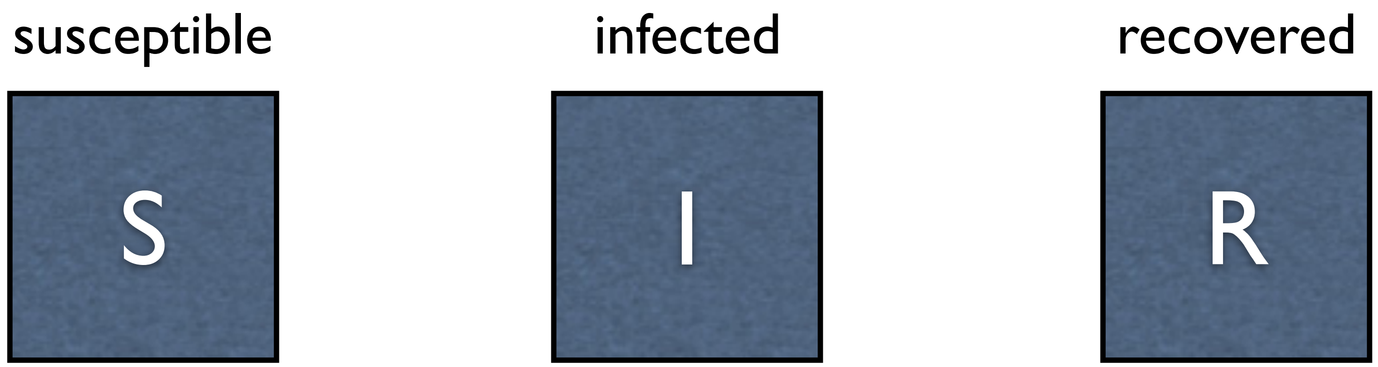
1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



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

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

susceptible	infected	recovered
S	I	R

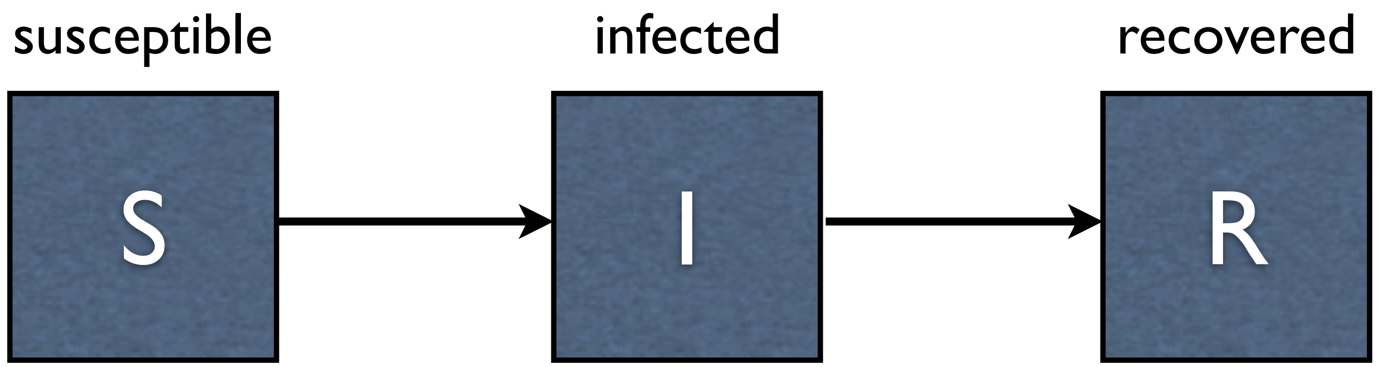
What are the big assumptions here?

The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

everyone is either:



The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

everyone is either:

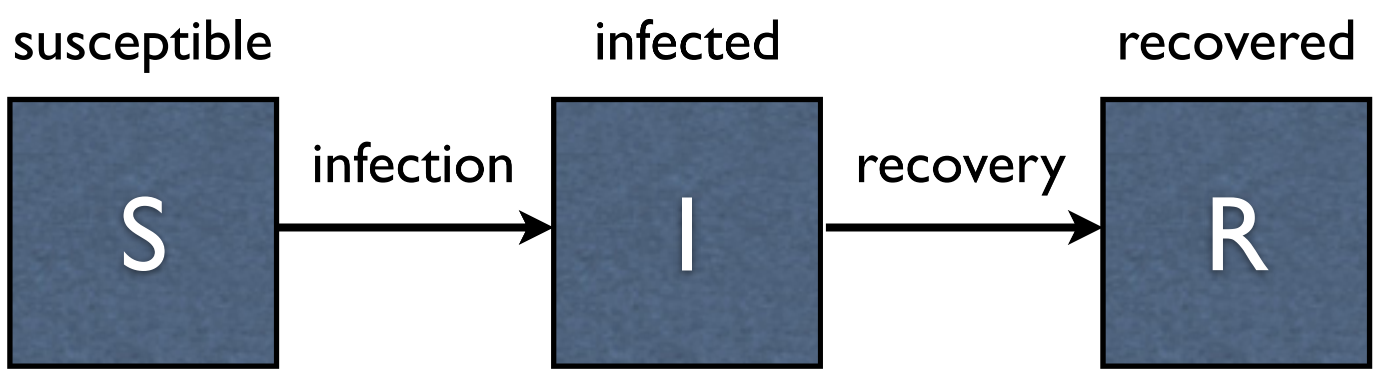
susceptible		infected		recovered
S	$\xrightarrow{\text{infection}}$	I	$\xrightarrow{\text{recovery}}$	R

The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

everyone is either:



people **mix uniformly (mass action)**

- les gens se mélangent uniformément

The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

susceptible | infected | recovered

everyone is either: $S \xrightarrow{\text{infection}} I \xrightarrow{\text{recovery}} R$

people **mix uniformly (mass action)**

no latent period (infectious when infected)

- les gens se mélangent uniformément
- pas de période de latence

The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

everyone is either: susceptible **S** $\xrightarrow{\text{infection}}$ infected **I** $\xrightarrow{\text{recovery}}$ recovered **R**

recovery is **permanent**

people **mix uniformly (mass action)**

no latent period (infectious when infected)

- les gens se mélangent uniformément
- pas de période de latence
- la récupération est permanente

The SIR model

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

susceptible — infected — recovered

everyone is either: $S \xrightarrow{\text{infection}} I \xrightarrow{\text{recovery}} R$

recovery is **permanent**

people **mix uniformly (mass action)**

no latent period (infectious when infected)

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

- les gens se mélangent uniformément
- pas de période de latence
- la récupération est permanente
- taille de population constante

The SIR model

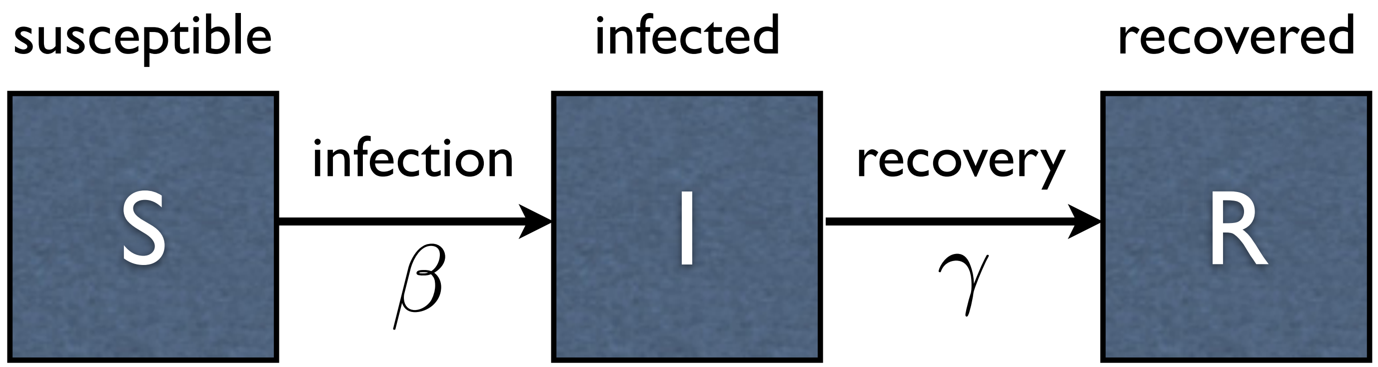
Parameters

β : transmission rate

γ : rate of recovery

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



The SIR model

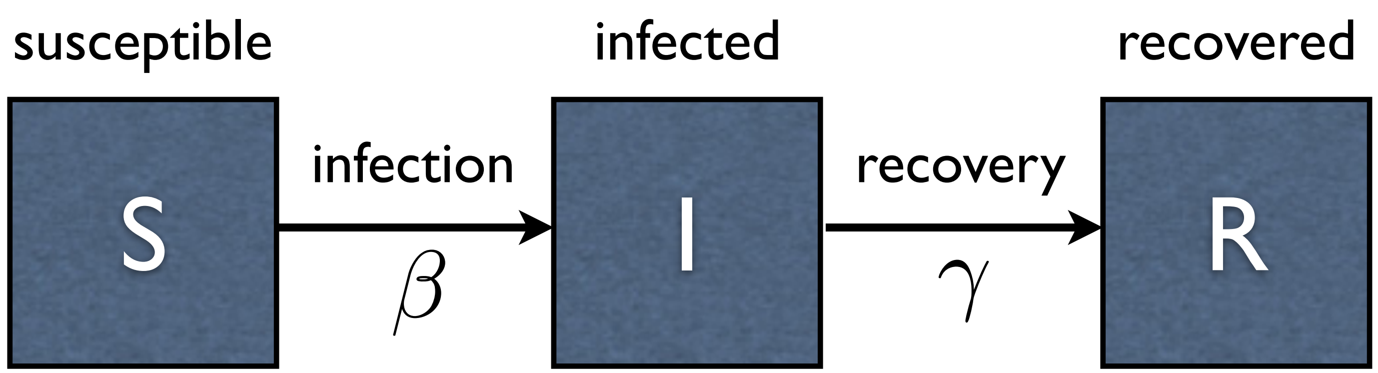
Parameters

β : transmission rate

γ : rate of recovery

Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



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

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

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

…multiply rates by box you start in….

The SIR model

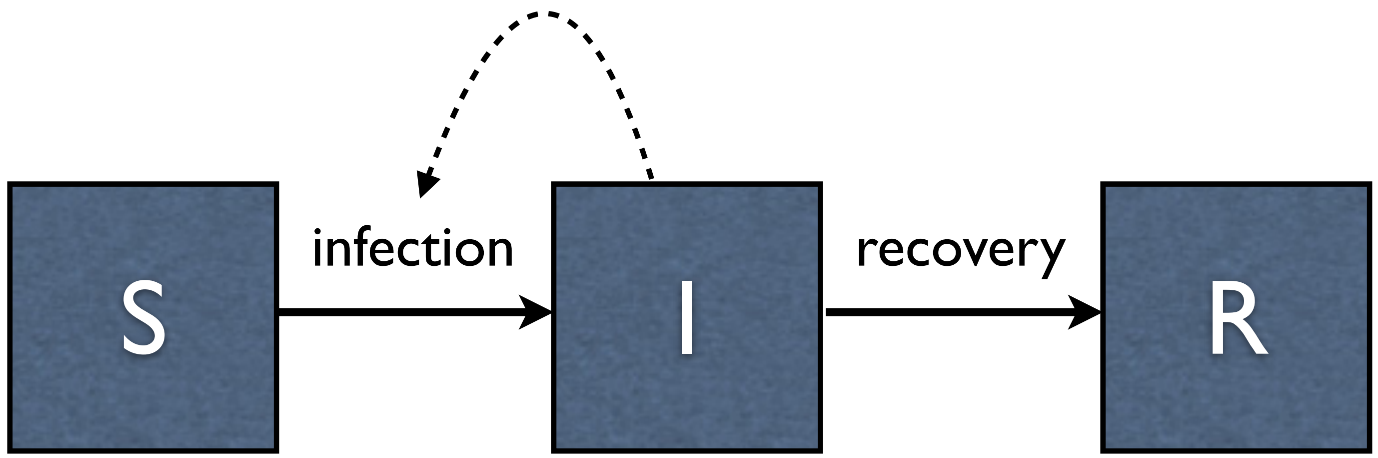
Parameters

β : transmission rate

γ : rate of recovery

<u>Compartmental models (Mechanistic Models)</u>

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically



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

…infected numbers shape infection….

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

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

…multiply rates by box you start in….

The SIR model

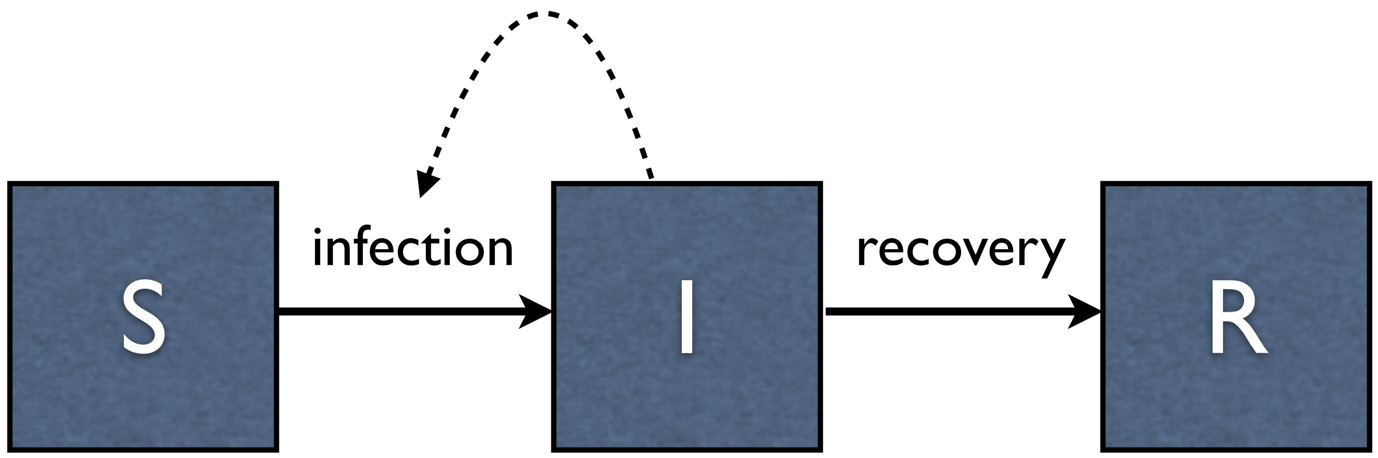
Parameters

β : transmission rate

γ : rate of recovery

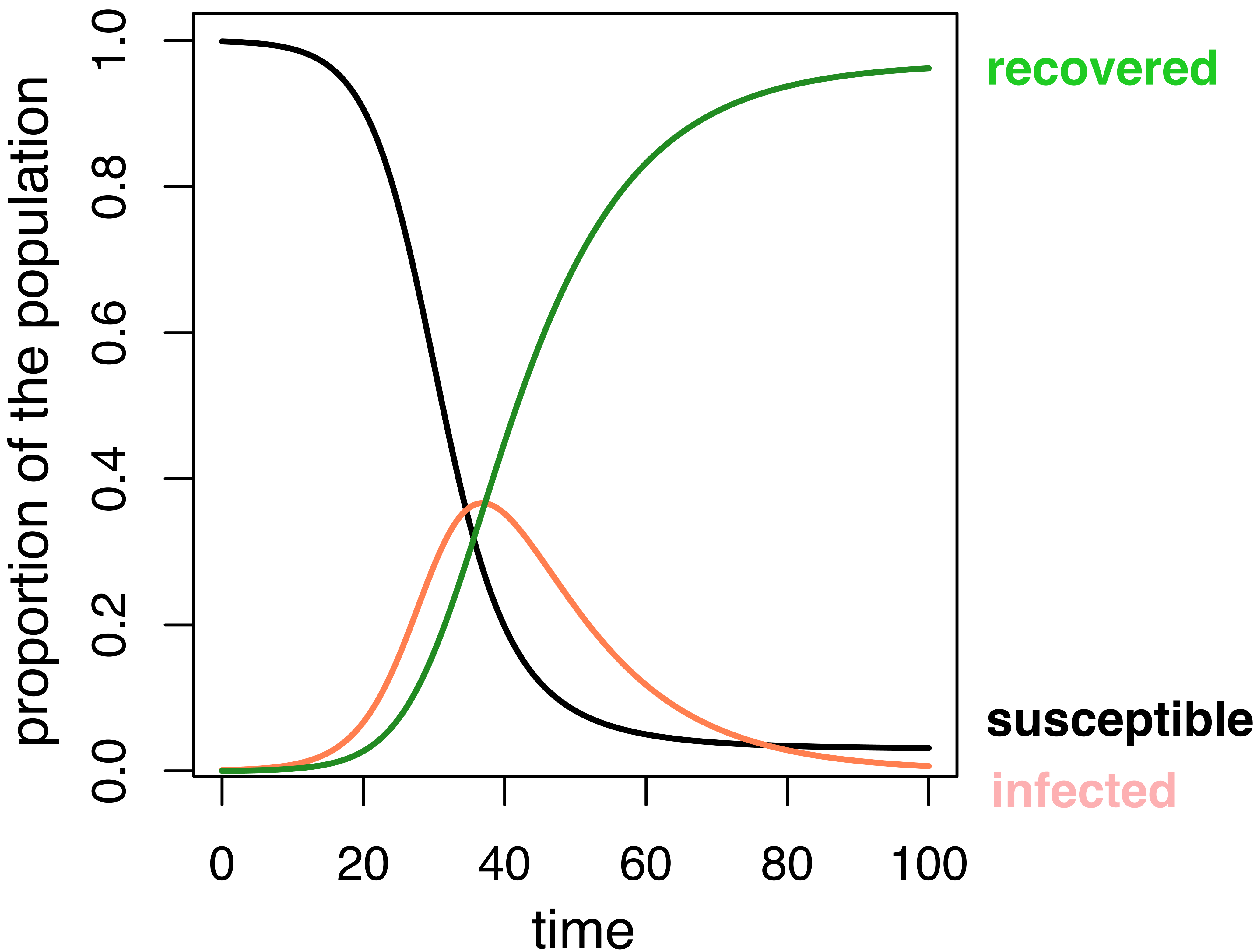
Compartmental models (Mechanistic Models)

1. Populations are divided into compartments
2. Compartments and transition rates are determined by biological systems
3. Rates of transferring between compartments are expressed mathematically

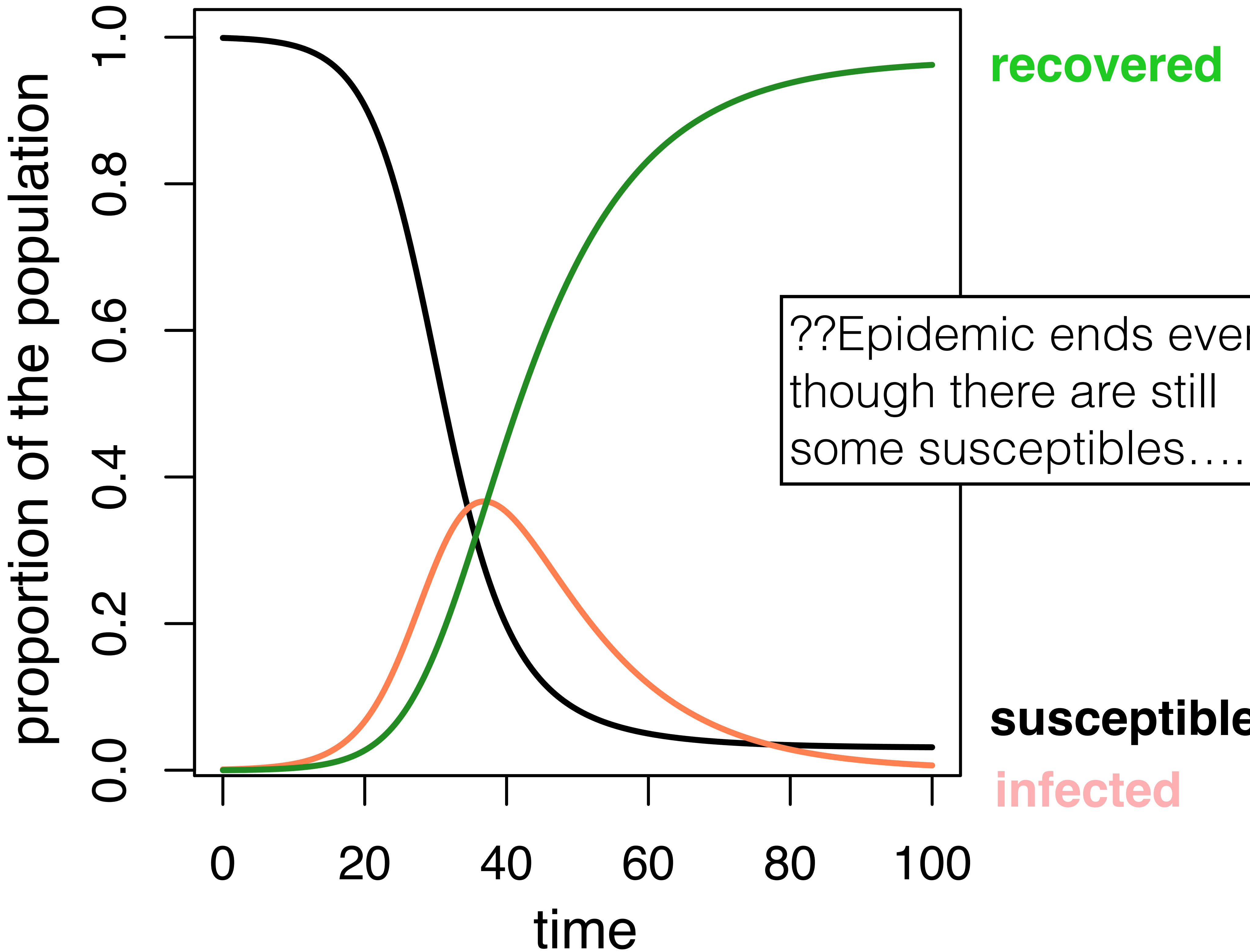


What will the dynamics look like?

The SIR model: dynamics

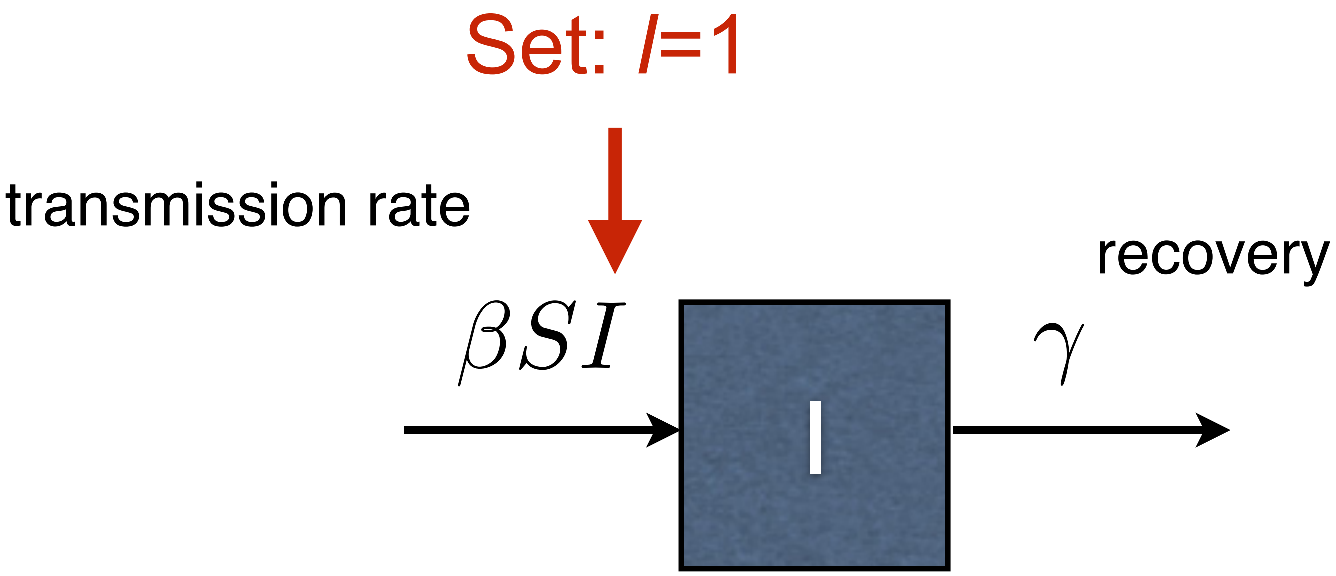


The SIR model: dynamics



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

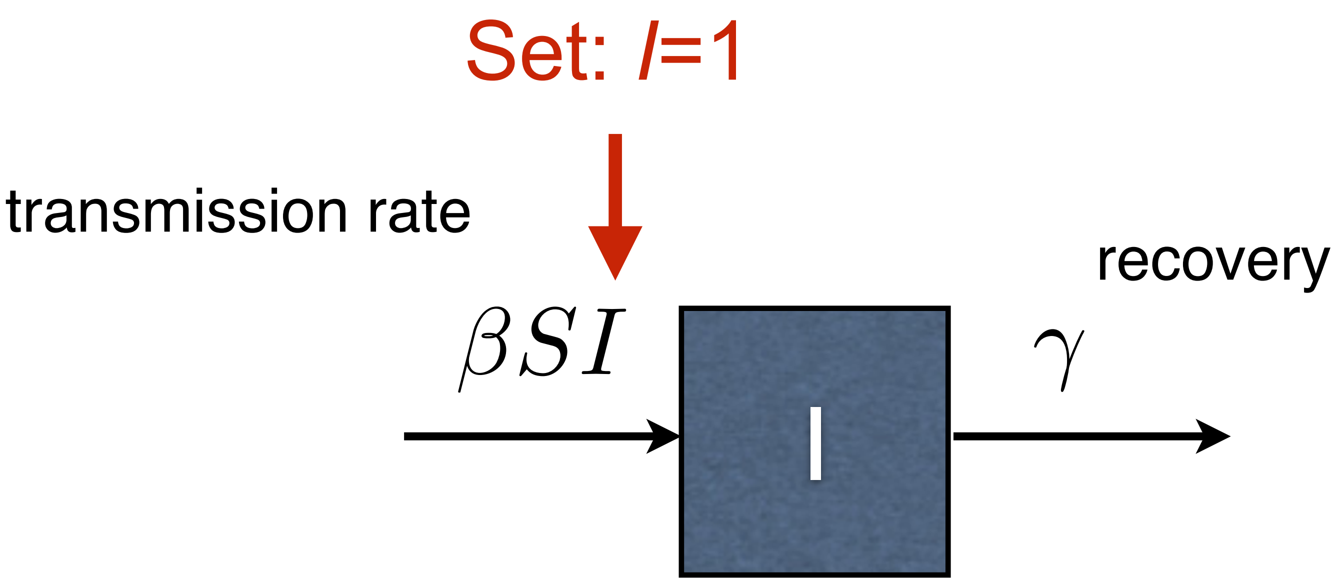
The SIR model: dynamics



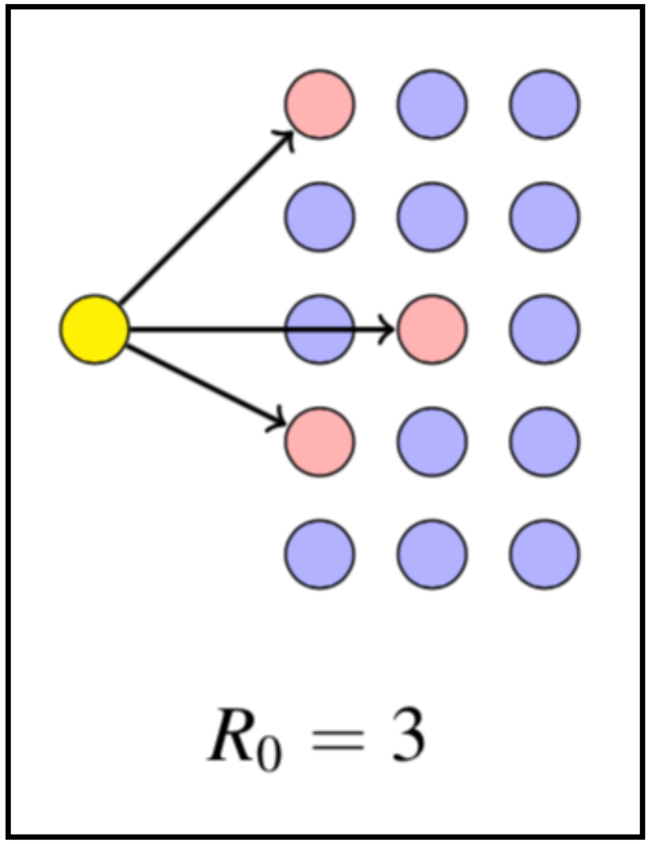
$$R_0 = \beta N/\gamma$$

The average number of persons infected by an infectious individual when everyone is susceptible (S=100%, or S=1, start of an epidemic)

The SIR model: dynamics

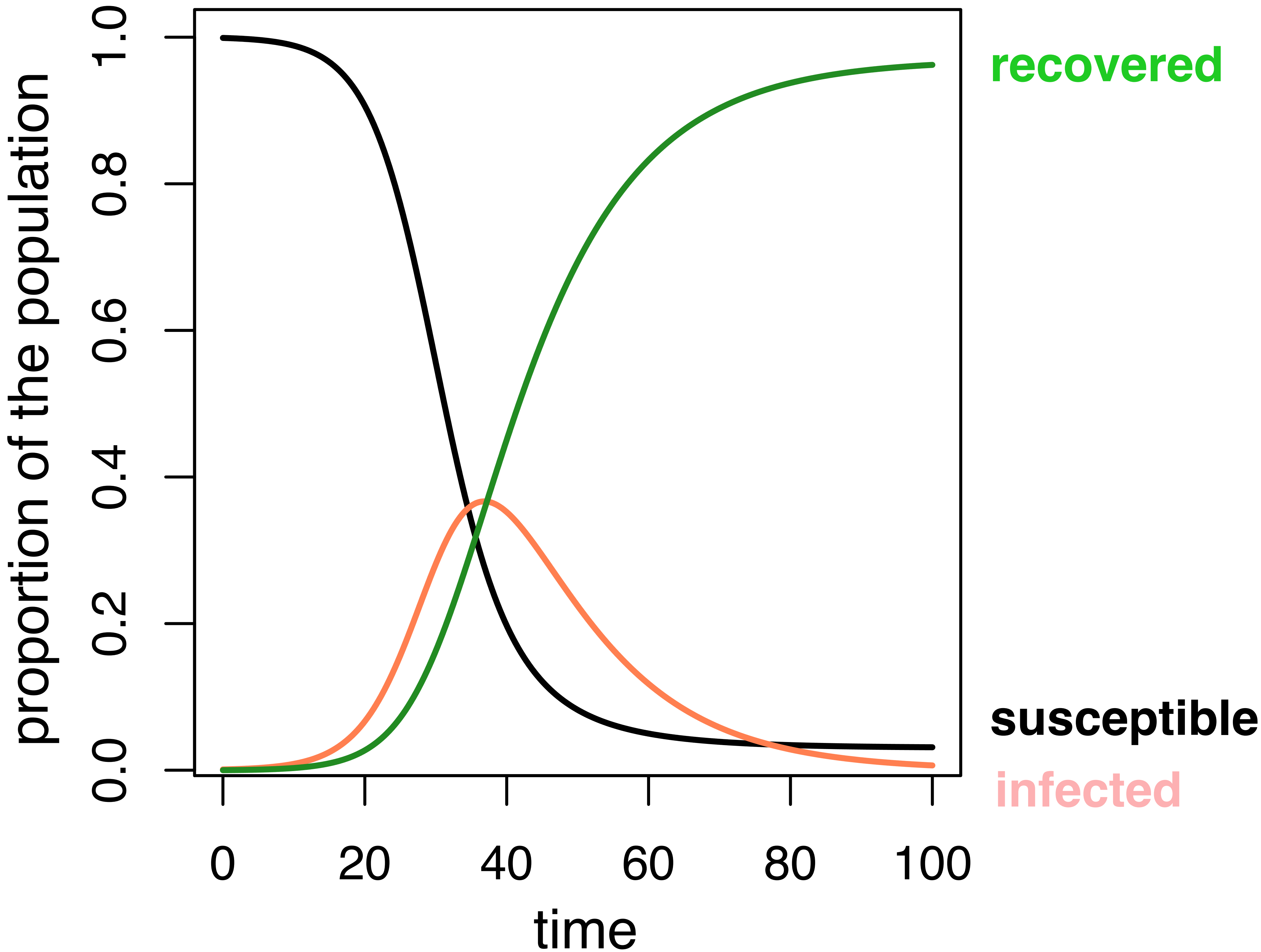


$$R_0 = \beta N / \gamma$$

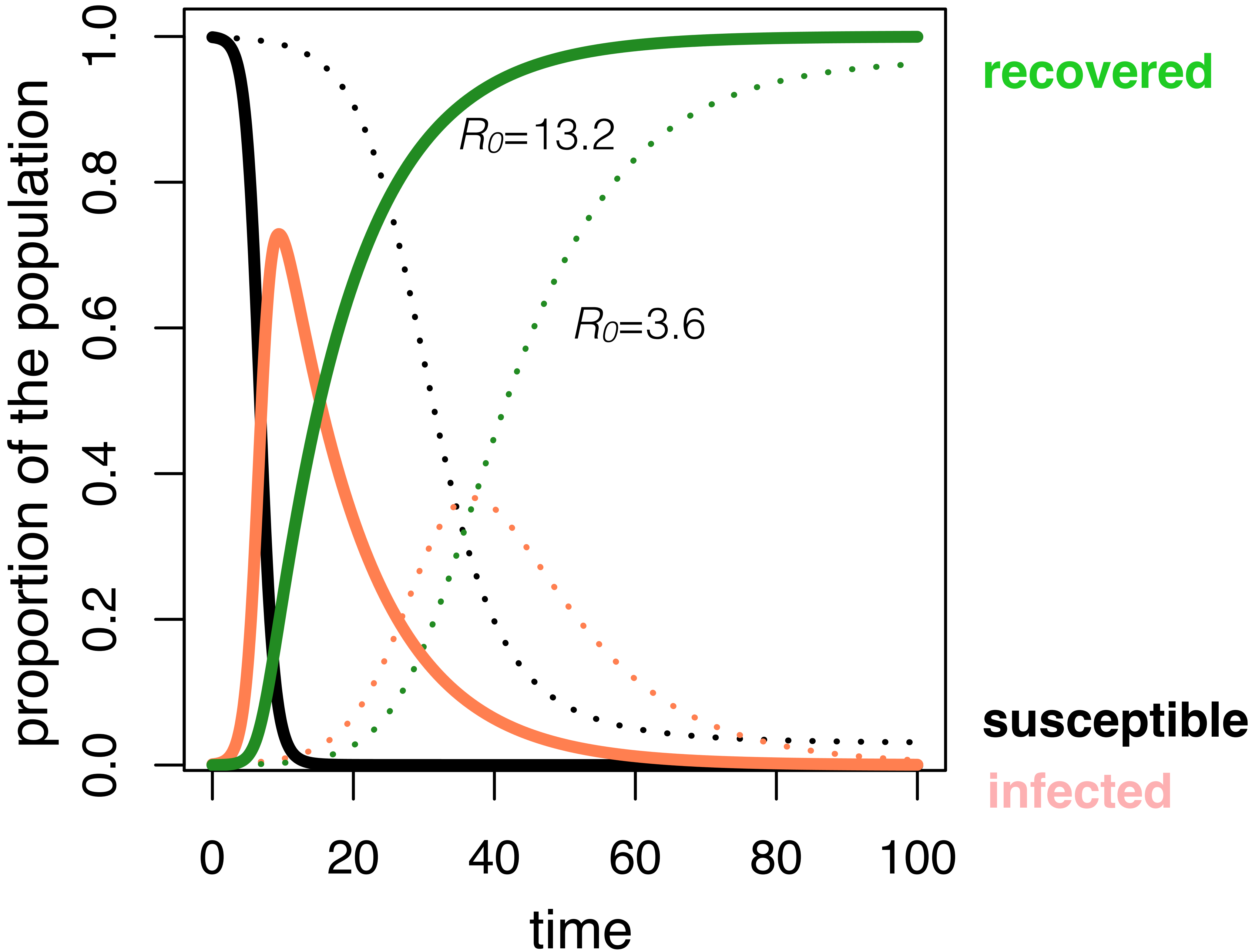


The average number of persons infected by an infectious individual when everyone is susceptible (S=100%, or S=1, start of an epidemic)

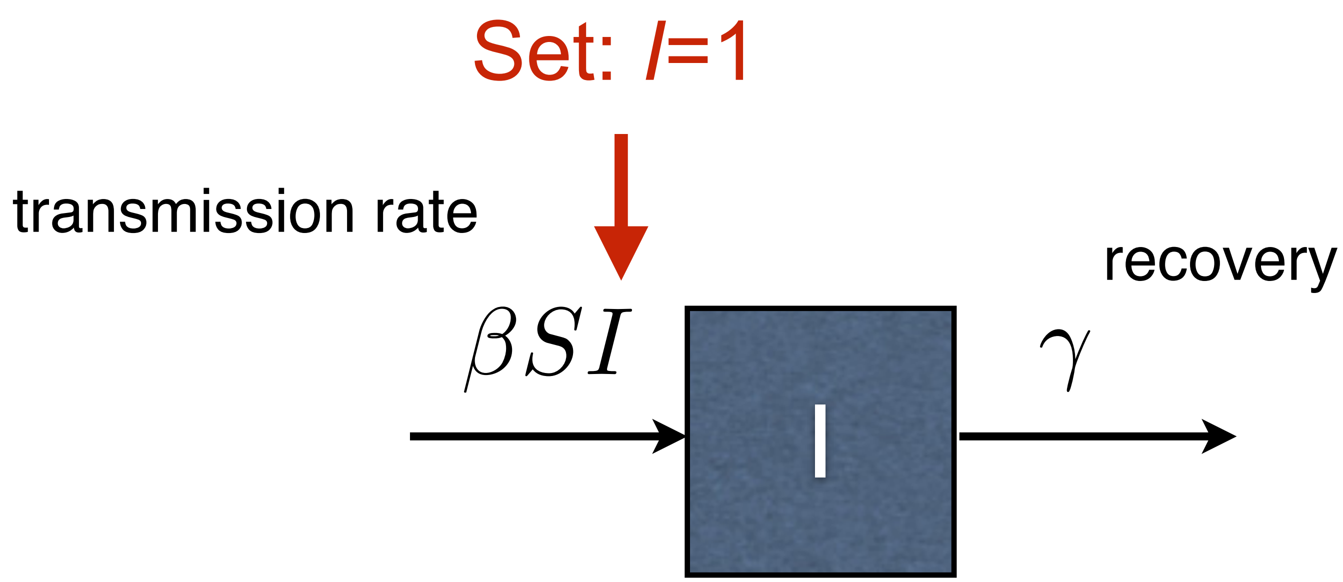
The SIR model: dynamics



The SIR model: dynamics



The SIR model: dynamics



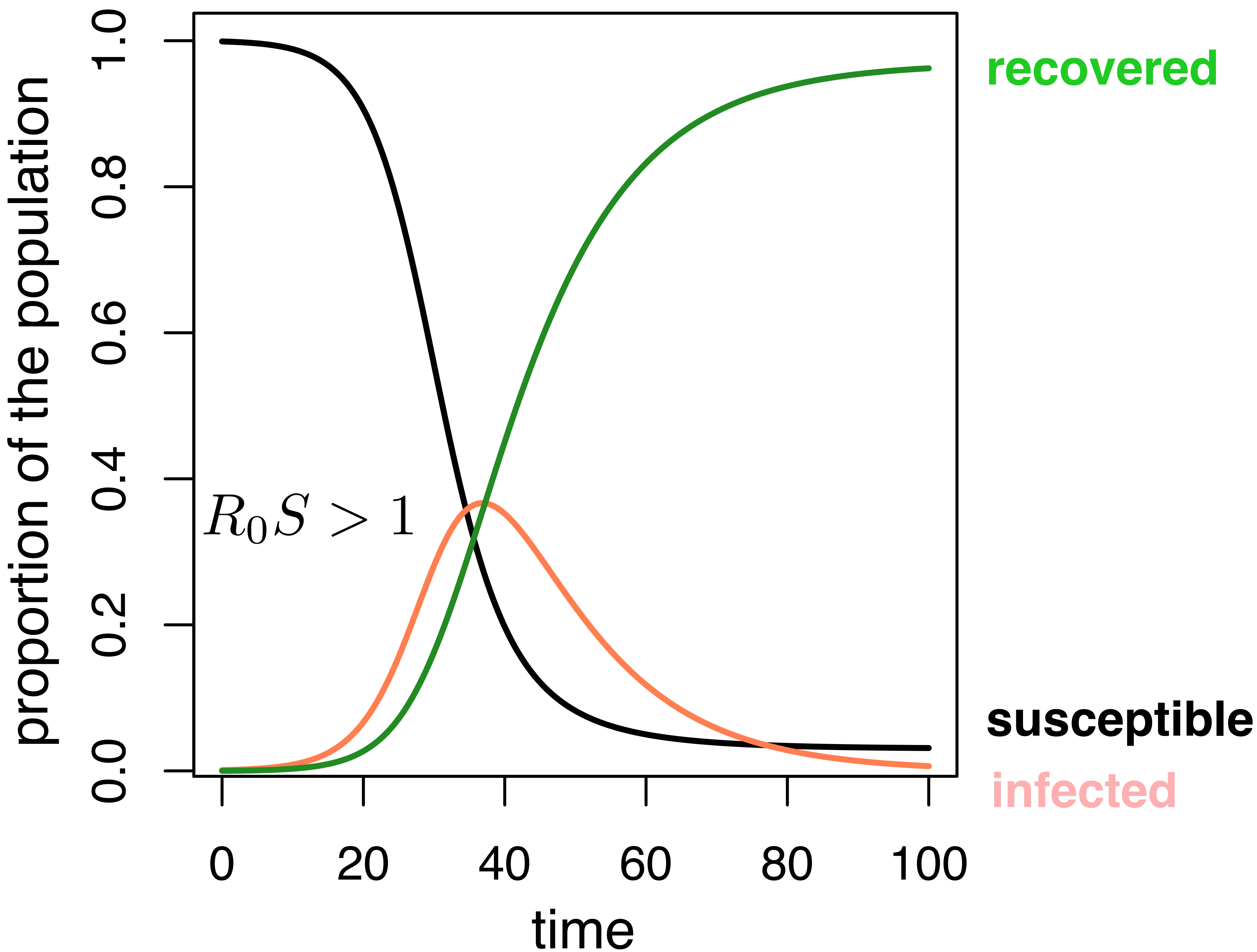
$$R_0 = \beta N / \gamma$$

The average number of persons infected by an infectious individual when everyone is susceptible (S=100%, or S=1, start of an epidemic) which is:

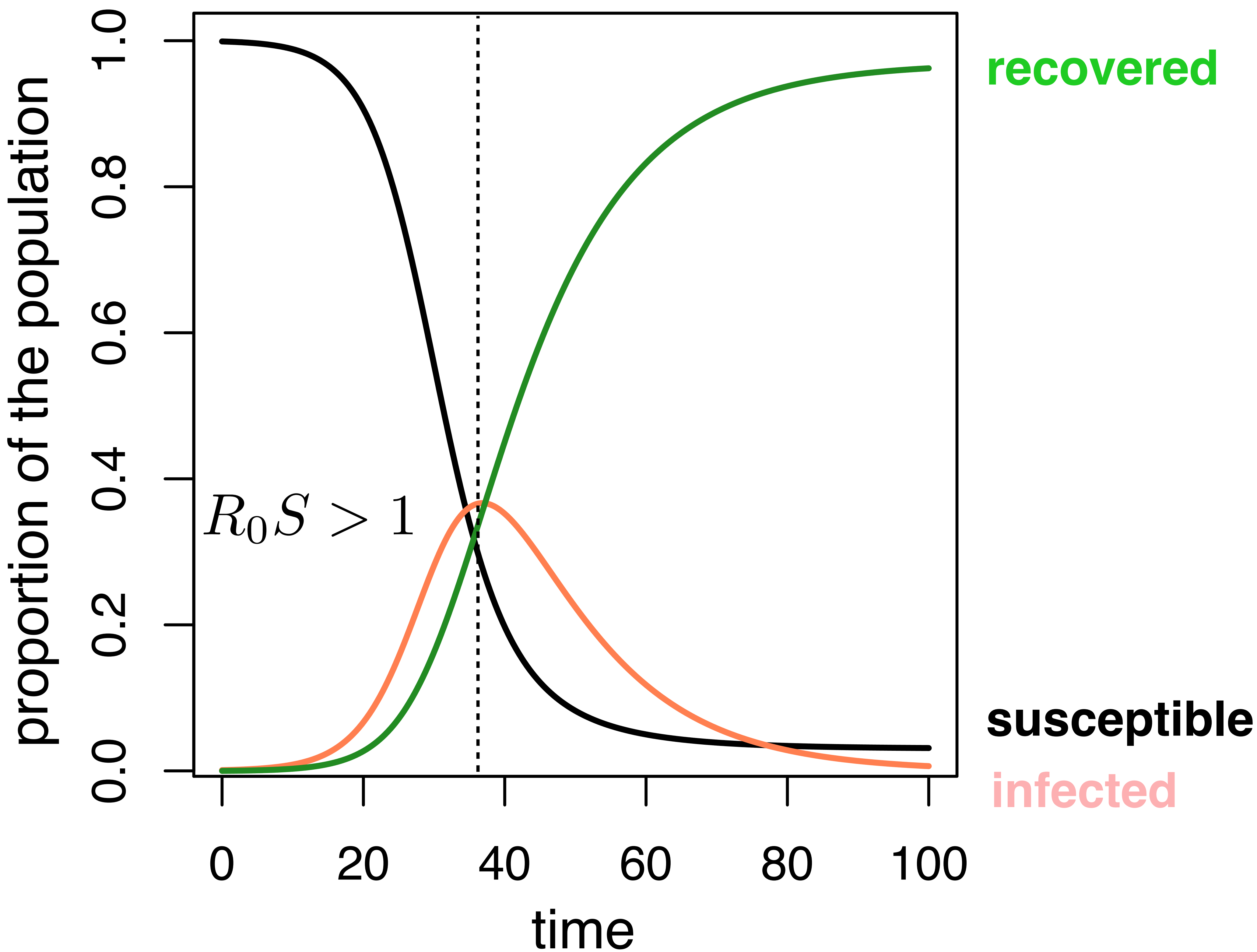
$$R_0 S$$

as the epidemic progresses and S falls

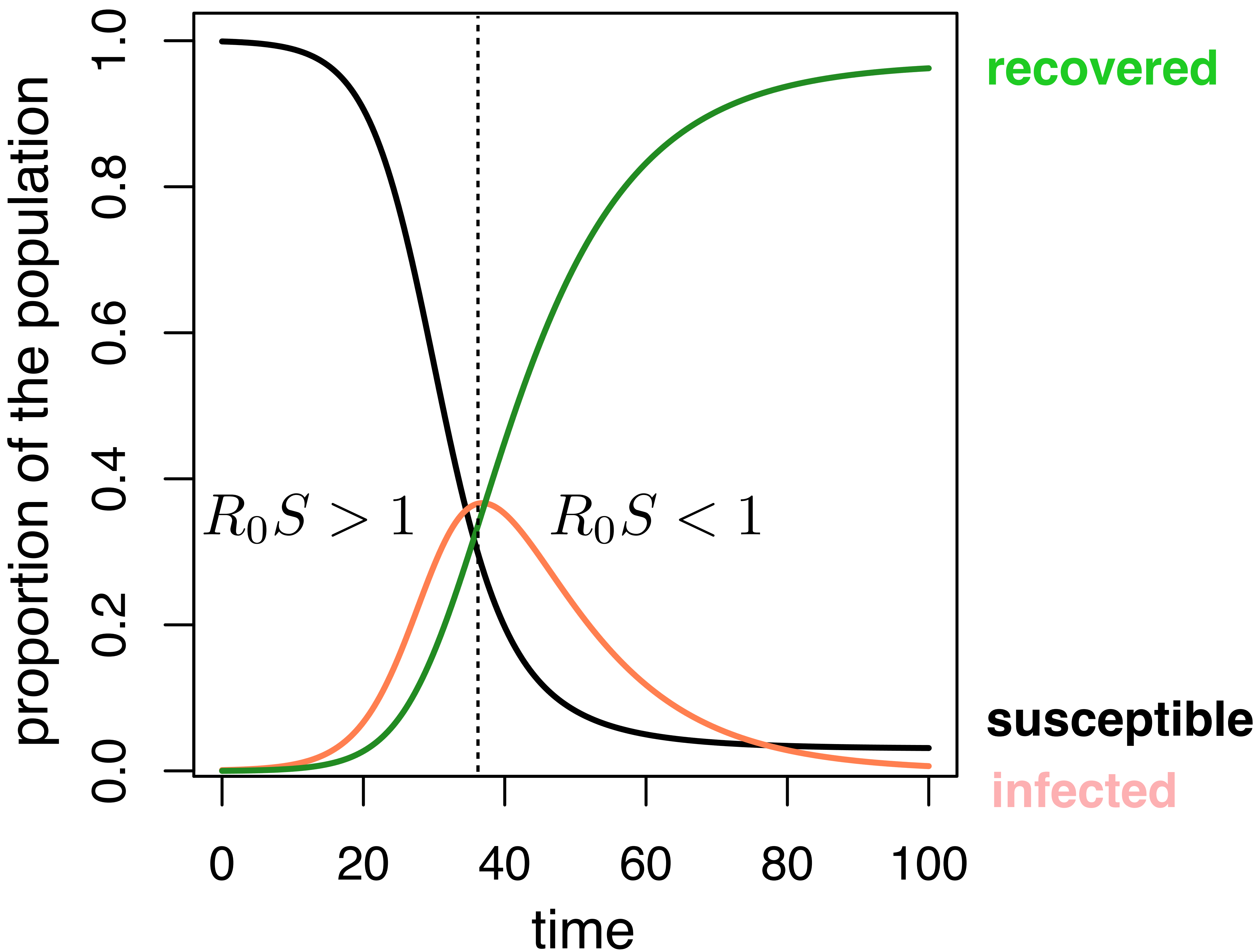
The SIR model: dynamics



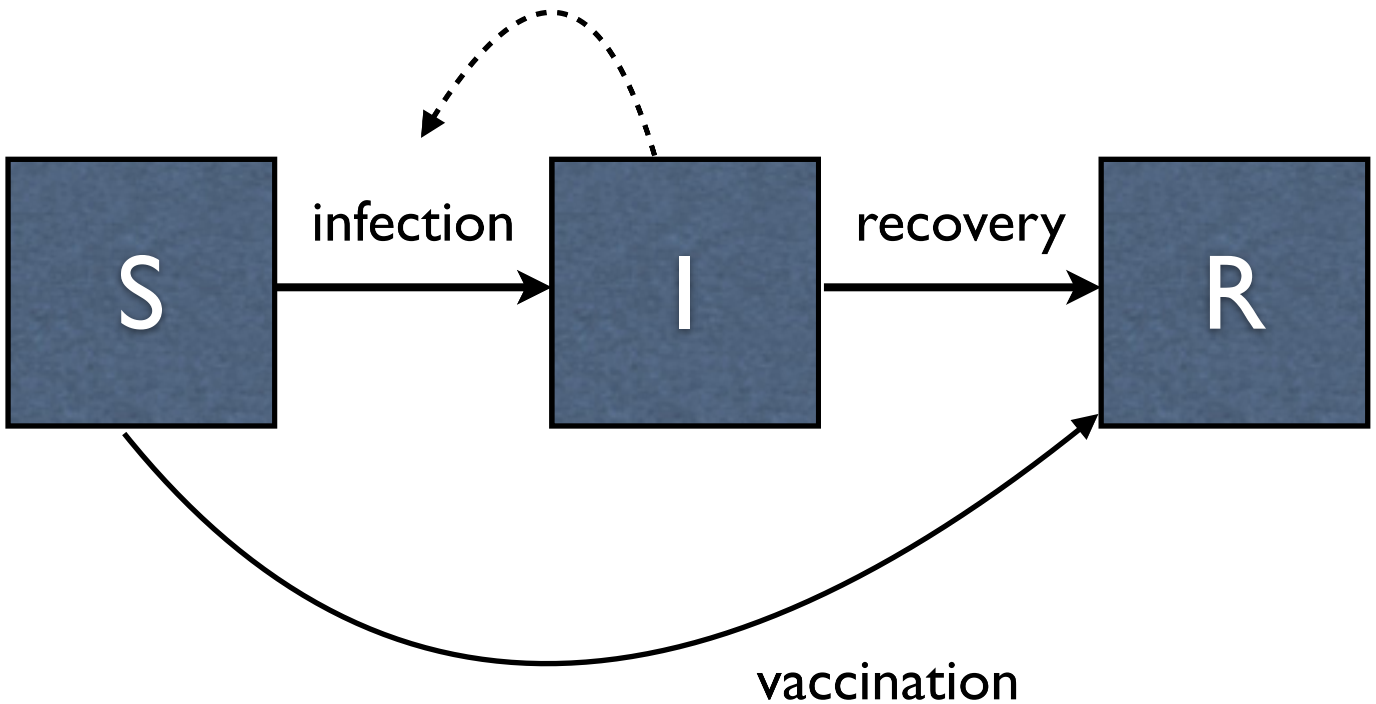
The SIR model: dynamics



The SIR model: dynamics

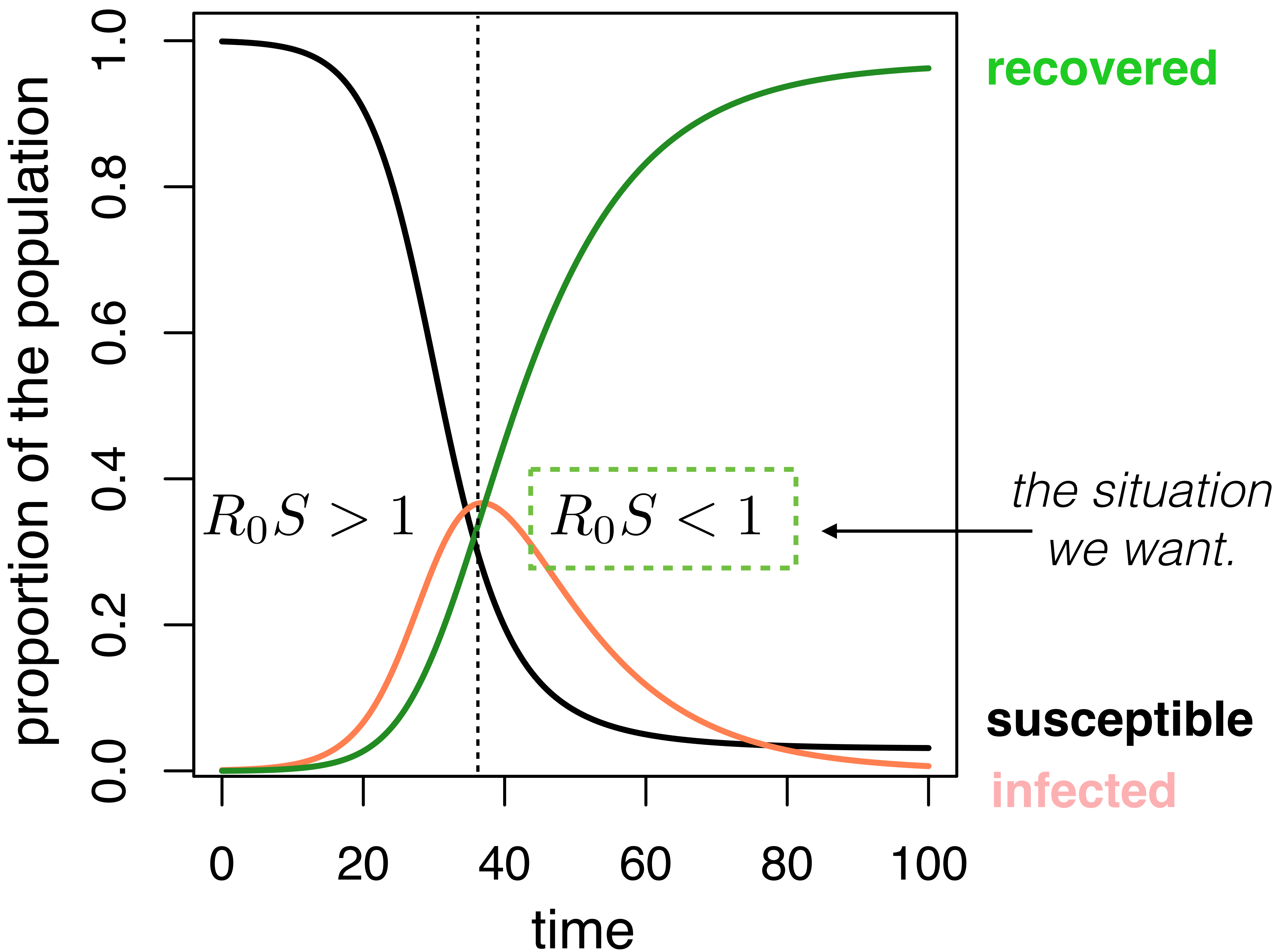


The SIR model: vaccination

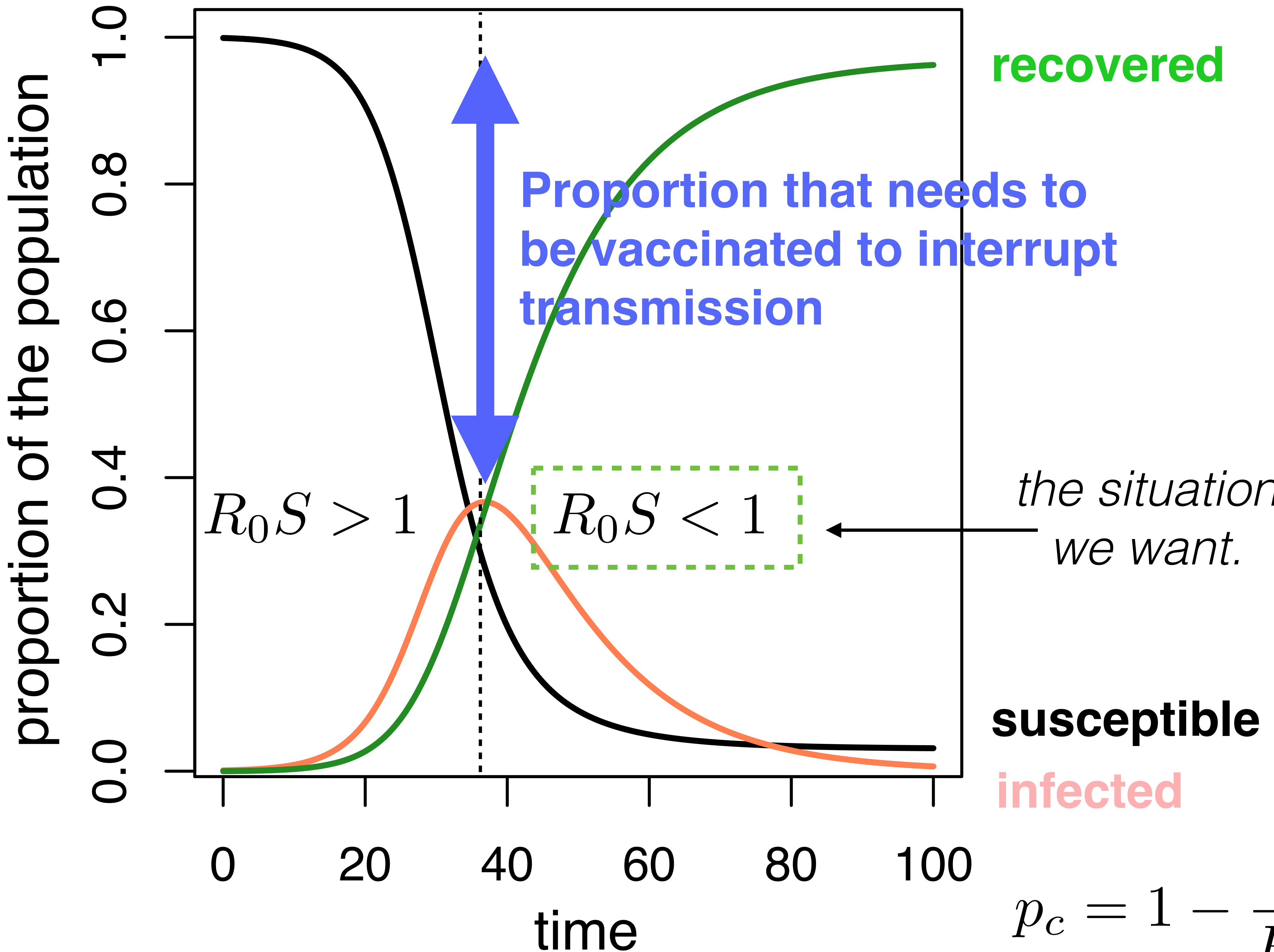


Vaccination moves people out of susceptibles into the immune (recovered) class.

The SIR model: dynamics



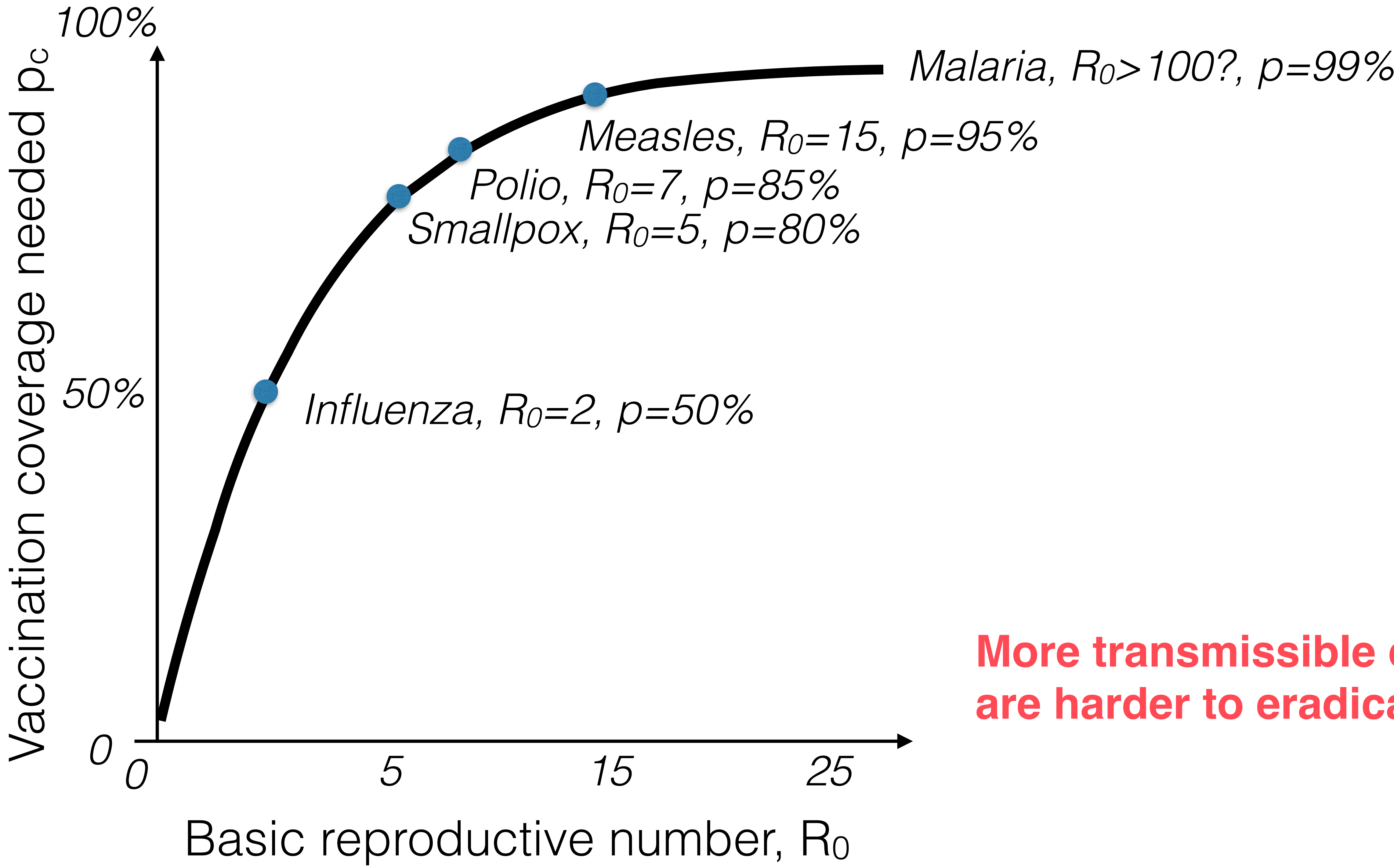
The SIR model: dynamics



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

The SIR model: eradication

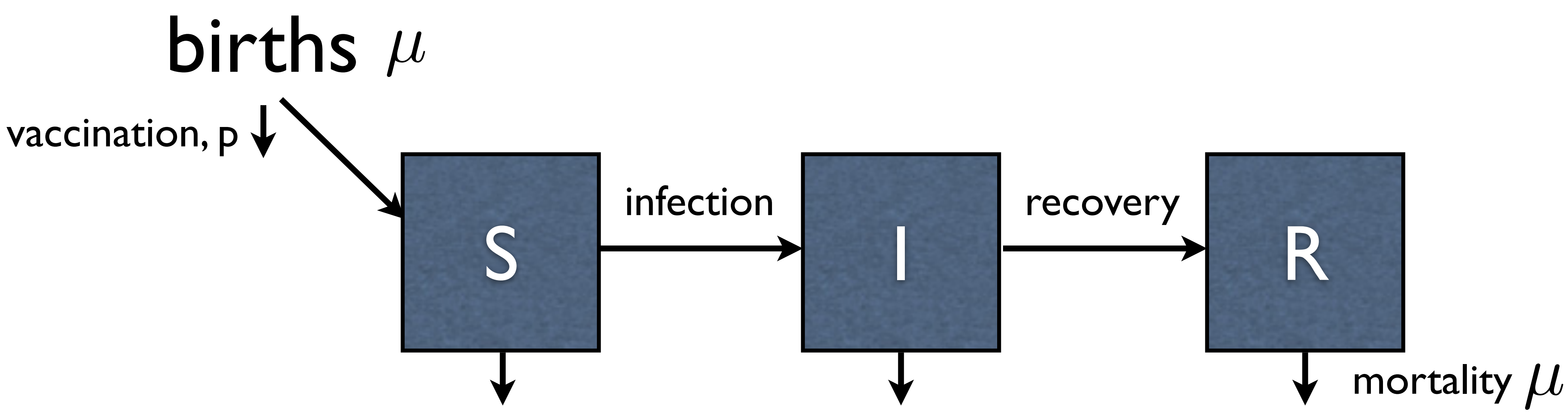
Same logic as without births: $p_c = 1 - \frac{1}{R_0}$



More transmissible diseases are harder to eradicate

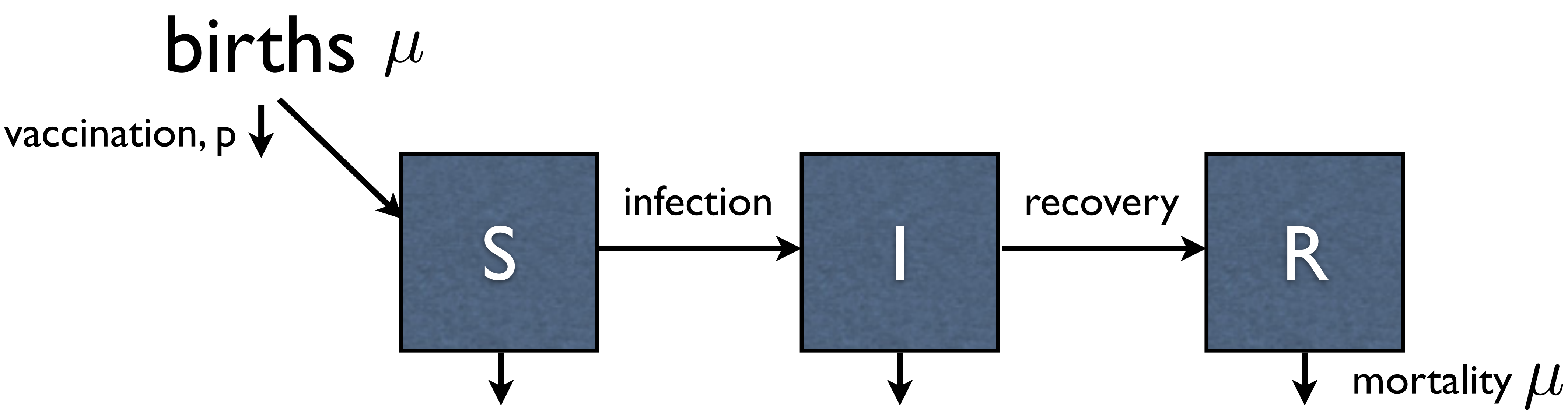
The SIR model: extensions

Moving beyond a ‘closed’ population



The SIR model: extensions

Moving beyond a 'closed' population

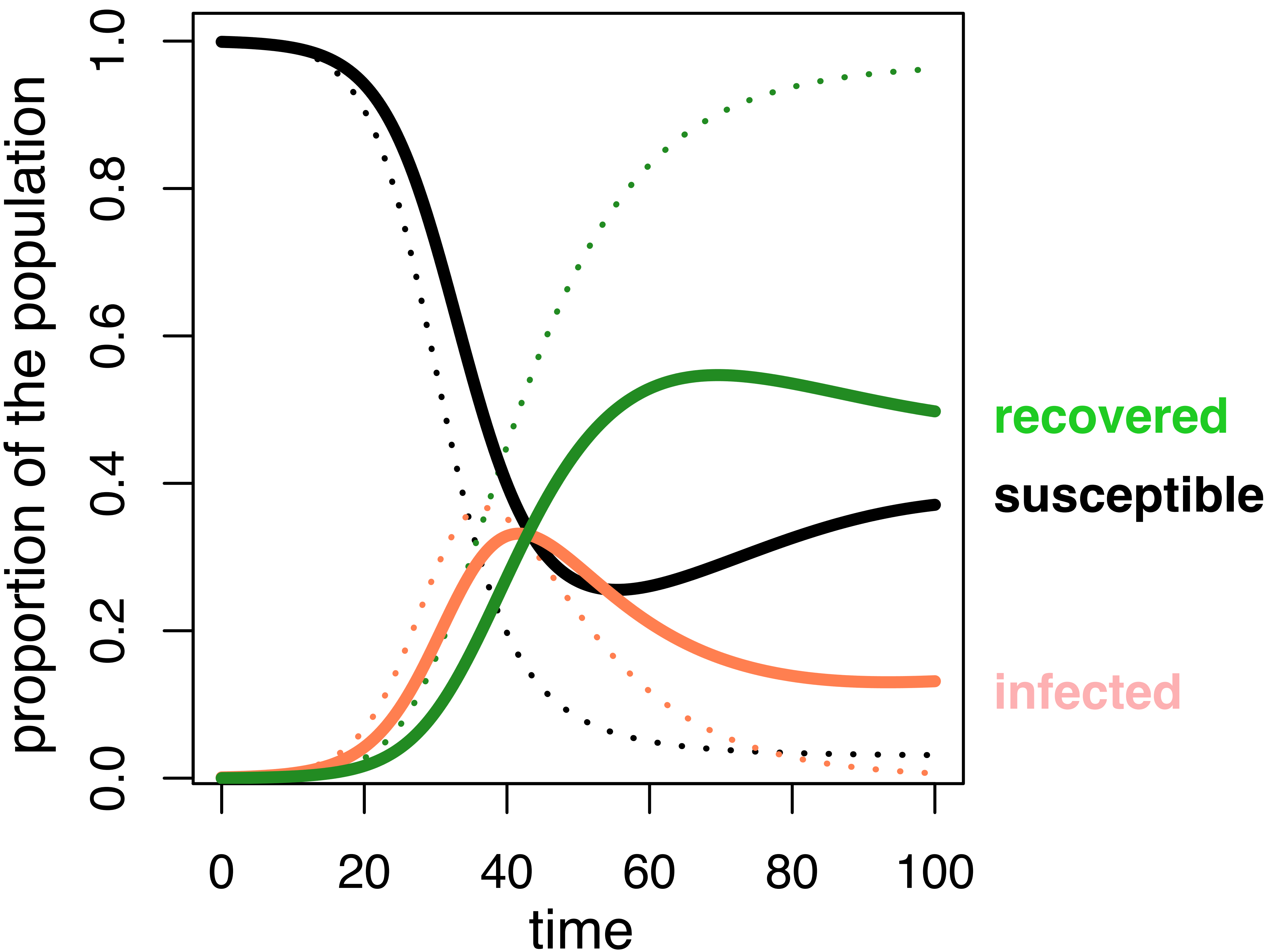


$$\frac{dS(t)}{dt} = \mu(1-p) - \beta S(t)I(t) - \mu S(t)$$

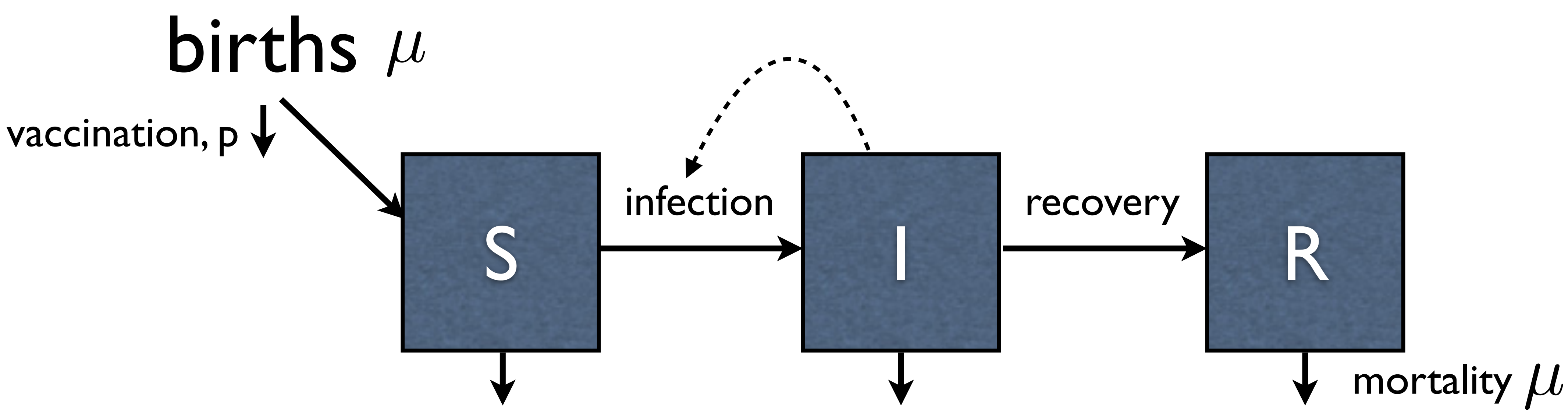
$$\frac{dI(t)}{dt} = \beta S(t)I(t) - \gamma I(t) - \mu I$$

What is likely to be the BIGGEST dynamical difference?

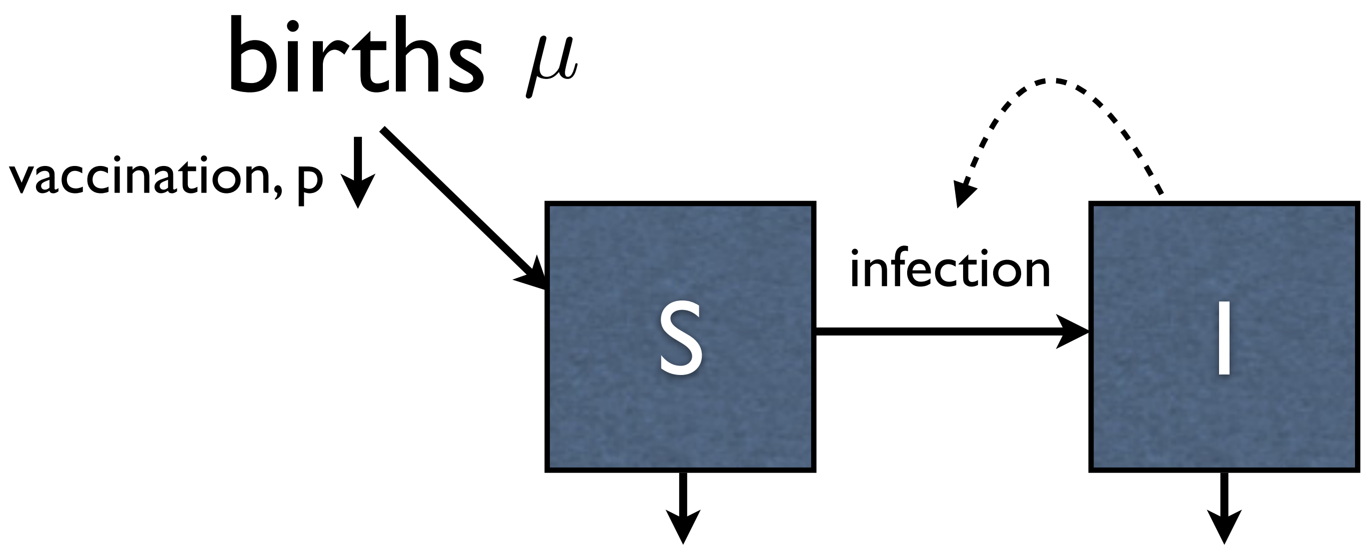
The SIR model: add births



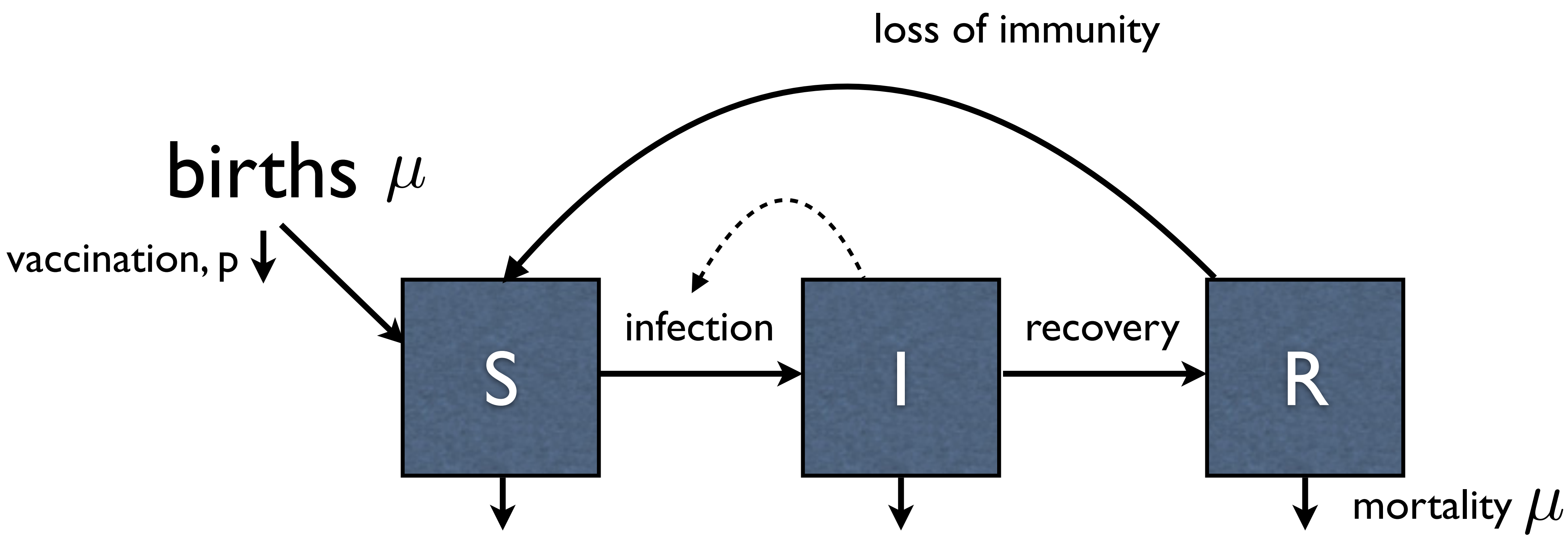
Beyond the SIR model



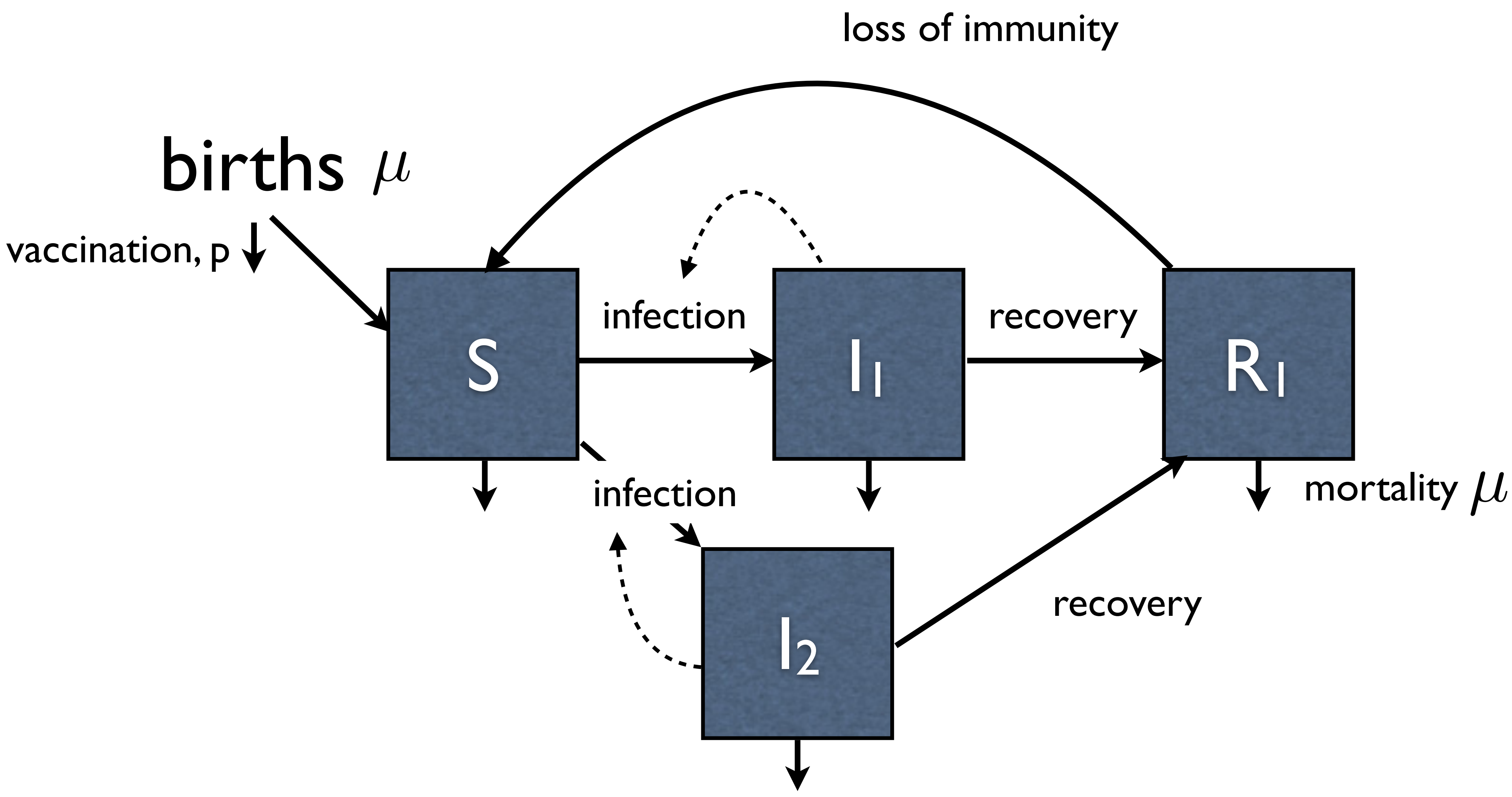
Beyond the SIR model



Beyond the SIR model



Beyond the SIR model



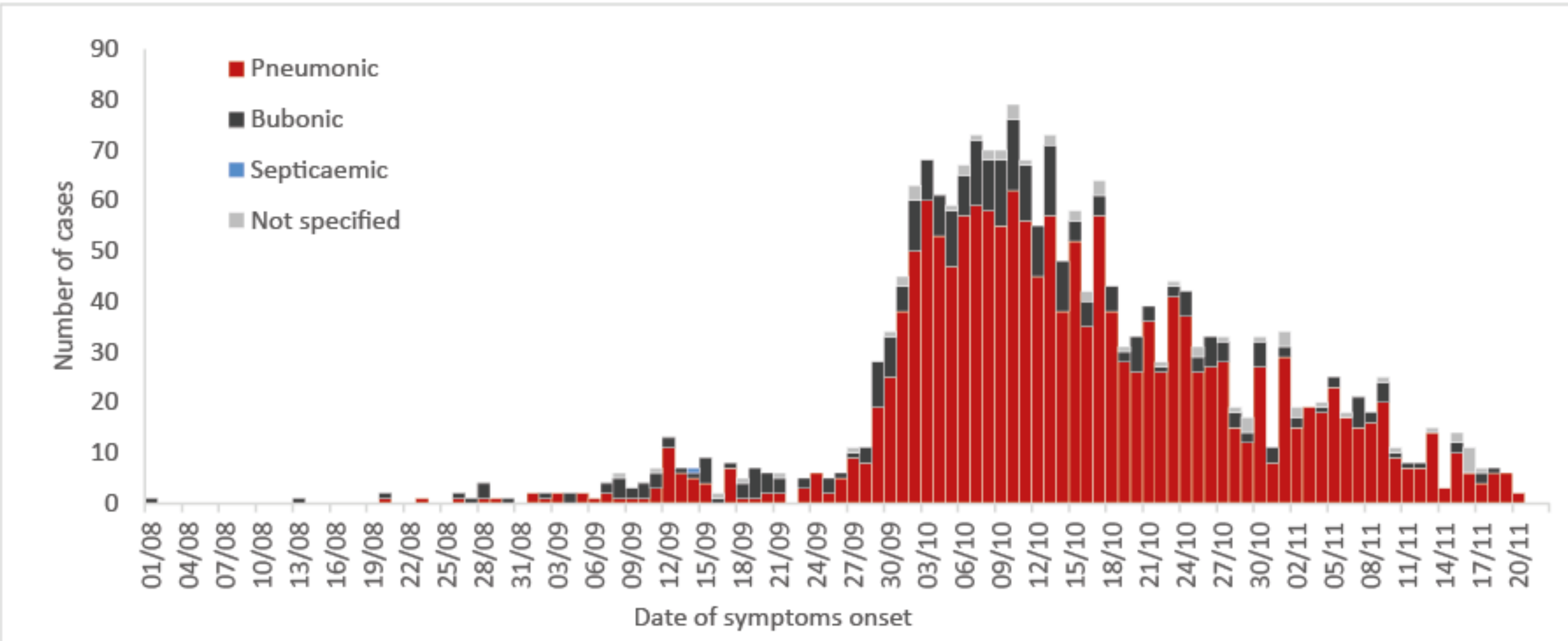
Key concepts

-Les modèles SIR ressemblent en essence a des modèles de dynamic predator-prey

-Pour des pathogènes avec un cycle de vie qui resemble a SIR, en ajoutant quelques details de realism on peut prédire la trajectoire future de l'infection avec grande exactitude.

*-Il y a une énorme variété de modèles, avec different '**states**', et different '**processus**' qui pourrait mieux refléter des cas biologiques spécifiques.*

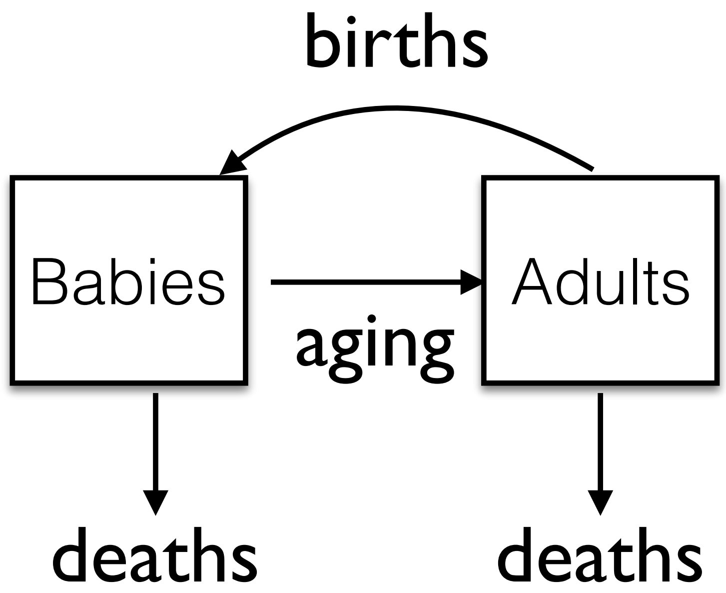
Which model?



http://www.who.int/csr/don/27-november-2017-plague-madagascar/en/

Extra Slides

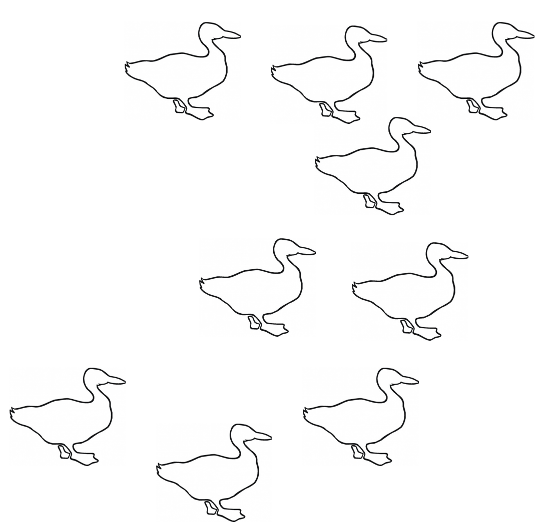
Structured population model



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

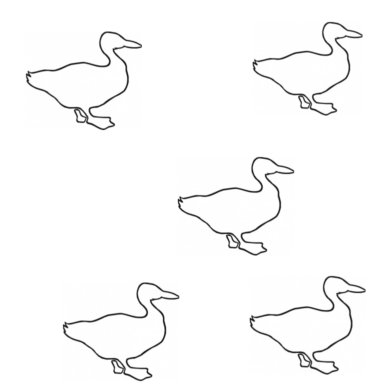
Assumes no role of chance

starting population



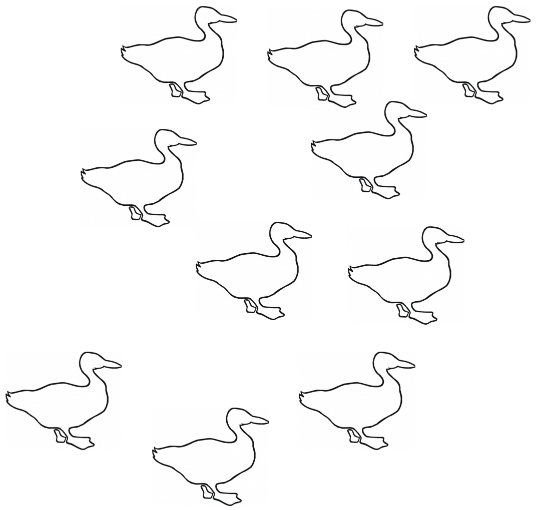
probability of
survival = 0.5

if deterministic

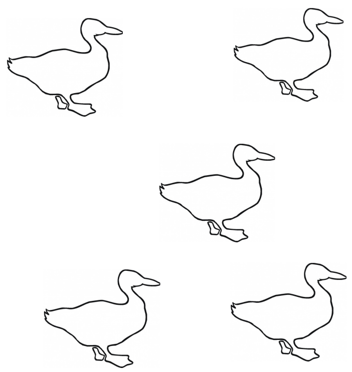


starting population

if deterministic

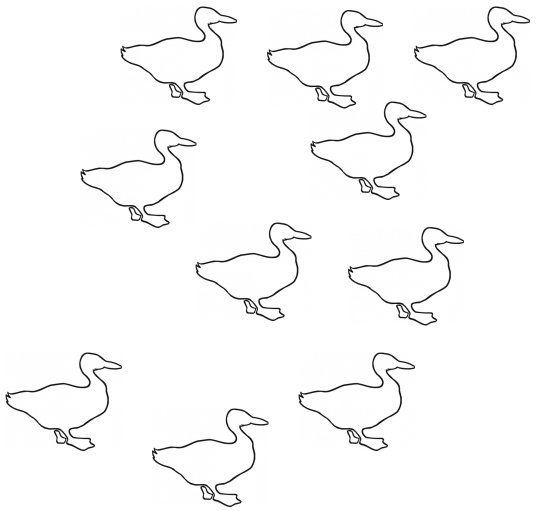


probability of
survival = 0.5



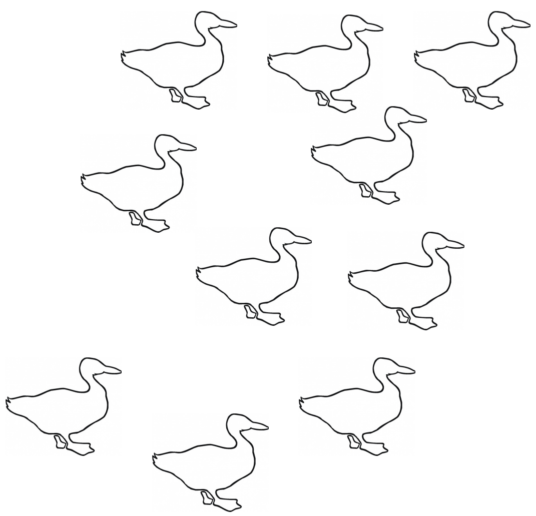
starting population

if stochastic?



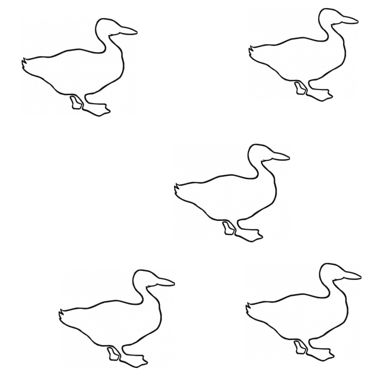
probability of
survival = 0.5

starting population

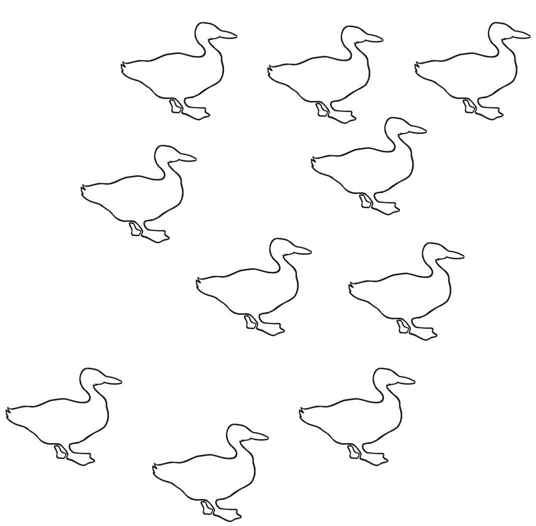


probability of
survival = 0.5

if deterministic

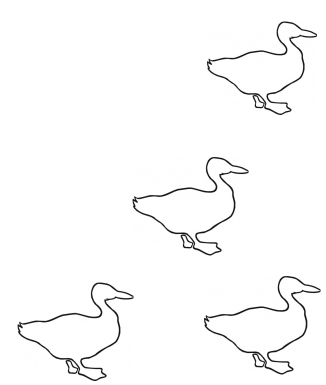


starting population



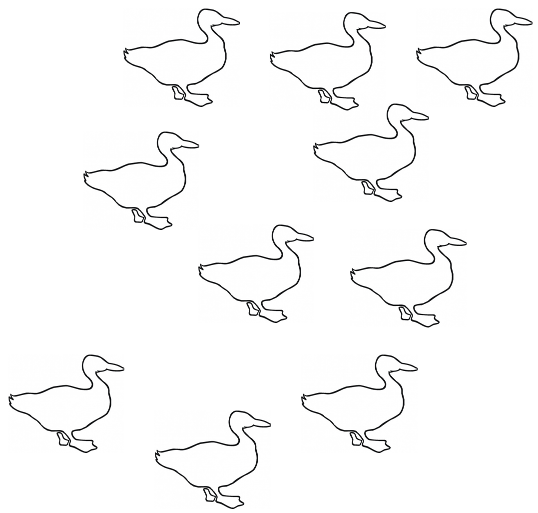
probability of
survival = 0.5

if stochastic?



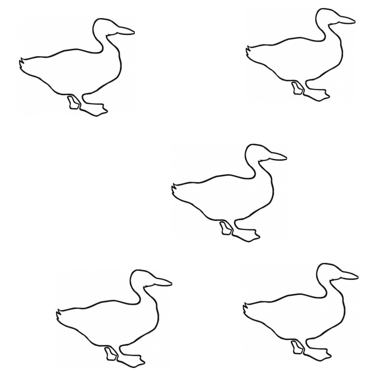
Flip a coin for
every duck;

starting population

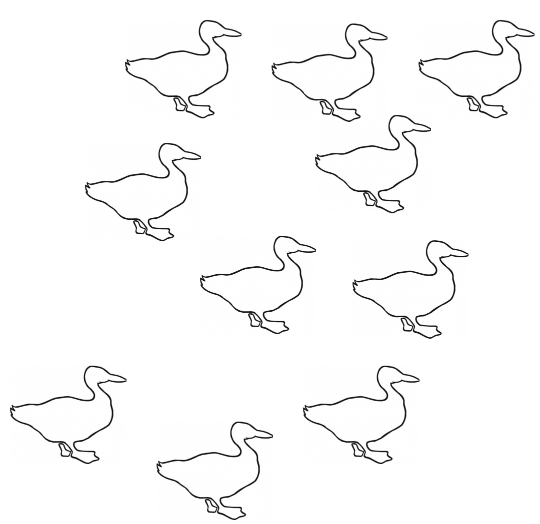


probability of survival = 0.5

if deterministic

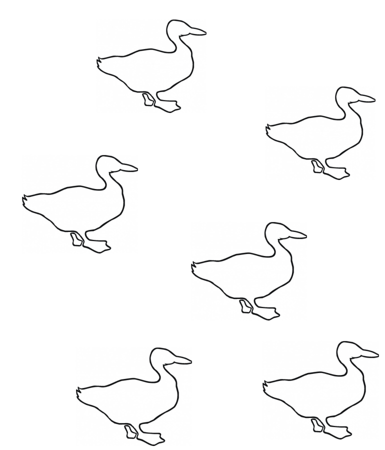


starting population



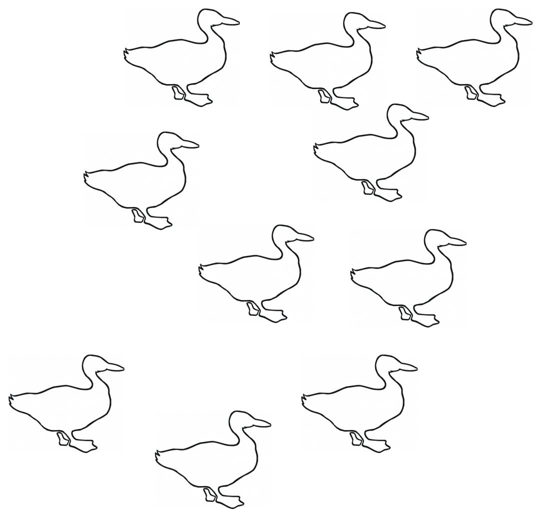
probability of survival = 0.5

if stochastic?



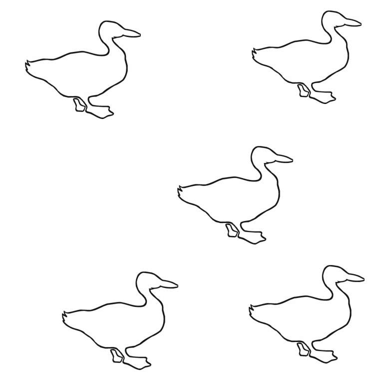
Flip a coin for every duck;

starting population

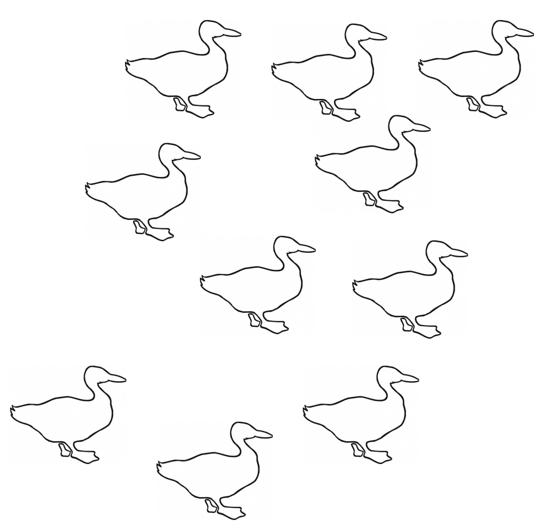


probability of survival = 0.5

if deterministic

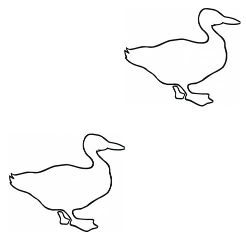


starting population



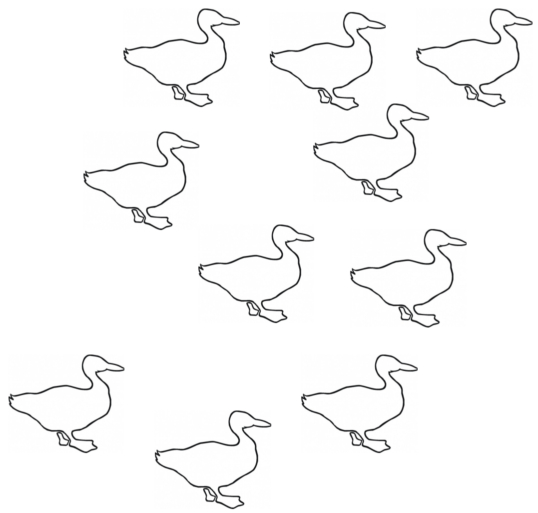
probability of survival = 0.5

if stochastic?



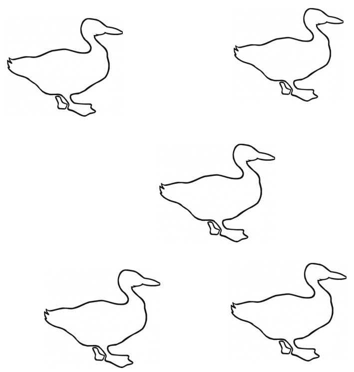
Flip a coin for every duck;

starting population

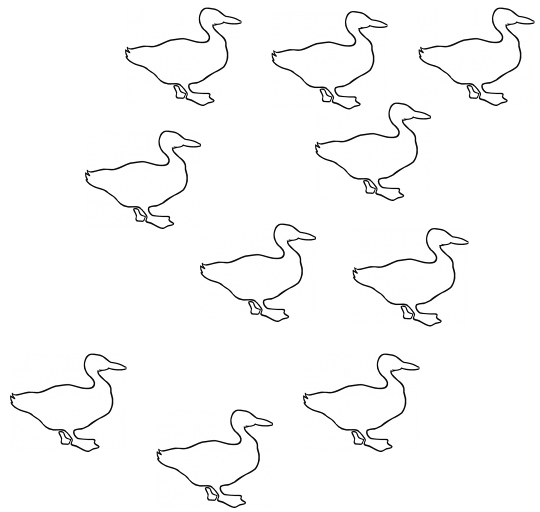


probability of survival = 0.5

if deterministic

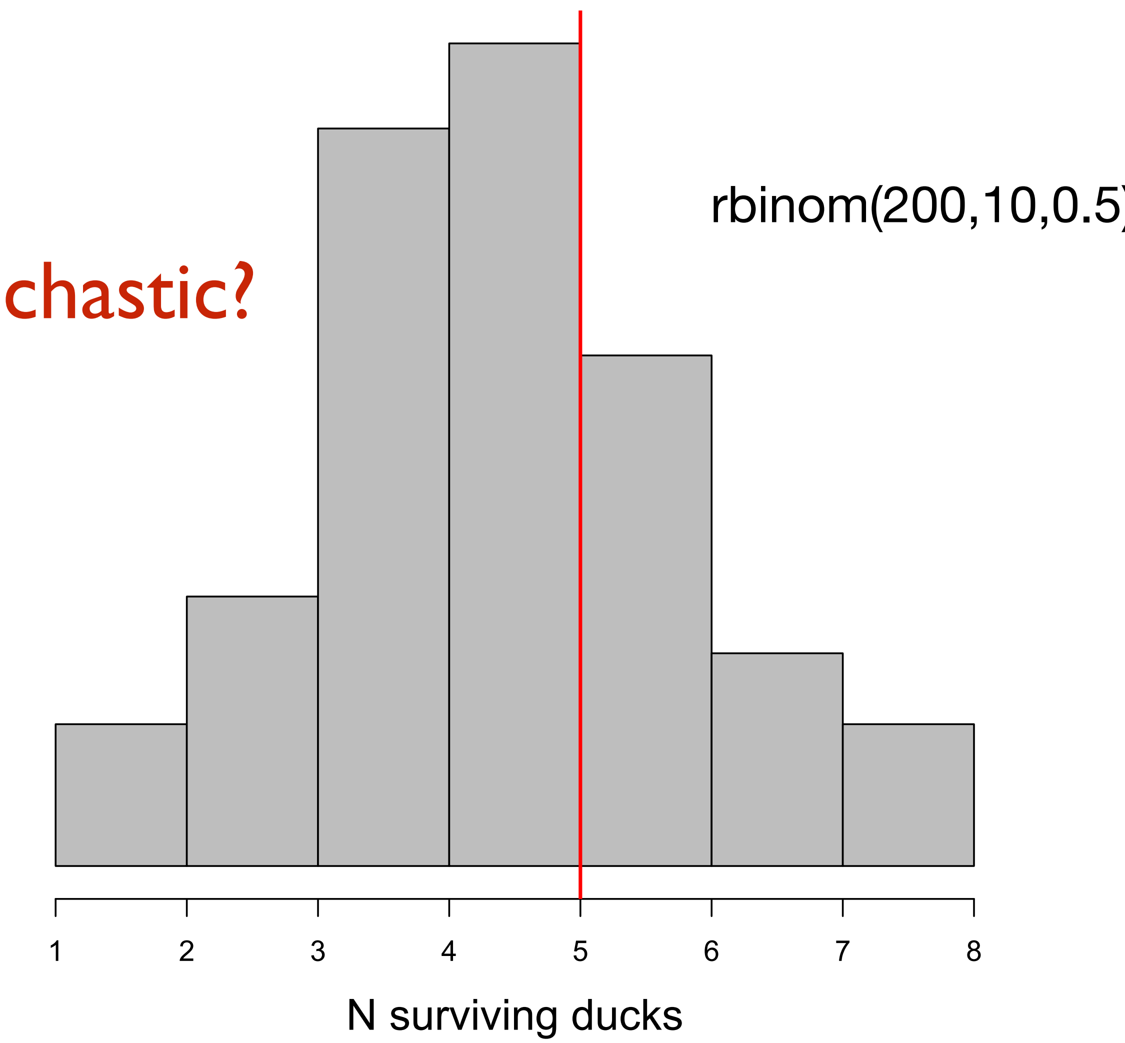


starting population

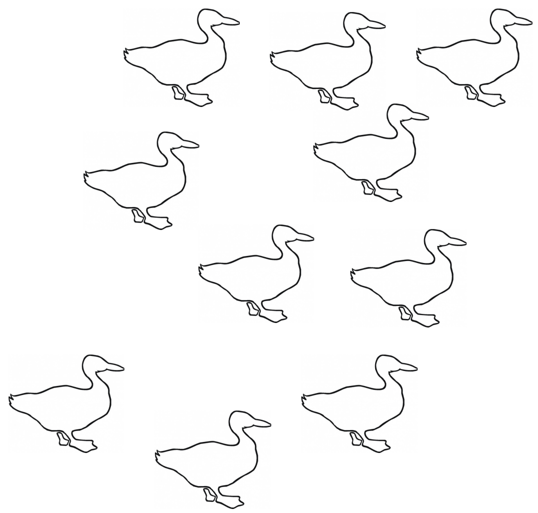


probability of survival = 0.5

if stochastic?

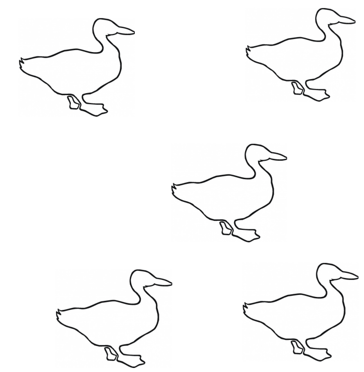


starting population

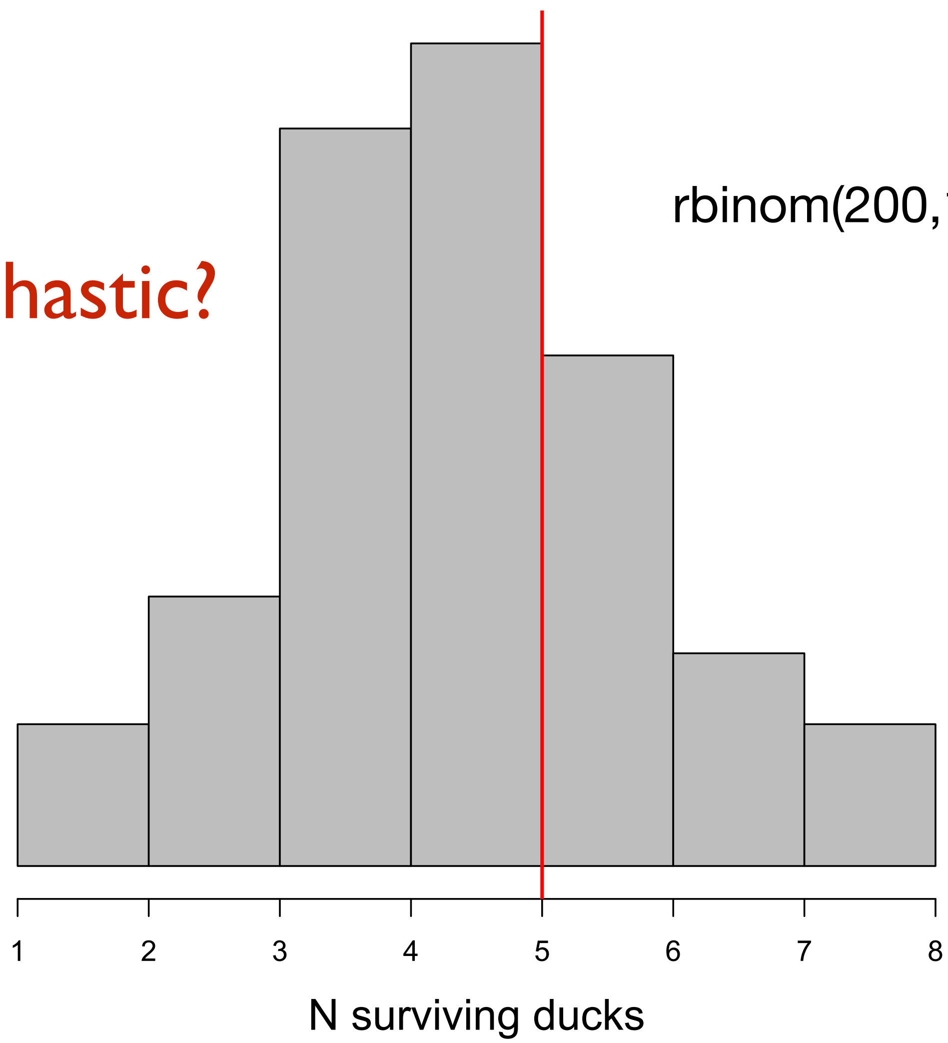


probability of
survival = 0.5

if deterministic

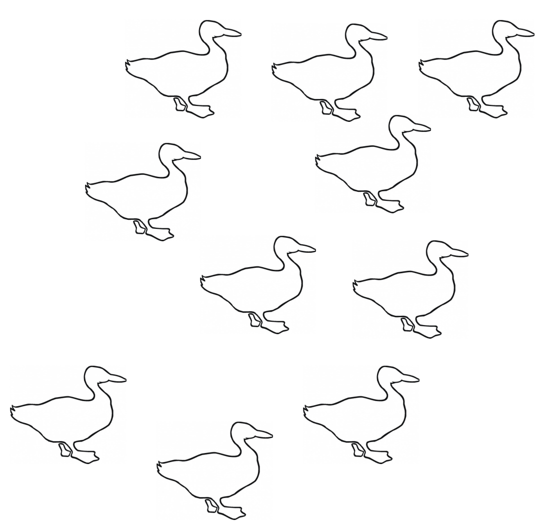


If you test your 10 ducks
many times, on average
you get 5



rbinom(200,10,0.5)

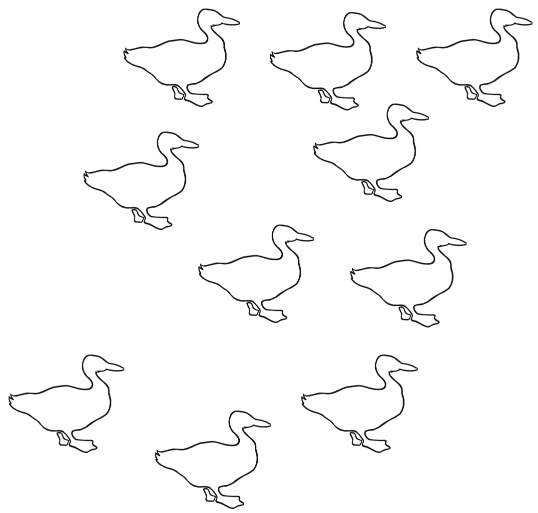
starting population



probability of
survival = 0.5

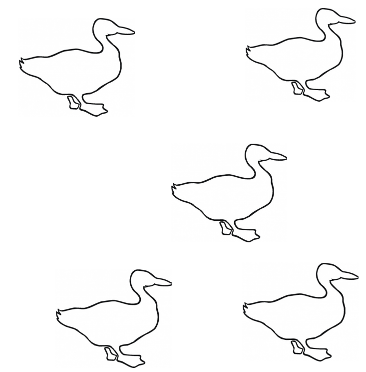
if stochastic?

starting population

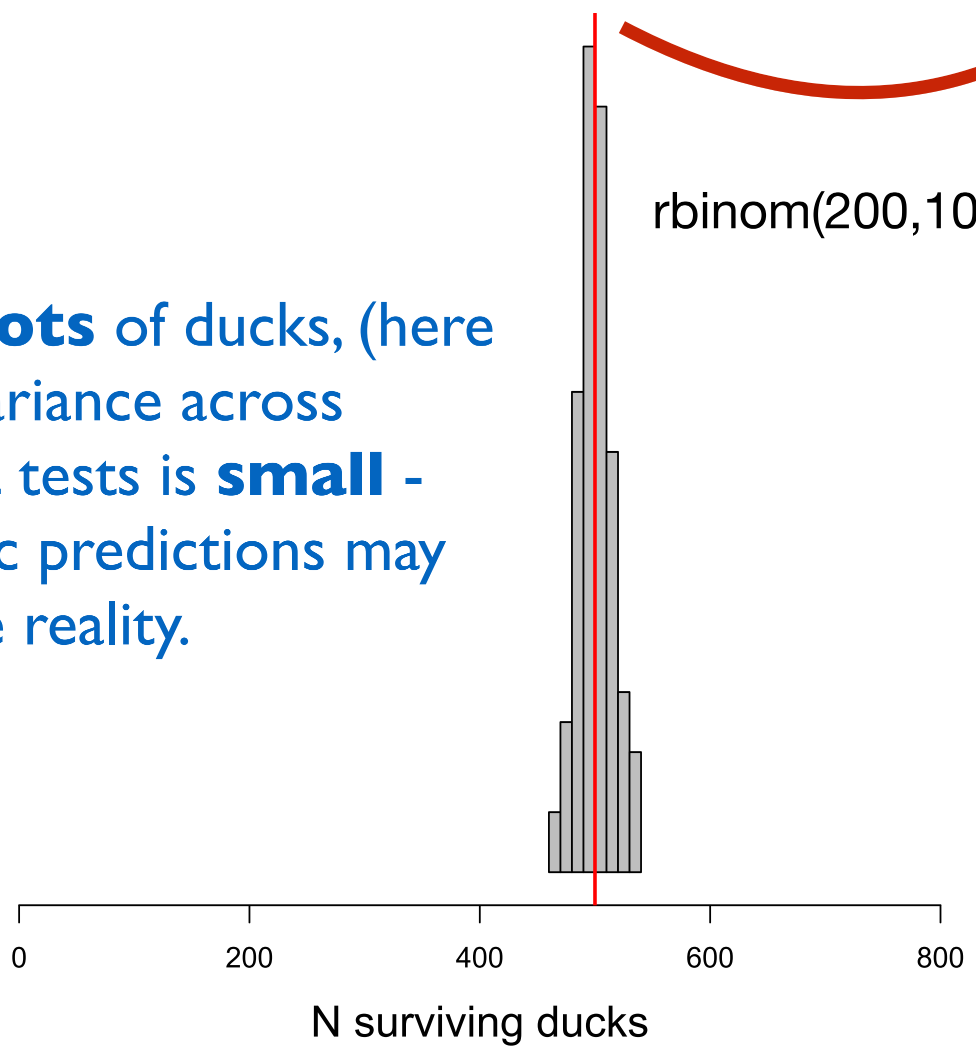


probability of survival = 0.5

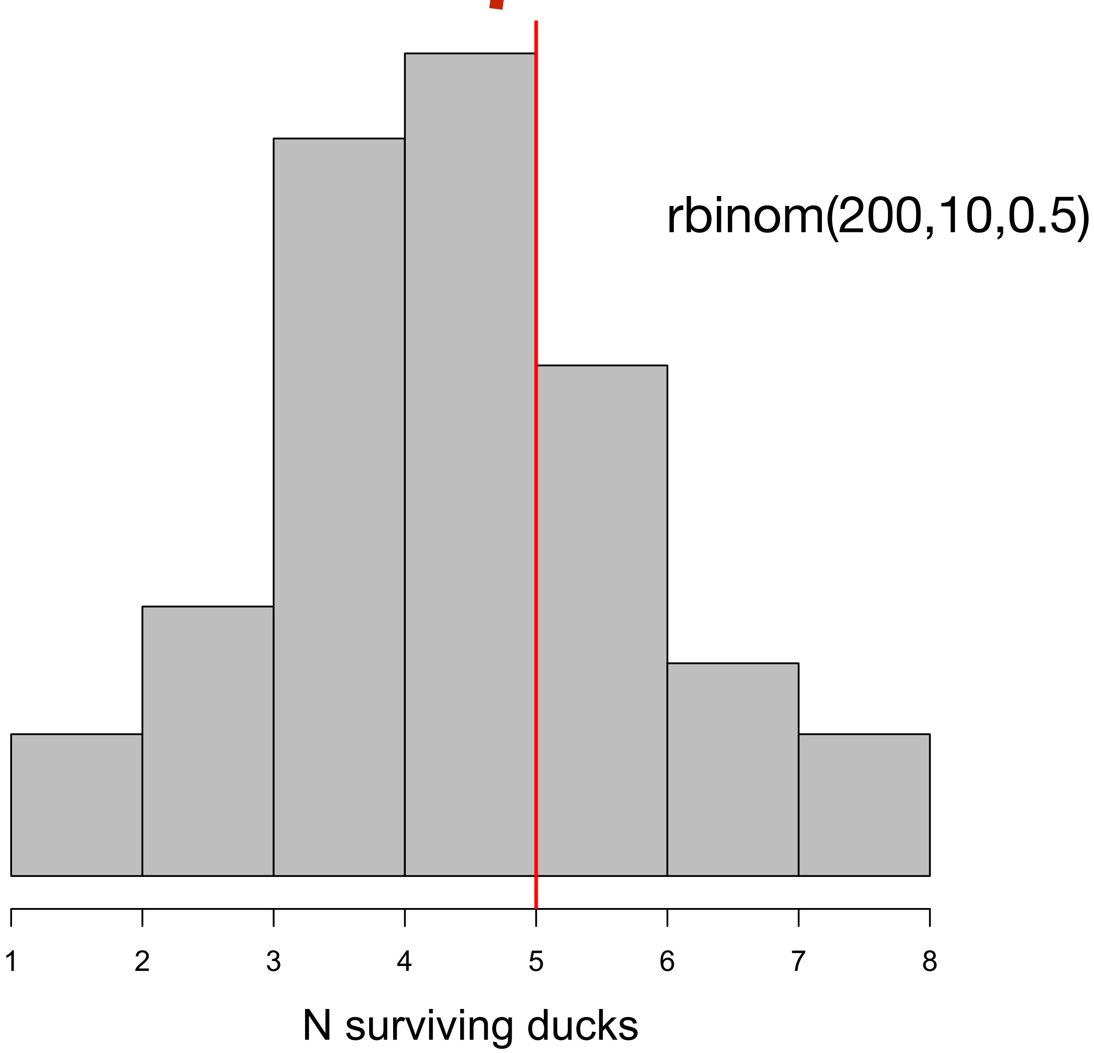
if deterministic



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



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.***

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 [‡]C
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 rainfall. Climatic unpredictability is associated with unpredictable patterns of fruiting and flowering. It is argued that these features