

Introduction to Compartmental Models and Differential Equations

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Slides and tutorial from Jess Metcalf
(Princeton University)



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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)



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Populations are divided into compartments

Les populations sont subdivisées en compartiments



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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



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Rates of transferring between compartments
are expressed mathematically

Taux de transition entre les compartiments sont exprimés
mathématiquement



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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?**



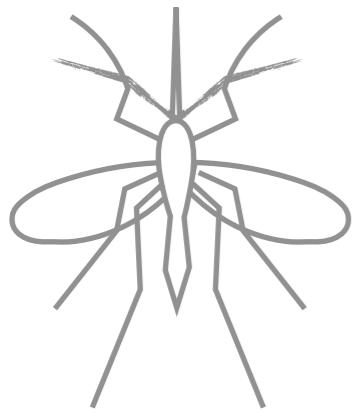
How are these different from statistical models?

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)



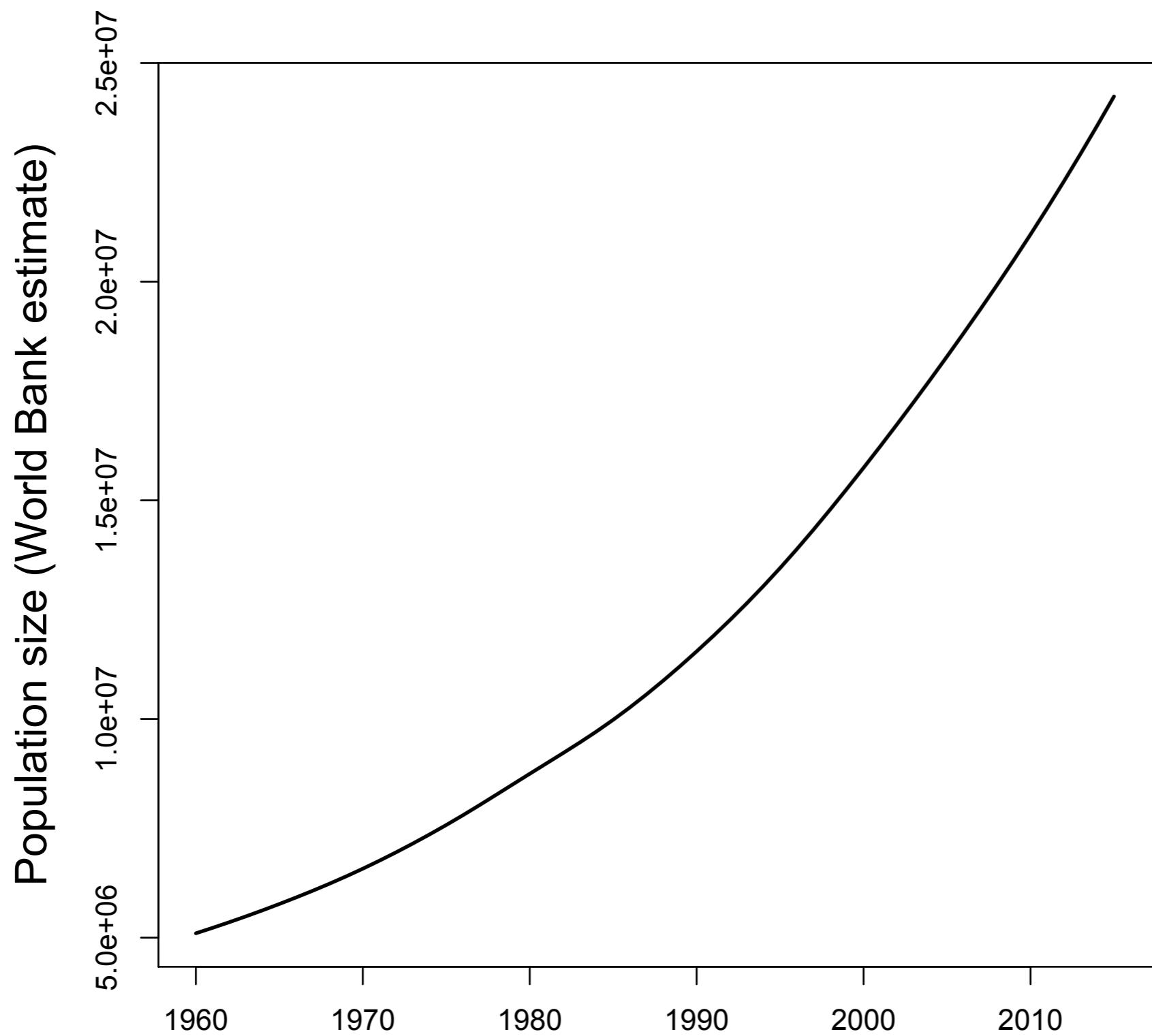


I. Population Models

I. 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)

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How could we build a compartmental model of population growth?

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



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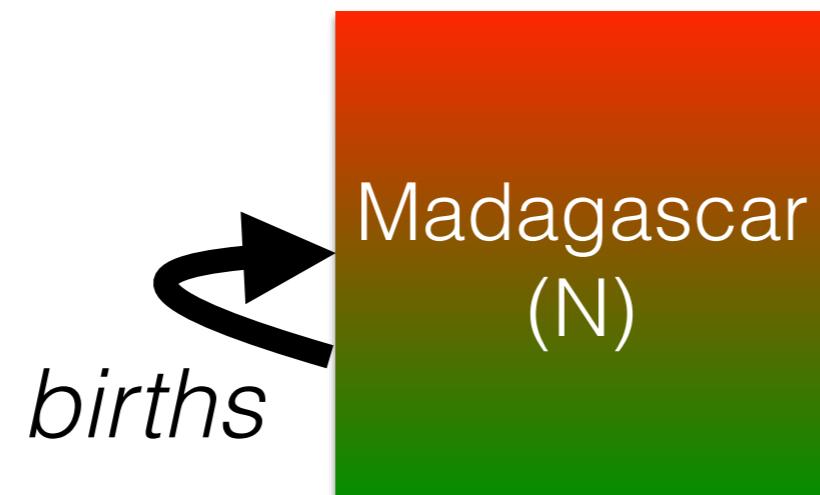
How does the population increase?



The basic population model

Compartmental models (Mechanistic Models)

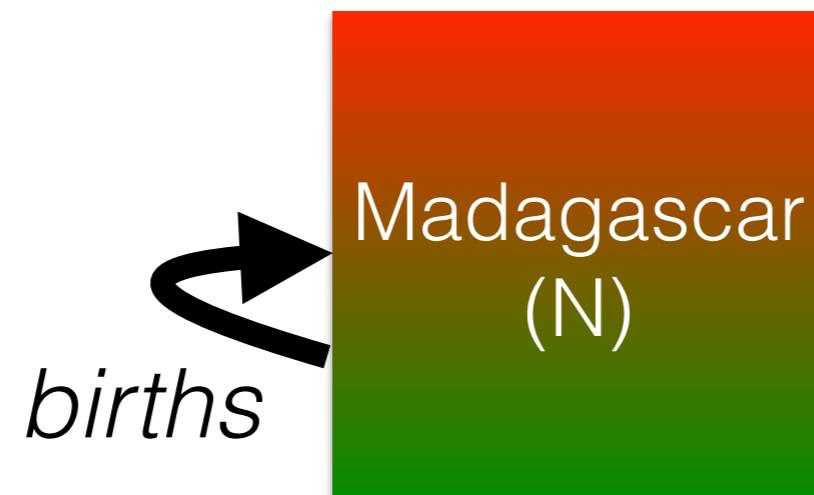
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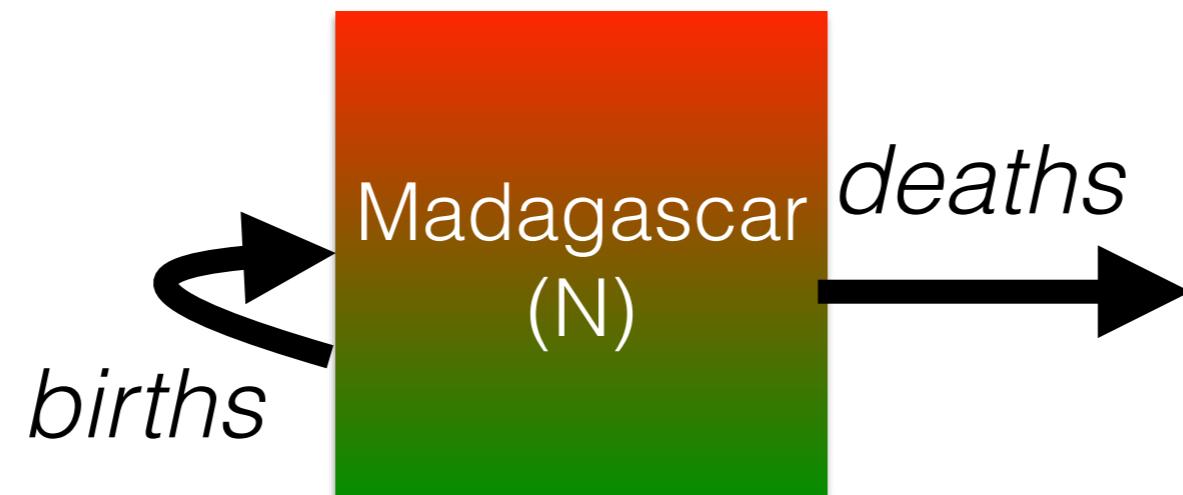
How does the population decrease?



The basic population model

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$$N_{t+1} =$$



The basic population model

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



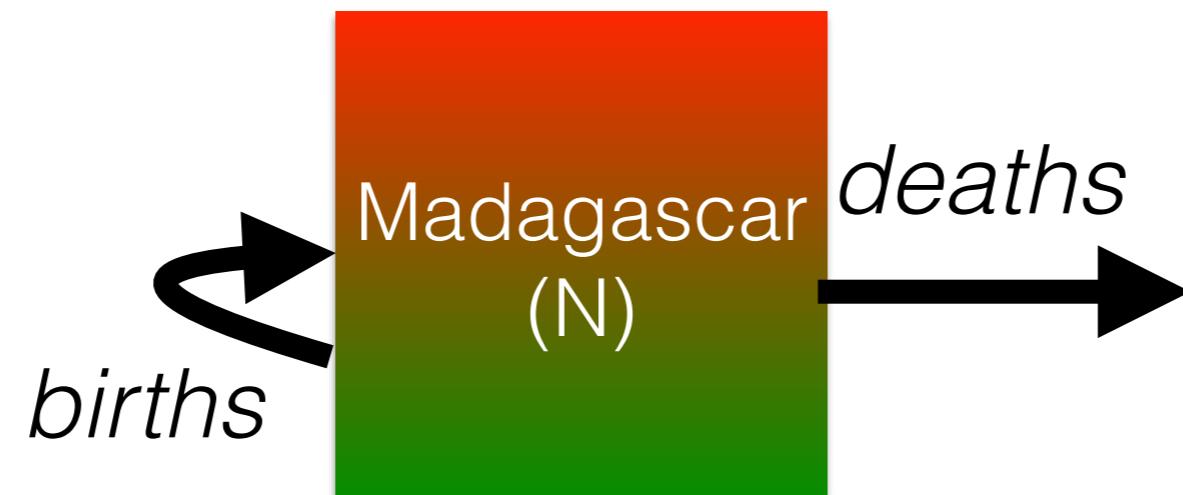
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$$N_{t+1} = \text{births} * N_t - \text{deaths} * N_t$$



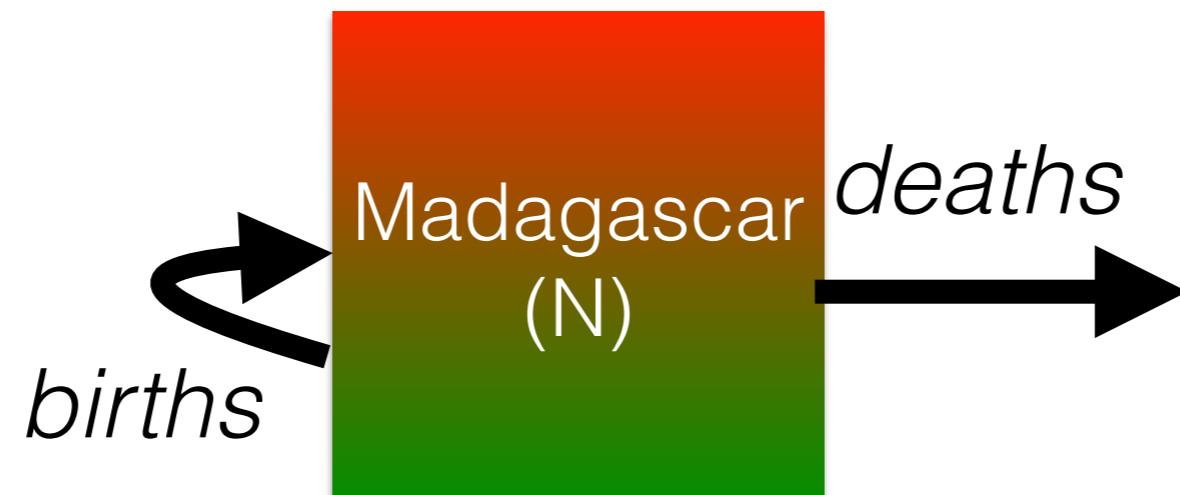
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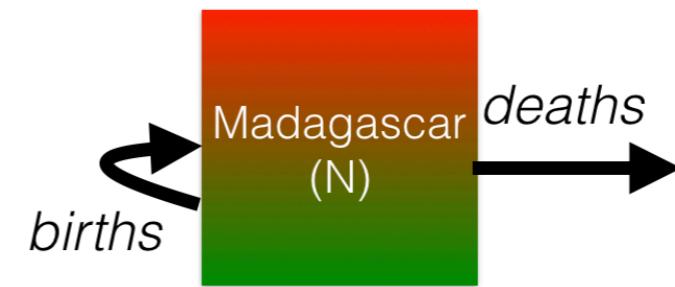
$$N_{t+1} = \text{births} * N_t - \text{deaths} * N_t$$

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

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



The basic population model



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

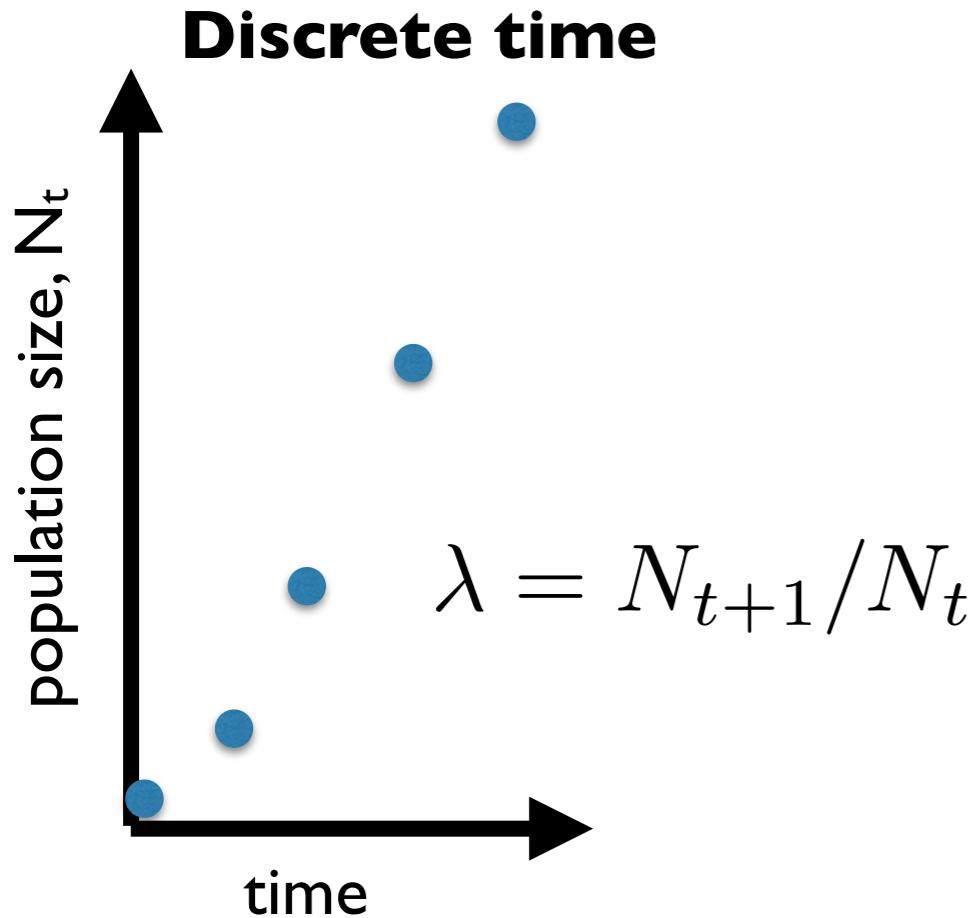
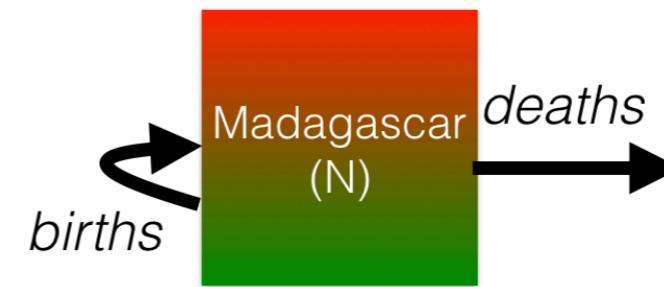
Population rate of increase

Taux d'accroissement de la population

pop size at t
pop size at t+1



The basic population model



$$N_1 = \lambda N_0$$

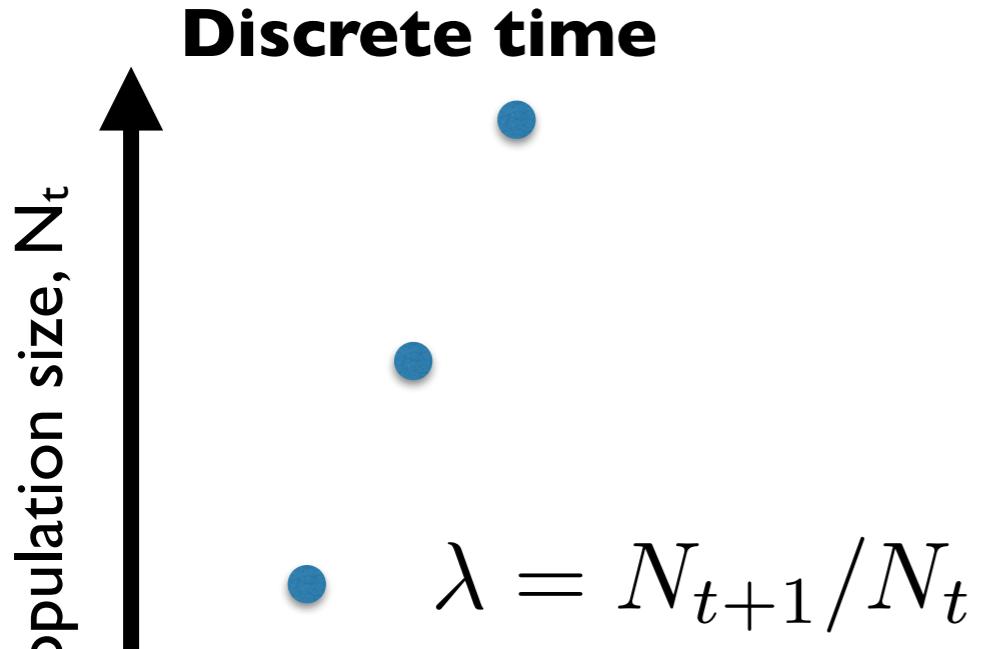
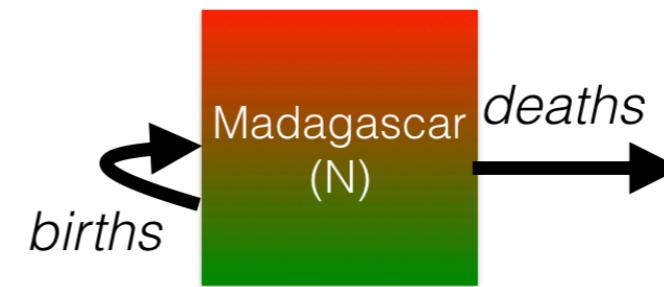
$$N_2 = \lambda[\lambda N_0] = \lambda^2 N_0$$

$$N_3 = \lambda^3 N_0$$

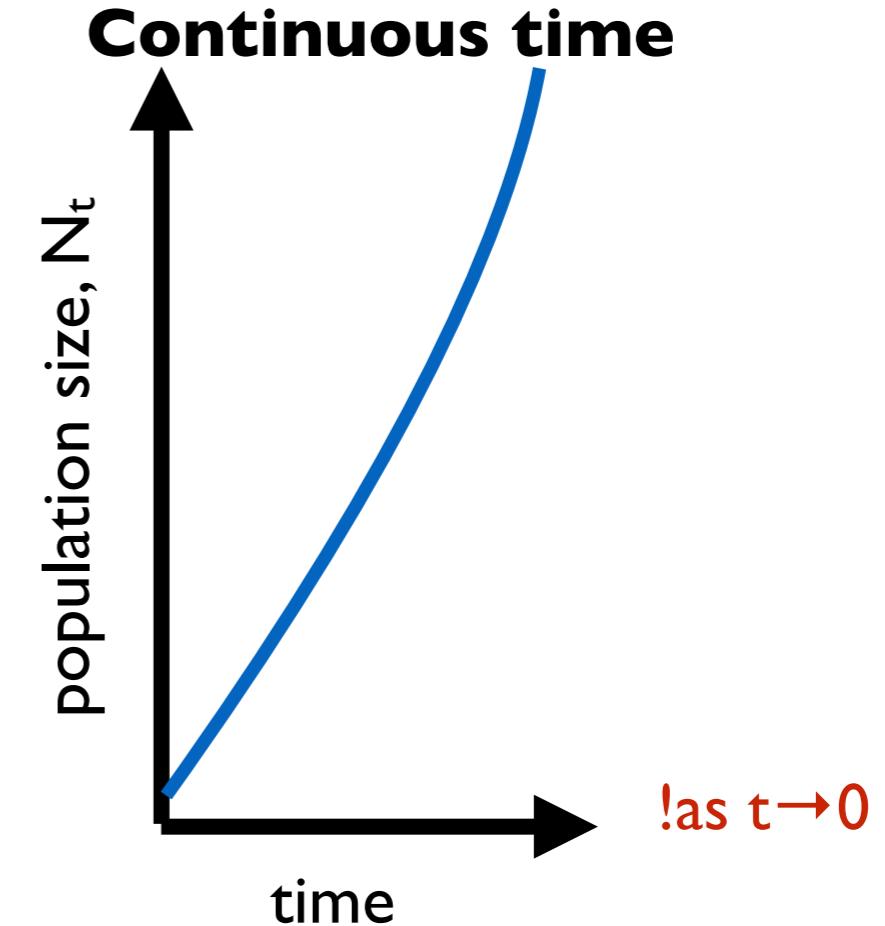
$$N_t = \lambda^t N_0$$



The basic population model



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



$$\frac{dP}{dt} = rP$$
$$r = [P(t) - P(0)]/t$$

$$N_1 = \lambda N_0$$

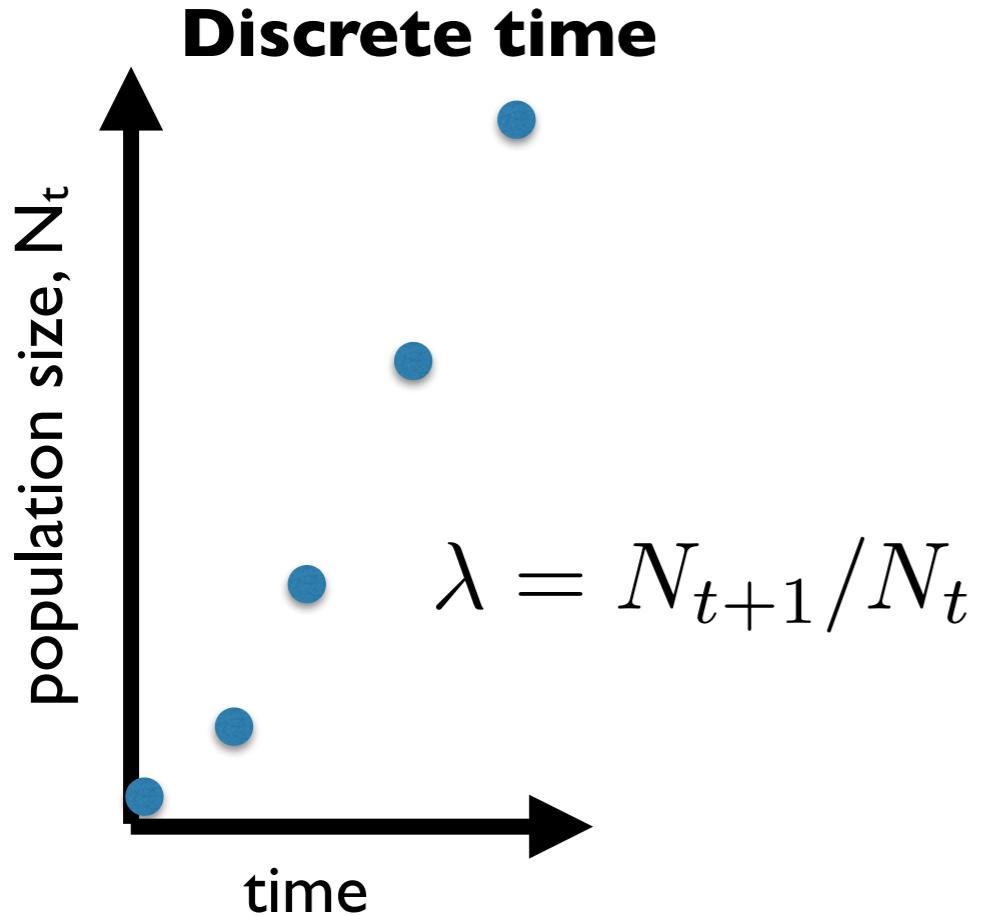
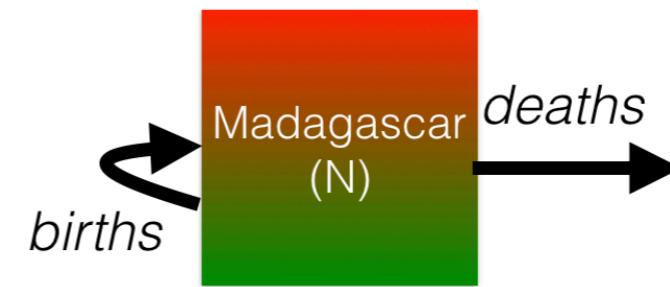
$$N_2 = \lambda [\lambda N_0] = \lambda^2 N_0$$

$$N_3 = \lambda^3 N_0$$

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The basic population model



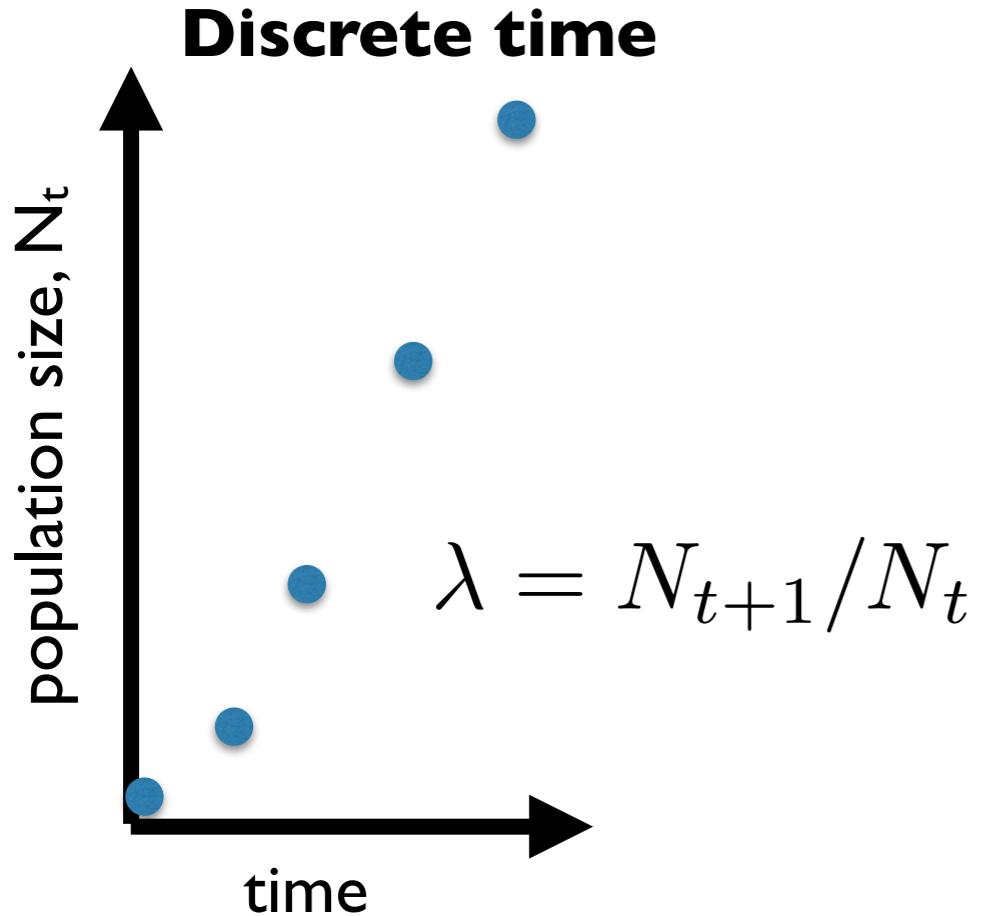
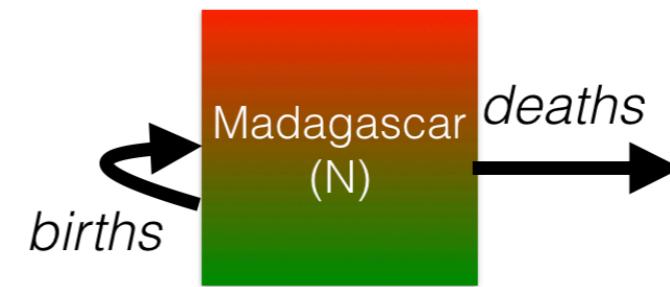
Continuous time

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

$$\begin{aligned}N_1 &= \lambda N_0 \\N_2 &= \lambda[\lambda N_0] = \lambda^2 N_0 \\N_3 &= \lambda^3 N_0 \\N_t &= \lambda^t N_0\end{aligned}$$



The basic population model



Continuous time

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

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

$$N_1 = \lambda N_0$$

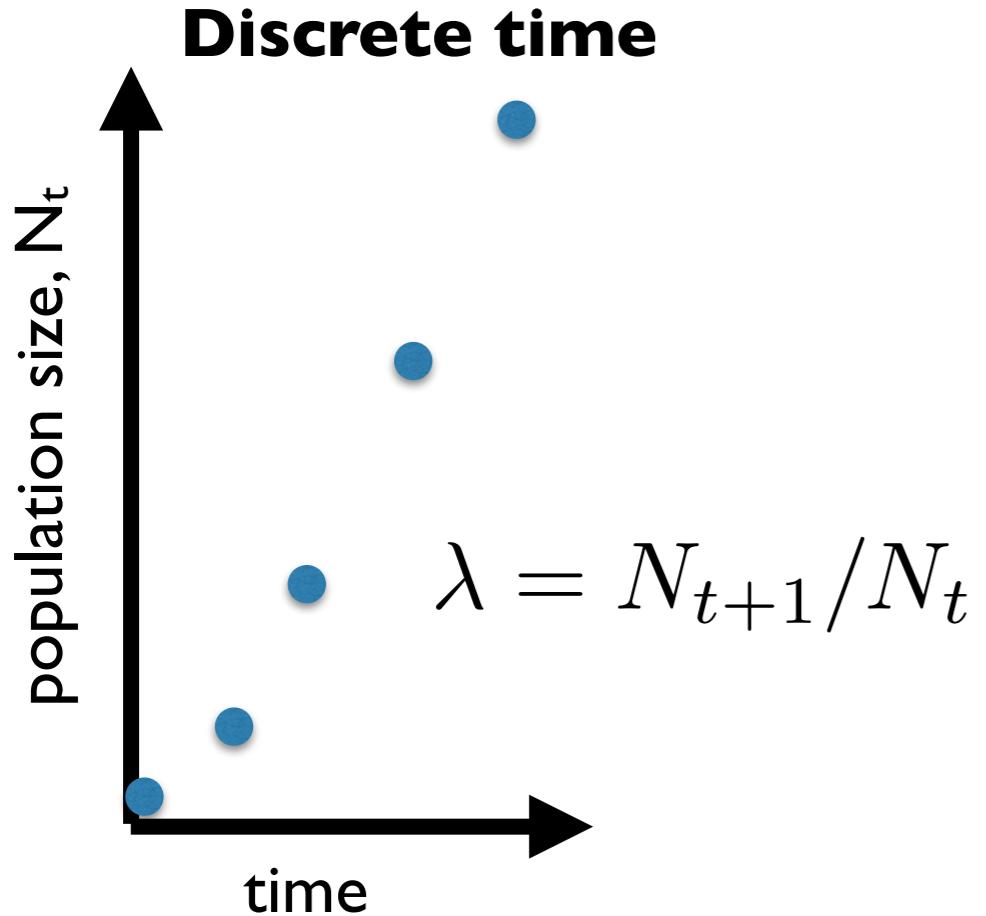
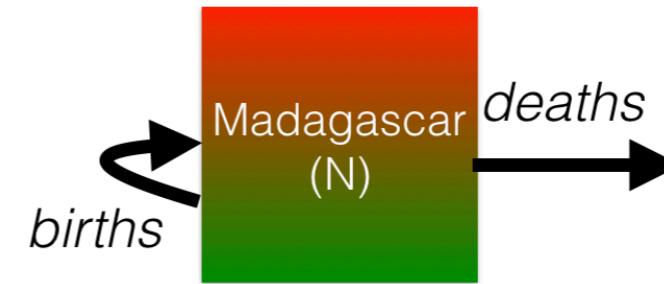
$$N_2 = \lambda [\lambda N_0] = \lambda^2 N_0$$

$$N_3 = \lambda^3 N_0$$

$$N_t = \lambda^t N_0$$



The basic population model



Continuous time

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

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

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

$$N_1 = \lambda N_0$$

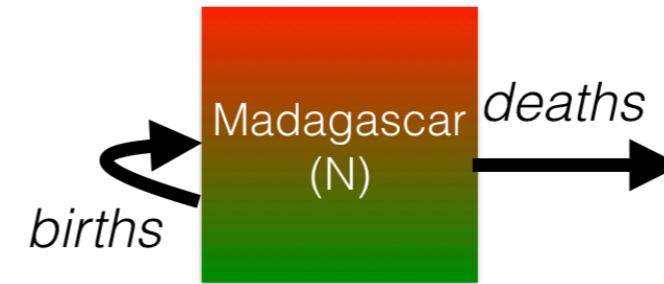
$$N_2 = \lambda [\lambda N_0] = \lambda^2 N_0$$

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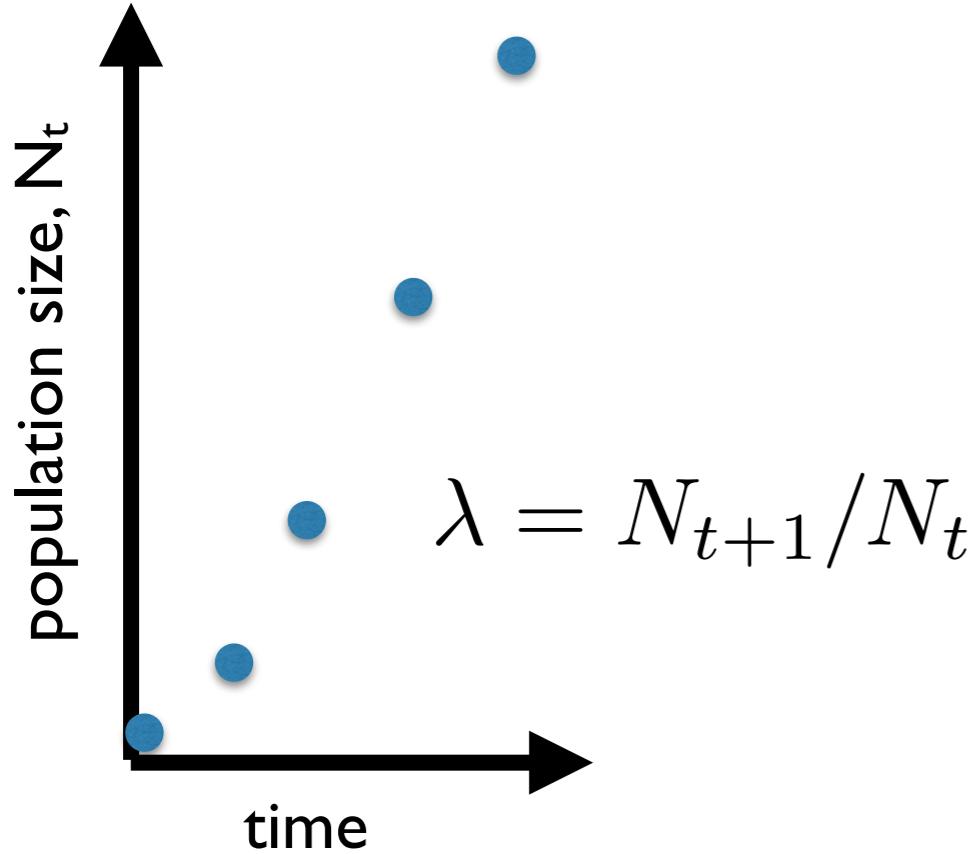
$$N_t = \lambda^t N_0$$



The basic population model



Discrete time



$$N_1 = \lambda N_0$$

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

$$N_3 = \lambda^3 N_0$$

$$N_t = \lambda^t N_0$$

Continuous time

$$\frac{dP(t)}{dt} = rP(t)$$

Separation of variables:
 $\frac{dP(t)}{P(t)} = r dt$

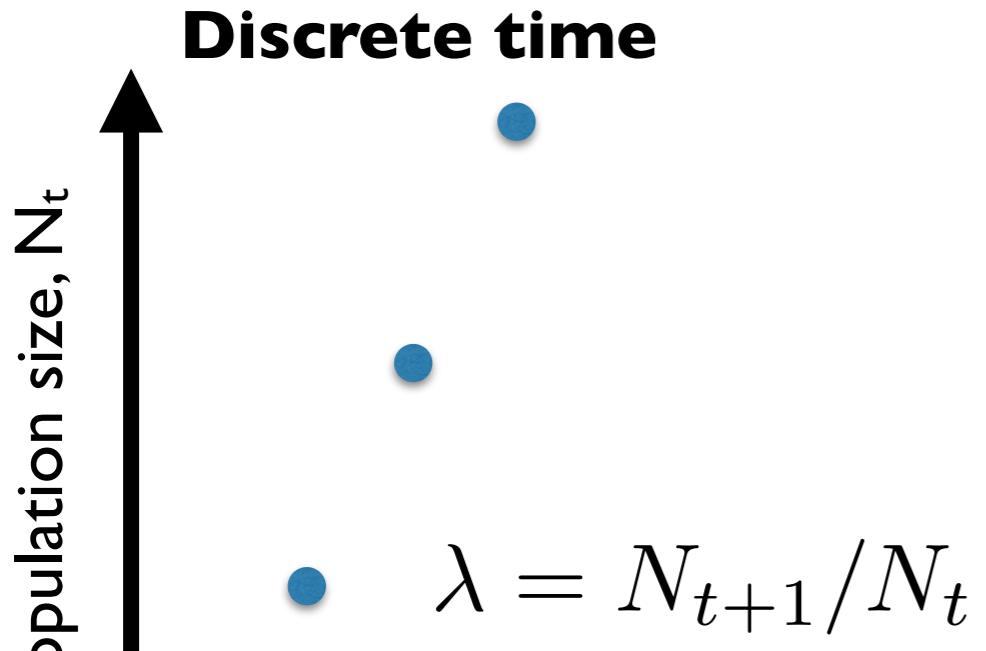
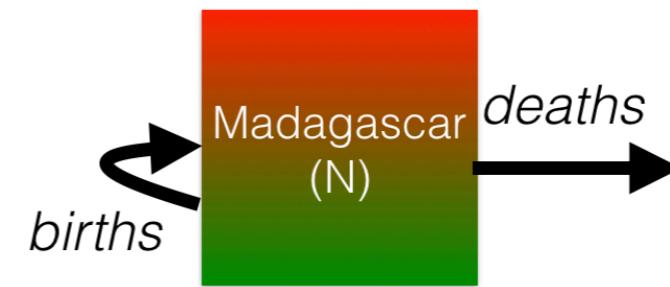
Integrate both sides:
 $\int \frac{dP(t)}{P(t)} = \int r dt$

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

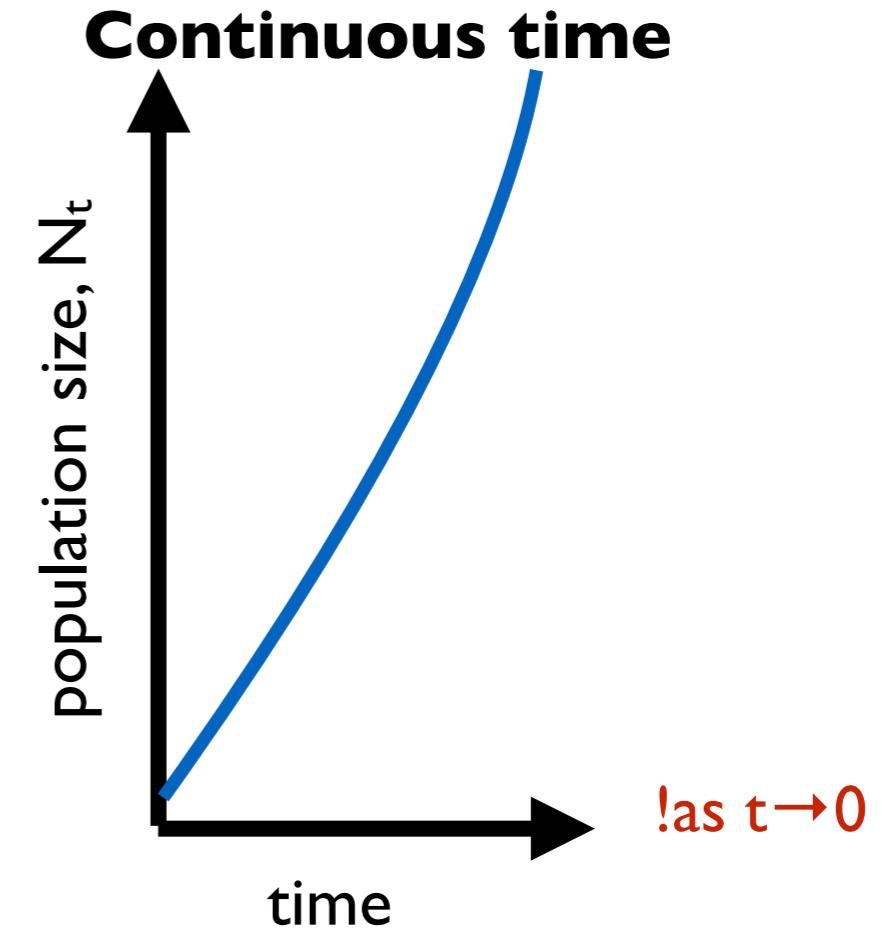
Take exponentials:
 $P(t) = e^{rt + c} = C e^{rt}$
 $P(t) = P(0)e^{rt}$



The basic population model



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



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

$$N_1 = \lambda N_0$$

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

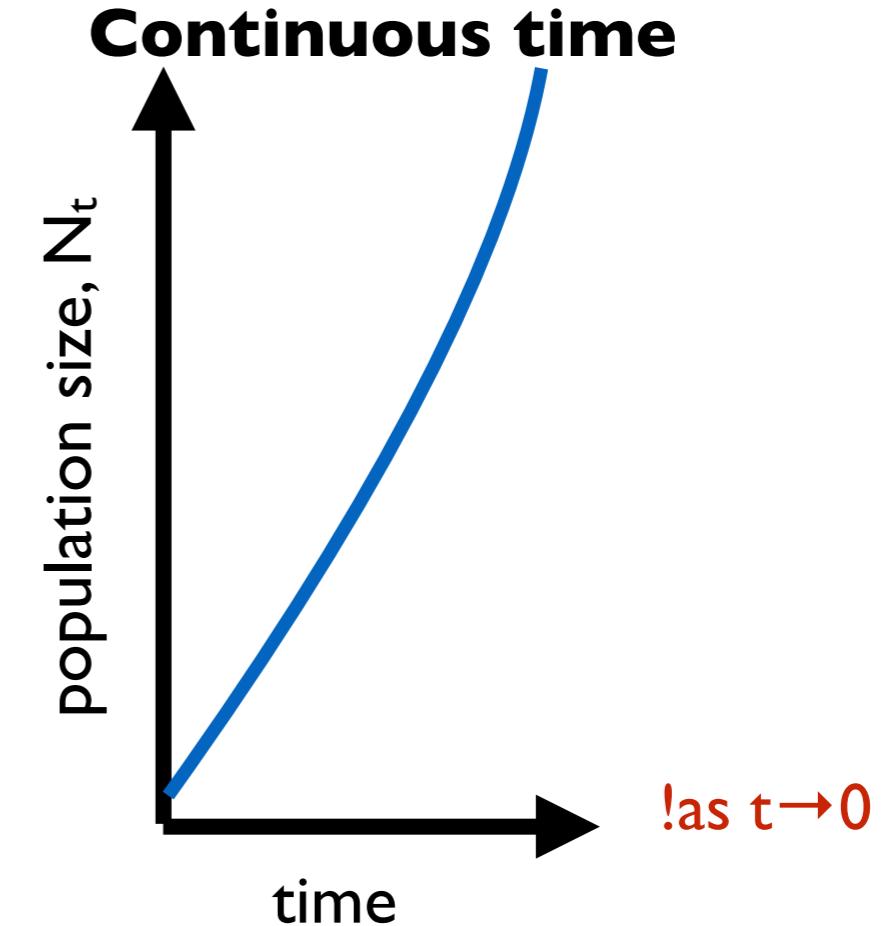
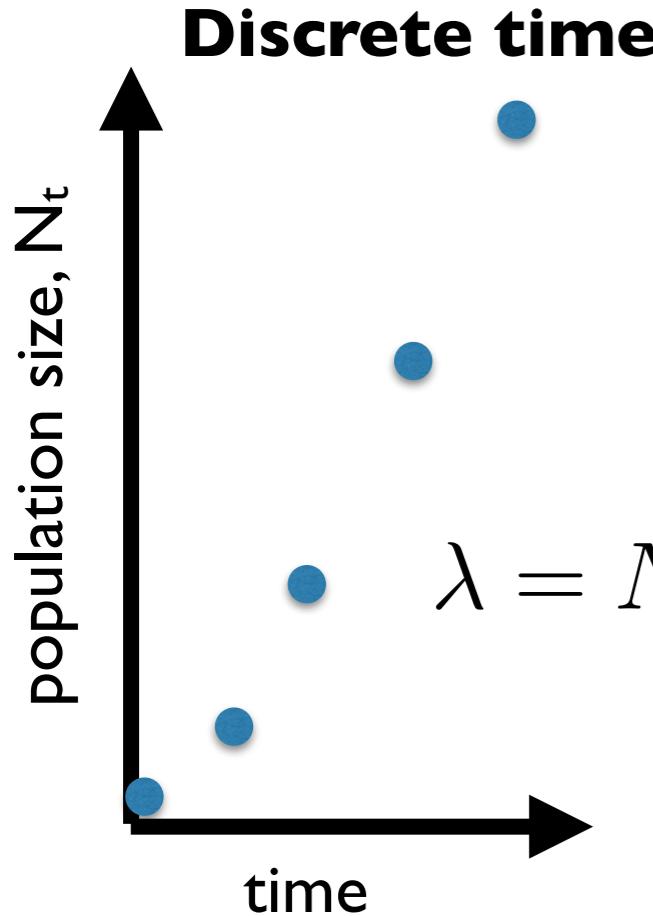
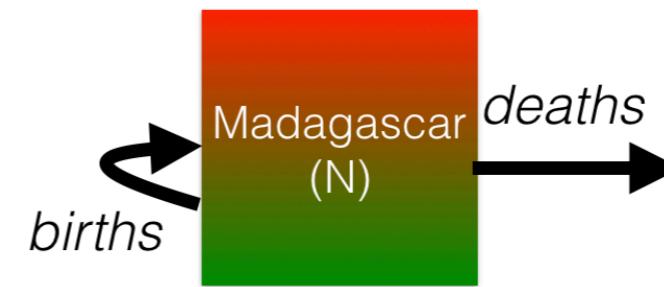
$$N_3 = \lambda^3 N_0$$

$$N_t = \lambda^t N_0$$

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



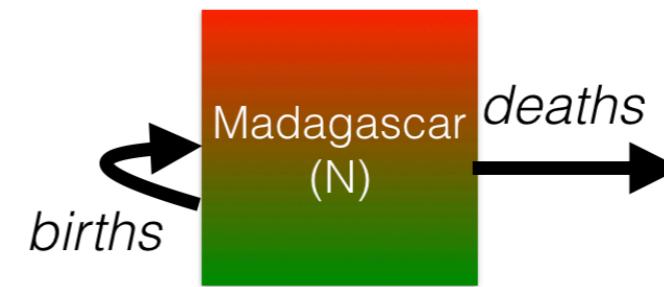
The basic population model



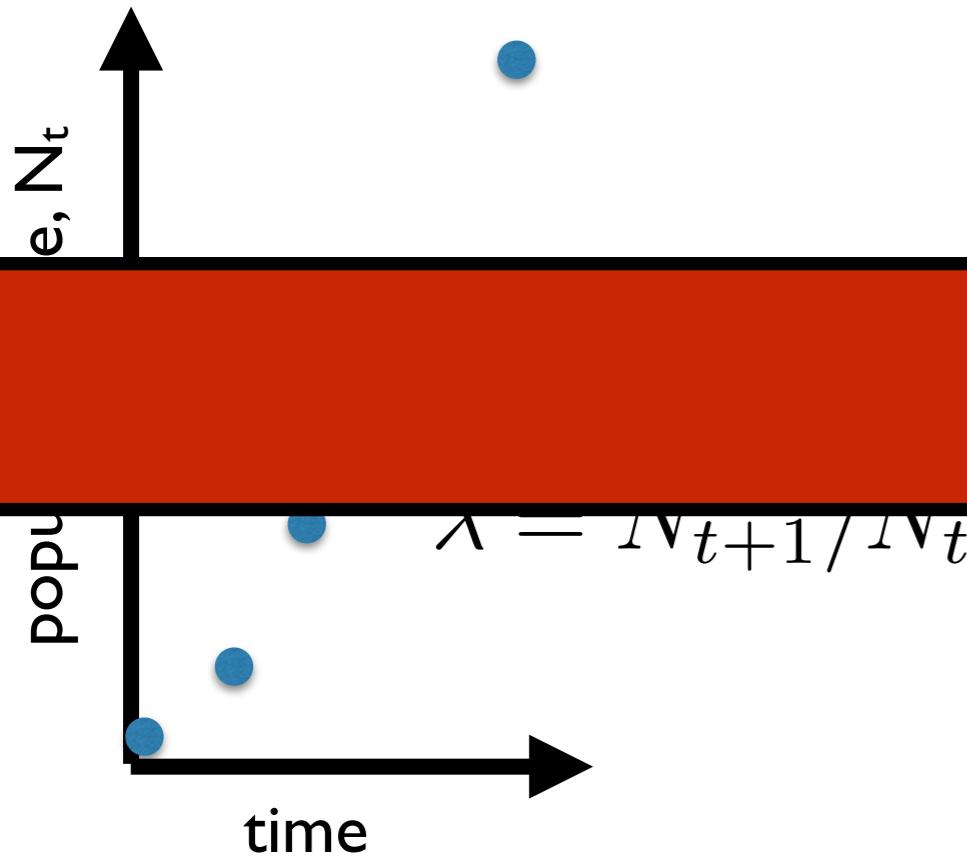
Continuous models can be discretized; discrete models can be approximated by continuous ones. The appropriate framing may depend on the data / question.



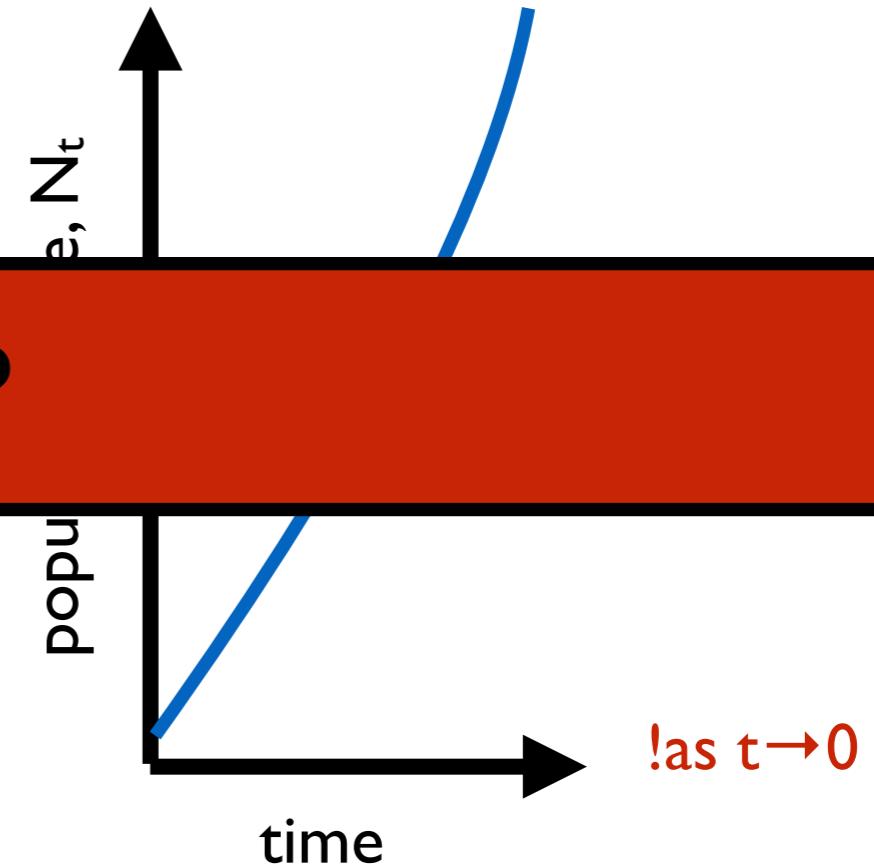
The basic population model



Discrete time



Continuous time



mazava?

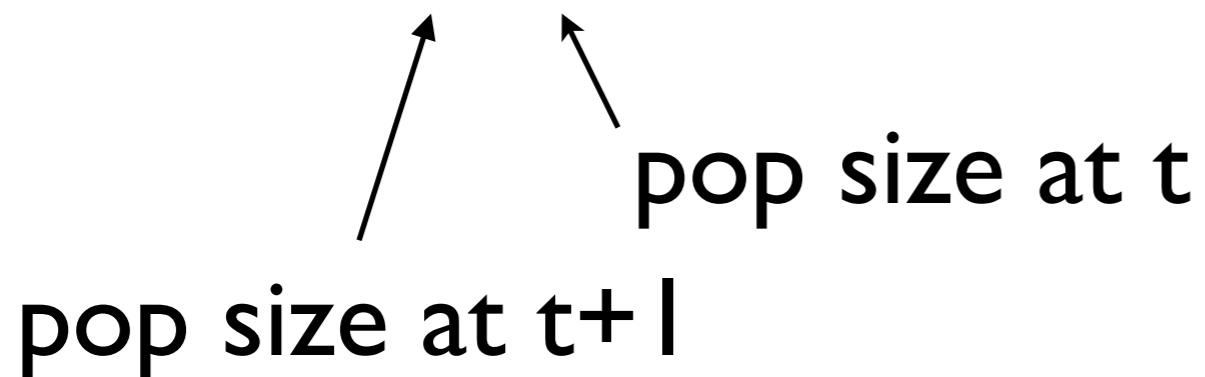
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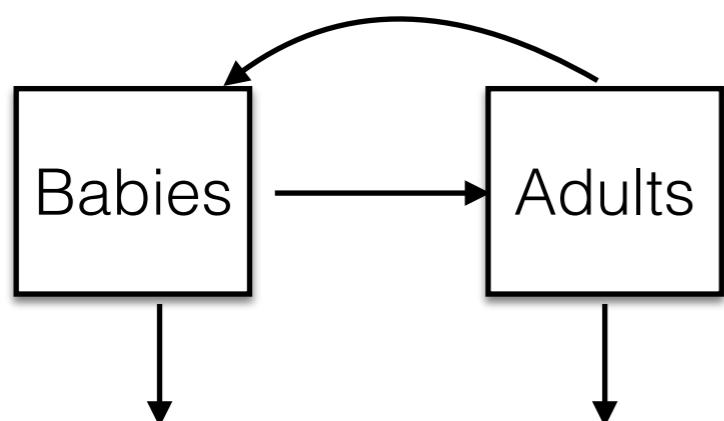
The basic population model

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

Population rate of increase



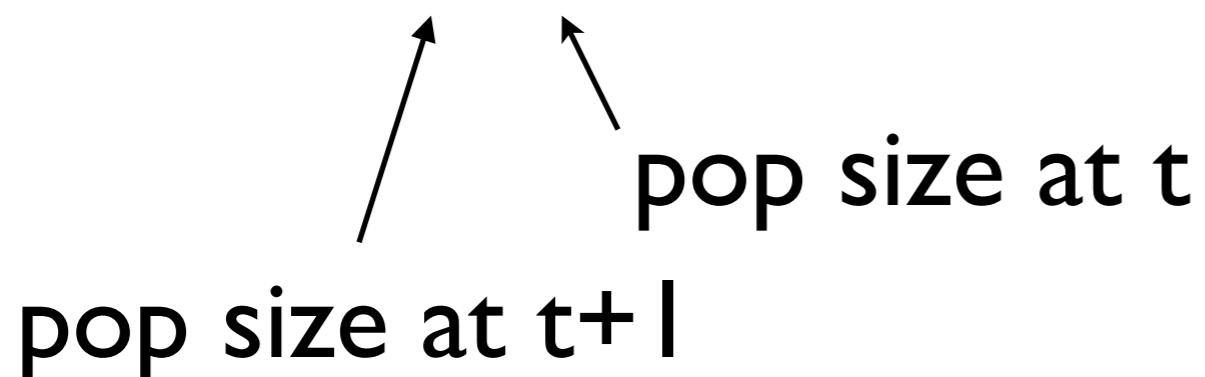
Structured population model



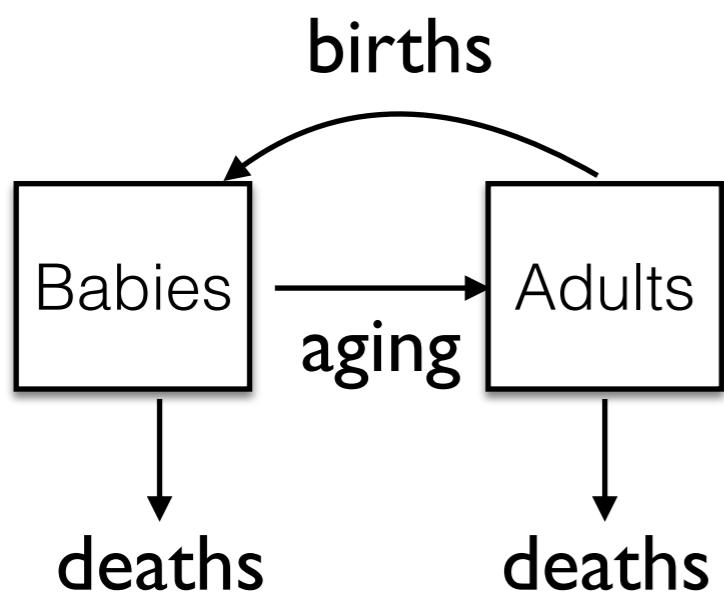
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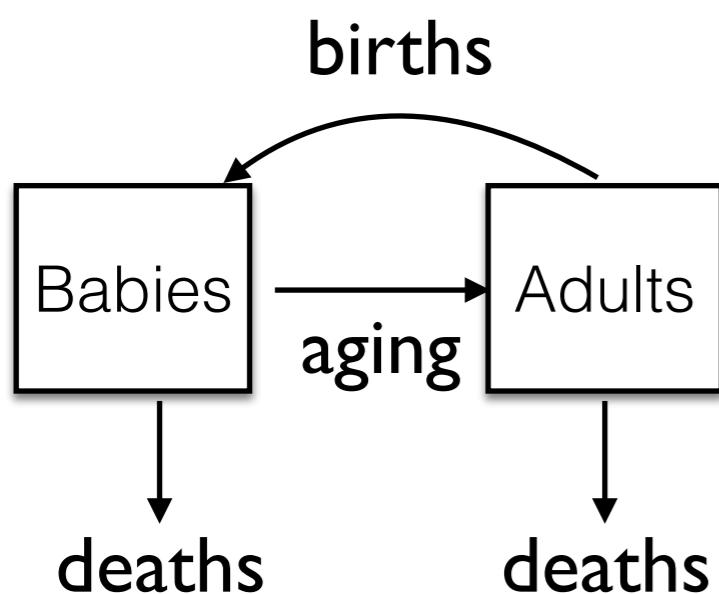
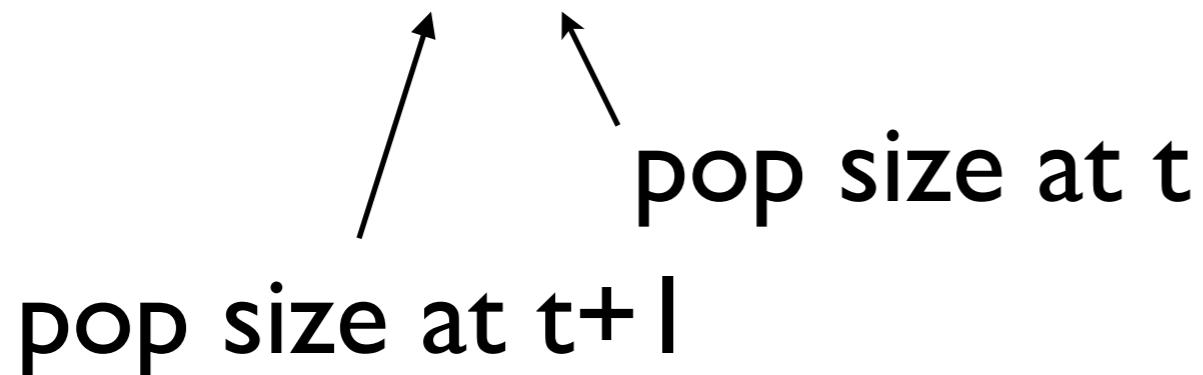
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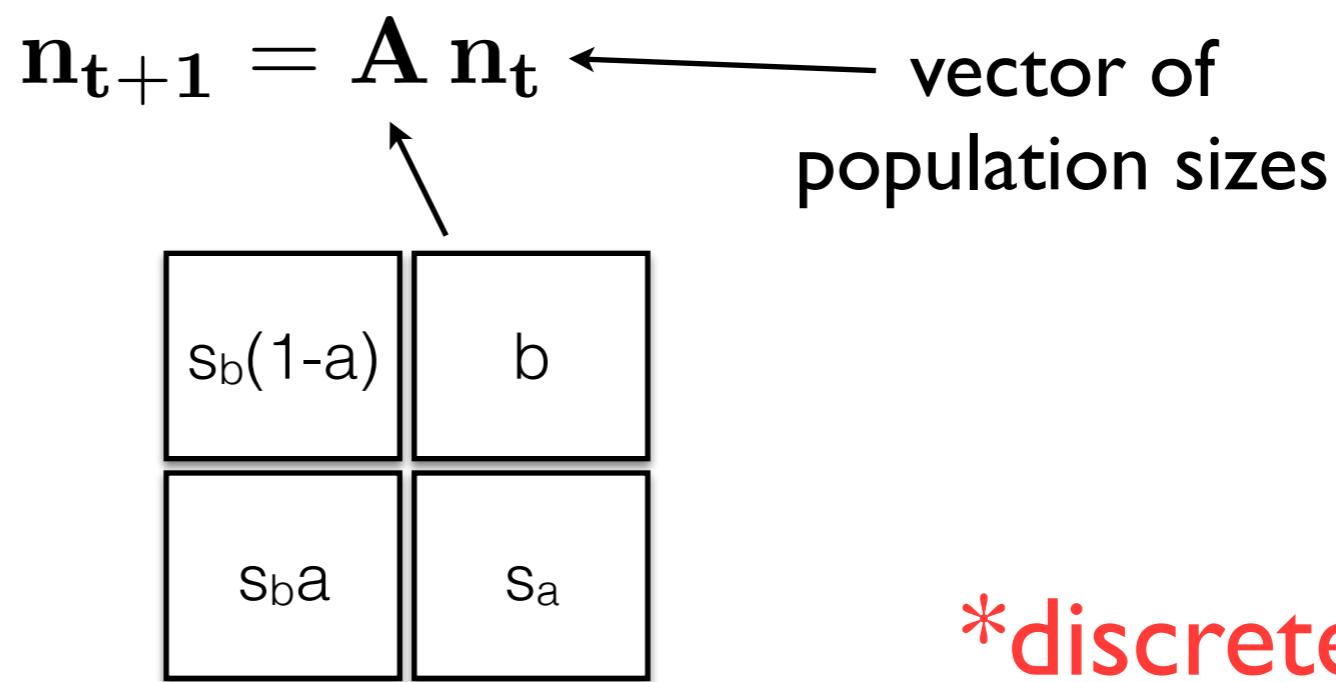
The basic population model

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Population rate of increase



Structured population model



*discrete time



Key concepts

-Continuous vs. discrete models

Modèles en temps continue vs. modèles en temps discret

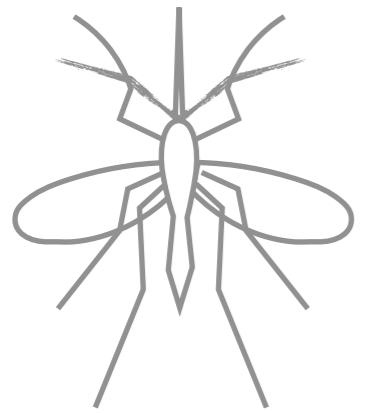
-Deterministic vs. stochastic models

Modèles déterministique vs. stochastique

-Structured models

Modèles structurés .





2. Multiple Life Stage Model



The life stage 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 different life stages of a mosquito?

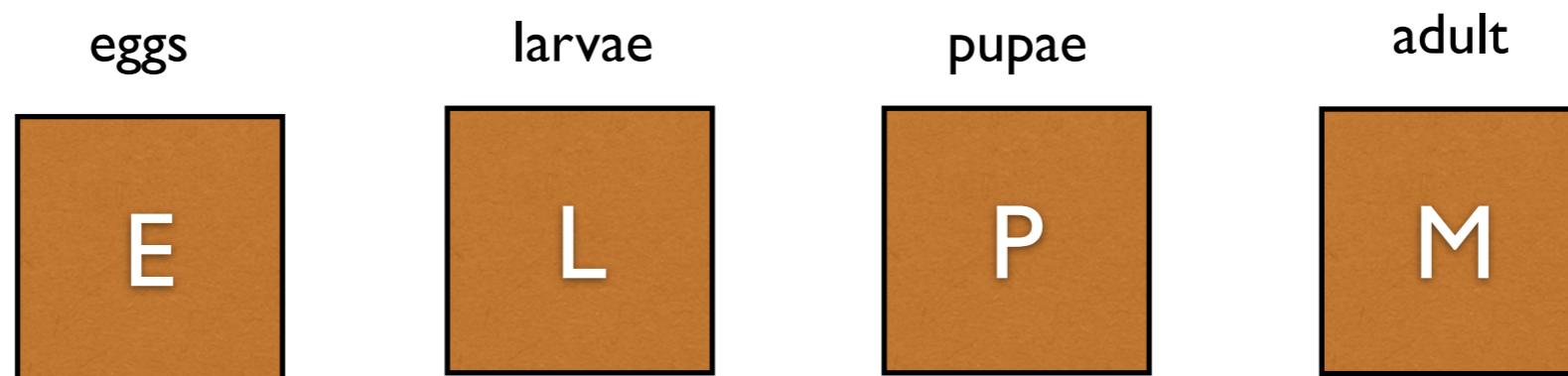


The life stage model

Compartmental models (Mechanistic Models)

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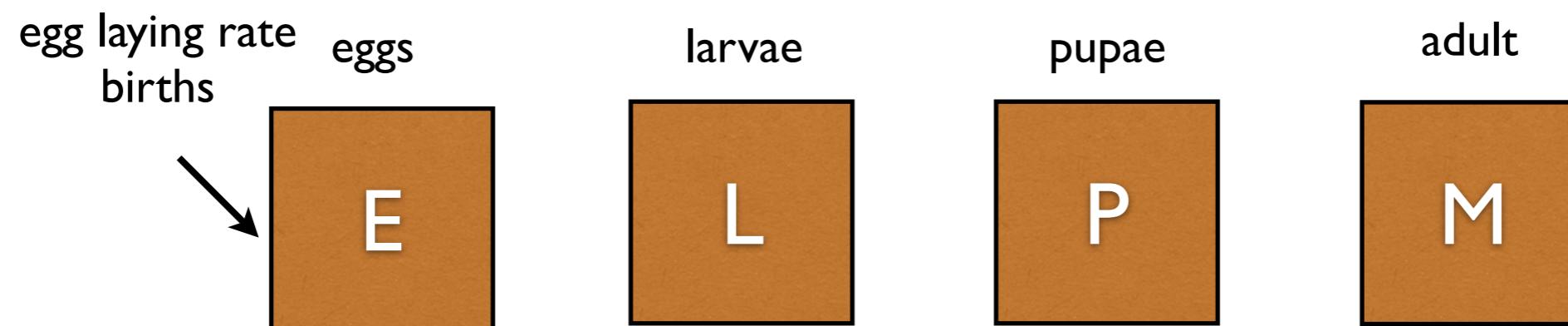
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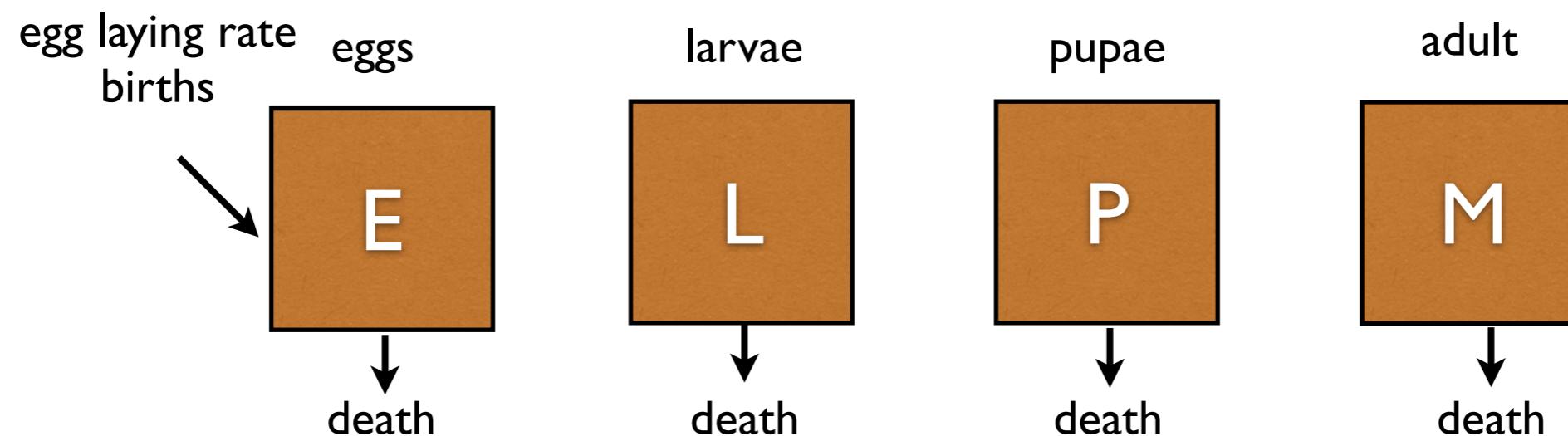
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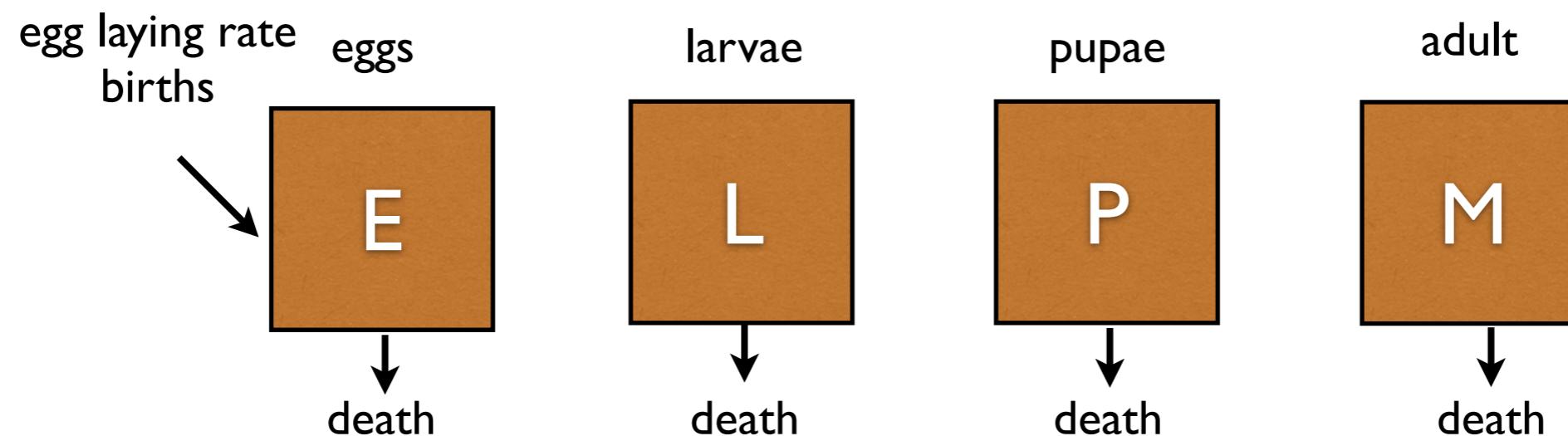
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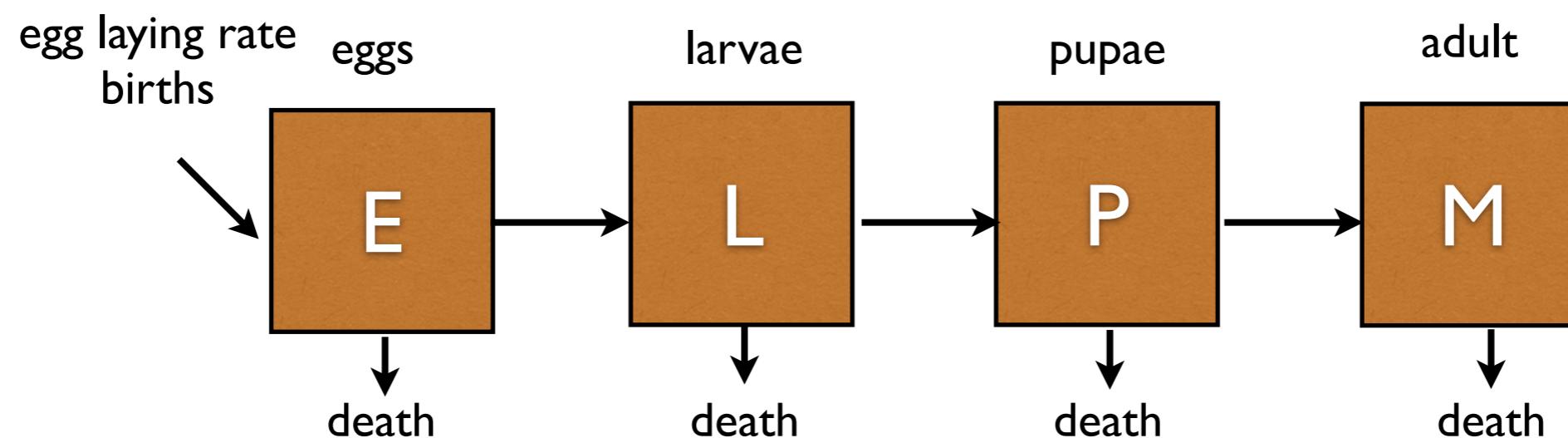
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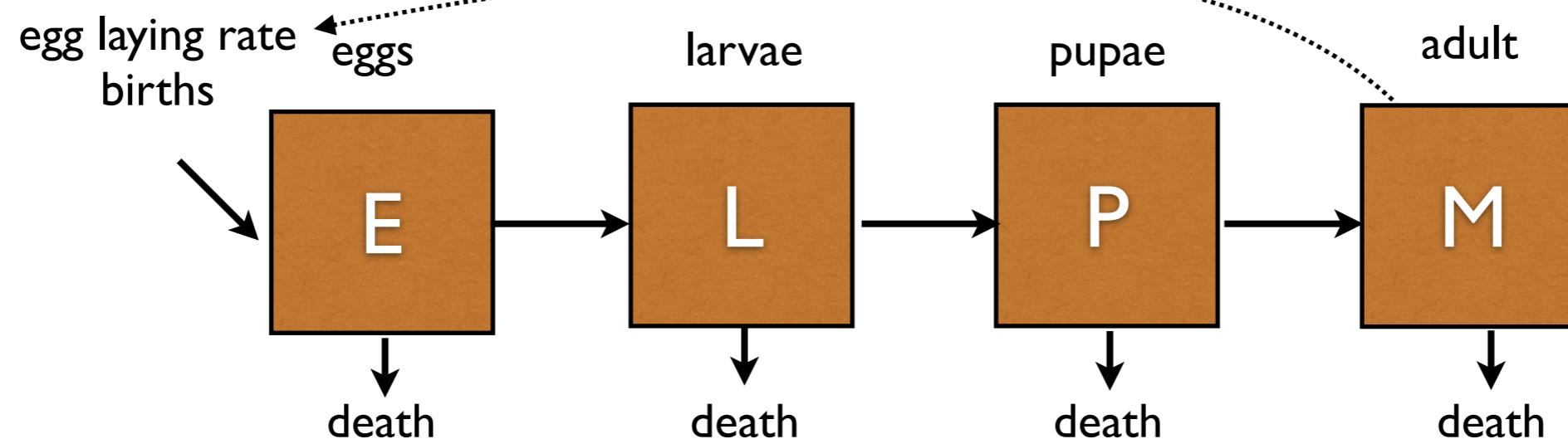
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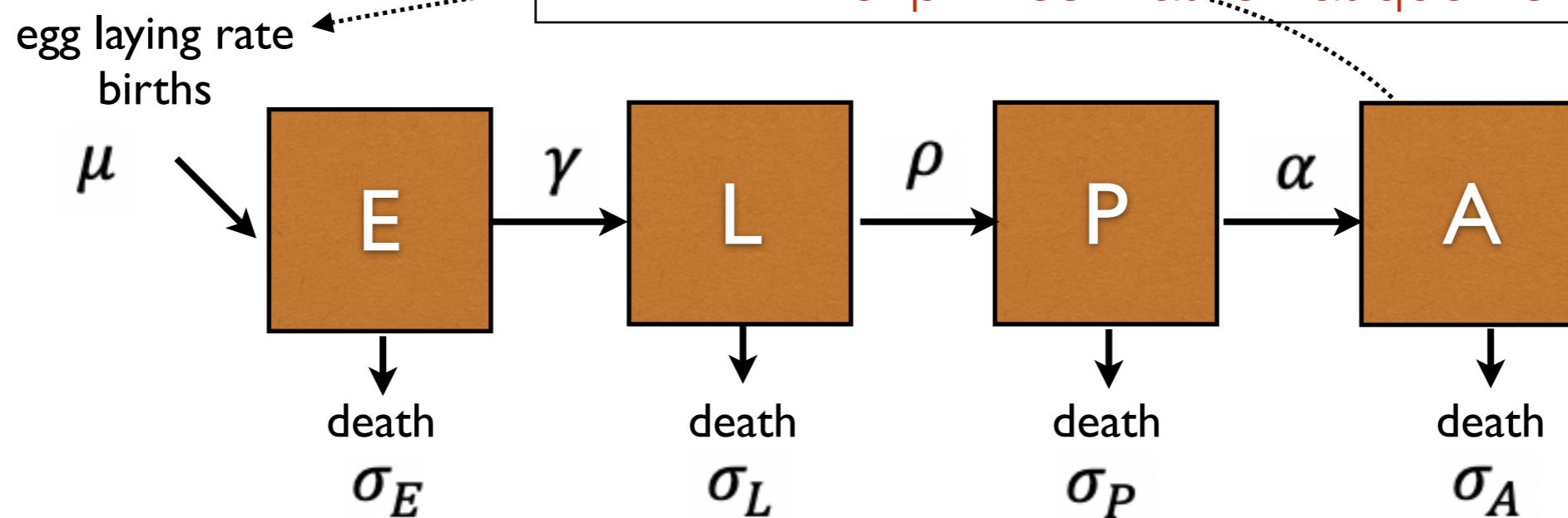
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Parameters

: egg laying rate

: egg death rate

: aging egg to larvae

: larvae death rate

: aging larvae to pupae

: pupae death rate

: aging pupae to adult

: adult death rate



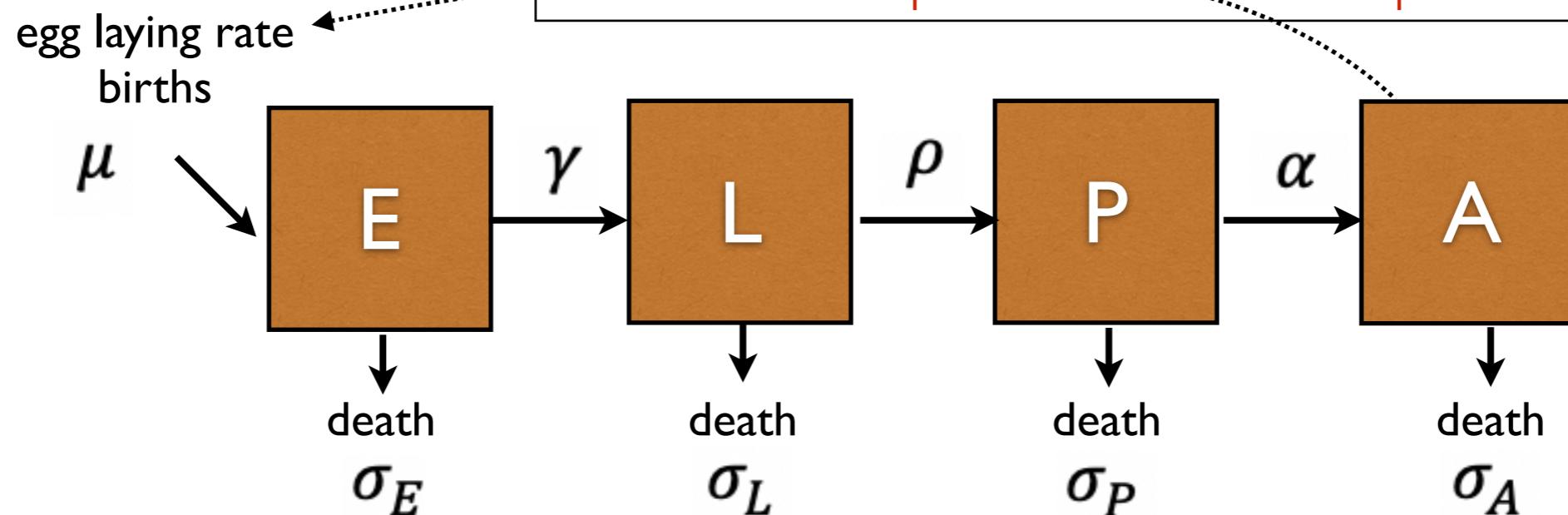
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Parameters

μ : egg laying rate

ρ : aging larvae to pupae

σ_E : egg death rate

σ_P : pupae death rate

γ : aging egg to larvae

α : aging pupae to adult

σ_L : larvae death rate

σ_A : adult death rate

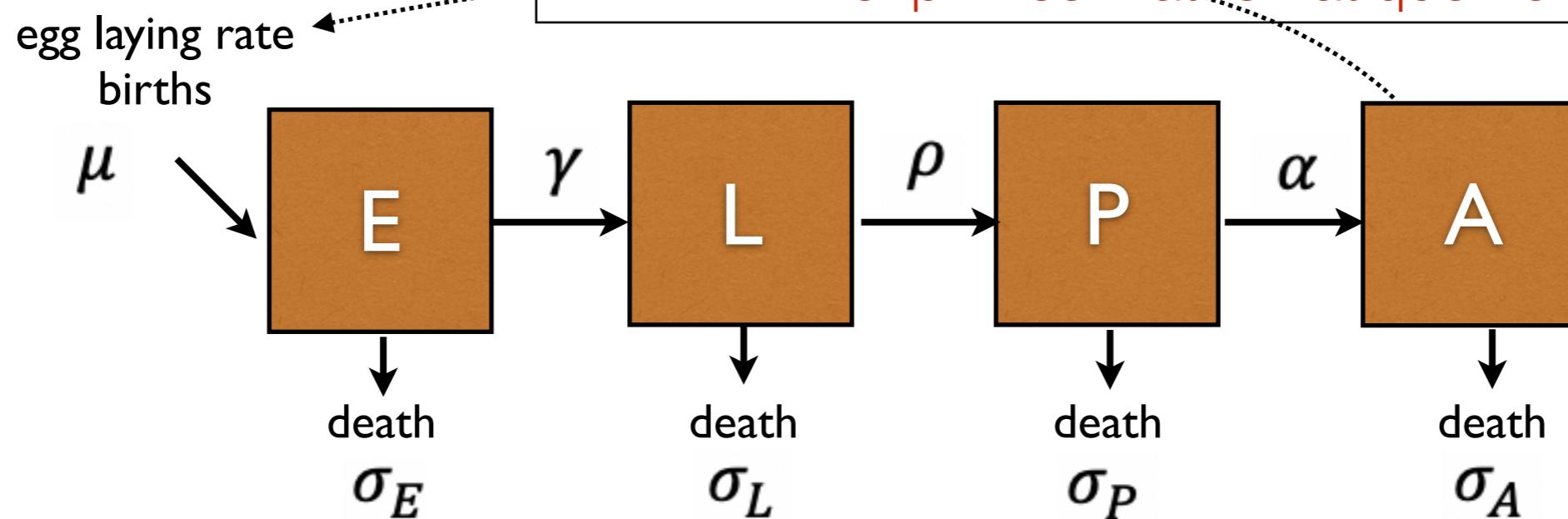


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$$\frac{dE}{dt} = \mu A - \gamma E - \sigma_E E$$

$$\frac{dL}{dt} = \gamma E - \rho L - \sigma_L L$$

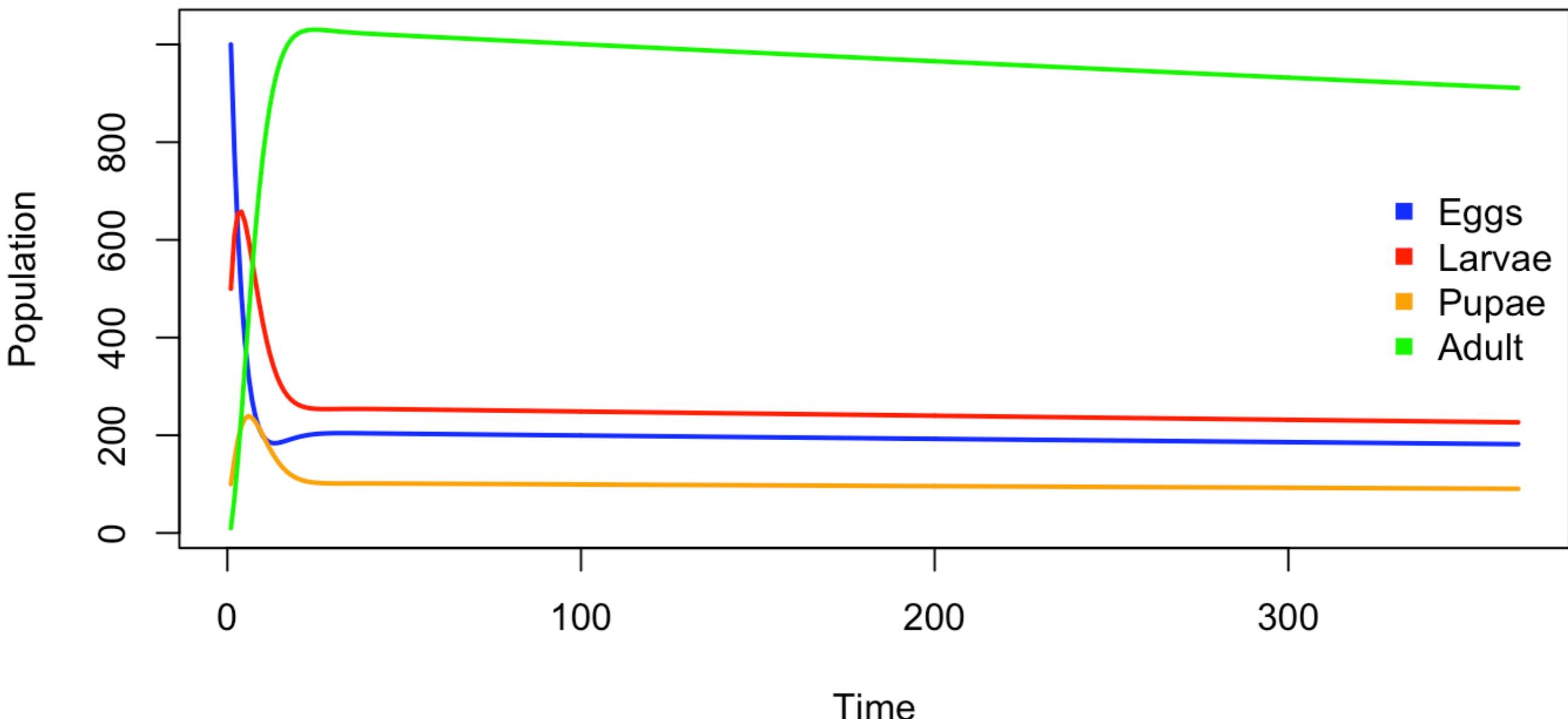
$$\frac{dP}{dt} = \rho L - \alpha P - \sigma_P P$$

$$\frac{dA}{dt} = \alpha P - \sigma_A A$$



The life stage model

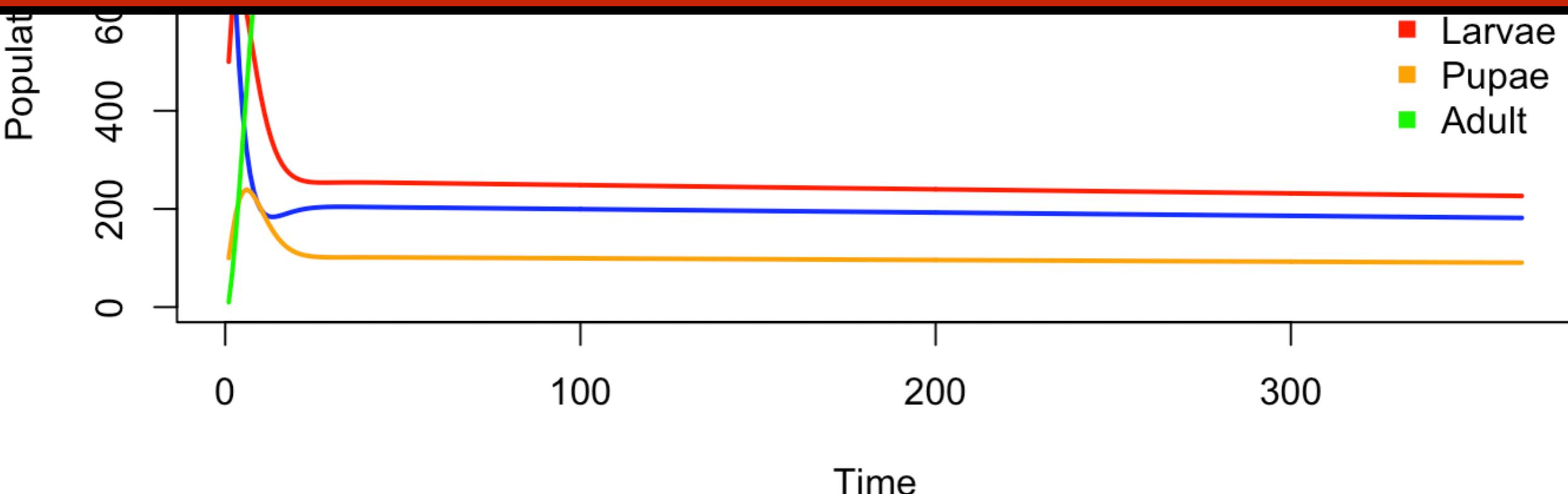
```
initial.pops<-c(E = 1000, L = 500, P = 100, A = 10)
mosq.pop.params<-c(mu = 0.05, gamma = 1/4, sigmaE = 0.001, rho = 1/5, sigmaL = 0
.001, alpha = 1/2, sigmaP = 0.001, sigmaA = 0.05)
```

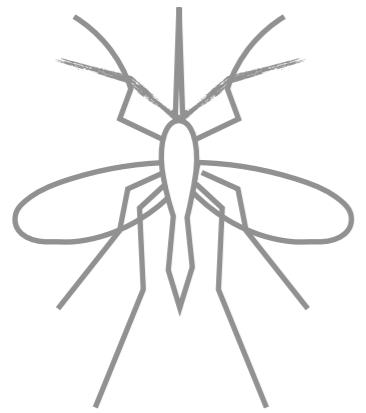


The life stage model

```
initial.pops<-c(E = 1000, L = 500, P = 100, A = 10)
mosq.pop.params<-c(mu = 0.05, gamma = 1/4, sigmaE = 0.001, rho = 1/5, sigmaL = 0
.001, alpha = 1/2, sigmaP = 0.001, sigmaA = 0.05)
```

mazava?





3. 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 (lemur)?

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



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

lemur
x

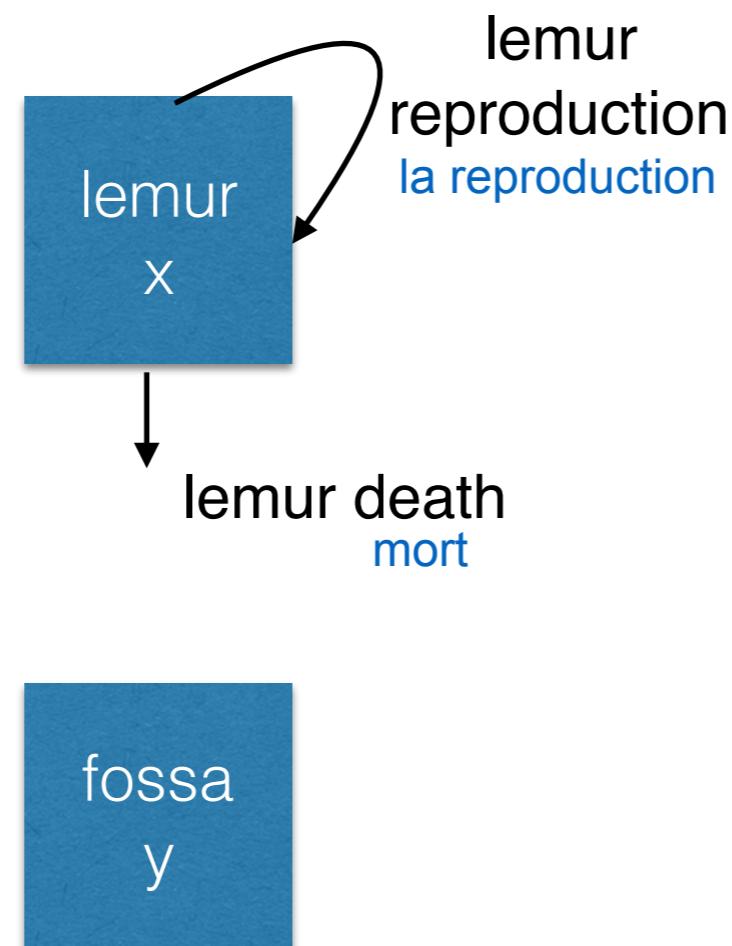
fossa
y



The predator prey model

Compartmental models (Mechanistic Models)

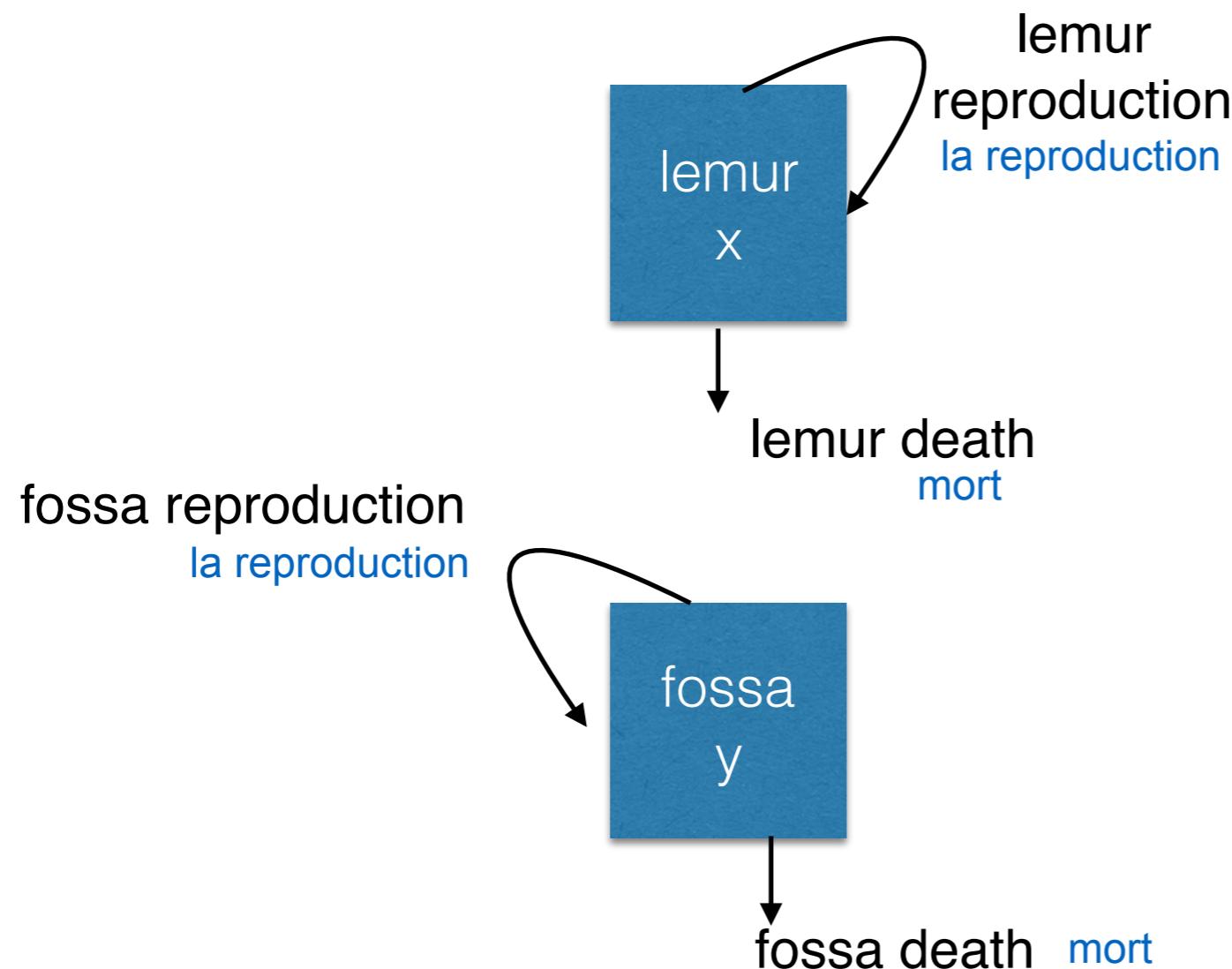
1. Les populations sont subdivisées en compartiments
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3. Taux de transition entre les compartiments sont exprimés mathématiquement



The predator prey model

Compartmental models (Mechanistic Models)

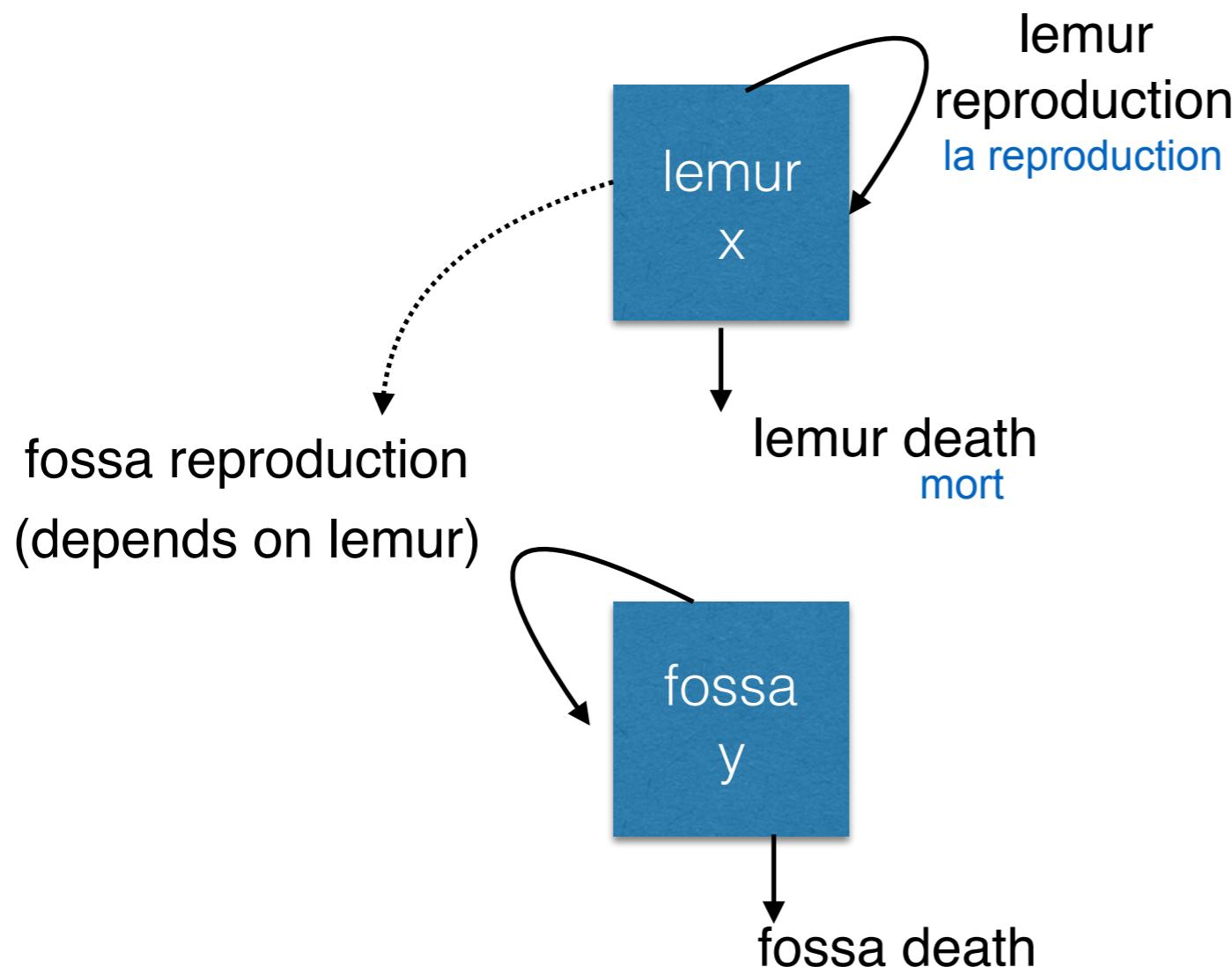
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The predator prey model

Compartmental models (Mechanistic Models)

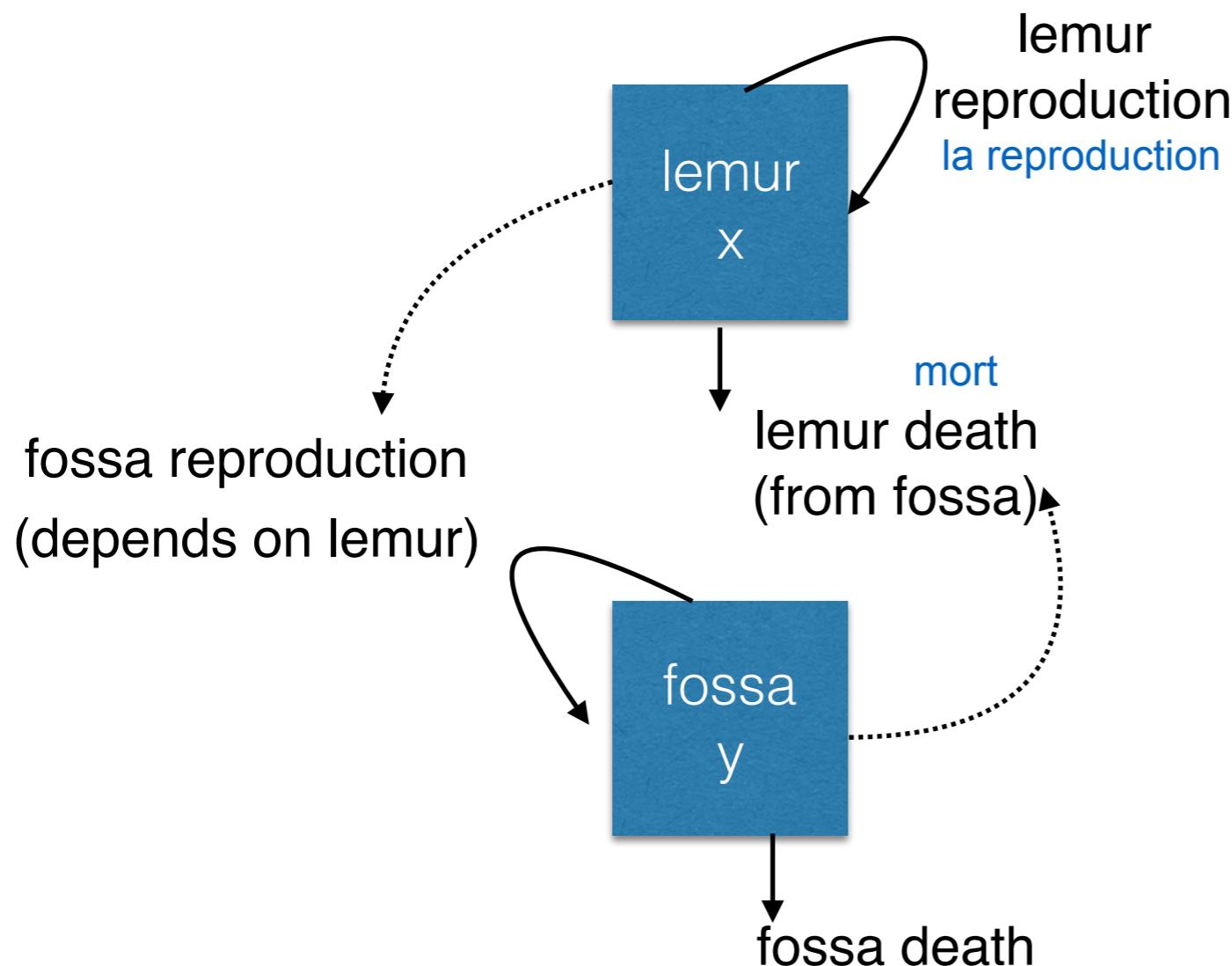
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The predator prey model

Compartmental models (Mechanistic Models)

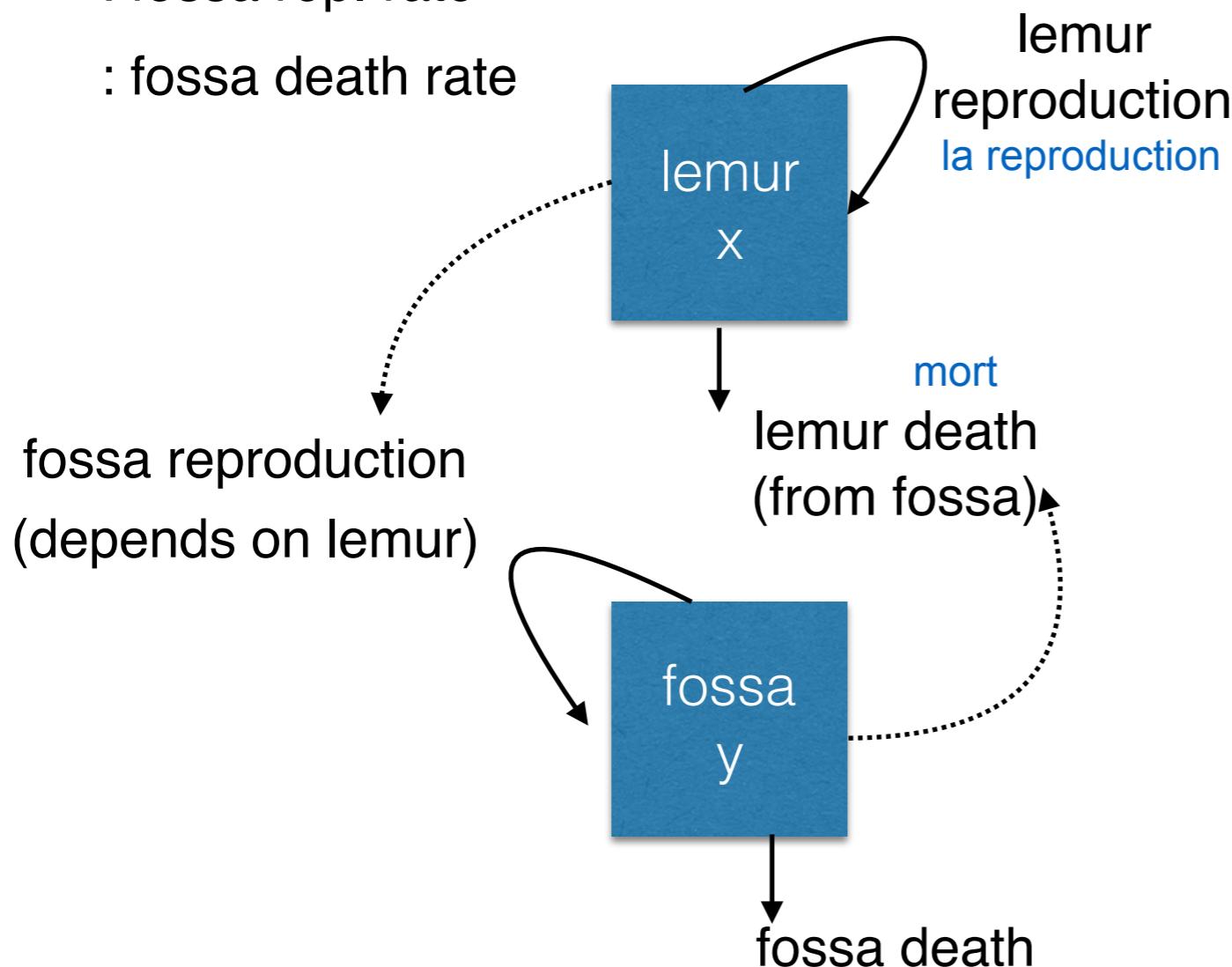
1. Les populations sont subdivisées en compartiments
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3. Taux de transition entre les compartiments sont exprimés mathématiquement



The predator prey model

Parameters

- : lemur rep. rate
- : lemur death rate
- : fossa rep. rate
- : fossa death rate



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 predator prey model

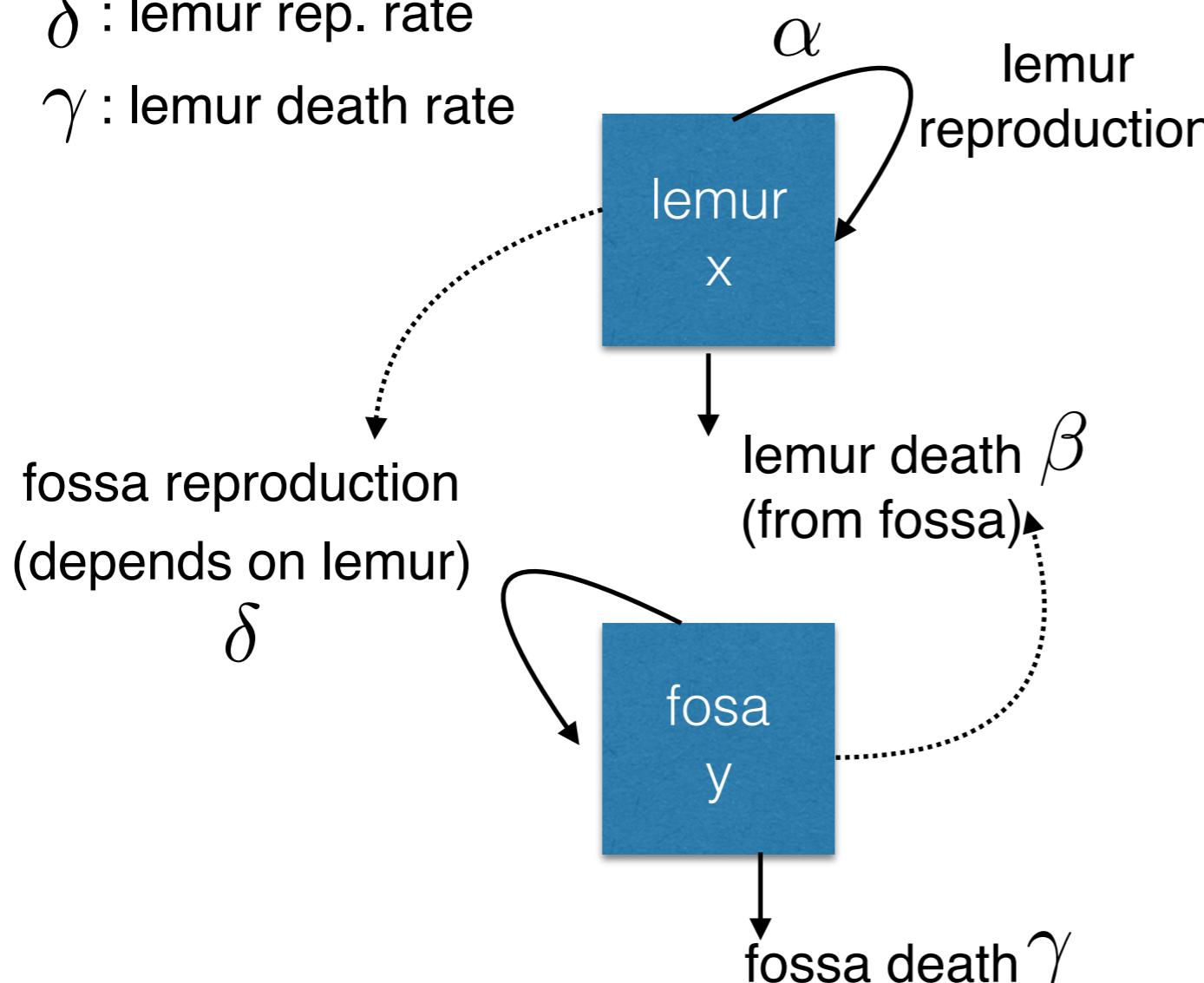
Parameters

α : lemur rep. rate

β : lemur death rate

δ : lemur rep. rate

γ : lemur death rate



Compartmental models (Mechanistic Models)

1. Les populations sont subdivisées en compartiments
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3. Taux de transition entre les compartiments sont exprimés mathématiquement



The predator prey model

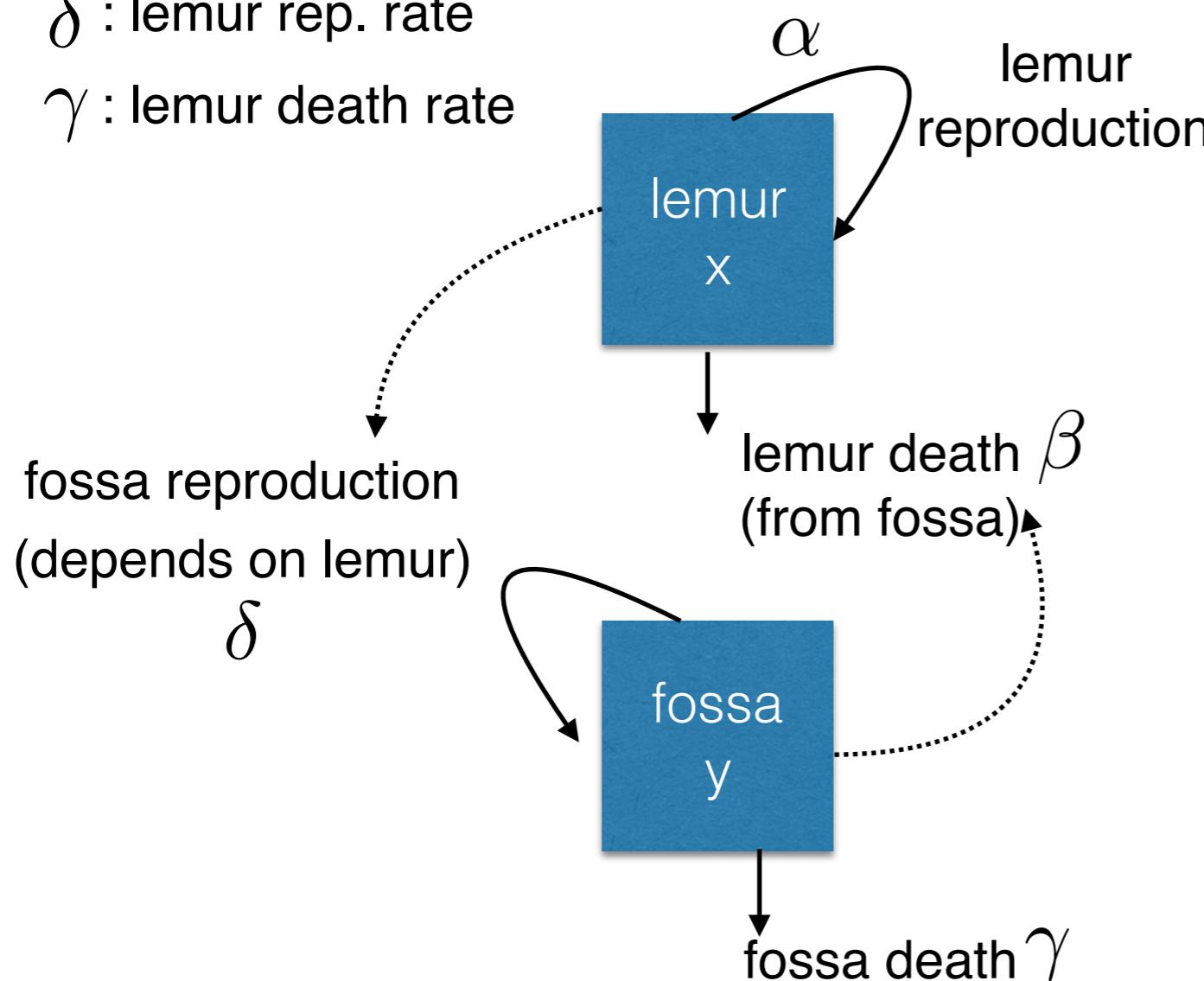
Parameters

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δ : lemur rep. rate

γ : lemur death rate



Compartmental models (Mechanistic Models)

1. Les populations sont subdivisées en compartiments
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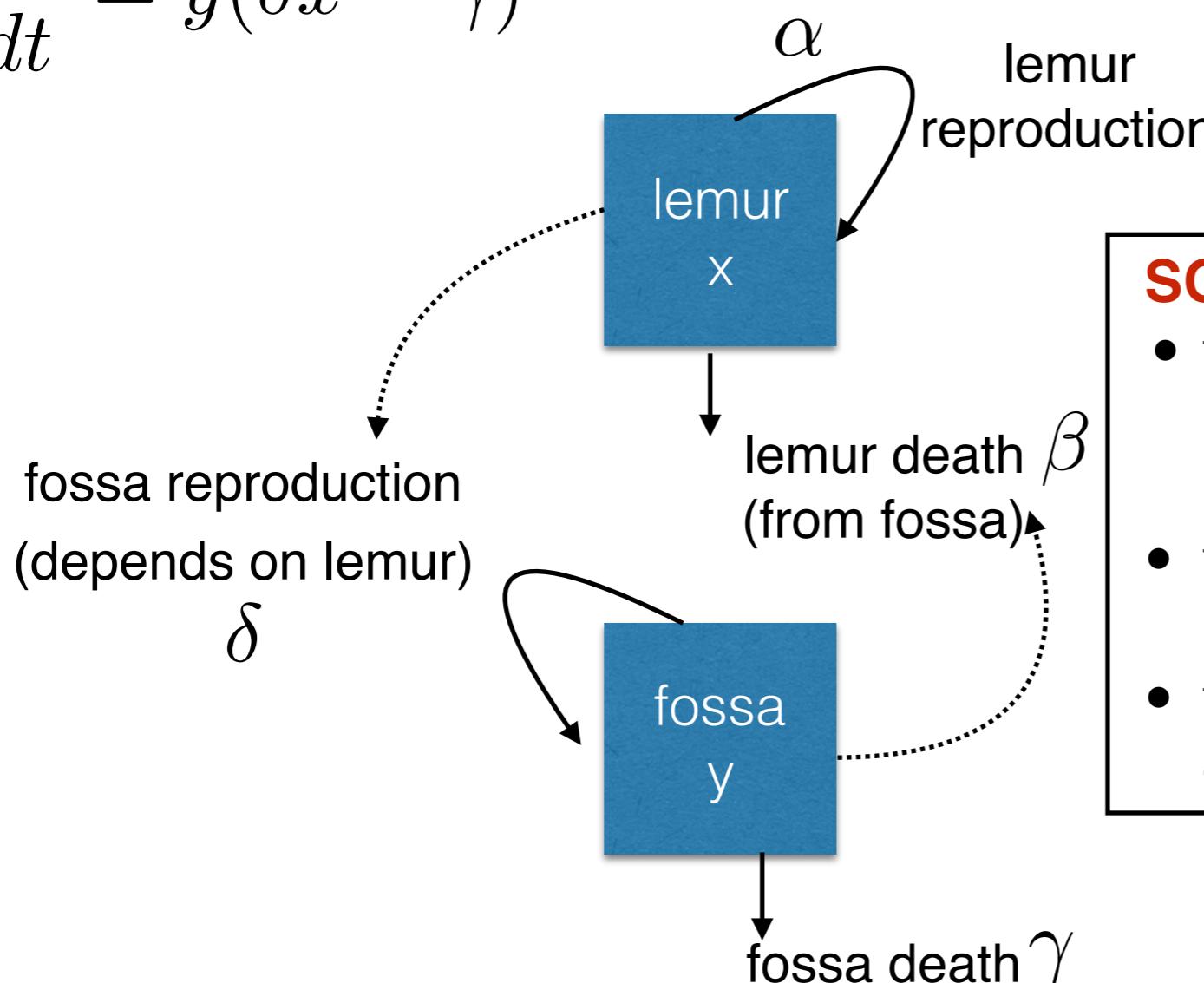
$$\frac{dx}{dt} = x(\alpha - \beta y)$$
$$\frac{dy}{dt} = y(\delta x - \gamma)$$



The predator prey model

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

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



Compartmental models (Mechanistic Models)

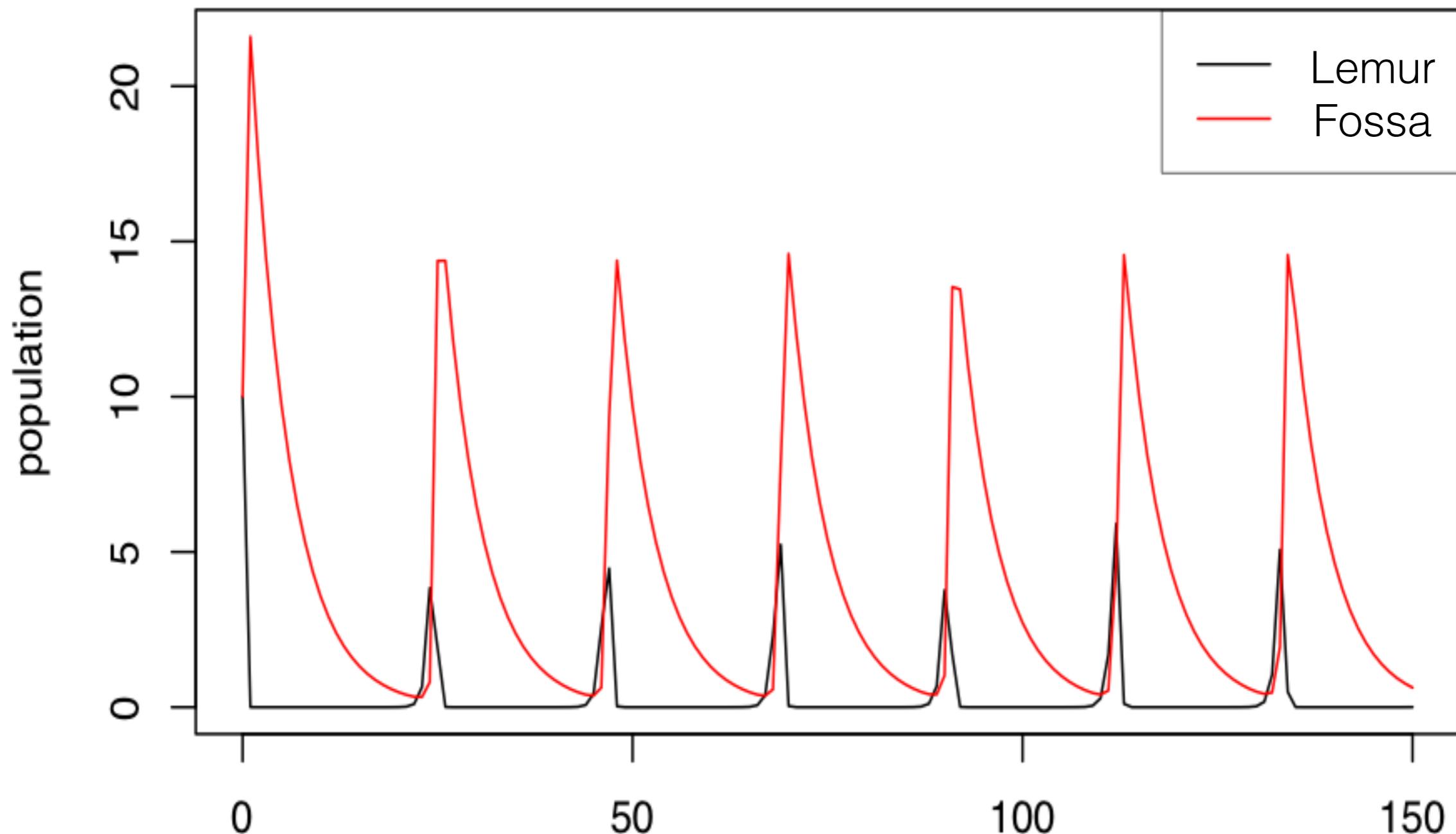
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SOME ASSUMPTIONS

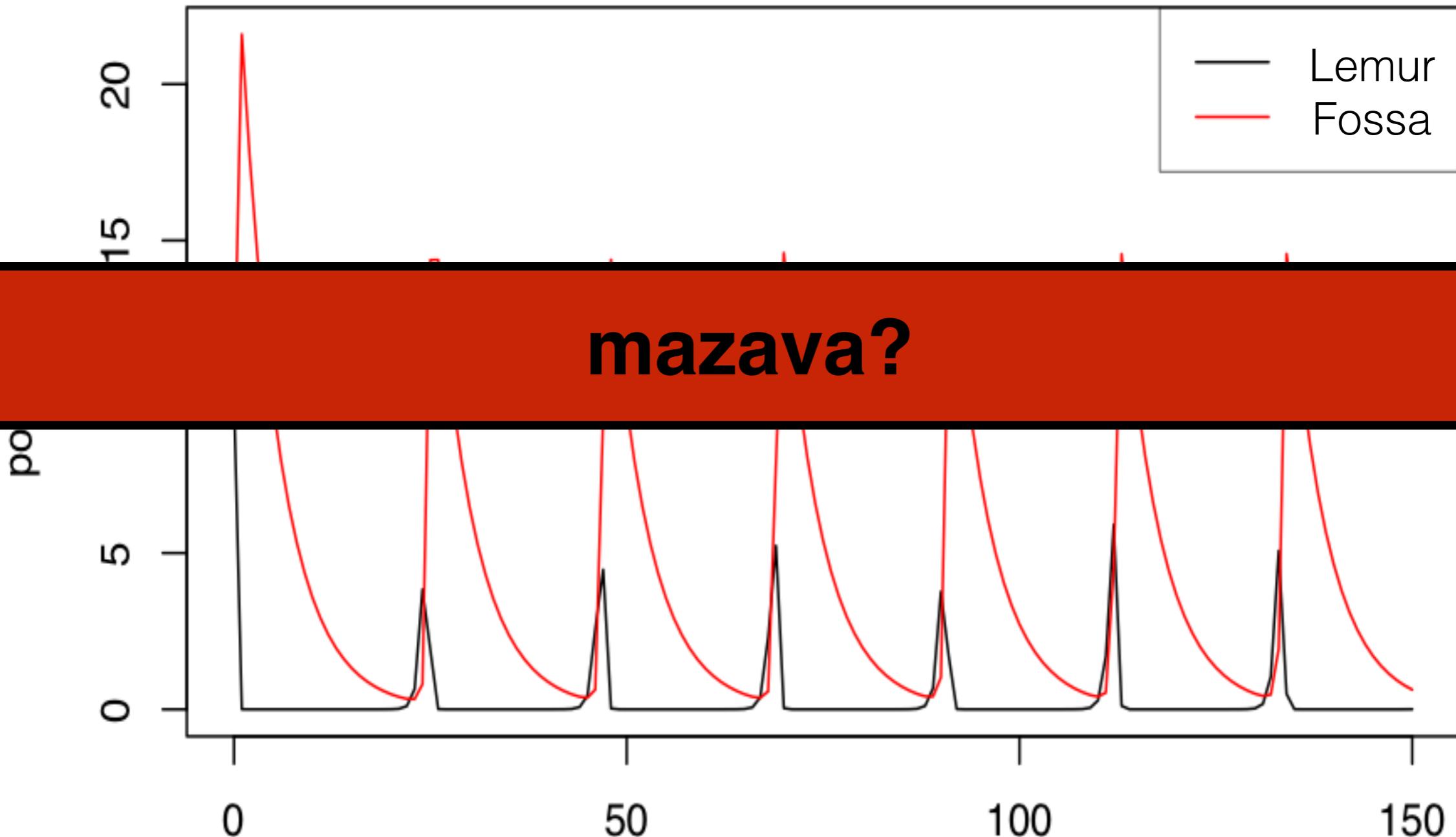
- the **fossa** is totally dependent on a single prey species (**the lemur**) as its only food supply,
- the **lemur** has an unlimited food supply,
- there is no threat to the **lemur** other than the specific predator.



The predator prey model



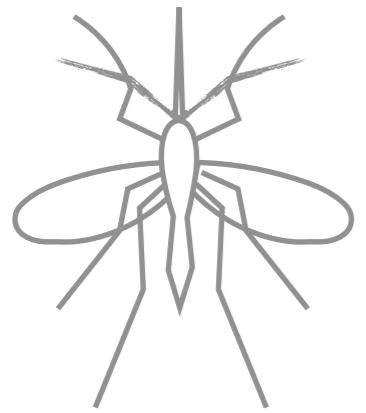
The predator prey model



Key concepts

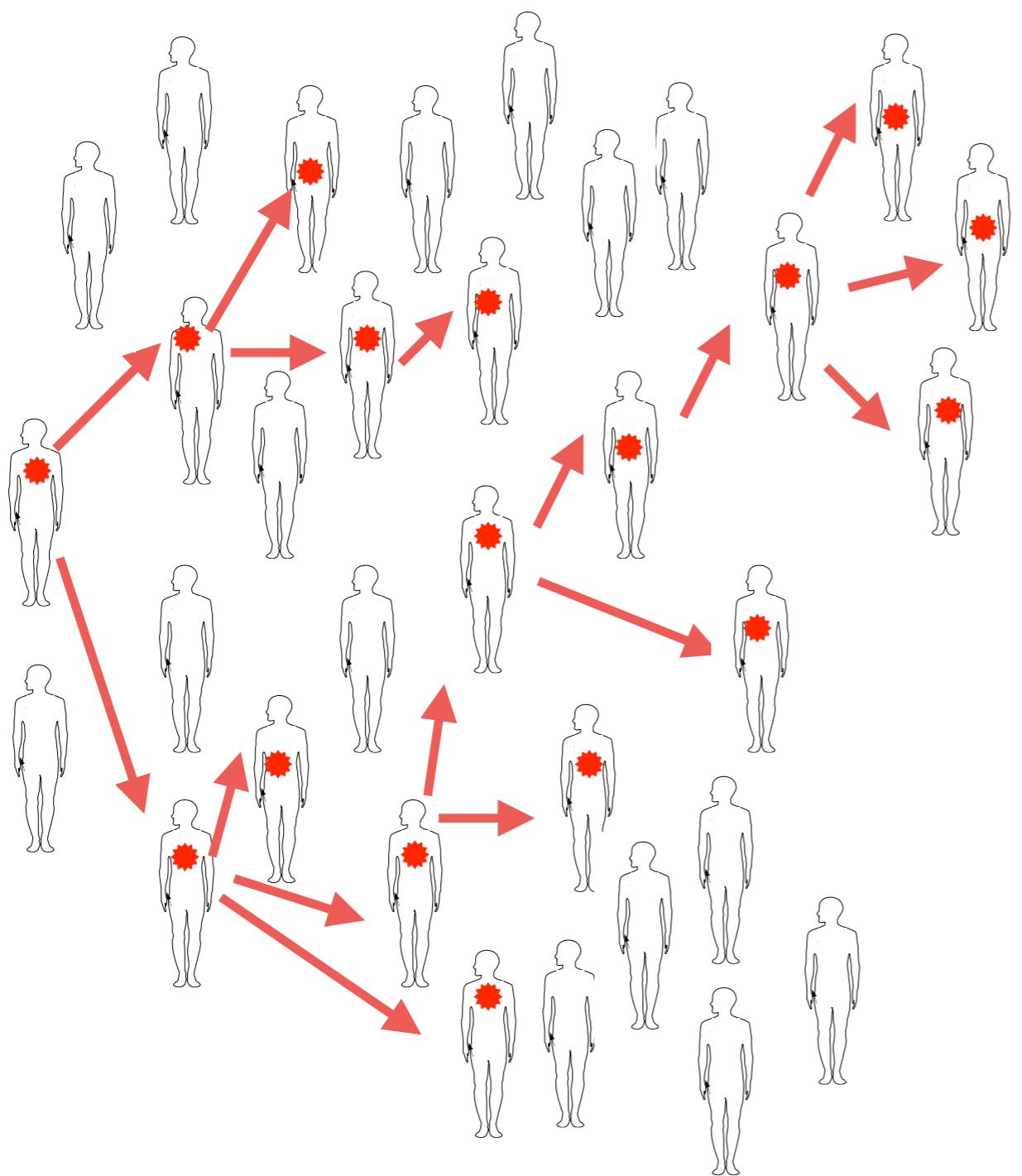
- Inter-dependence de la démographie des espèces (nous avons parlé de **predation**, mais la **competition** est aussi possible)
- Les cycles peuvent émerger de forces internes, sans un rôle d'environnement, saisonnalité, etc.
- Beaucoup d'assumptions dans ce modèle simple! On pourrait ajouter des détails pour se rapprocher de vraies systèmes.





4. 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

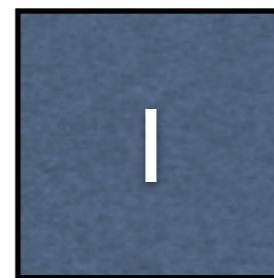
Compartmental models (Mechanistic Models)

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

susceptible



The SIR model

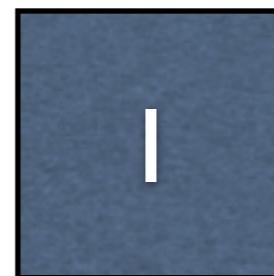
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3. Taux de transition entre les compartiments sont exprimés mathématiquement

susceptible



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

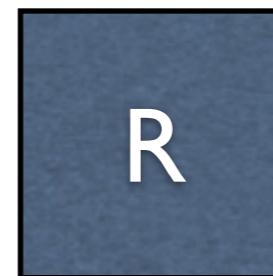
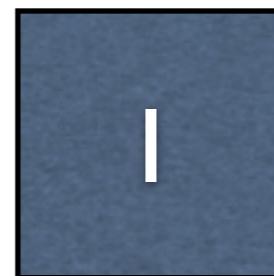
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2. Les compartiments et les taux de transition sont déterminés par les systèmes biologiques

3. Taux de transition entre les compartiments sont exprimés mathématiquement

susceptible



What are the big assumptions here?



The SIR model

Compartmental models (Mechanistic Models)

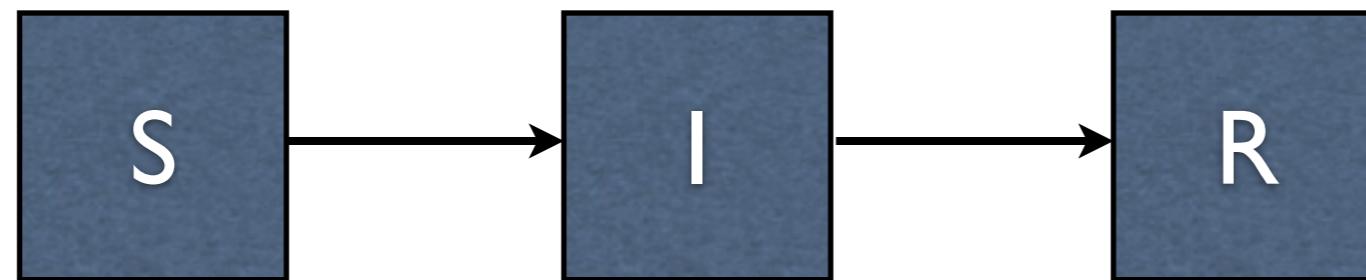
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susceptible

everyone is either:



The SIR model

Compartmental models (Mechanistic Models)

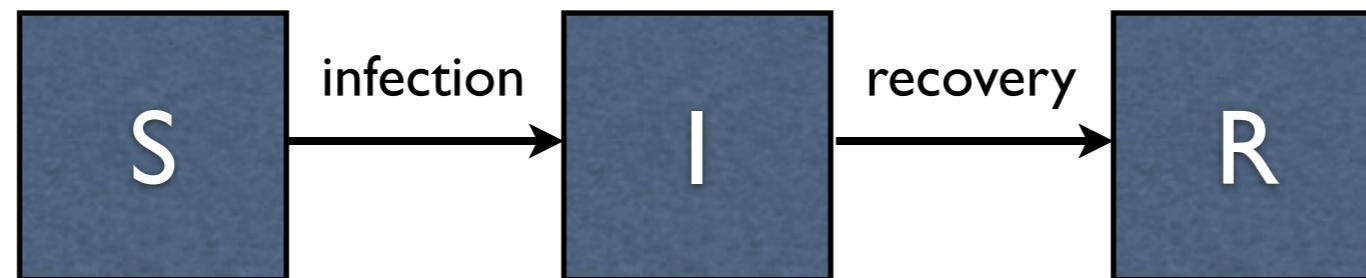
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susceptible

everyone is either:



The SIR model

Compartmental models (Mechanistic Models)

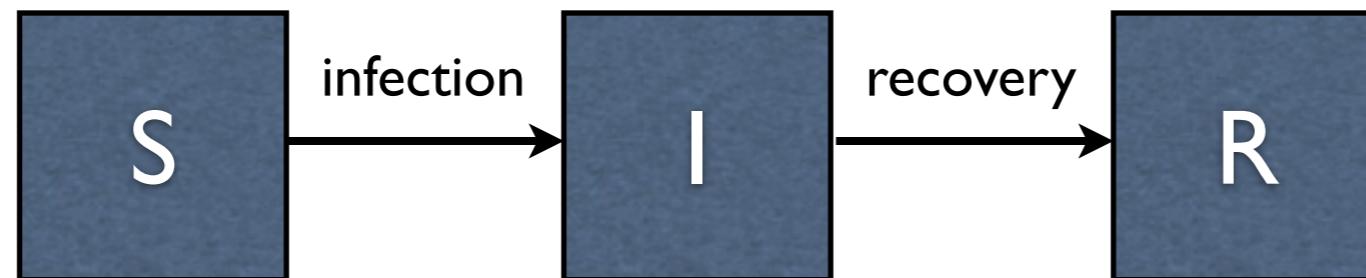
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susceptible

everyone is either:



people mix
uniformly
**(mass
action)**

- les gens se mélagent uniformément



The SIR model

Compartmental models (Mechanistic Models)

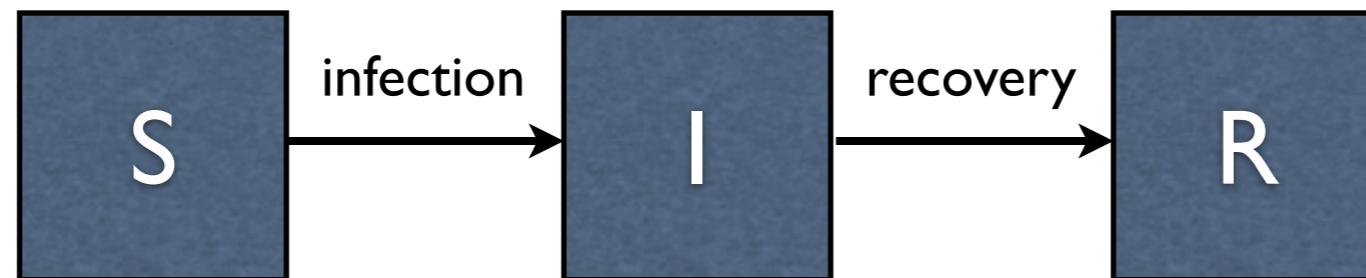
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susceptible

everyone is either:



people mix uniformly (mass action)

no latent period
(infectious when infected)

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



The SIR model

Compartmental models (Mechanistic Models)

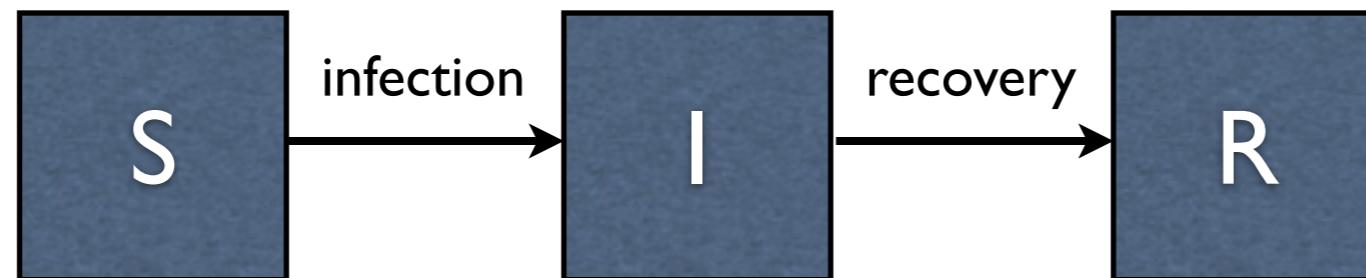
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susceptible

everyone is either:



recovery is permanent

people mix uniformly (mass action)

no latent period
(infectious when infected)

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



The SIR model

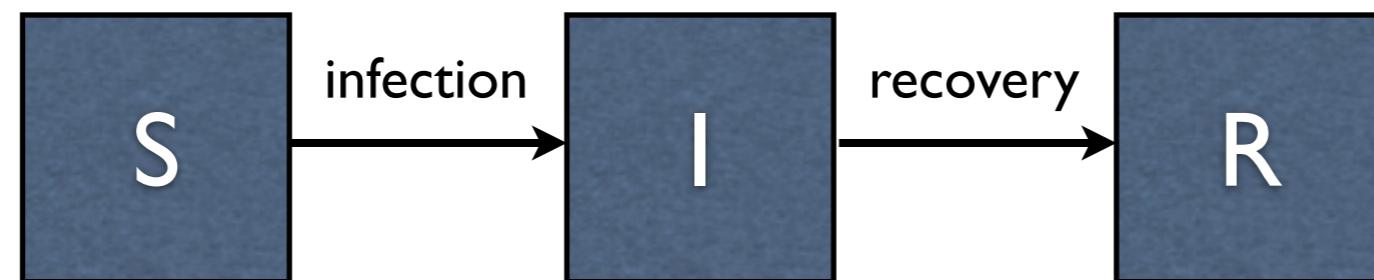
Compartmental models (Mechanistic Models)

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3. Taux de transition entre les compartiments sont exprimés mathématiquement

susceptible



recovery is
permanent

everyone is either:

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

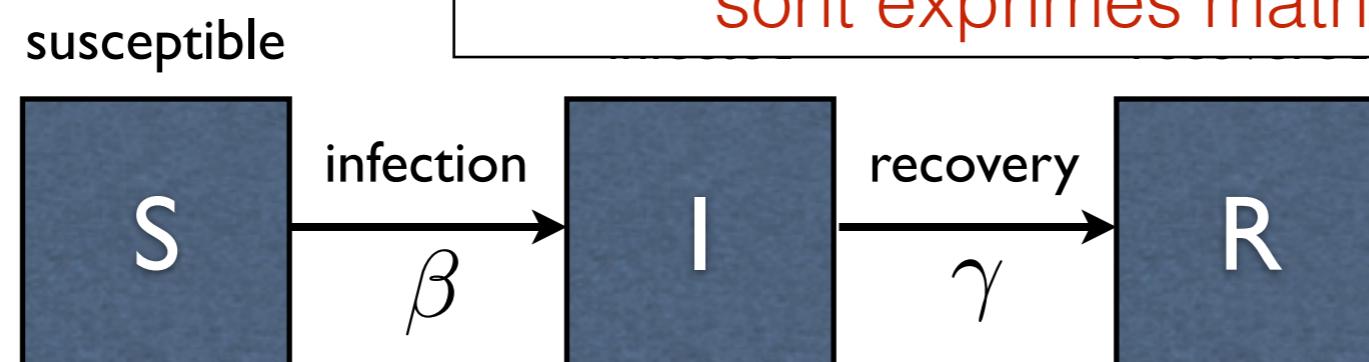
γ : rate of recovery

Compartmental models (Mechanistic Models)

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The SIR model

Parameters

β : transmission rate

γ : rate of recovery

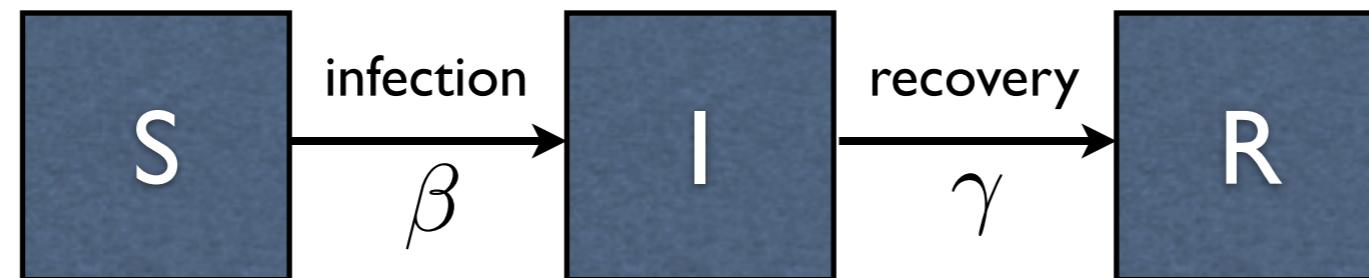
Compartmental models (Mechanistic Models)

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3. Taux de transition entre les compartiments sont exprimés mathématiquement

susceptible



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

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

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

...multiply rates by
box you start in....



The SIR model

Parameters

β : transmission rate

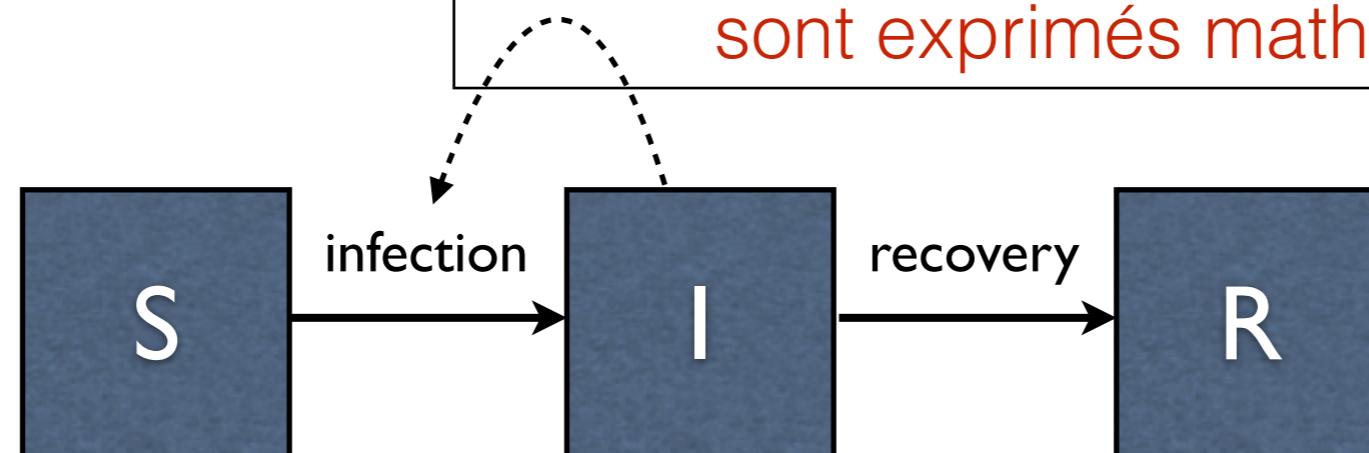
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Compartmental models (Mechanistic Models)

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

...infected numbers shape infection....

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

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

...multiply rates by box you start in....



The SIR model

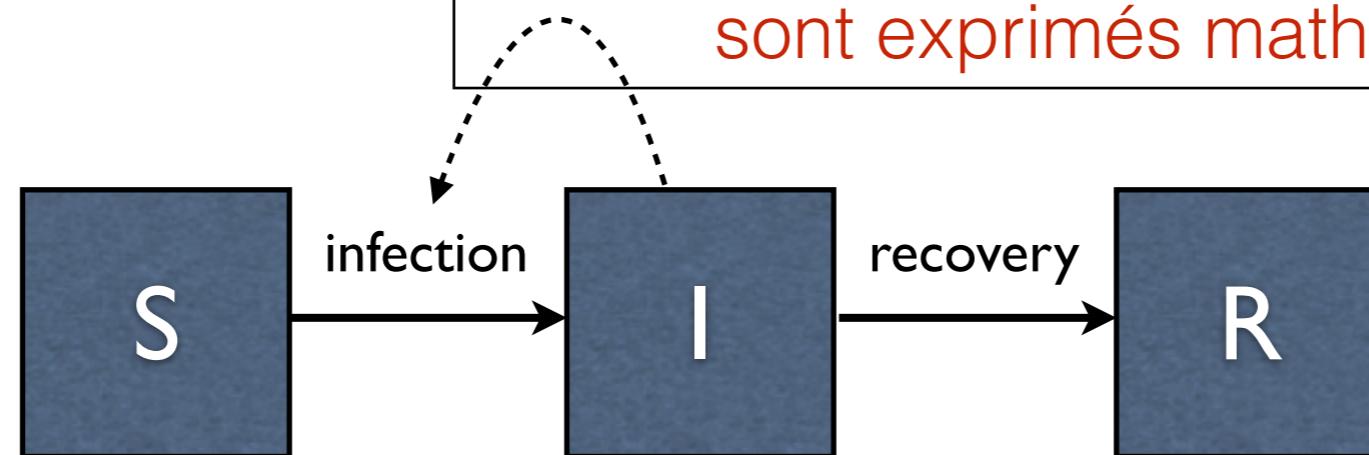
Parameters

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Compartmental models (Mechanistic Models)

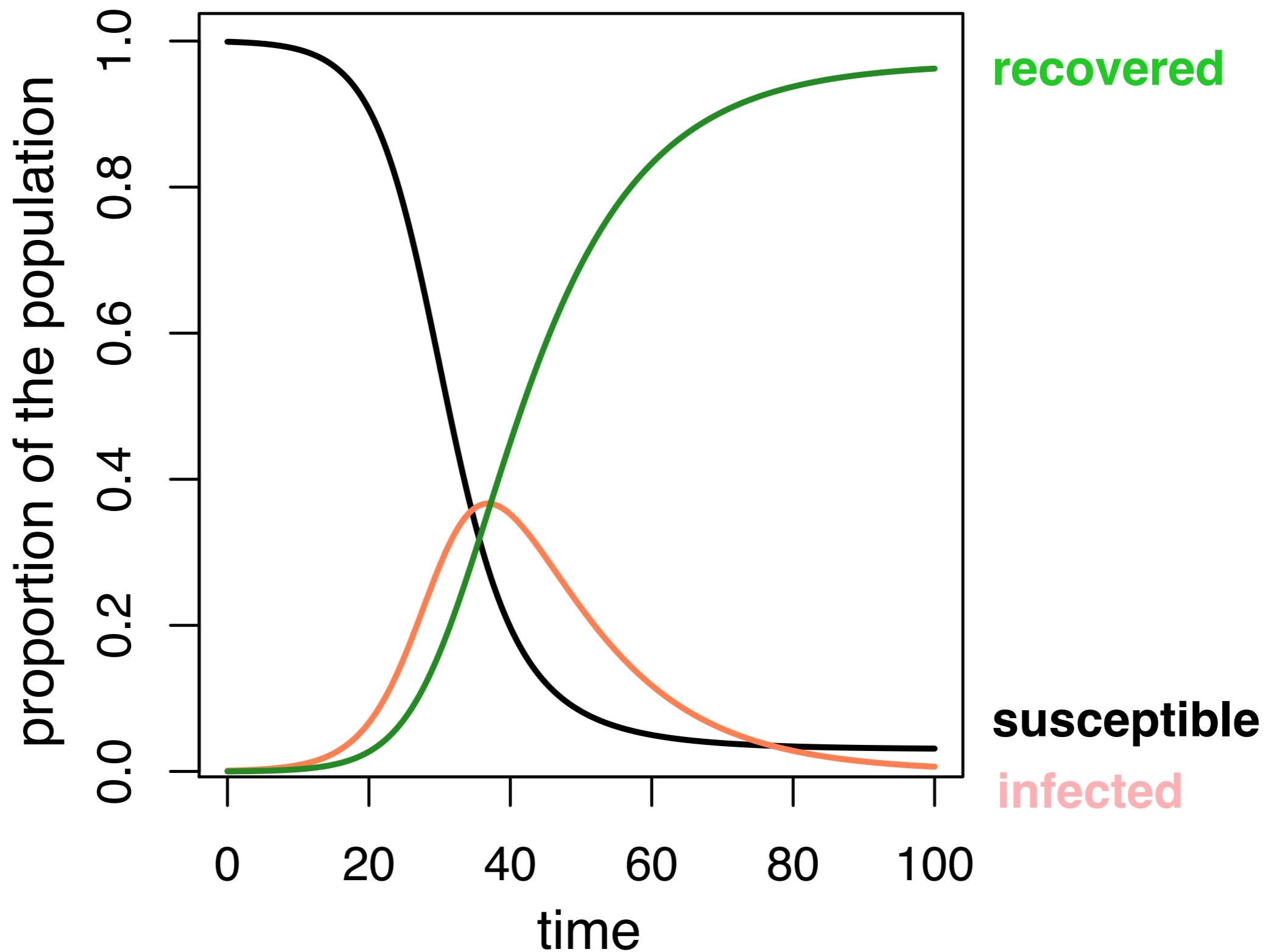
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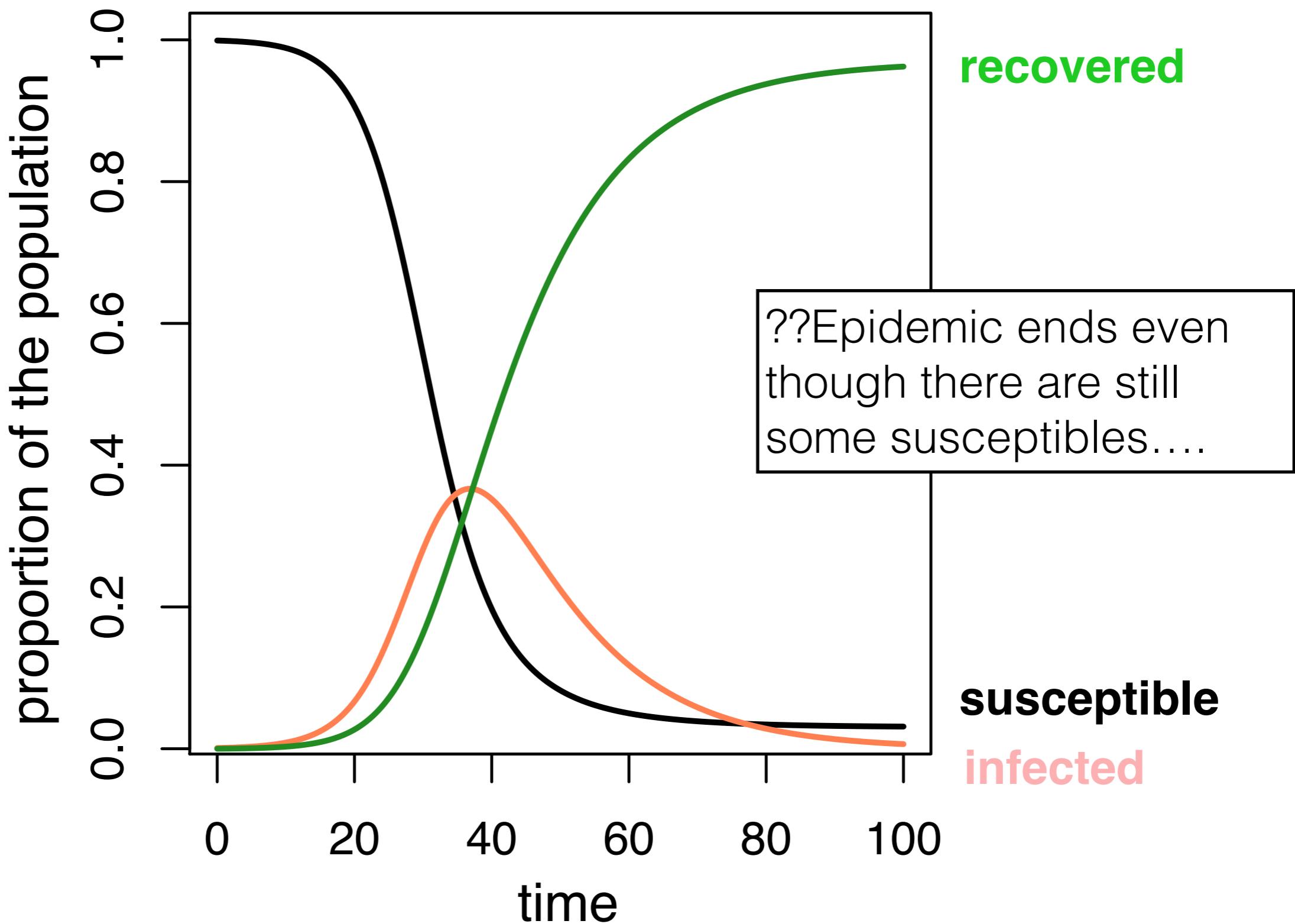
What will the dynamics look like?



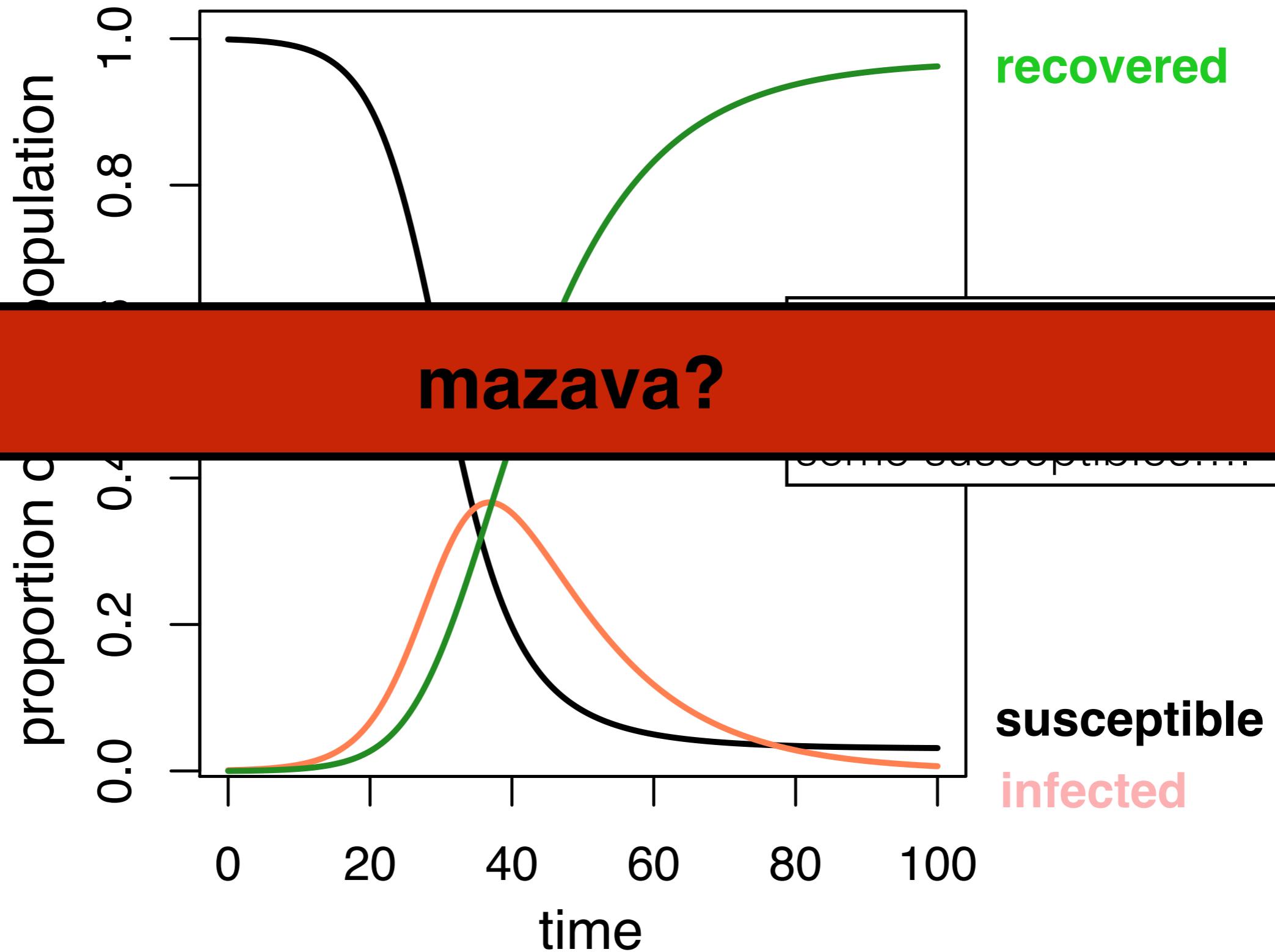
The SIR model: dynamics



The SIR model: dynamics

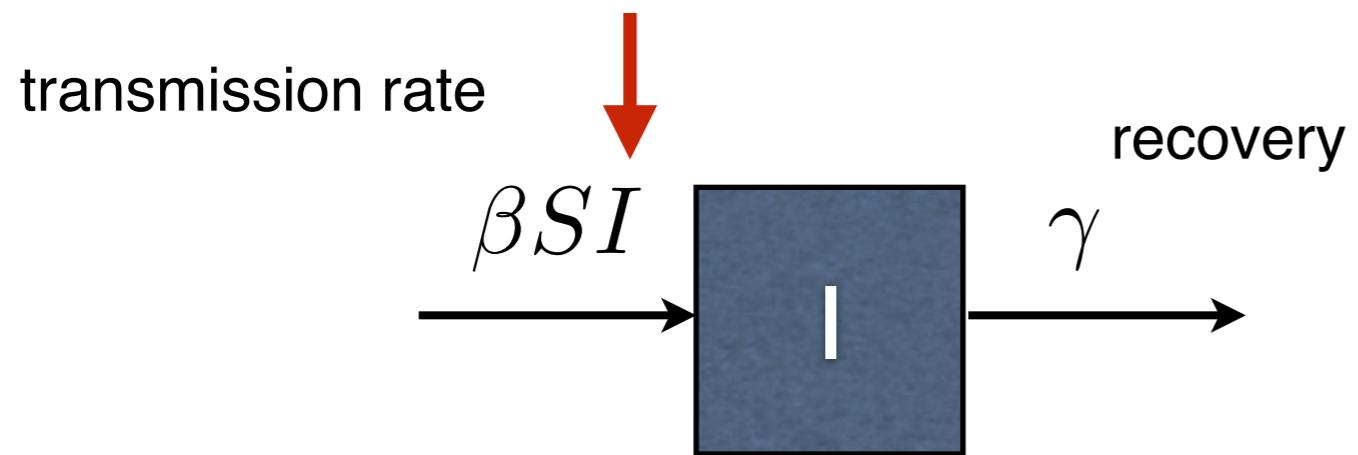


The SIR model: dynamics



The SIR model: dynamics

Set: $I=1$

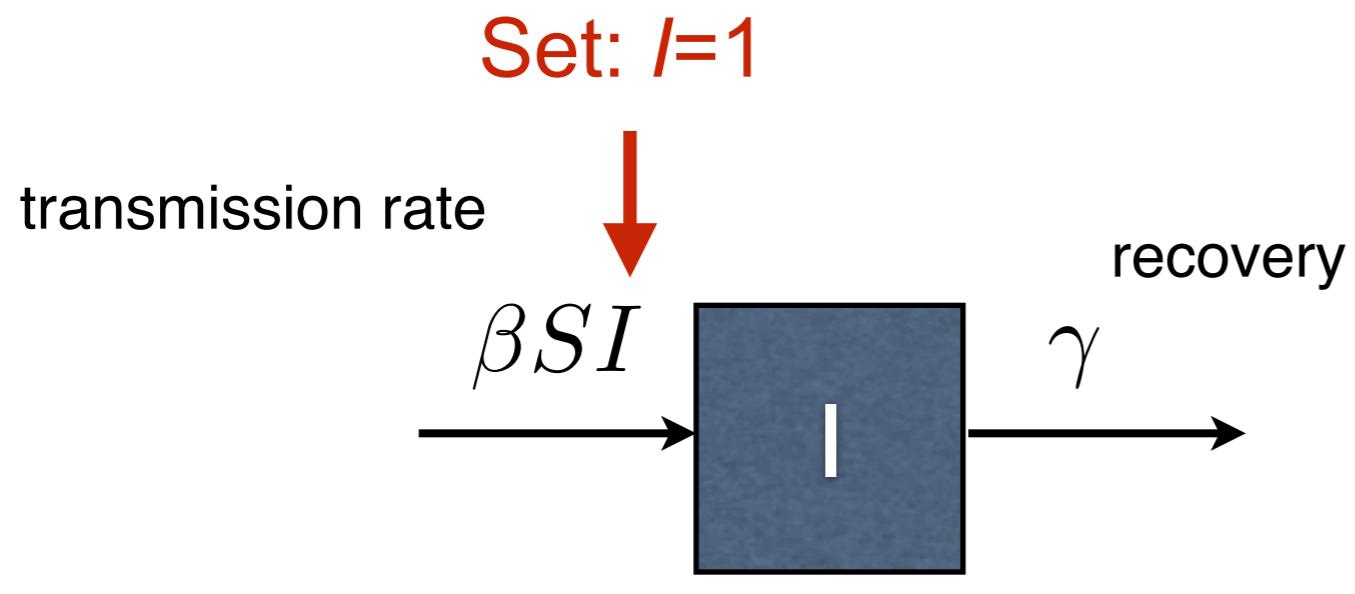


$$R_0 = \beta N / \gamma$$

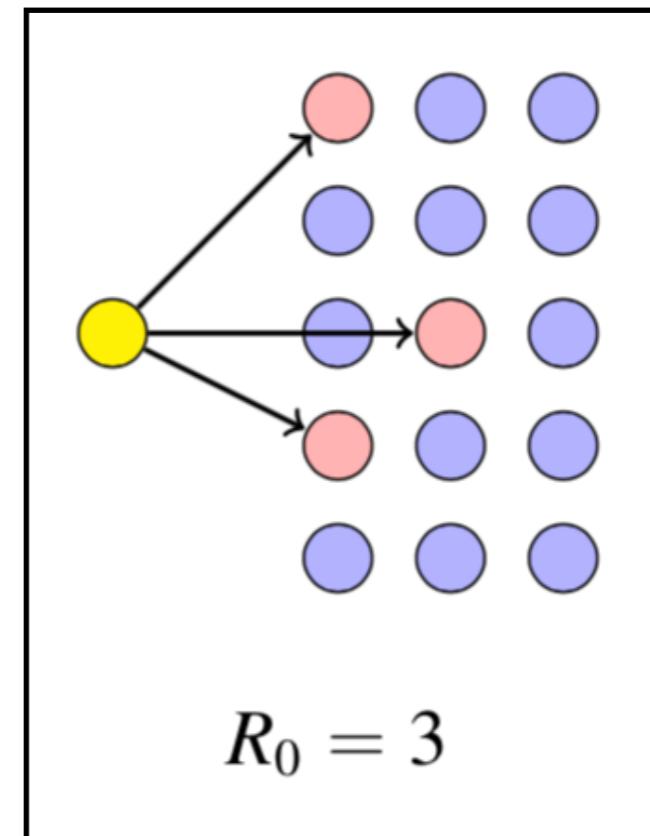
The average number of persons infected by an infectious individual when everyone is susceptible ($S=100\%$, or $S=1$, start of an epidemic)



The SIR model: dynamics



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

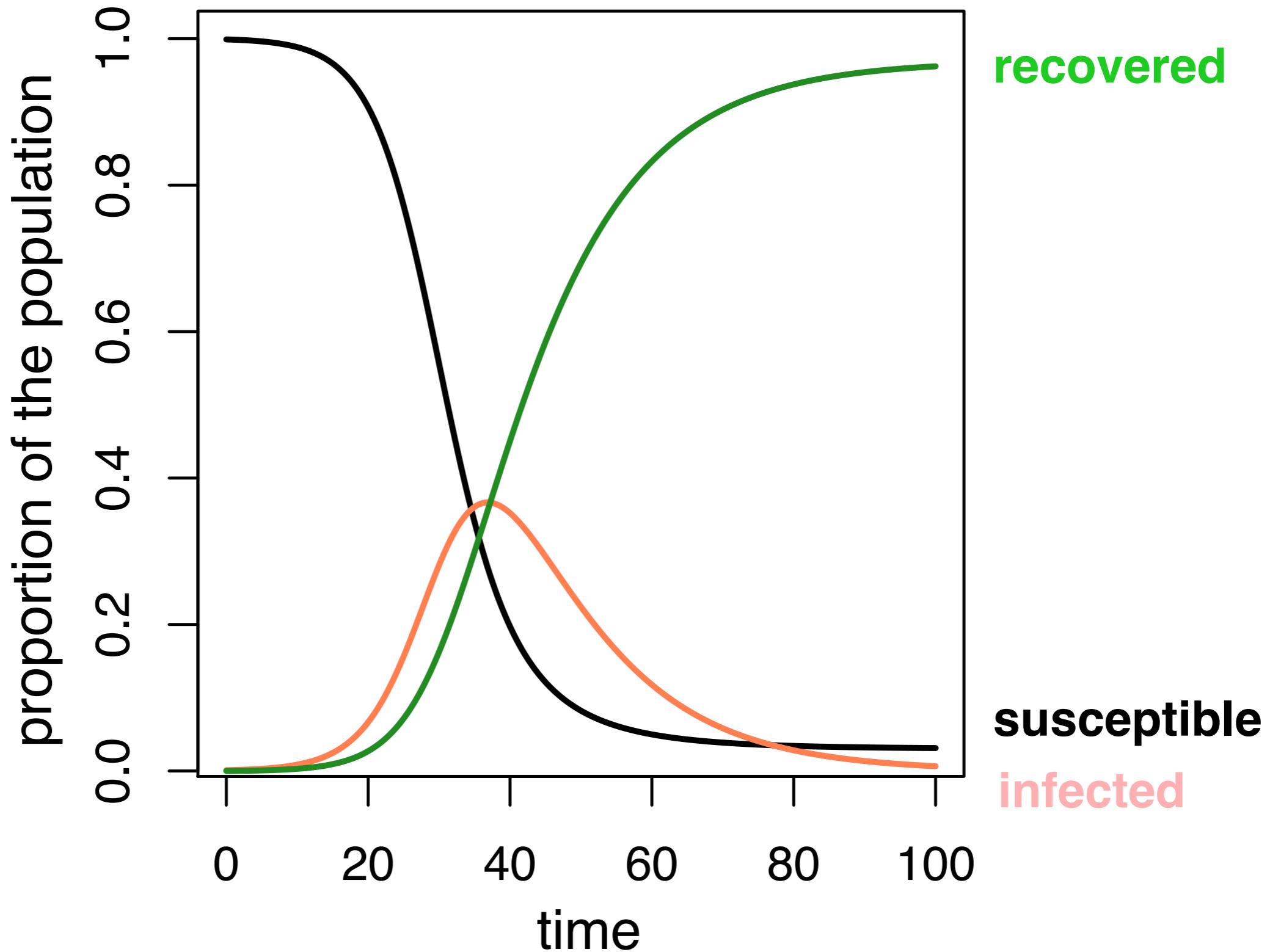


The average number of persons infected by an infectious individual when everyone is susceptible ($S=100\%$, or $S=1$, start of an epidemic)

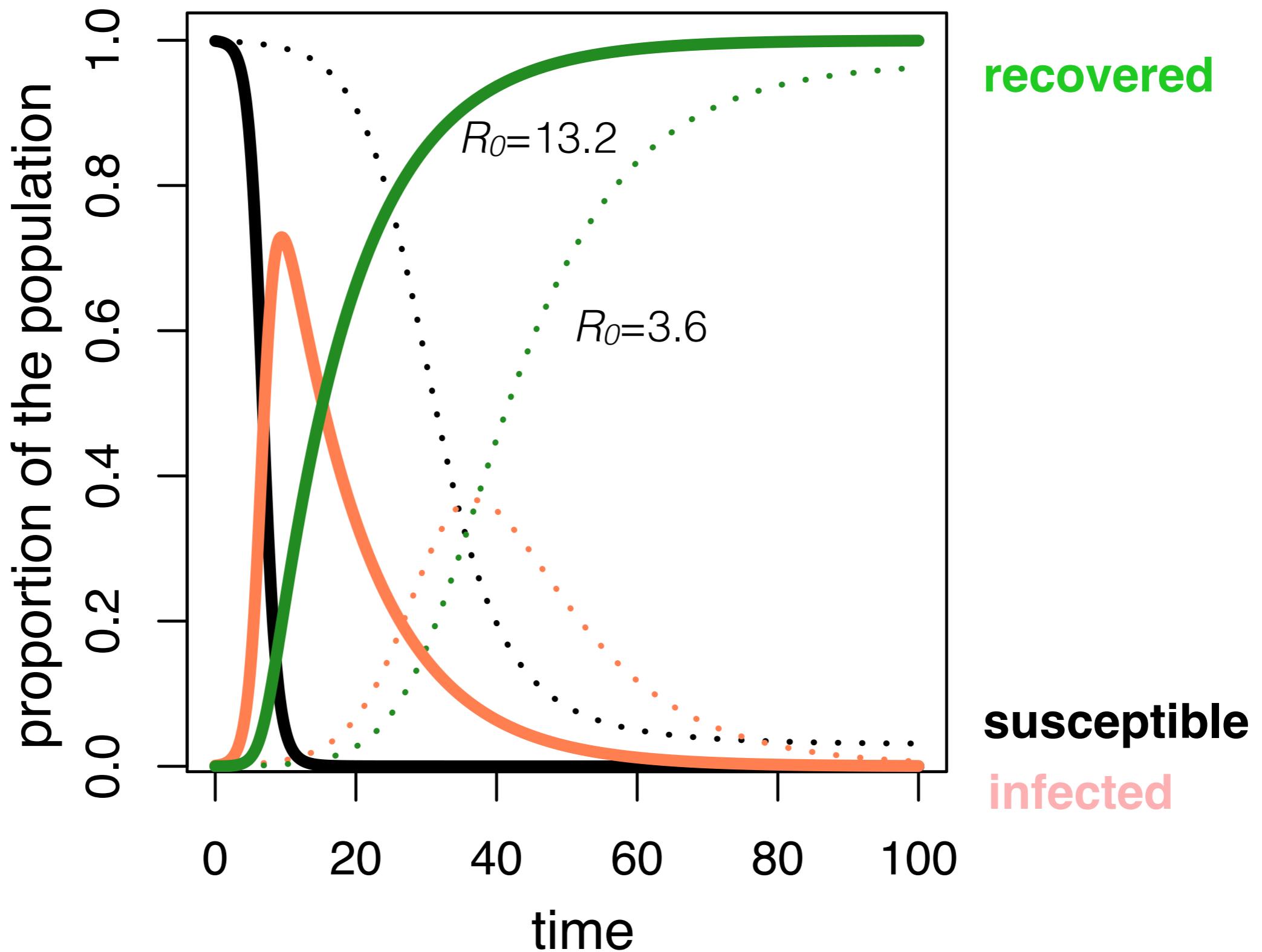
Le nombre moyen de personnes infectées par un individu infectieux lorsque tout le monde est susceptible



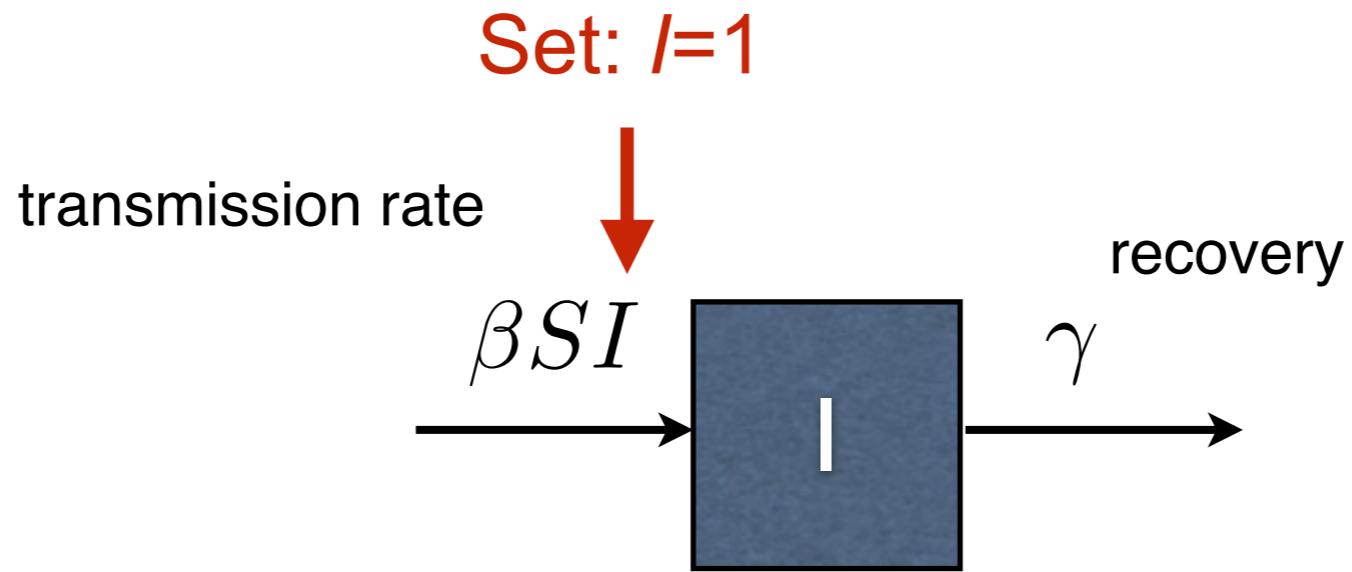
The SIR model: dynamics



The SIR model: dynamics



The SIR model: dynamics



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

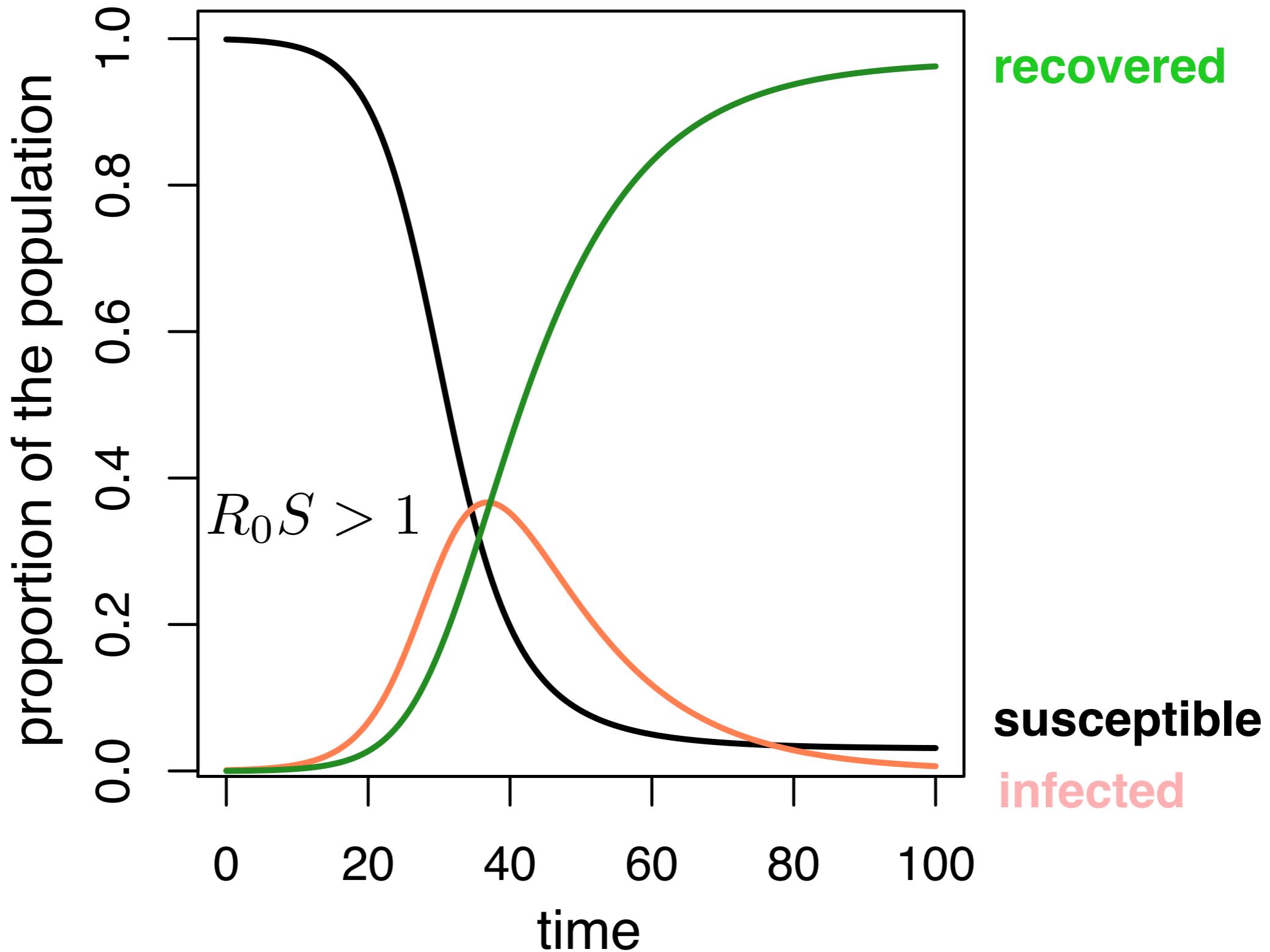
The average number of persons infected by an infectious individual when everyone is susceptible ($S=100\%$, or $S=1$, start of an epidemic) which is:

$$R_0 S$$

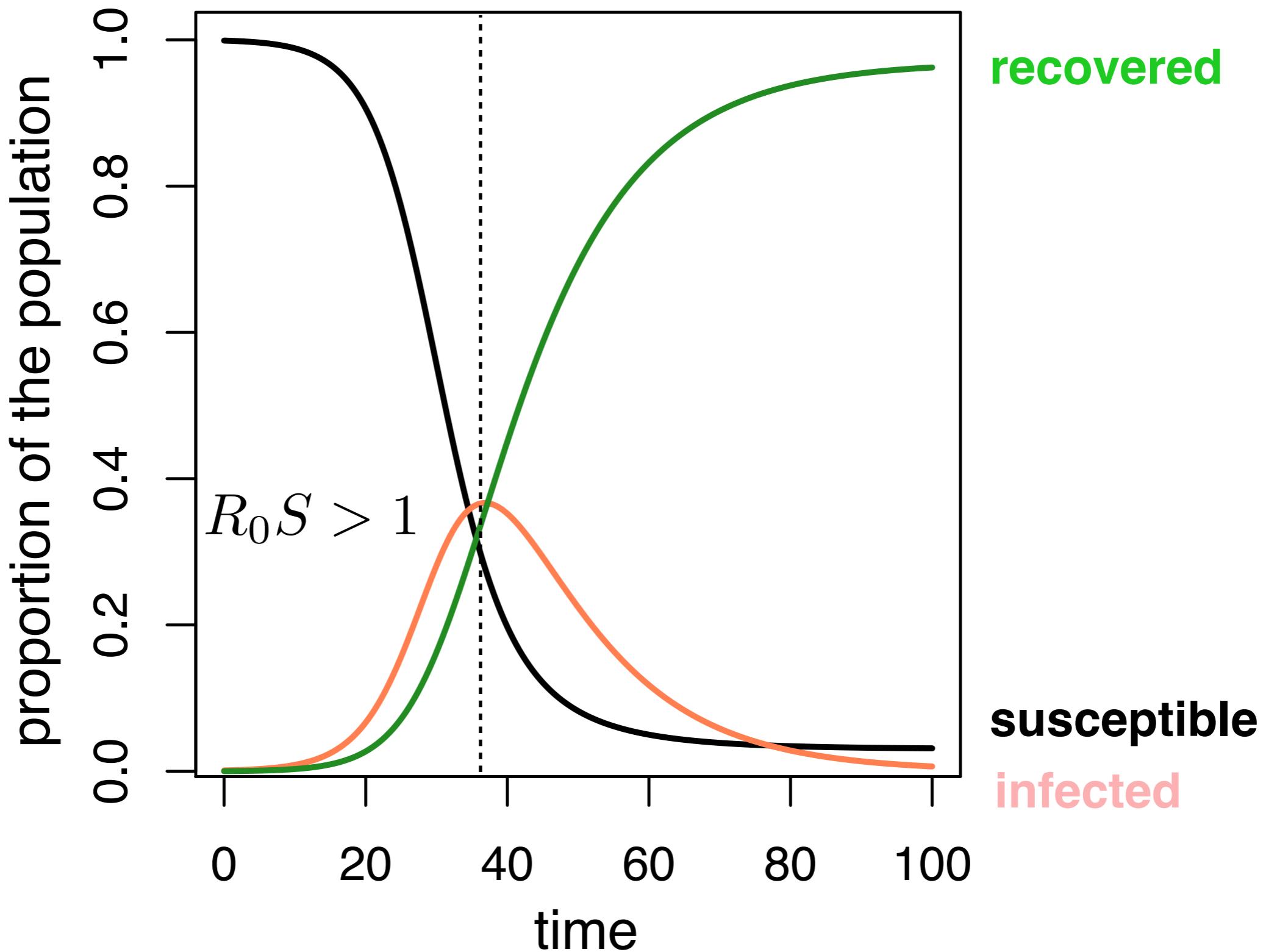
as the epidemic progresses and S falls



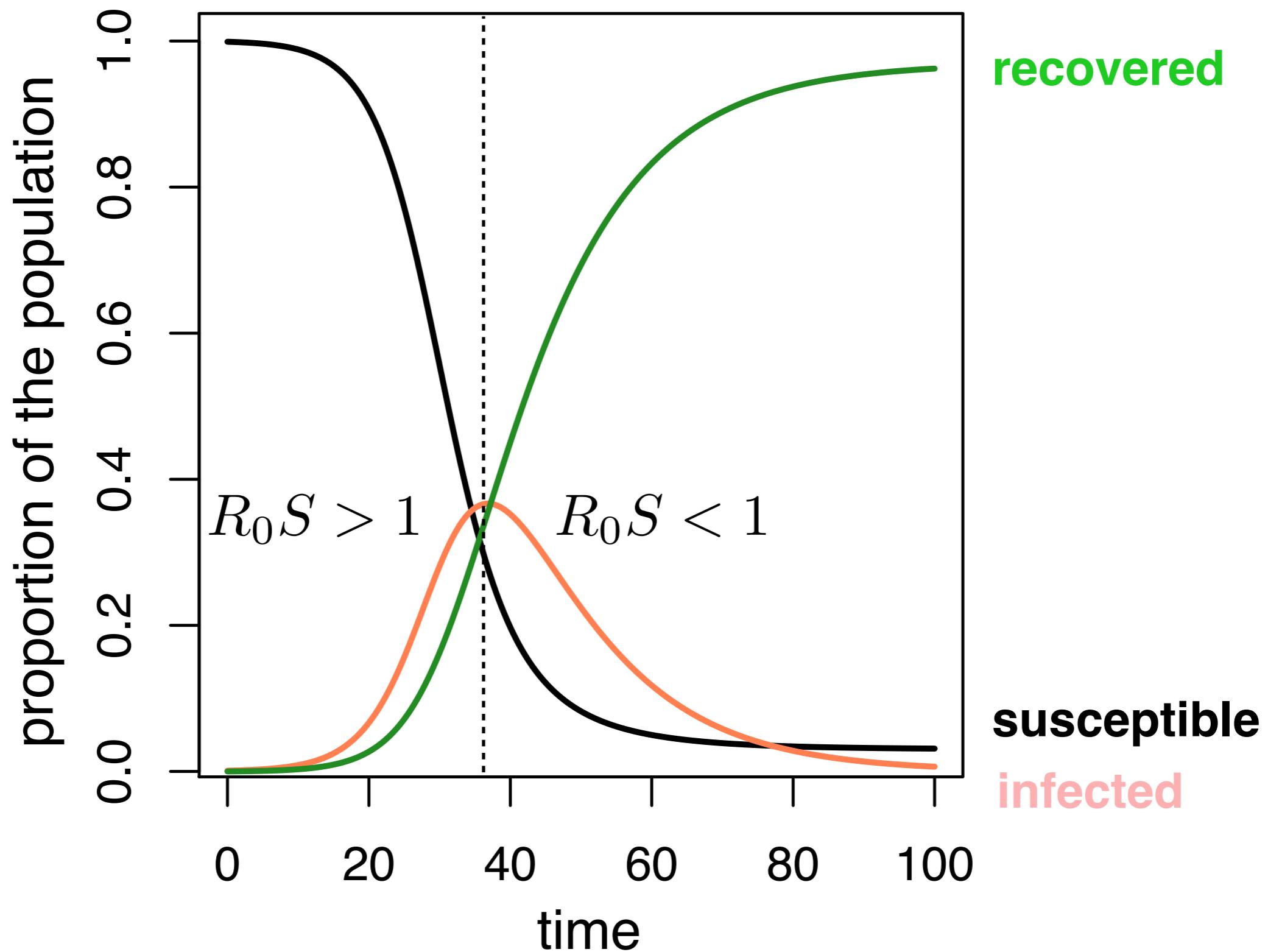
The SIR model: dynamics



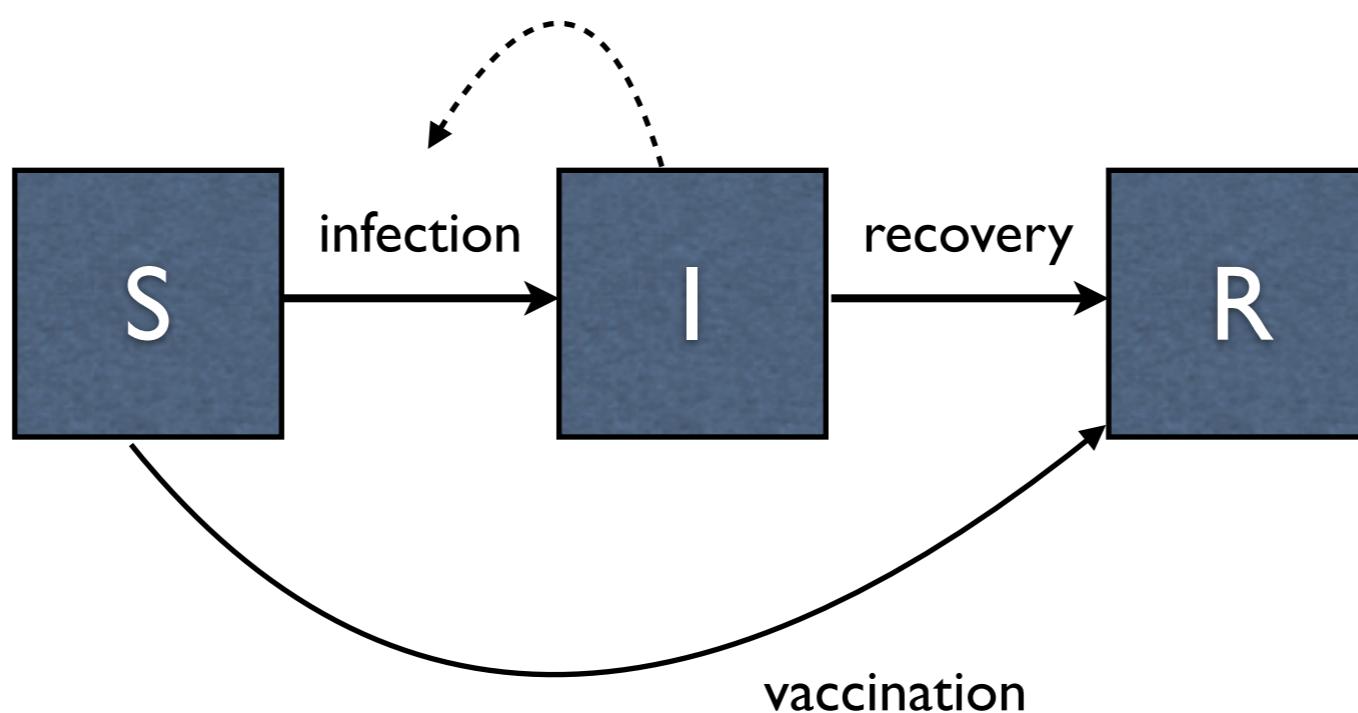
The SIR model: dynamics



The SIR model: dynamics



The SIR model: vaccination

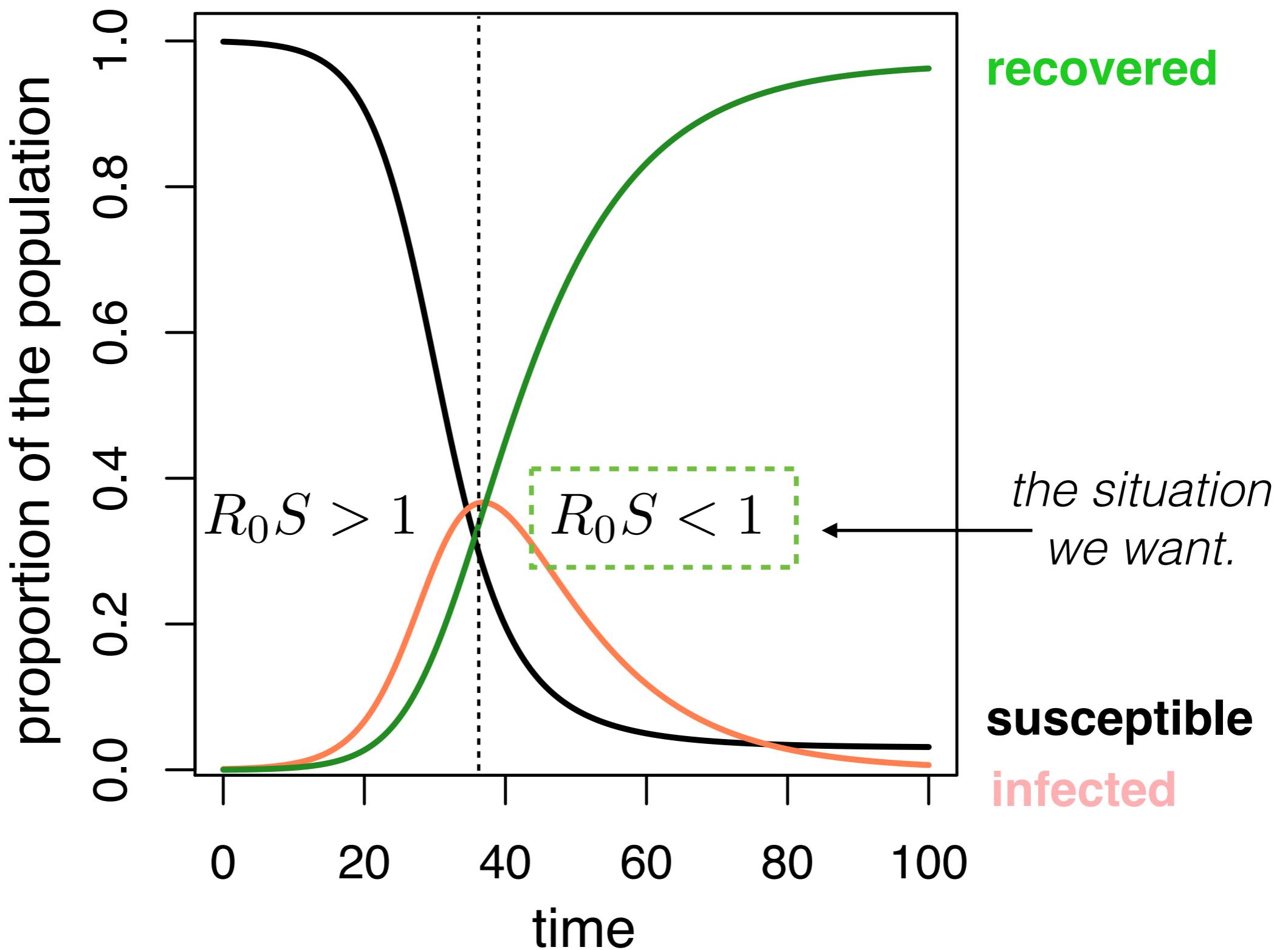


Vaccination moves people out of susceptibles into the immune (recovered) class.

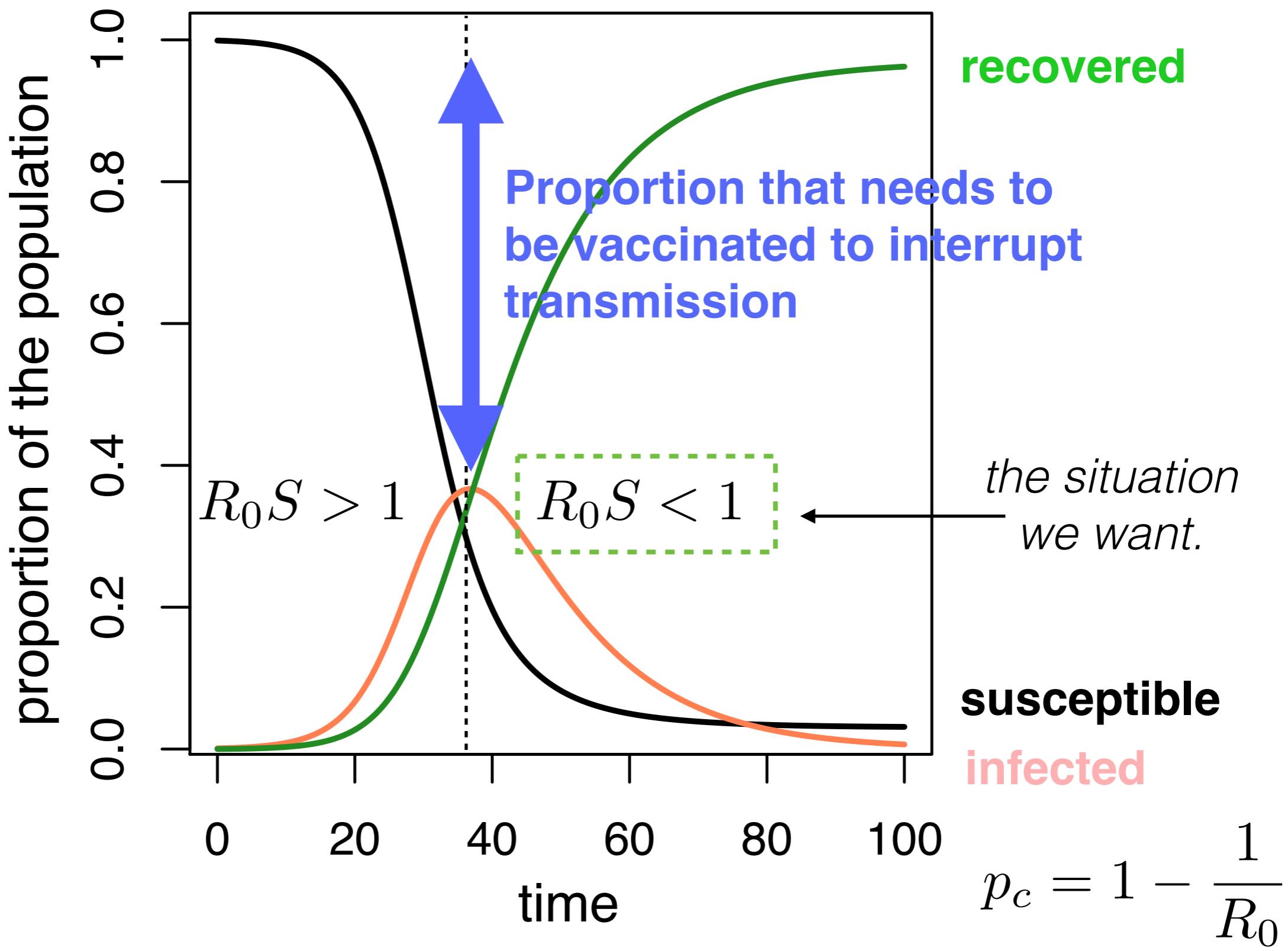
La vaccination éloigne les personnes sensibles de la maladie dans la classe immunitaire (rétablie).



The SIR model: dynamics

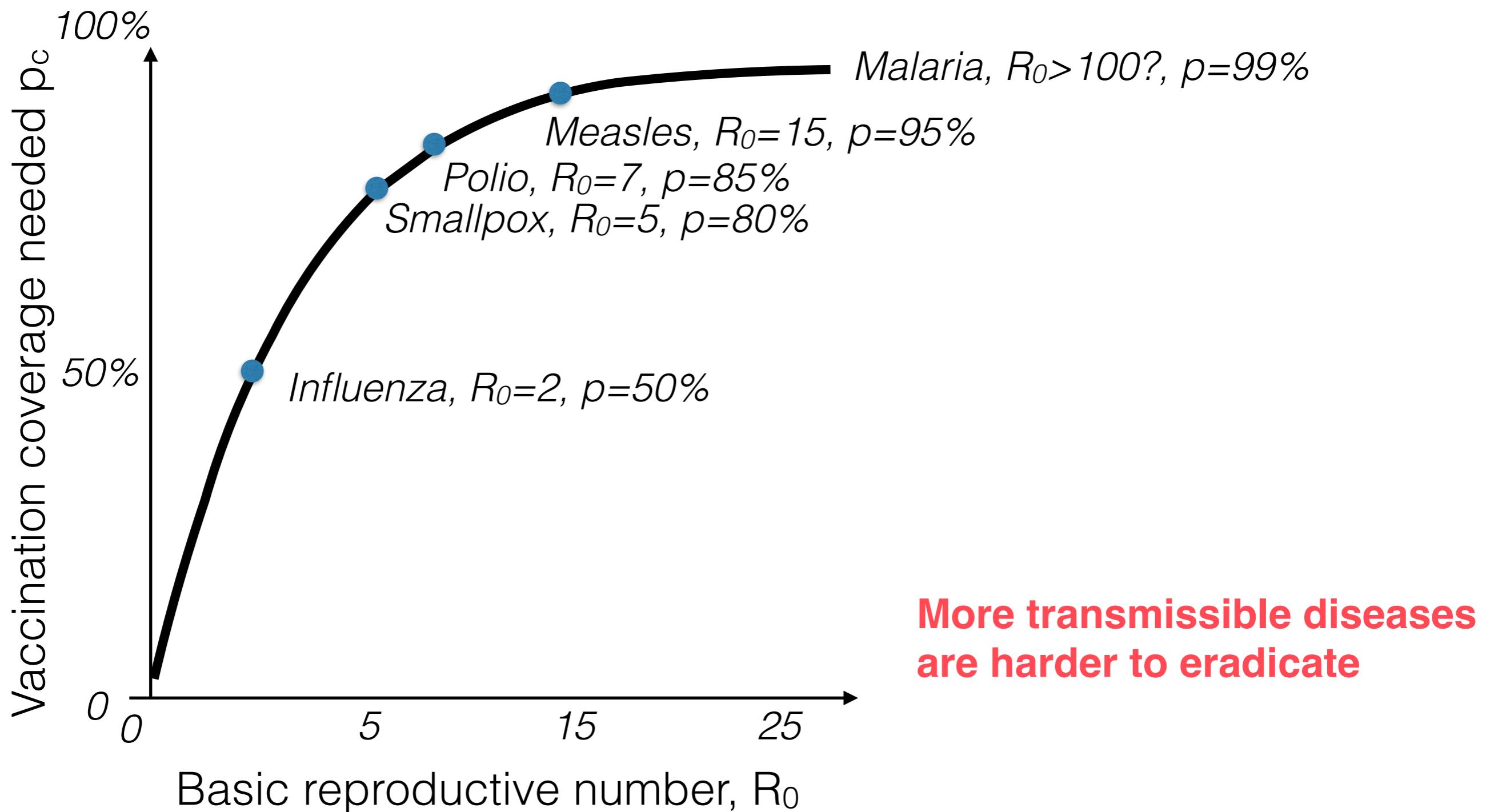


The SIR model: dynamics



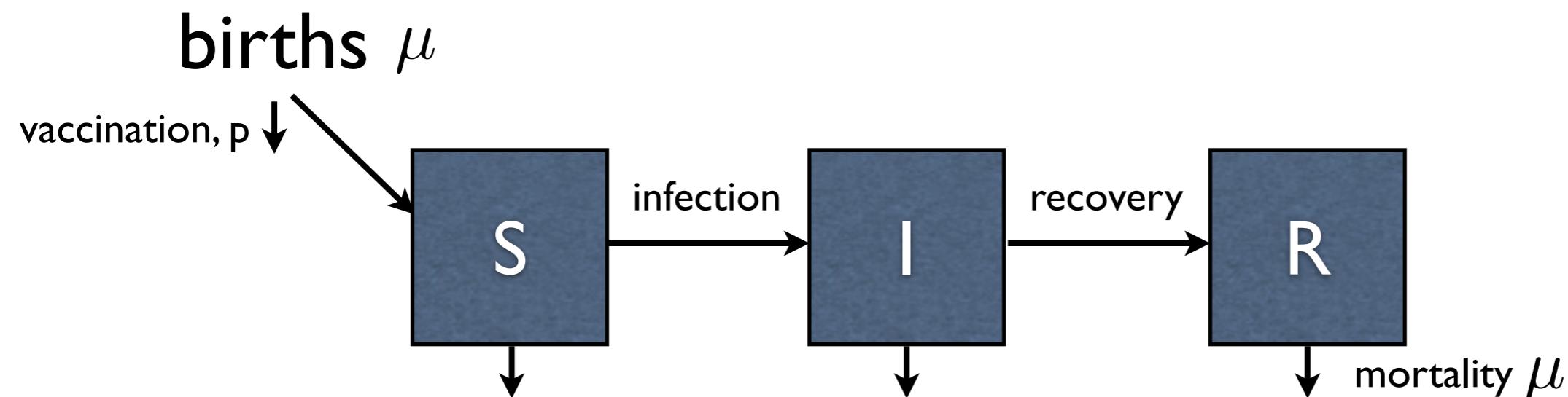
The SIR model: eradication

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



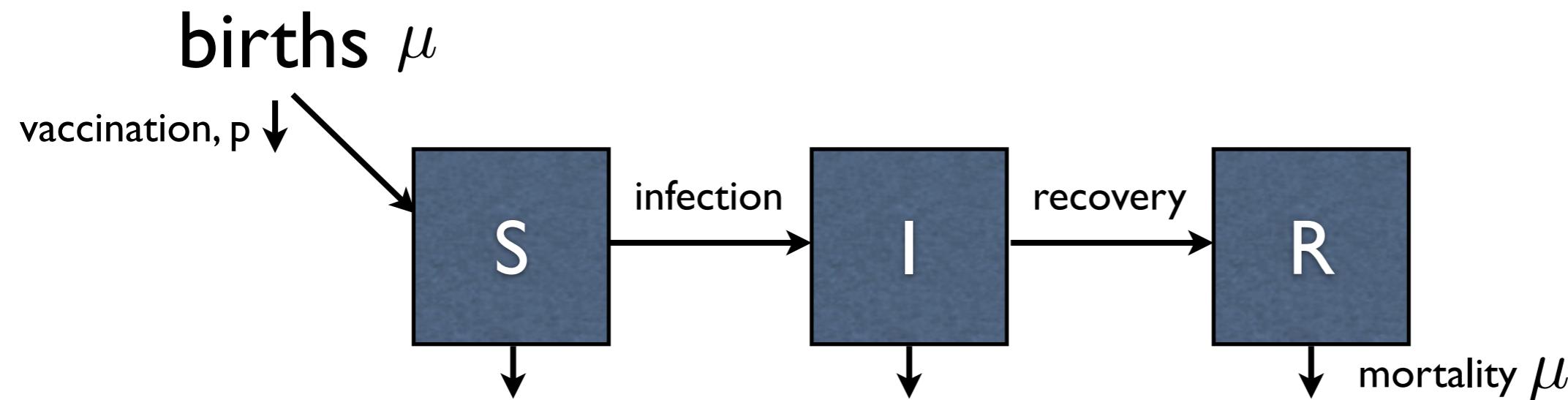
The SIR model: extensions

Moving beyond a ‘closed’ population



The SIR model: extensions

Moving beyond a ‘closed’ population



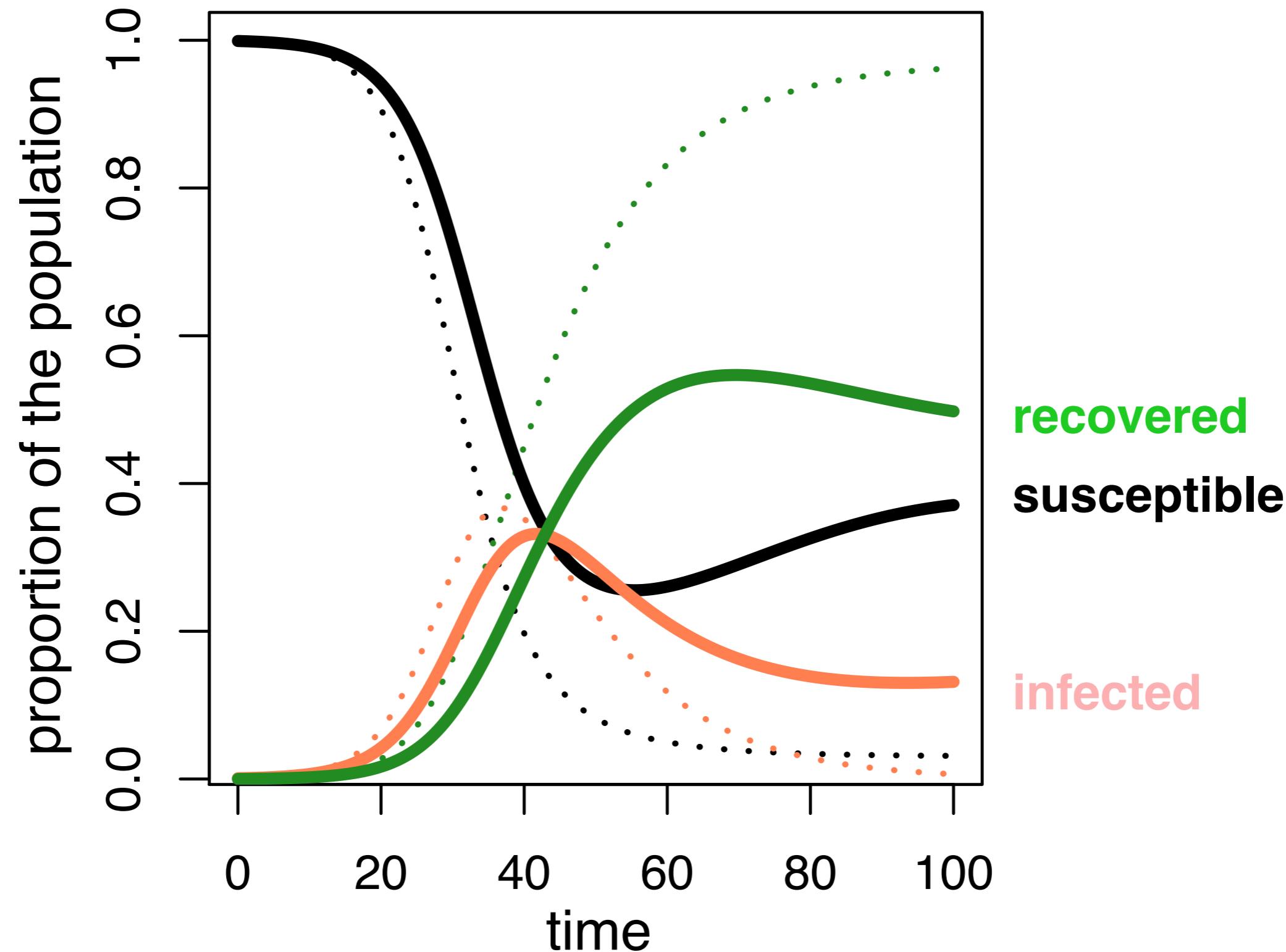
$$\frac{dS(t)}{dt} = \mu(1 - p) - \beta S(t)I(t) - \mu S(t)$$

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

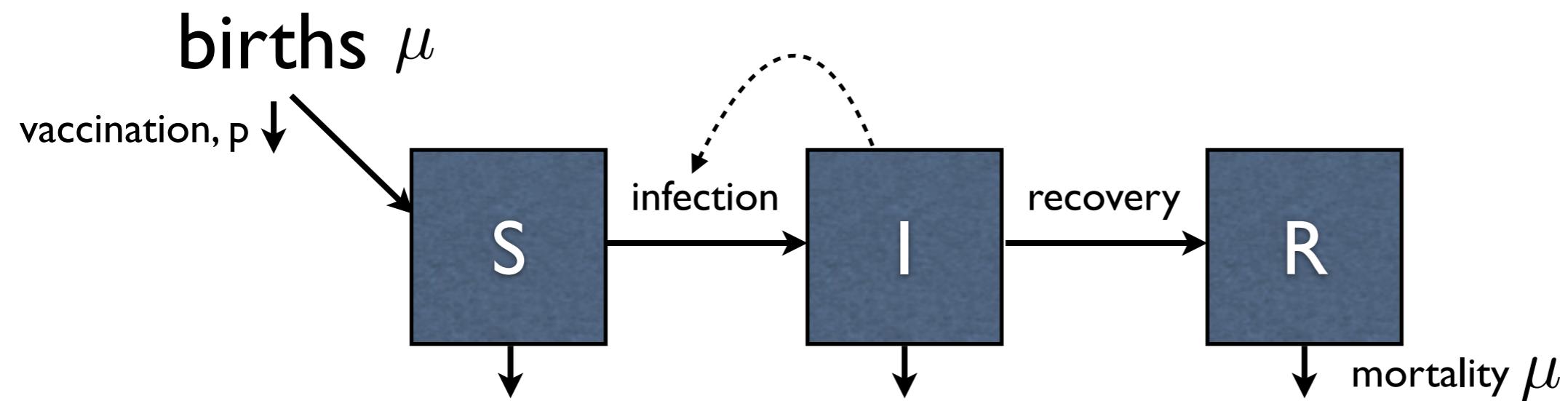
What is likely to be the BIGGEST dynamical difference?



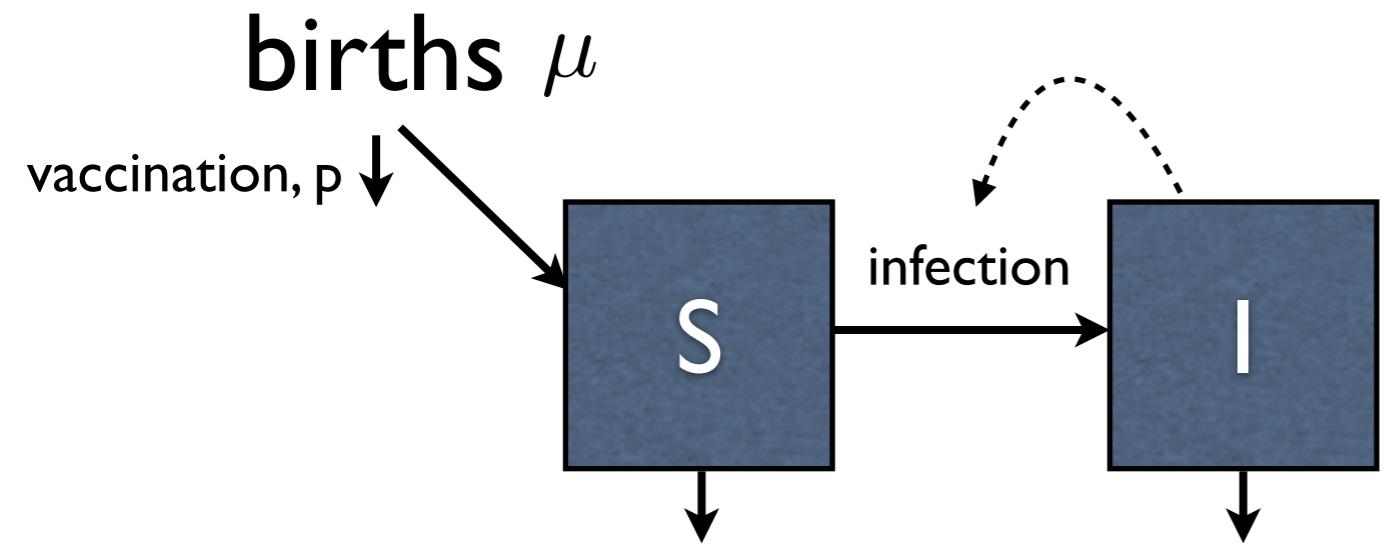
The SIR model: add births



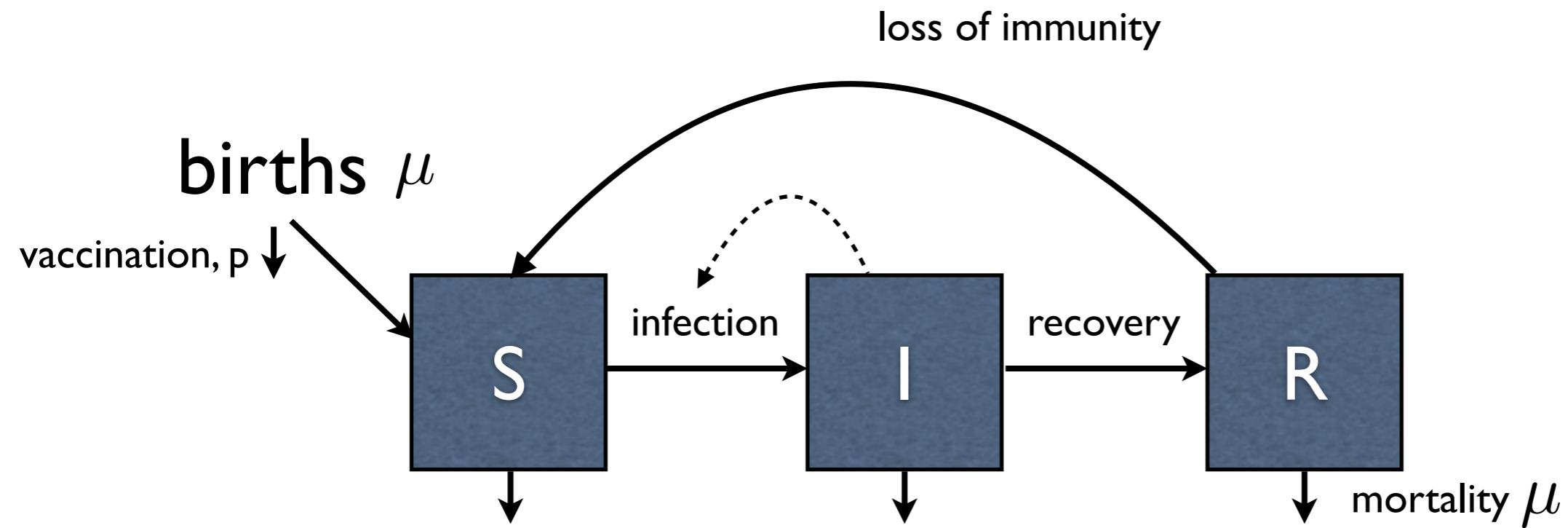
Beyond the SIR model



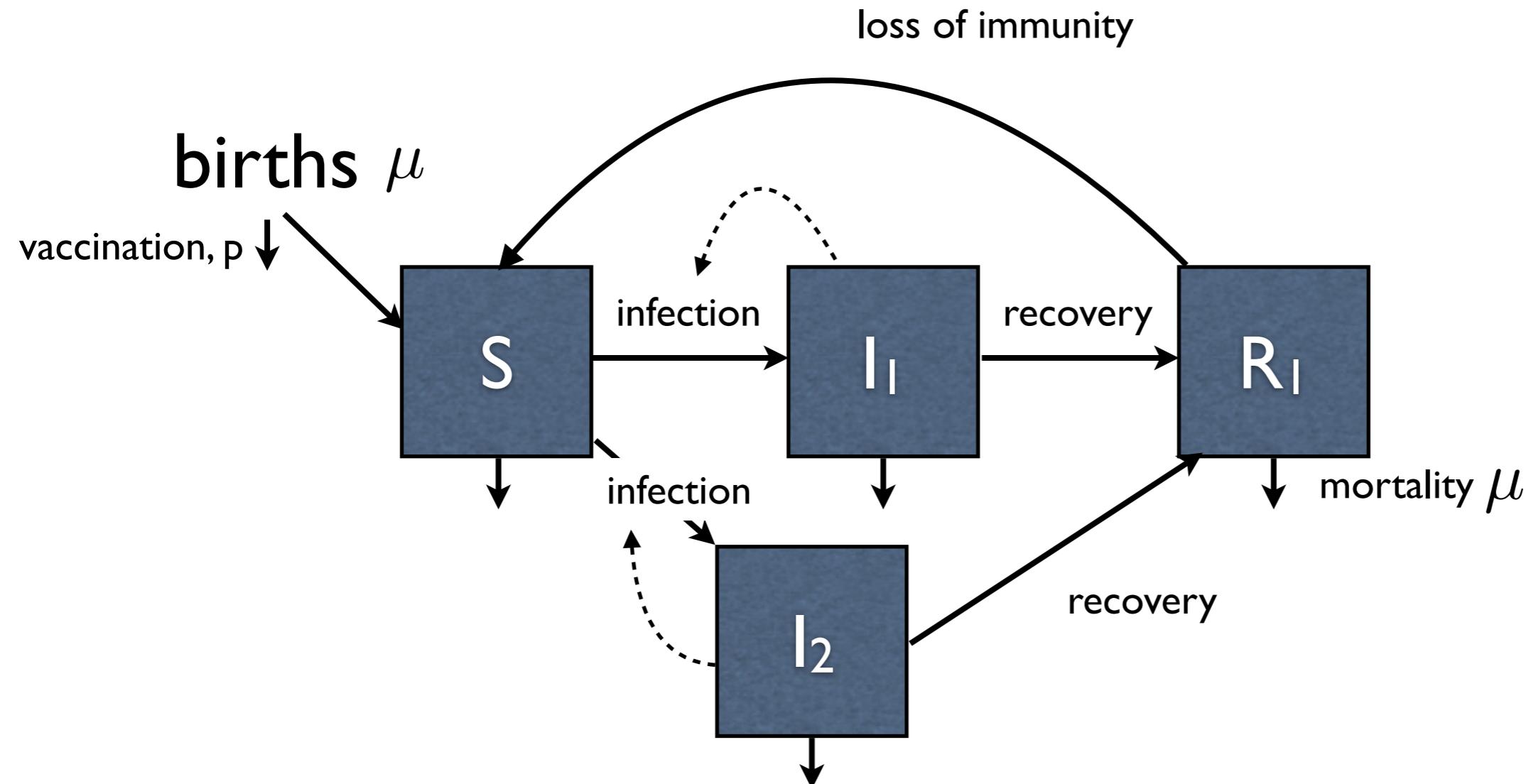
Beyond the SIR model



Beyond the SIR model



Beyond the SIR model

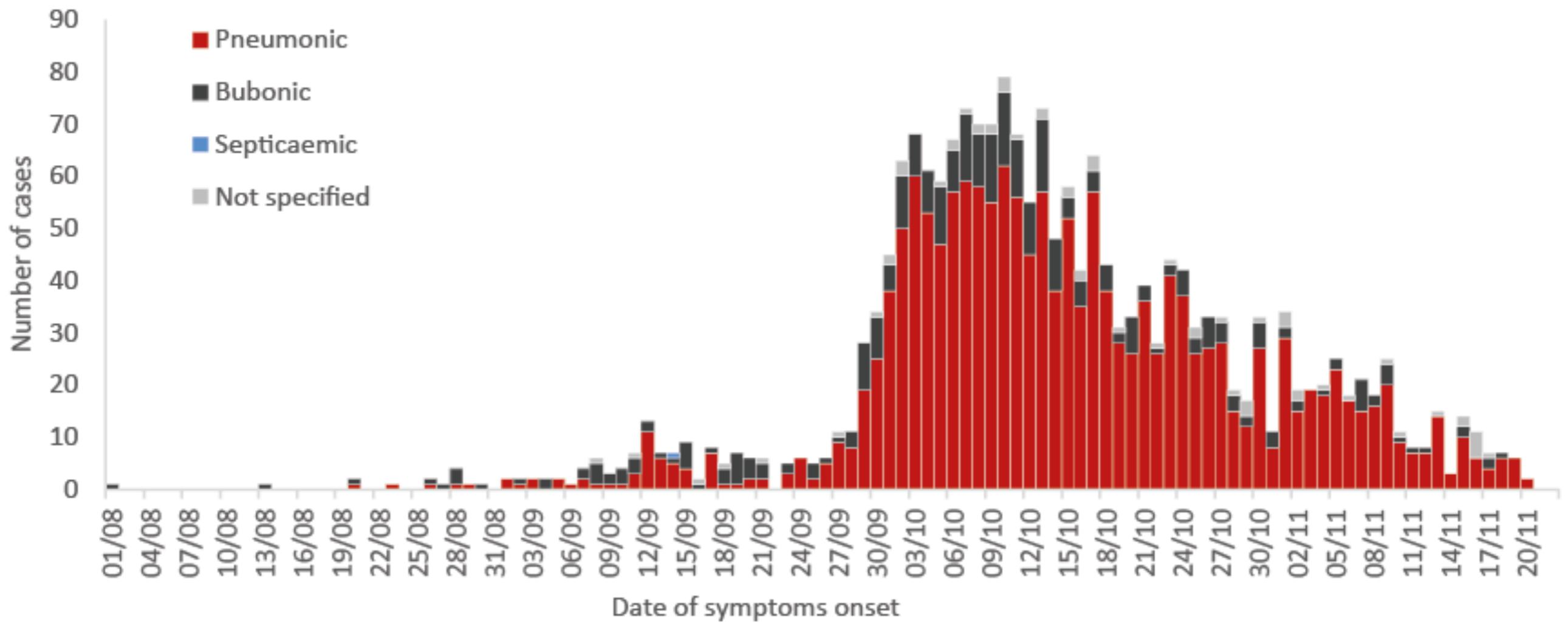


Key concepts

- Les modèles SIR ressemblent en essence à des modèles de dynamic predator-prey
- Pour des pathogènes avec un cycle de vie qui ressemble à 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.



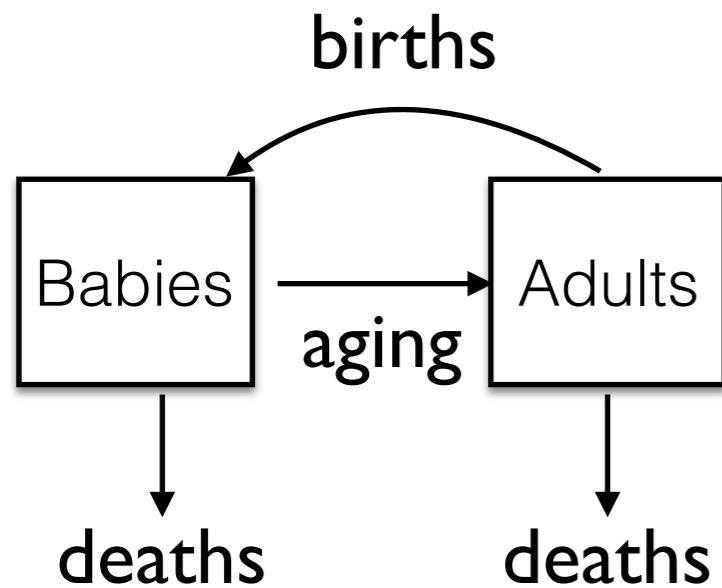
Which model?



Extra Slides



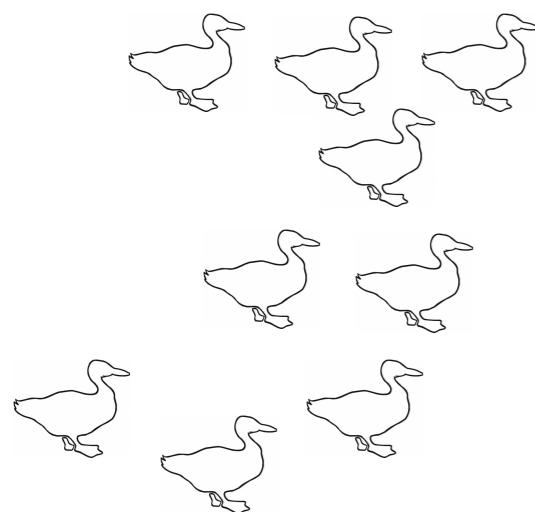
Structured population model



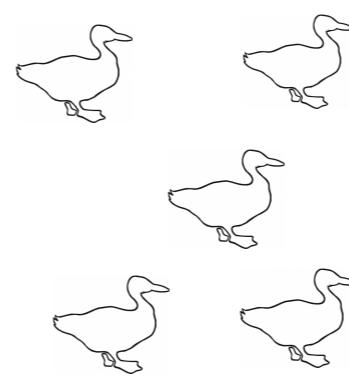
$$\mathbf{n}_{t+1} = \mathbf{A} \mathbf{n}_t$$

Assumes no role of chance

starting population



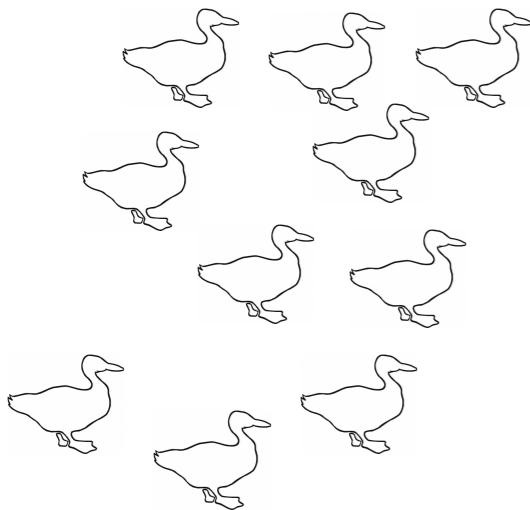
if deterministic



probability
of
survival = 0.5



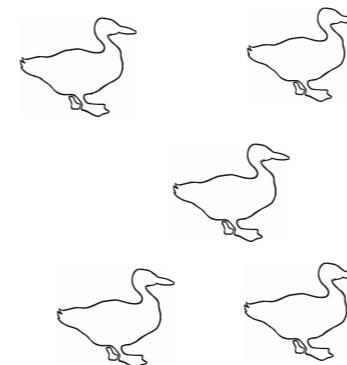
starting population



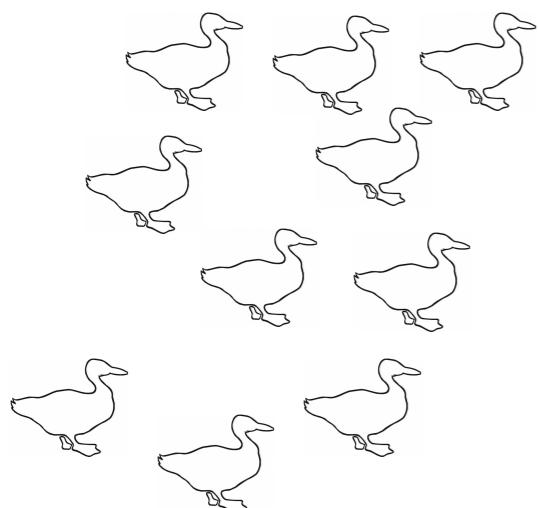
if deterministic



probability of
survival = 0.5



starting population



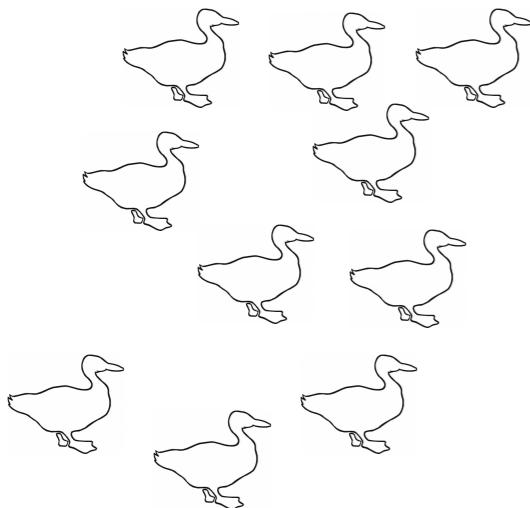
if stochastic?



probability of
survival = 0.5



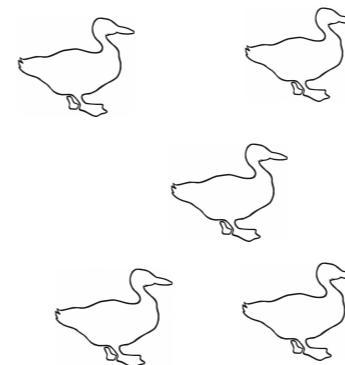
starting population



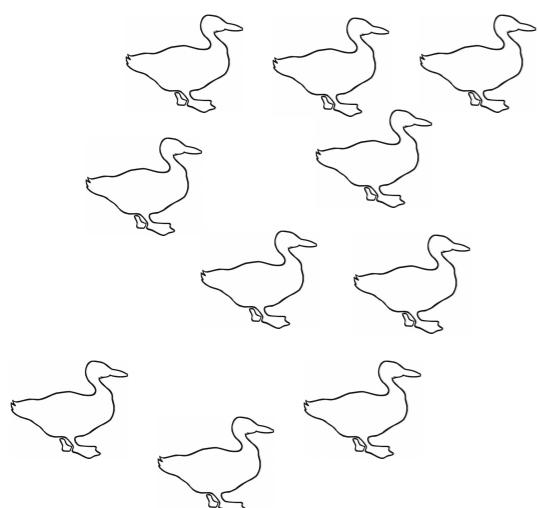
if deterministic



probability of
survival = 0.5



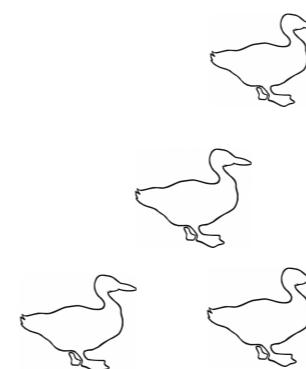
starting population



if stochastic?



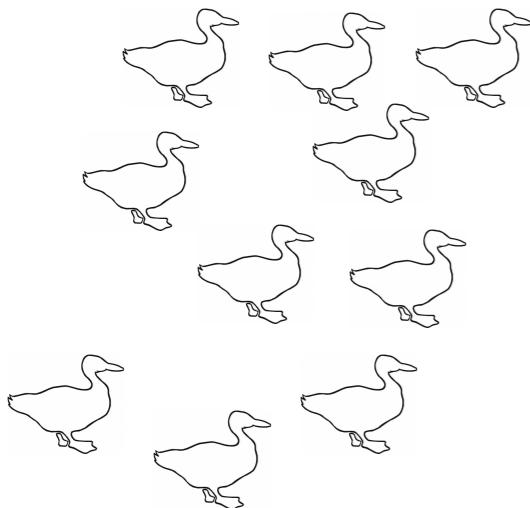
probability of
survival = 0.5



Flip a coin for
every duck;



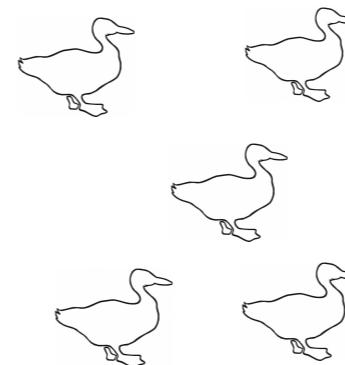
starting population



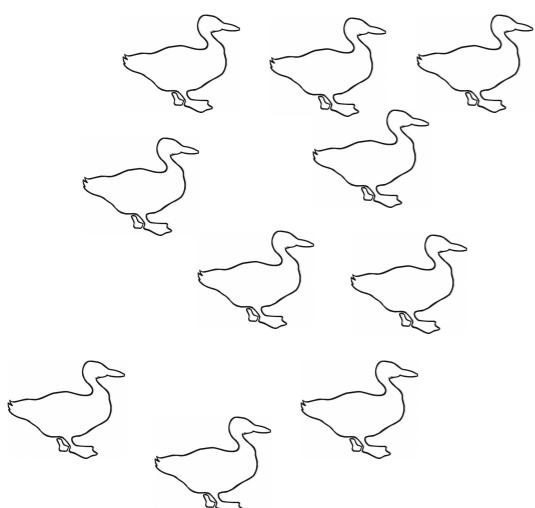
if deterministic



probability of
survival = 0.5

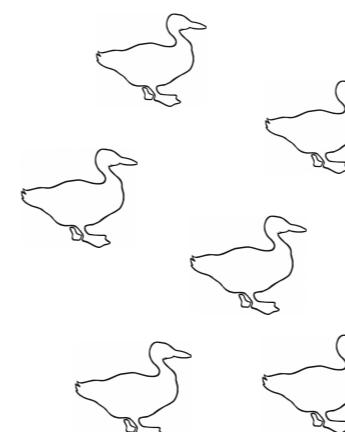


starting population



probability of
survival = 0.5

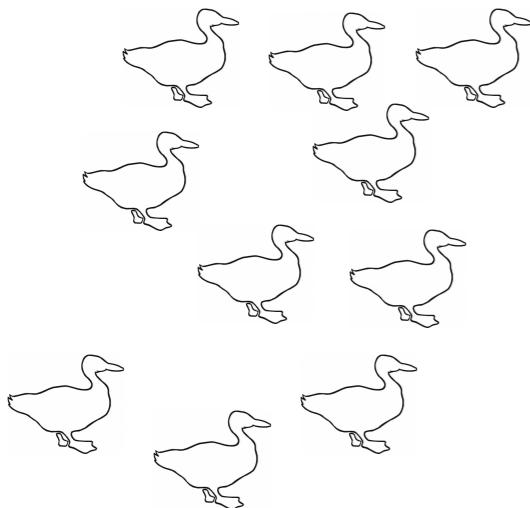
if stochastic?



Flip a coin for
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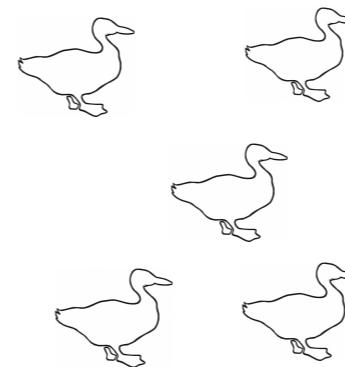
starting population



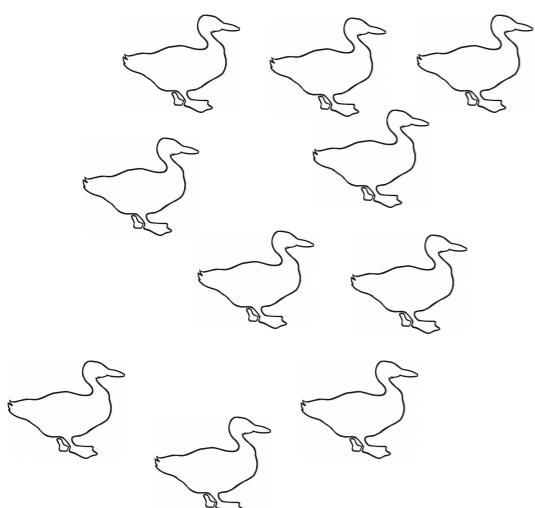
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probability of
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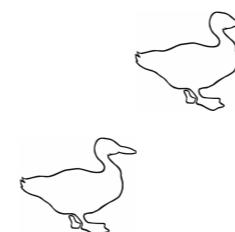
starting population



if stochastic?



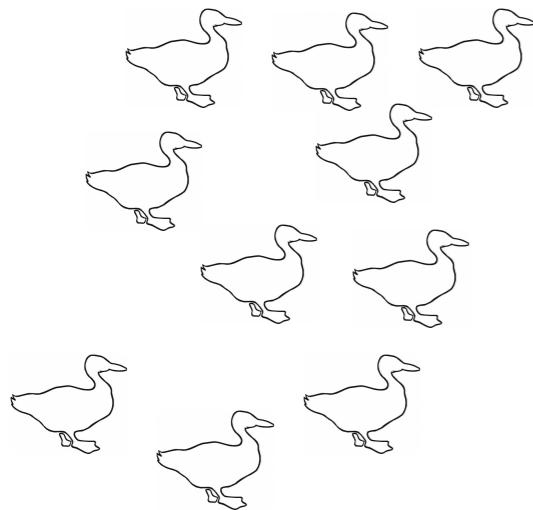
probability of
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Flip a coin for
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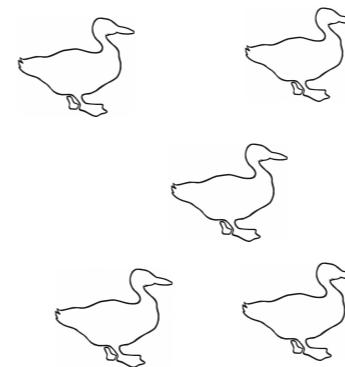
starting population



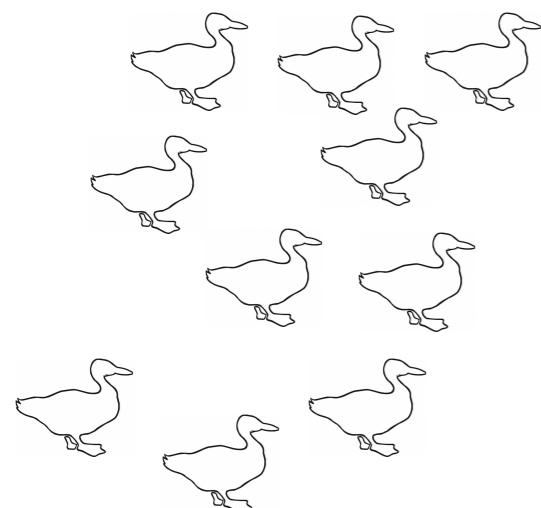
if deterministic



probability of
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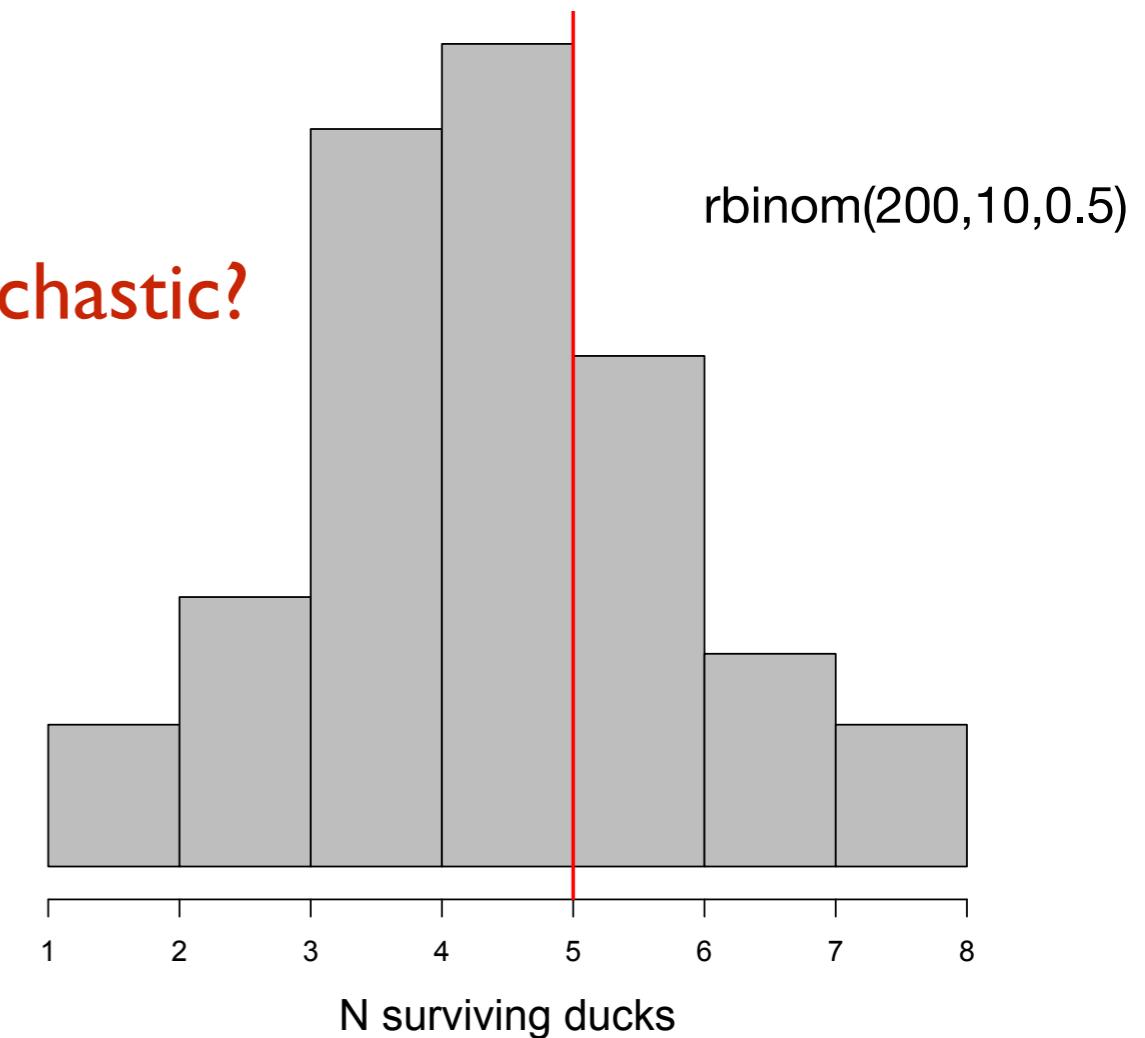
starting population



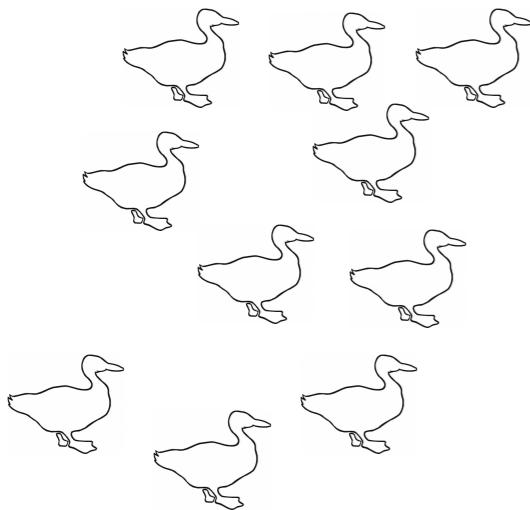
if stochastic?



probability of
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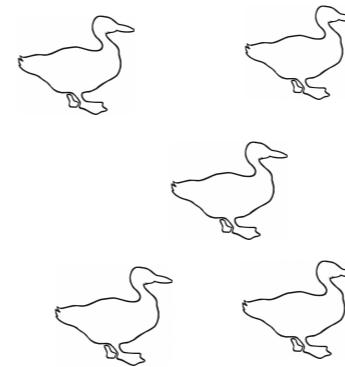


starting population



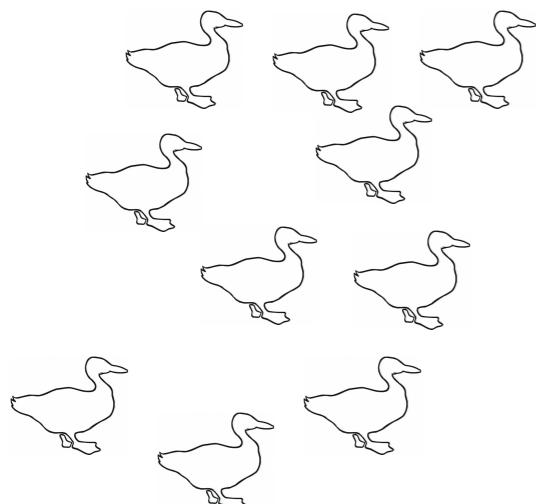
if deterministic

probability of survival = 0.5



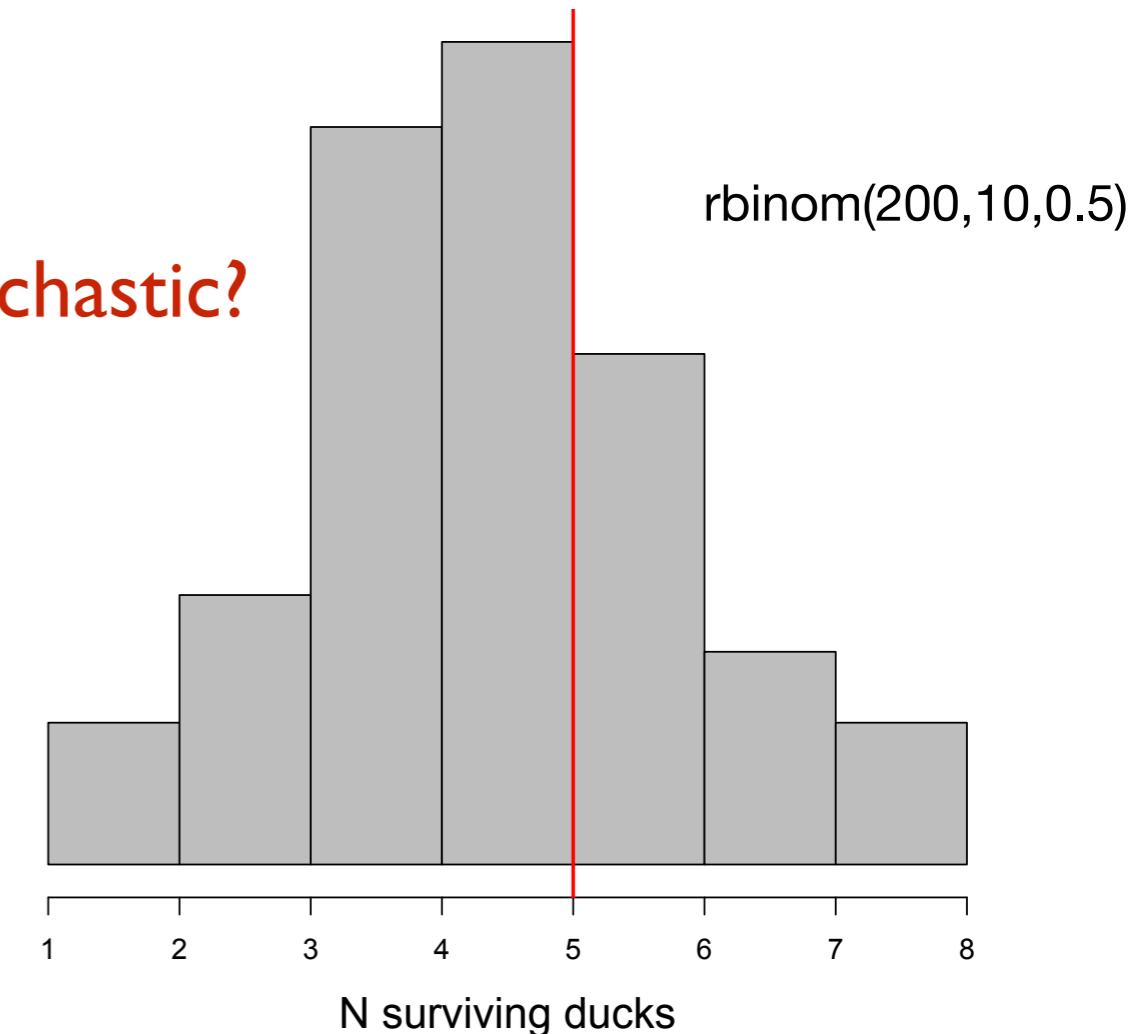
If you test your 10 ducks many times, on average you get 5

starting population

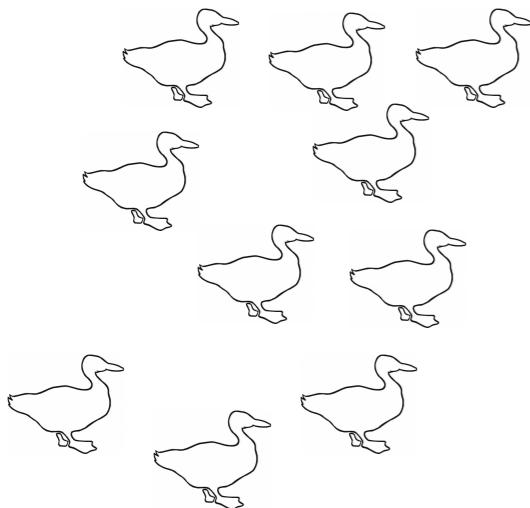


probability of survival = 0.5

if stochastic?

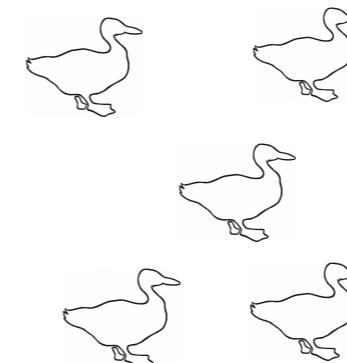


starting population



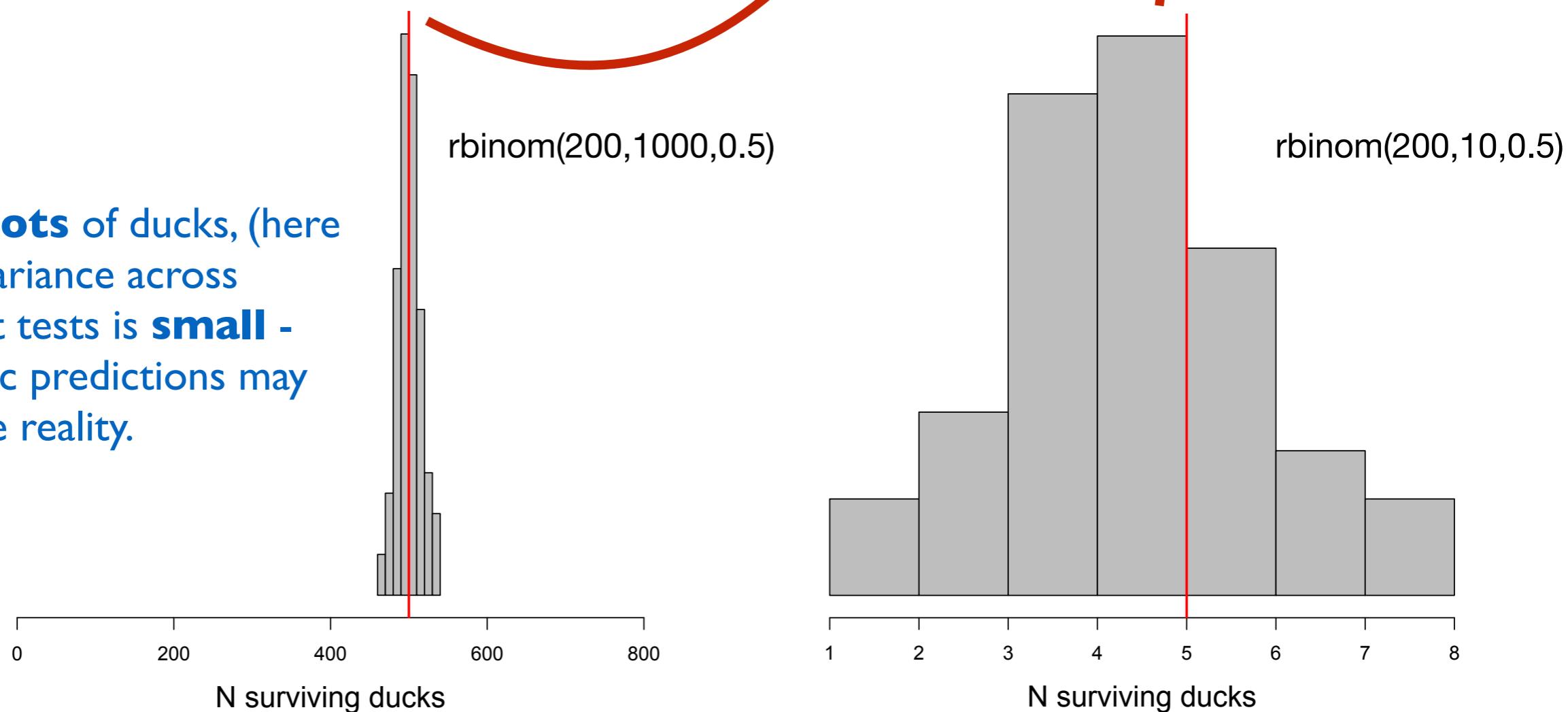
if deterministic

probability of survival = 0.5



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‡

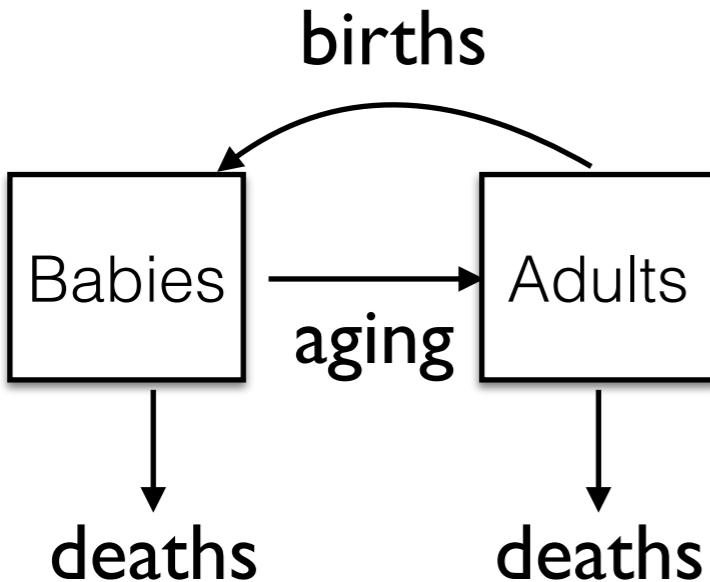
*McDonald Institute of Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, England; and ‡Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB3 0EQ, England; and †Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge 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 rainfall. Climatic unpredictability is associated with unpredictable patterns of fruiting and flowering. It is argued that these features



The basic population model



Structured population model

$$\mathbf{n}_{t+1} = \mathbf{A} \mathbf{n}_t$$

A diagram showing the matrix multiplication for a structured population model. On the left, a matrix \mathbf{A} is shown as a 2x2 grid:

$s_b(1-a)$	b
$s_b a$	s_a

To its right is a multiplication sign (\times). To the right of that is a vector \mathbf{n}_t as a 2x1 column:

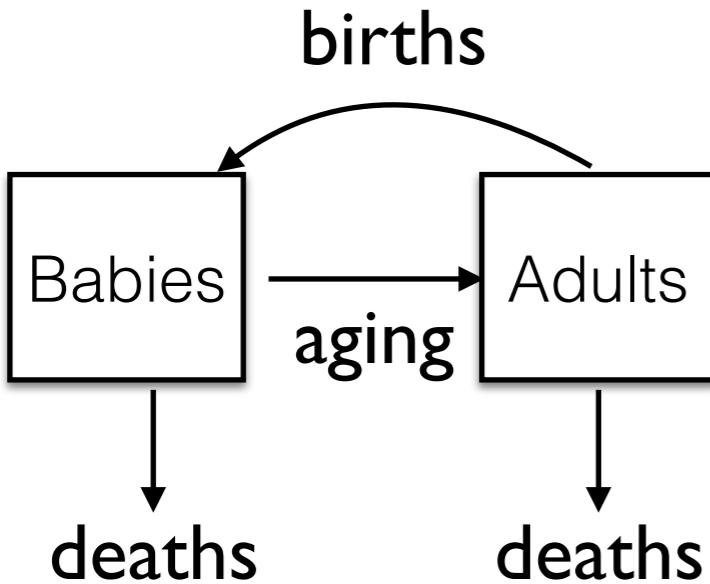
n_b
n_a

Between the multiplication sign and the vector is an equals sign (=). To the right of the equals sign is the resulting vector \mathbf{n}_{t+1} as a 2x1 column:

$s_b(1-a)n_b + b n_a$
$s_b a n_b + s_a n_a$



The basic population model



Structured population model

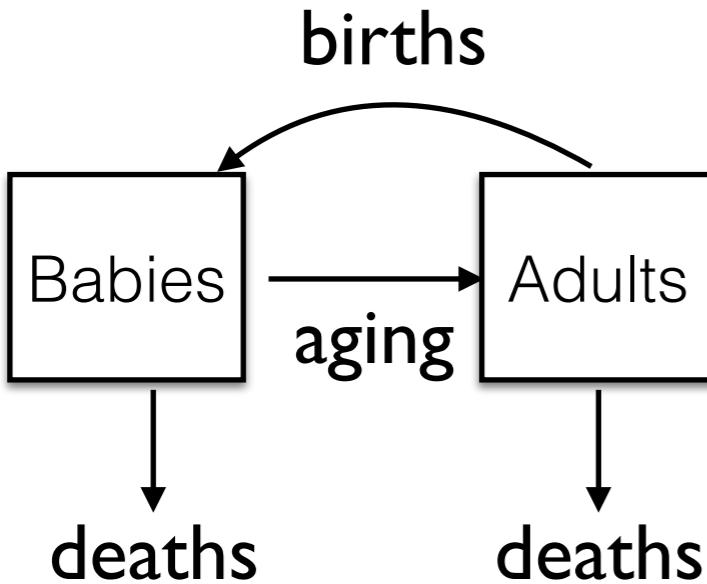
$$\mathbf{n}_{t+1} = \mathbf{A} \mathbf{n}_t$$

Population growth will depend on population structure

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



The basic population model



Structured population model

$$\mathbf{n}_{t+1} = \mathbf{A} \mathbf{n}_t$$

Dominant eigenvalue provides growth rate at equilibrium

A

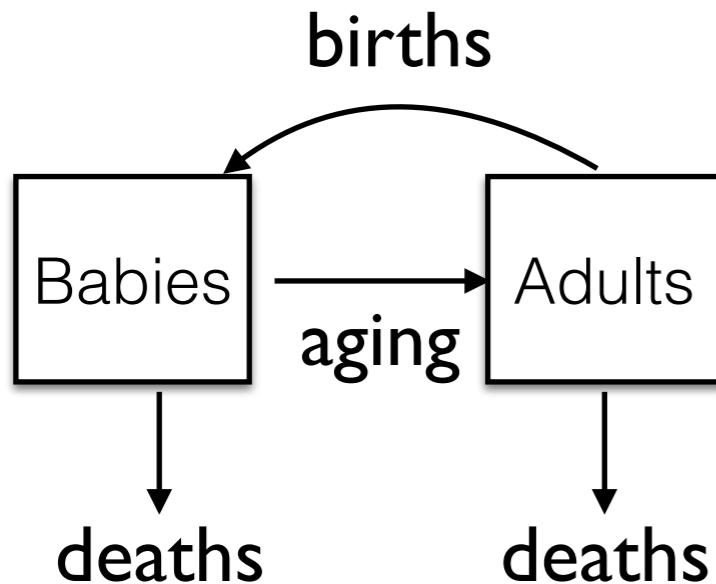
n_t

n_{t+1}

$$\begin{array}{c|c} s_b(1-a) & b \\ \hline s_b a & s_a \end{array} \times \begin{array}{c|c} n_b \\ \hline n_a \end{array} = \begin{array}{c|c} s_b(1-a)n_b + bn_a \\ \hline s_b a n_b + s_a n_a \end{array}$$



The basic population model



Structured population model

$$n_{t+1} = A n_t$$

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

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