

Qualitative behaviour of ecological models

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Introduction

- Population dynamics describe change over time
- Aim of population and community ecology is to understand the processes underlying patterns of change
- I hope this course will help in understanding the qualitative behaviour of mathematical models

Introduction

- Most models that are of interest in biology are non-linear dynamical systems
- Mathematical analysis tools are sharpest for linear systems
- Analysis is often only possible to a limited extent, but at the same time, provides a powerful tool to understand the dynamics

Introduction

- I will use dynamical systems theory and bifurcation theory and apply this to ecological models
- The ecological models mainly describe the interactions between one and two species
- I will try to provide a mix of biological background and justification and mathematical analysis, building on what you have done before in this course

Overview

- Single species models, stability, the metapopulation concept
- Interspecific competition, phase plane, eigenvalues & eigenvectors
- Alternative stable states, phase shifts and catastrophic transitions
- Chaos and unpredictability
- Predator-prey models, limit cycles, Hopf bifurcation
- Epidemiological models

Week 1:



Single species models, stability, the metapopulation

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Outline

- Exponential Growth
- Logistic growth
- Stability
- Metapopulations
- Pair approximations

Exponential Growth

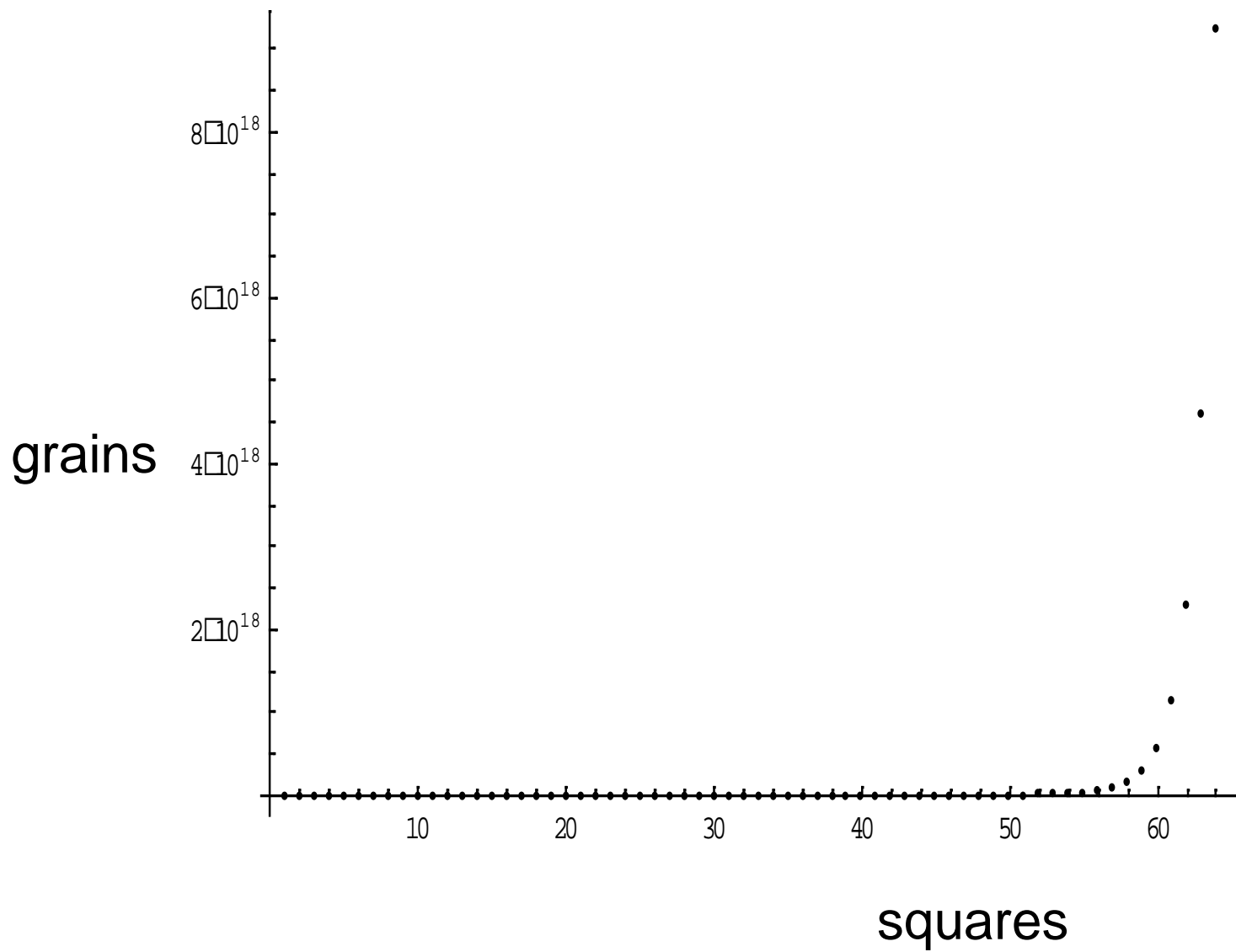
- The simplest model for growth is to assume that the net per capita growth is density independent
- It goes back many centuries

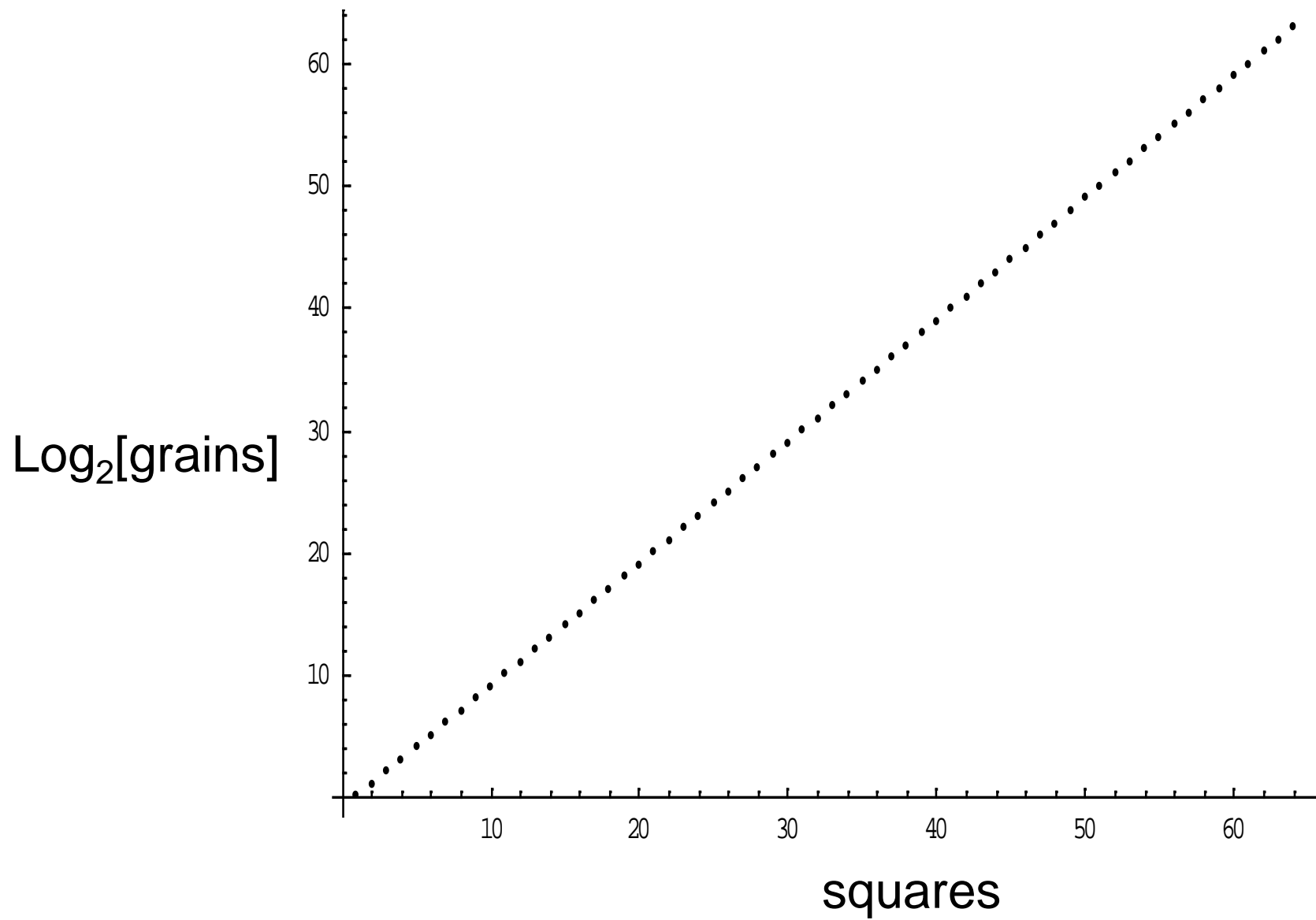


The courtier and the Persian king

Exponential Growth

- Sequence 1,2,4,8,16,32,64,128,256,512, etc.
- Or 2^0 , 2^1 , 2^2 , 2^3 , 2^4 etc
- He would get 18446744073709551615 grains of rice, that is about 5×10^{11} metric tons, more than 500 times the current yearly global rice production!





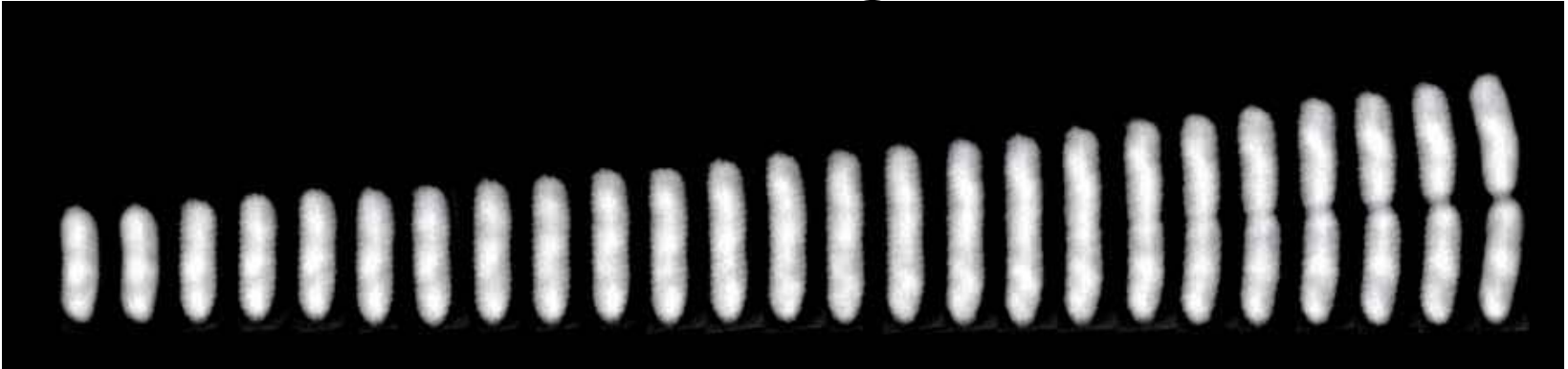
Humans vs Bacteria: the growth of the human population

Humans vs Bacteria:

- How does a population grow?
- Can we find any patterns or mechanisms in human population growth
- Malthus wrote an essay (1789) in which he claims that the human population grows geometrically
- This claim still resonates today, see e.g. [Albert Bartlett's view on human population growth](#)

Humans vs Bacteria:

Bacterial growth




A time series of a single E. coli cell dividing

- Bacteria multiply by dividing in 2
- So you get 1,2,4,8,16,32 etc bacteria
- This is a geometric series (all terms powers of 2)

Bacterial Growth


Escherichia coli
grown on
minimal salts and
complex medium

Absorbance



Time (mins)

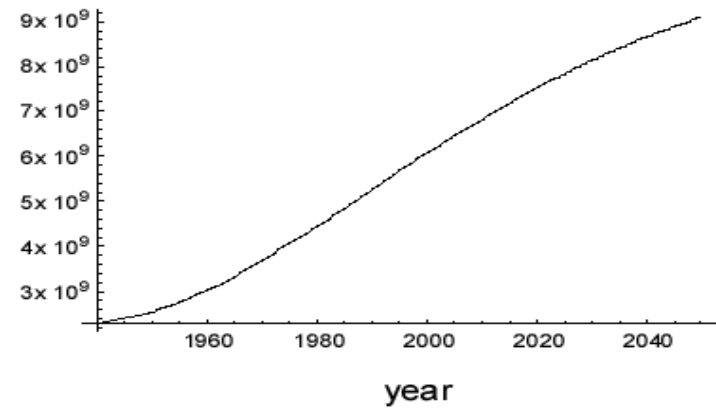
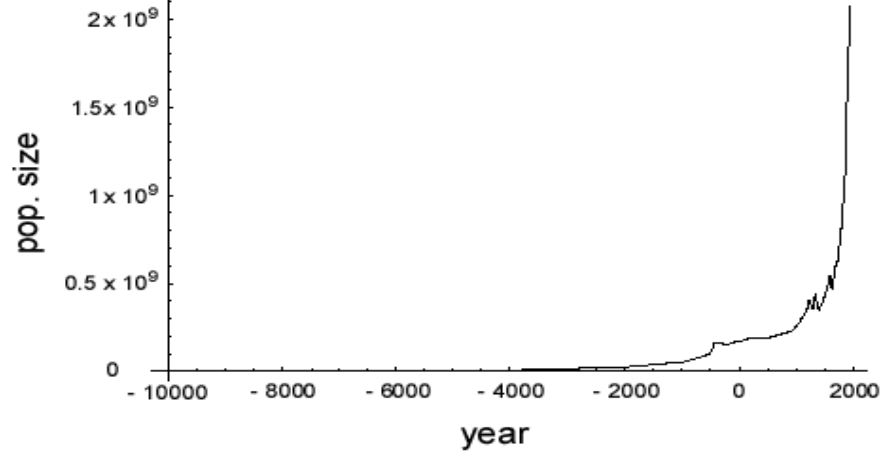
Absorbance



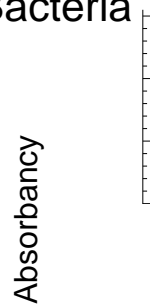
Time (mins)

Humans vs Bacteria

Humans



Bacteria



Time (mins)



Time (mins)

Do human bacterial populations grow in the same way?

Obviously the time scale is different

But is the growth curve the same or
different?

Exponential Population Growth

- If we assume births and death rates are proportional to the size of the population:

$$\text{Births} = b N_t$$

$$\text{Deaths} = d N_t$$

- This amounts to assuming that the probability of a person giving birth (or dying) is independent of population size.

b: *per capita* birth rate

d: *per capita* death rate

Exponential Growth (discrete time)

- With a constant per capita birth and death rate we find a growth process similar to the accumulation of interest:

$$N_{t+1} - N_t = bN_t - dN_t = rN_t \quad (r = b - d, \text{ is the net per capita growth rate})$$

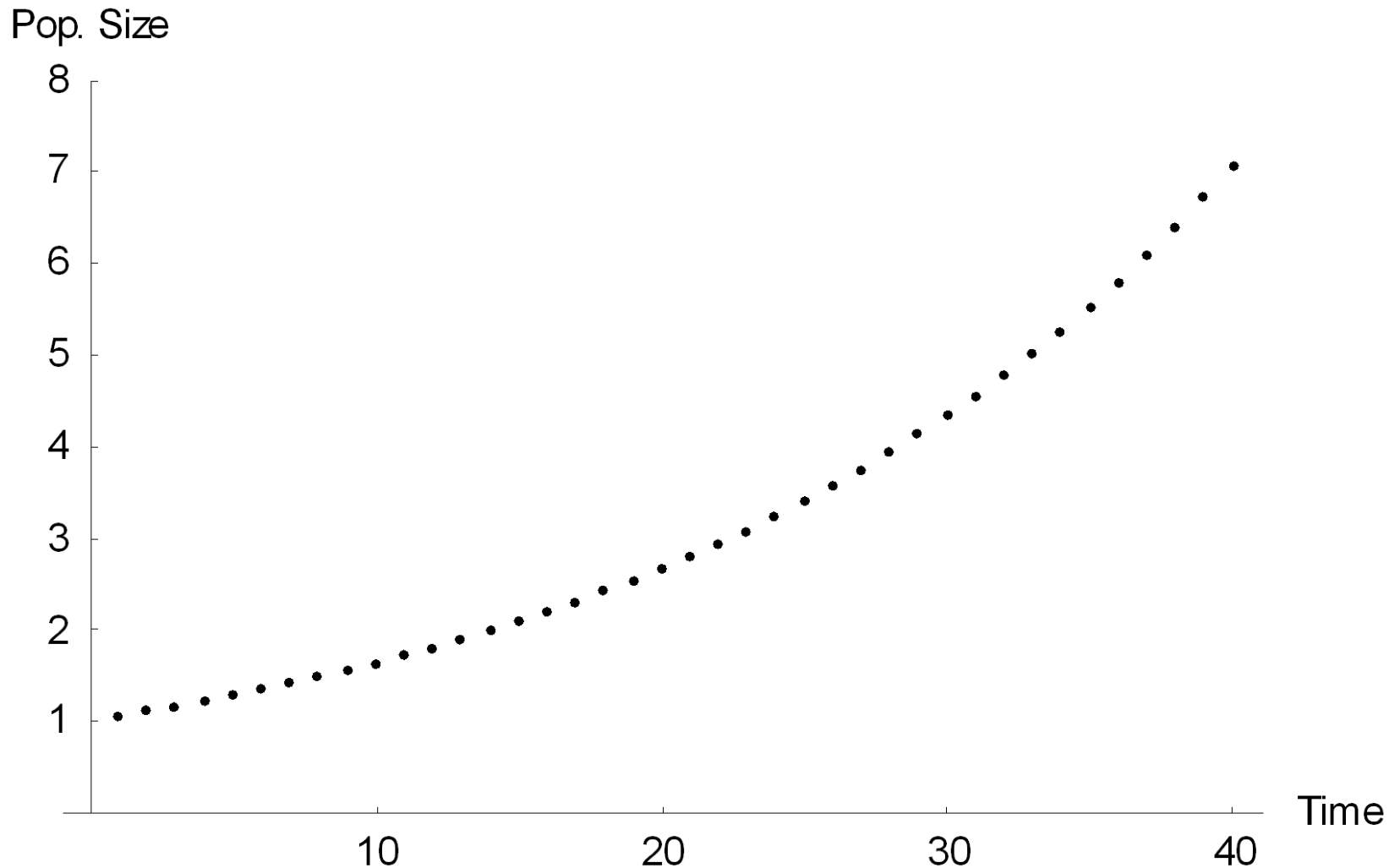
or

$$N_{t+1} = (1 + b - d) N_t = (1 + r) N_t$$

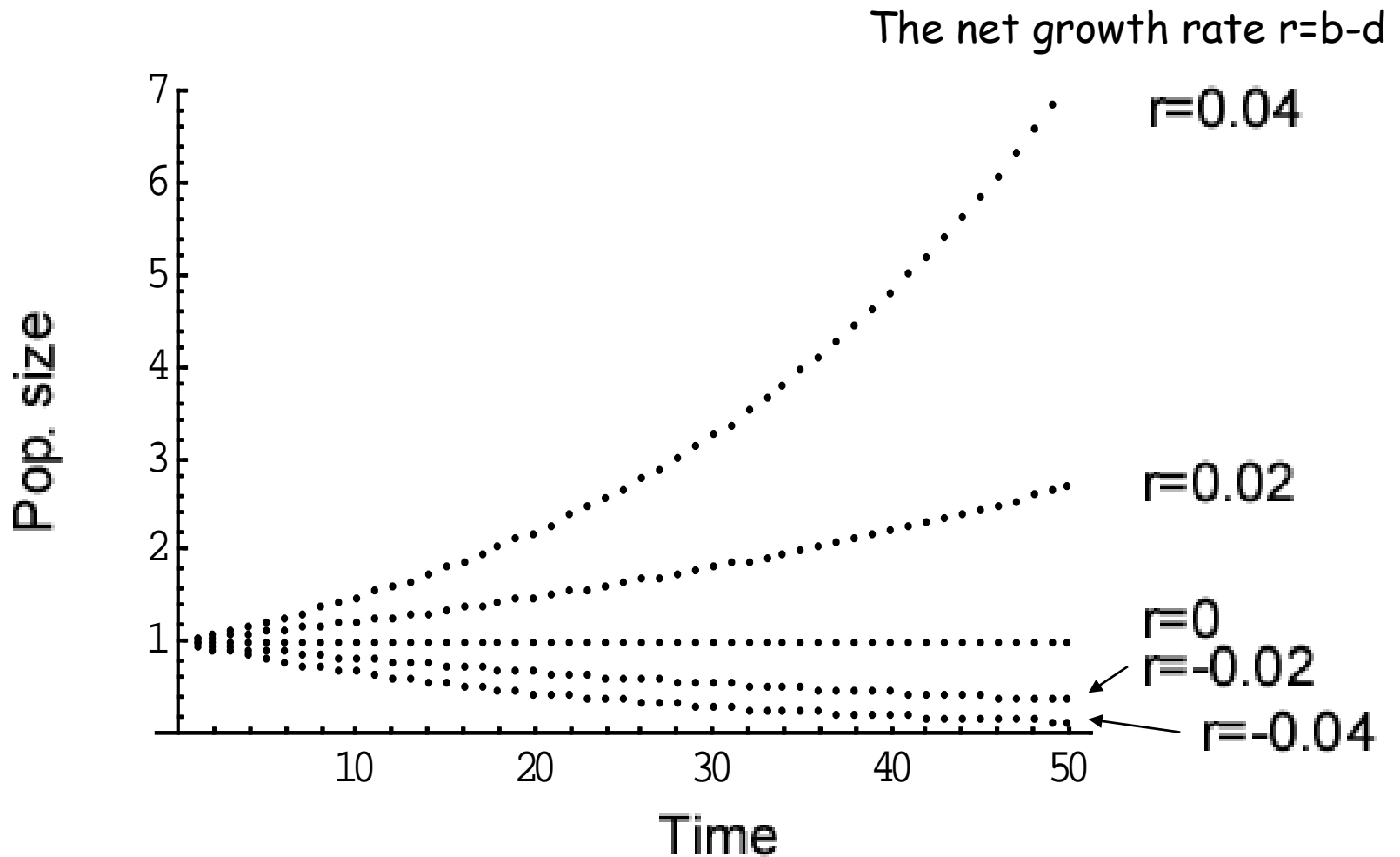
General solution:

$$N_t = N_0 (1 + r)^t$$

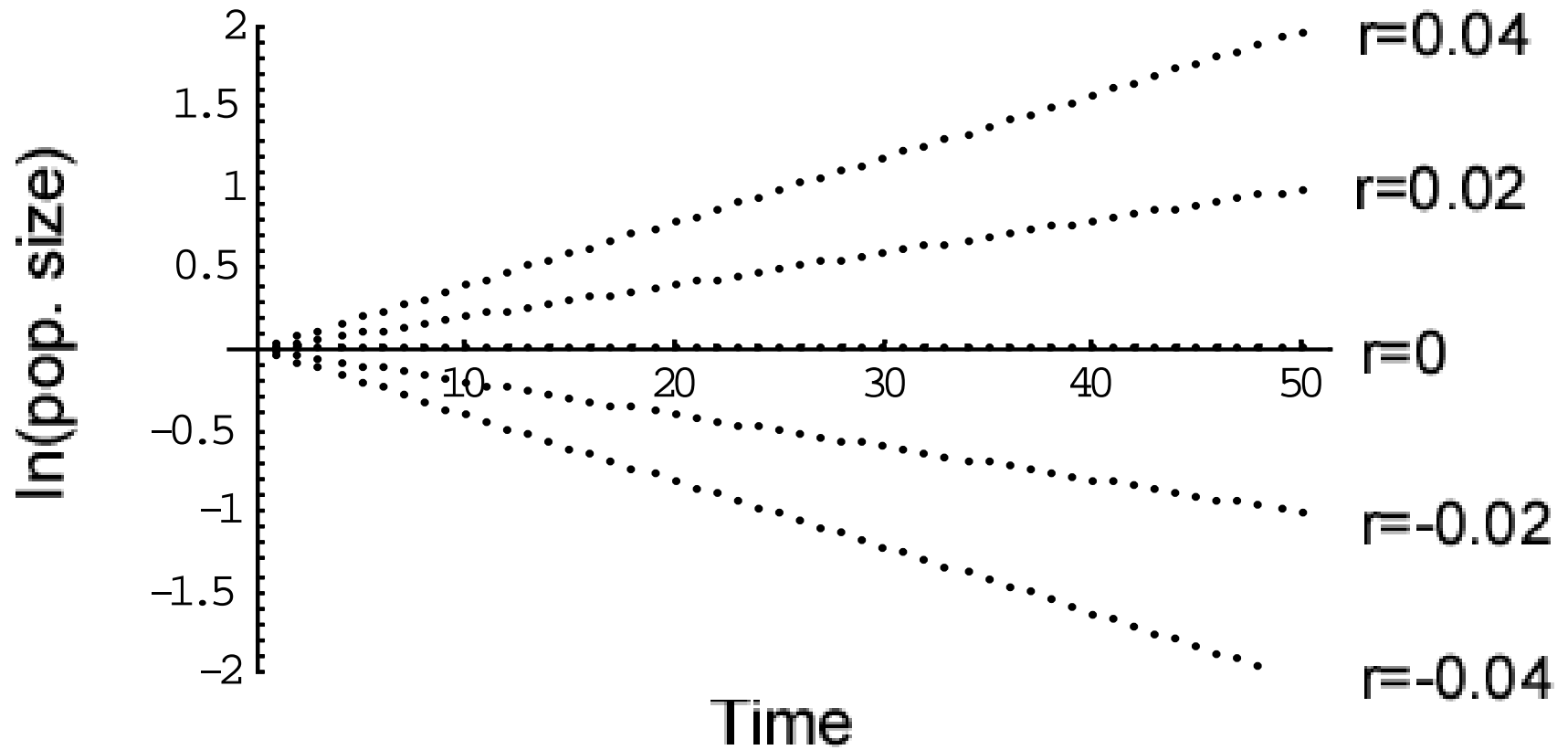
Exponential Growth



Exponential growth



Exponential growth



The Fibonacci sequence



Leonardo of Pisa
(Fibonacci)

(c. 1170 – c. 1250)

Page from the Liber Abaci, with the Fibonacci sequence

124

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 et geminant in secundo mense paria 2 concludatur. sic fit paria 4 in ipso mense.
 et quibus in ipso pariantur paria 3 et sic in quarto mense paria 8 et quibus
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The Fibonacci sequence

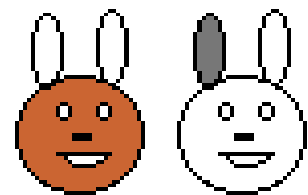


Leonardo of Pisa
(Fibonacci)
(c. 1170 – c. 1250)

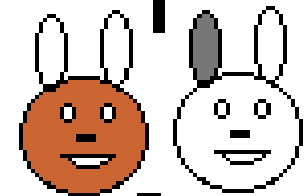
Suppose a newly-born pair of rabbits, one male, one female, are put in a field. Rabbits are able to mate at the age of one month so that at the end of its second month a female can produce another pair of rabbits. Suppose that our rabbits never die and that the female always produces one new pair (one male, one female) every month from the second month on. How many pairs will there be in one year ?

1,1,2,3,5,8,13,21,34,55,89,144

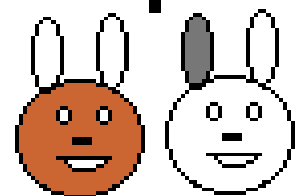
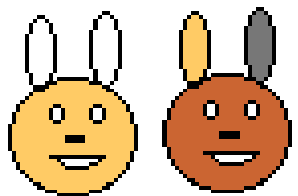
Number
of pairs



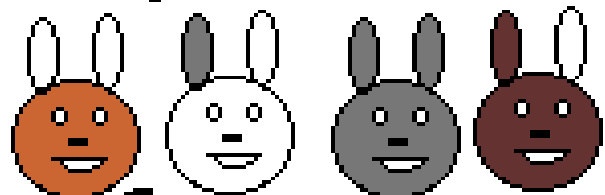
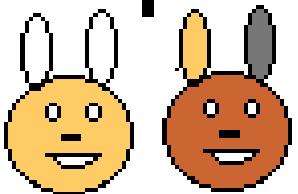
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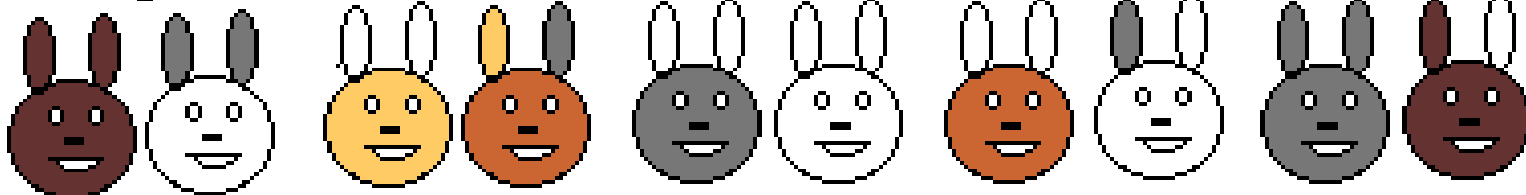
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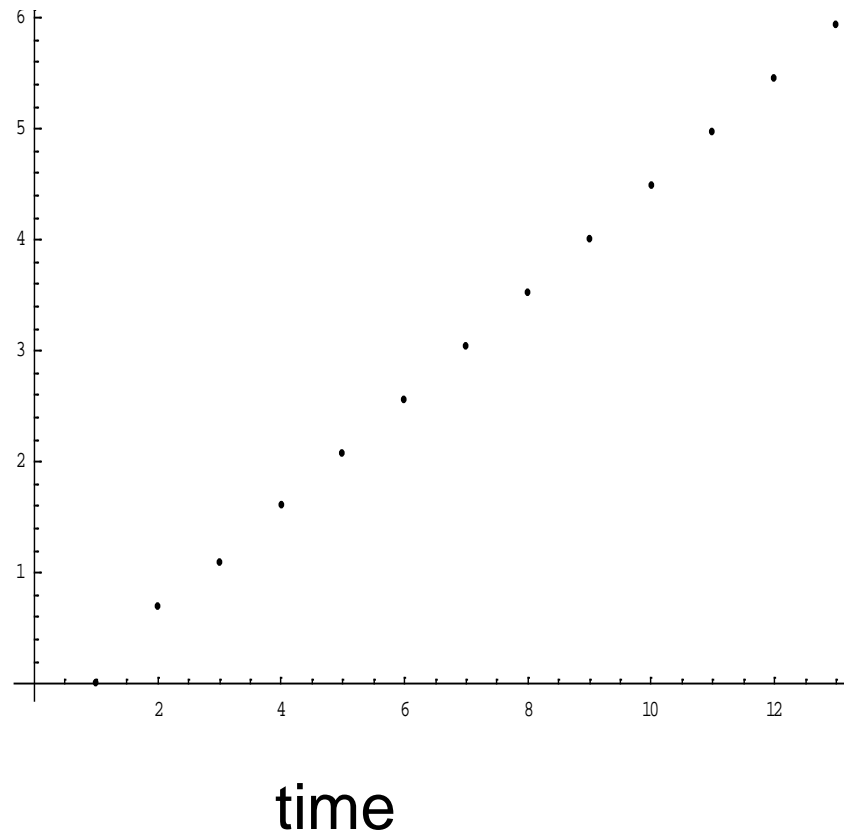
3



5

Fibonacci's rabbits

$\ln[\text{nr of rabbits}]$



Exponential growth

(continuous time)

If we assume constant per capita birth and death rates:

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

Which can be rewritten as

$$\frac{dN}{dt} = rN$$

where $r = b - d$ is the *per capita* growth rate .

This is the exponential growth model for overlapping generations

Exponential growth in continuous time

- Previous examples were in discrete time
- The differential equation

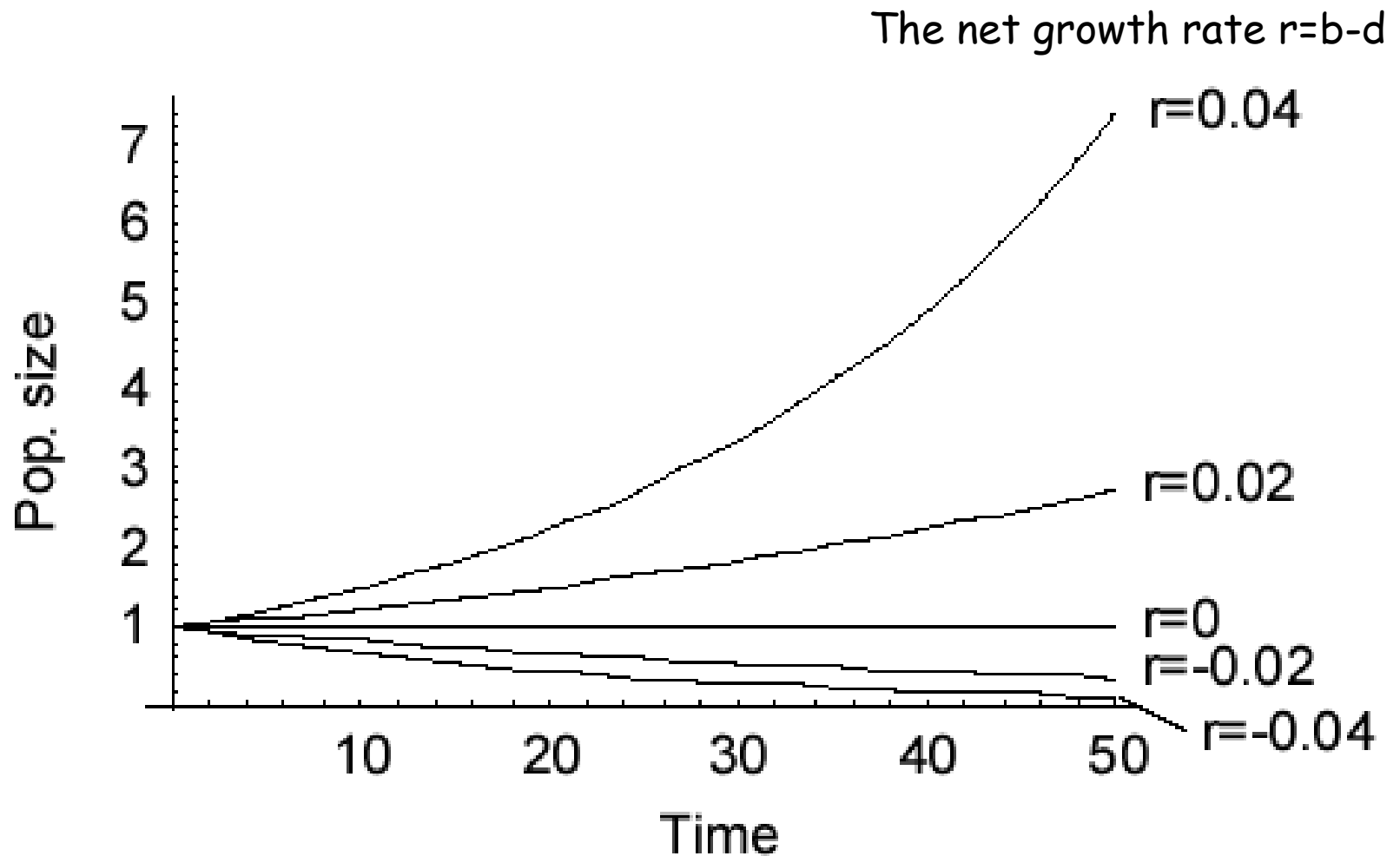
$$\frac{dN}{dt} = r N$$

Can be solved to give:

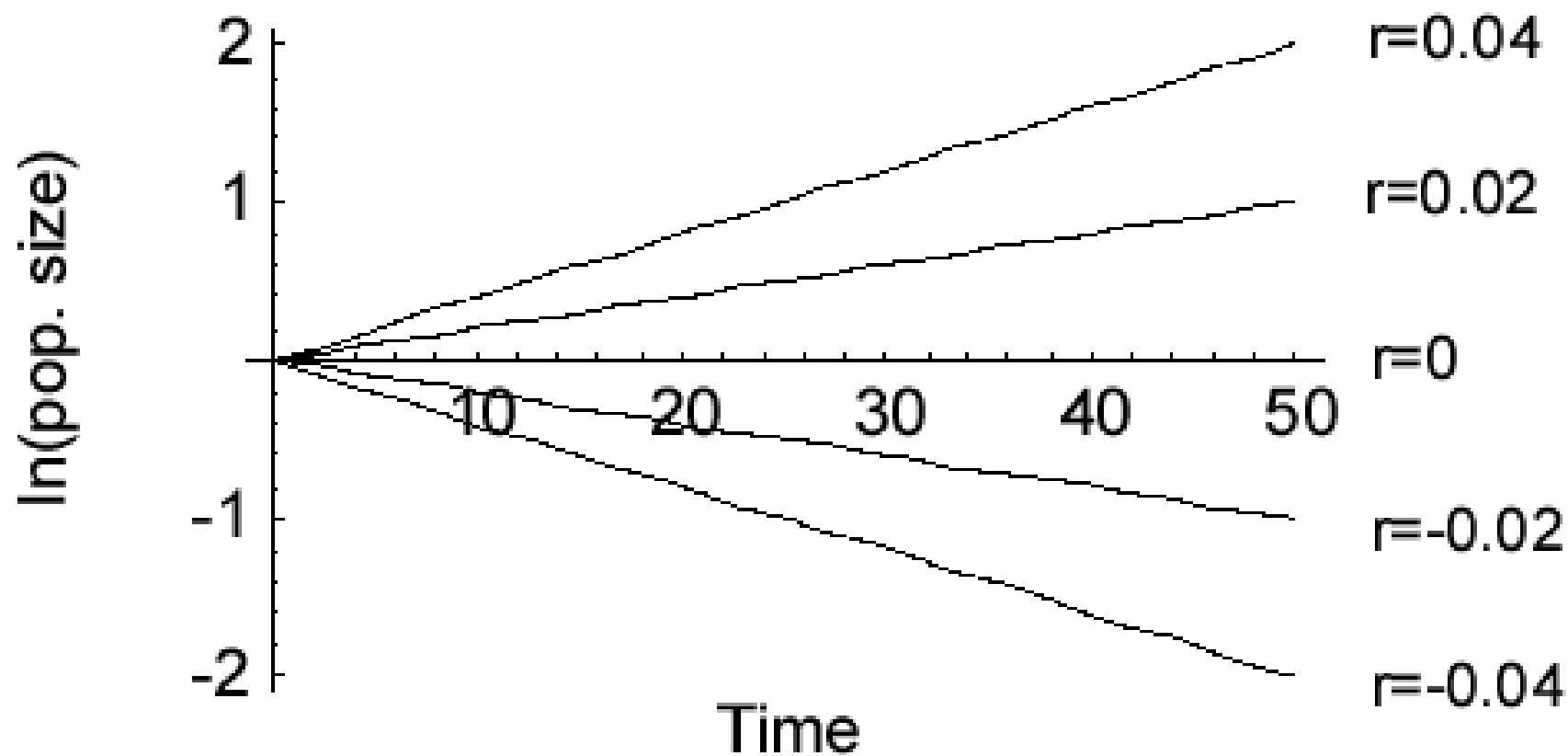
$$N(t) = N(0)e^{rt}$$

Where $N(0)$ is the population size at time $t=0$ and e is a constant (the base of the natural logarithm) with value ≈ 2.718

Exponential growth



Exponential growth

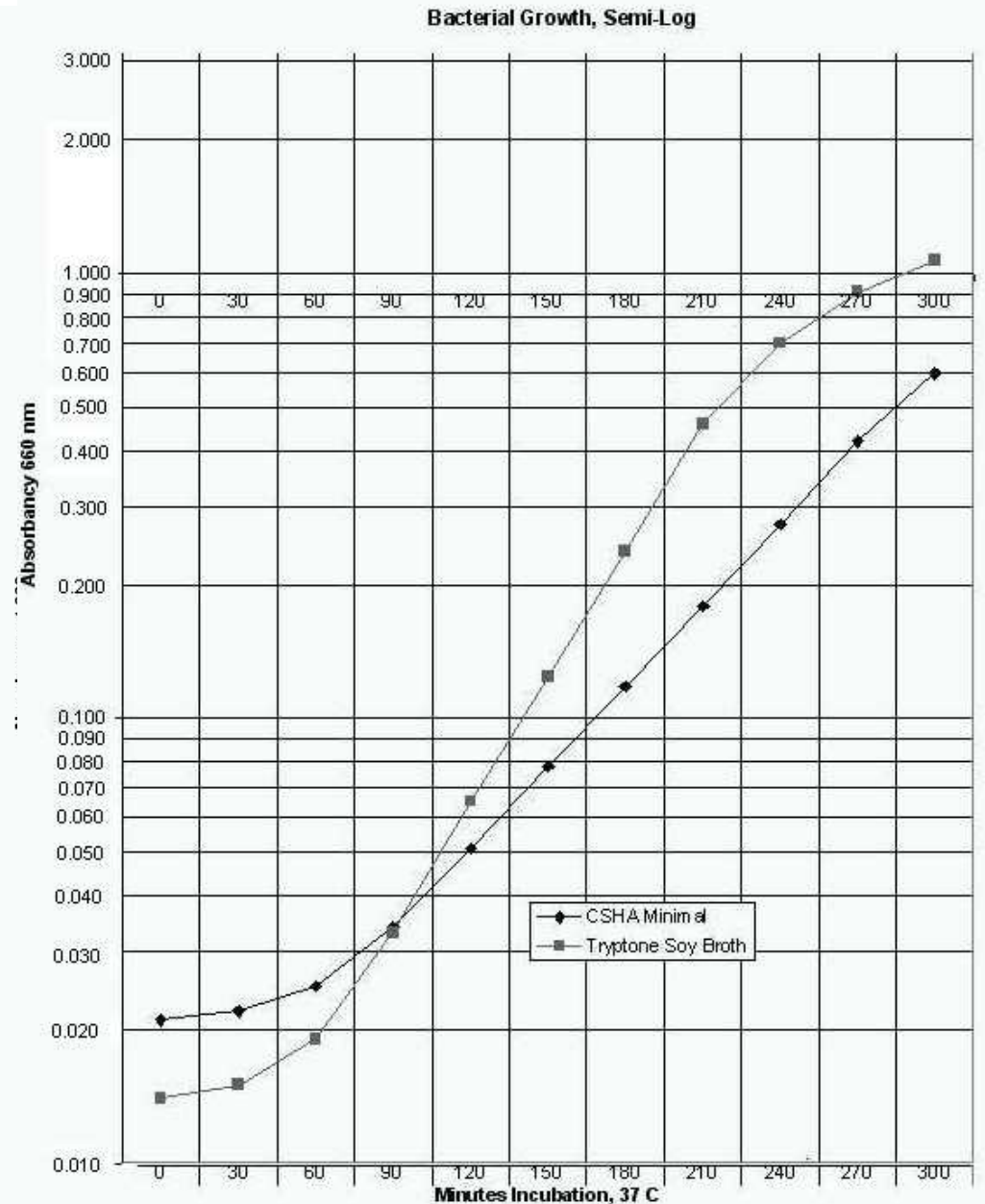


Humans vs Bacteria analysed

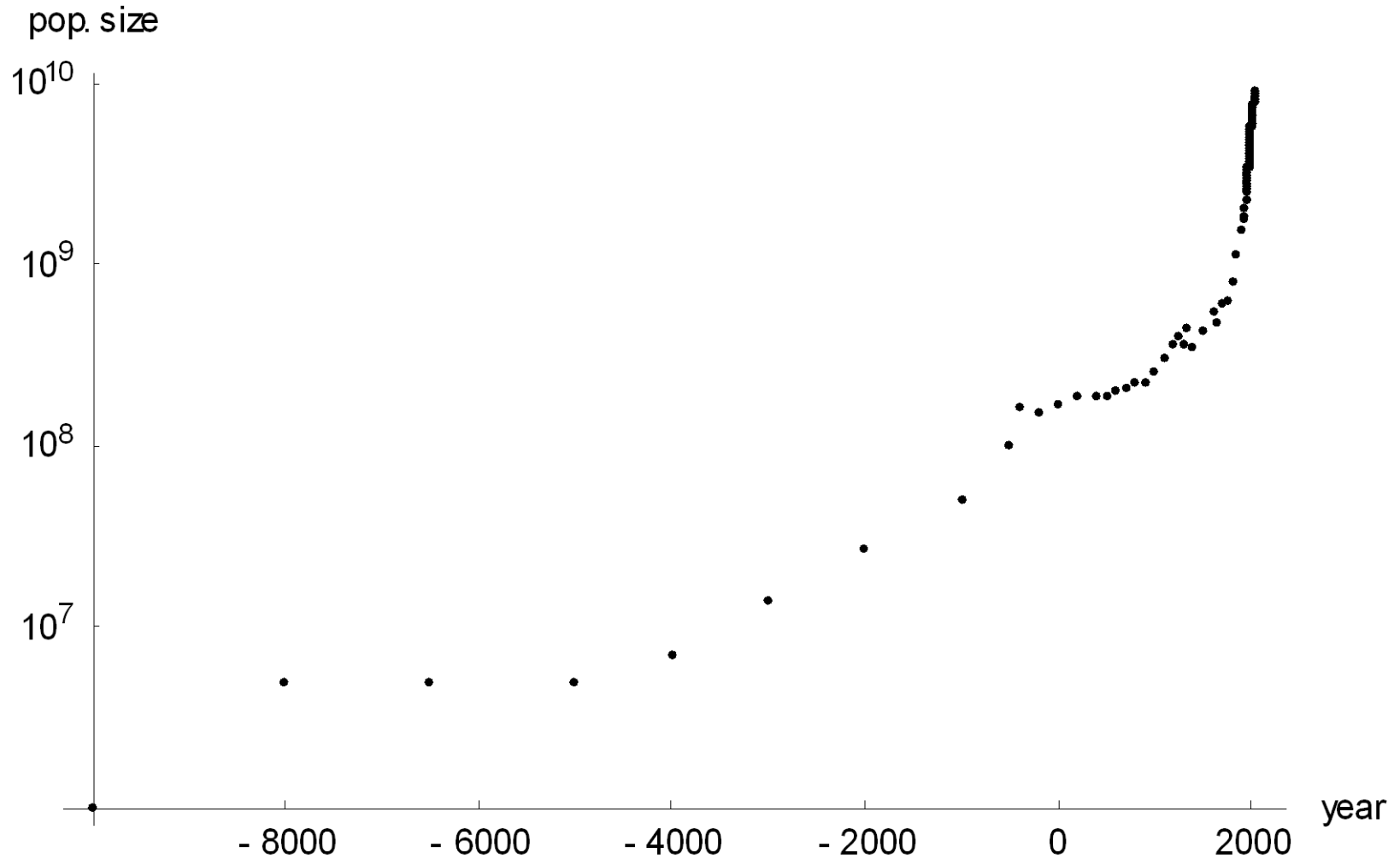
- So let's see, do humans or bacterial populations show exponential (=geometric growth)?

Example: Bacterial Growth

Escherichia coli
grown on
minimal salts vs
complex media



Human Population Growth



Growth Rate

- We can use the exponential model to calculate per capita growth rates
- If we measure the population at times 0 and T the model predicts:

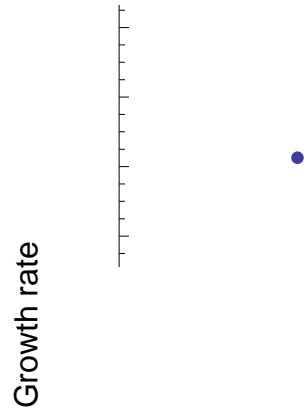
$$N(T) = N(0)e^{rT}$$

Solving for r we find

$$r = \frac{1}{T} \ln \frac{N(T)}{N(0)}$$

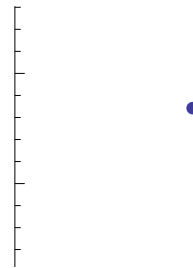
Are growth rates constant for bacteria?

Simple medium



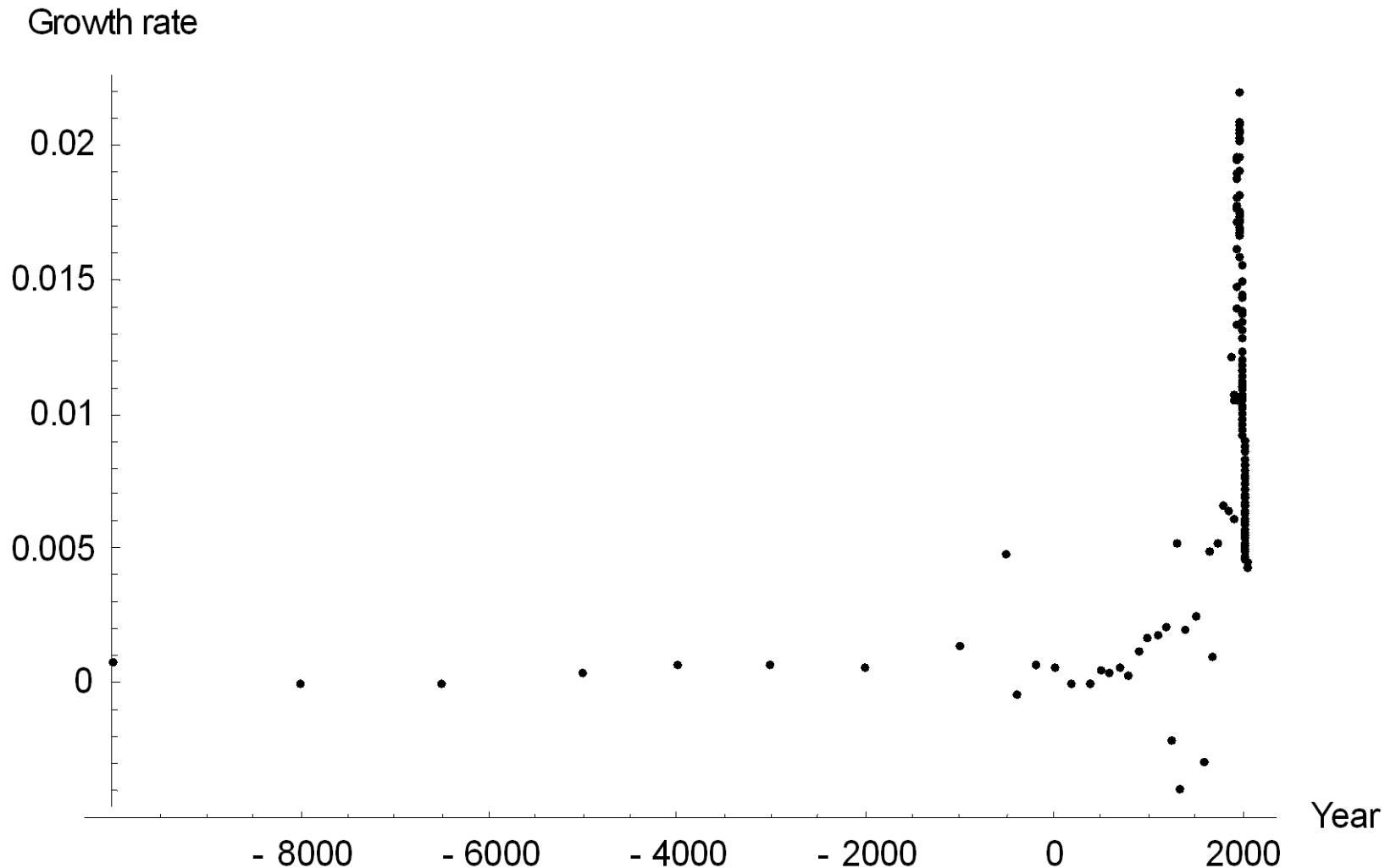
Time (mins)

Complex medium

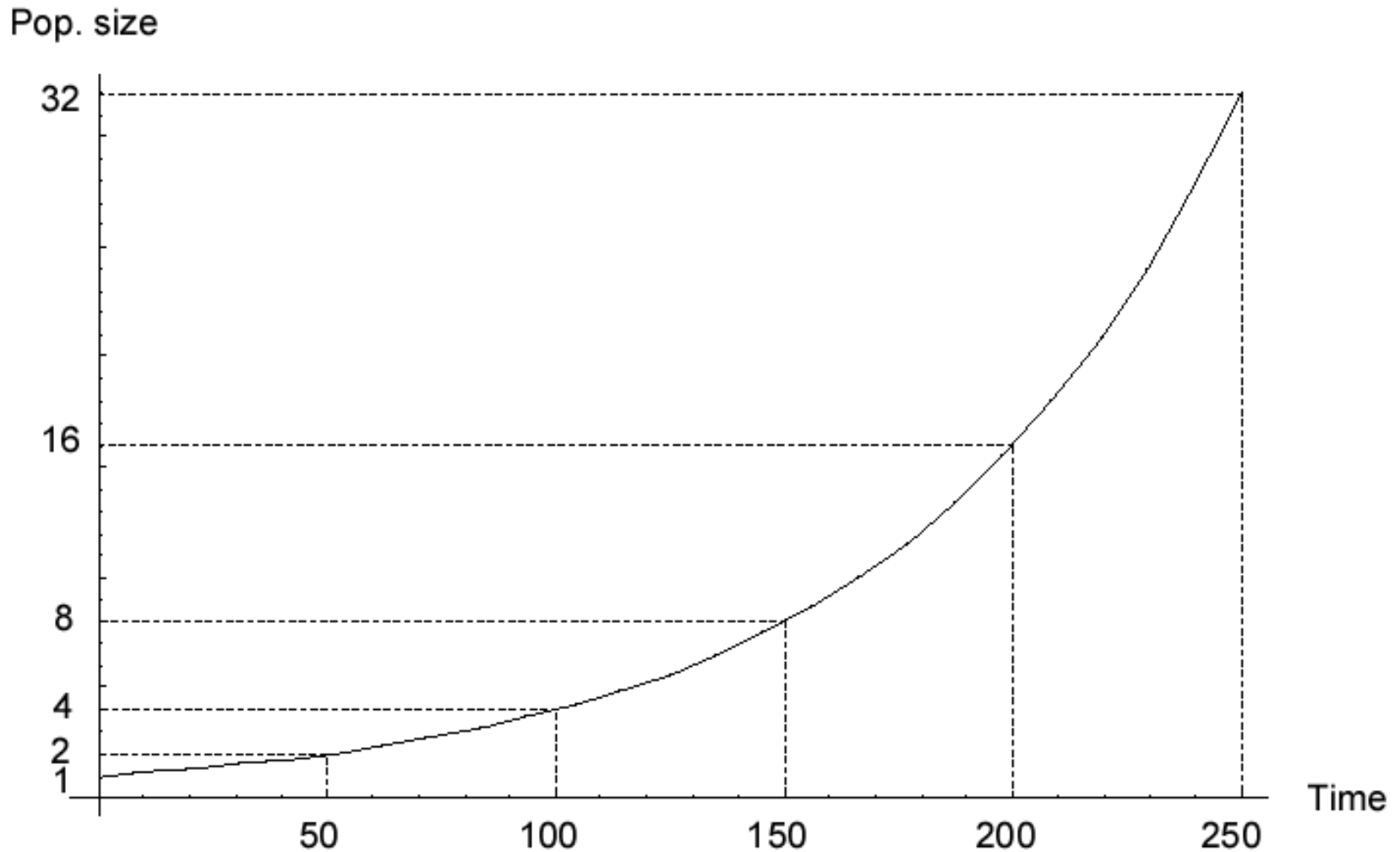


Time (mins)

Are human population growth rates constant?



Doubling Time



Doubling Time

- To calculate the doubling time we solve:
- Solving for t_{double} we find:

$$2N(0) = N(0)e^{rt_{double}}$$

$$t_{double} = \frac{1}{r} \ln 2$$

Doubling Time

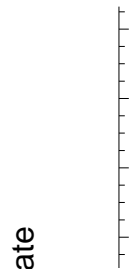
- The doubling time of the human population over the last 12000 year was approx. 900 years
- Over the last from 1950 until now it was approx. 35 years
- For the bacteria it is about 50 mins.

Density Dependence

- For the exponential growth rate we assumed the per capita growth rate is independent of the population size
- Let's see if that is correct

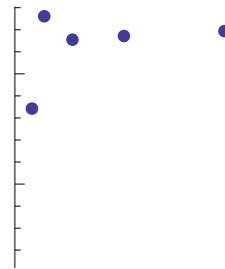
Are growth rates constant for bacteria?

Simple medium



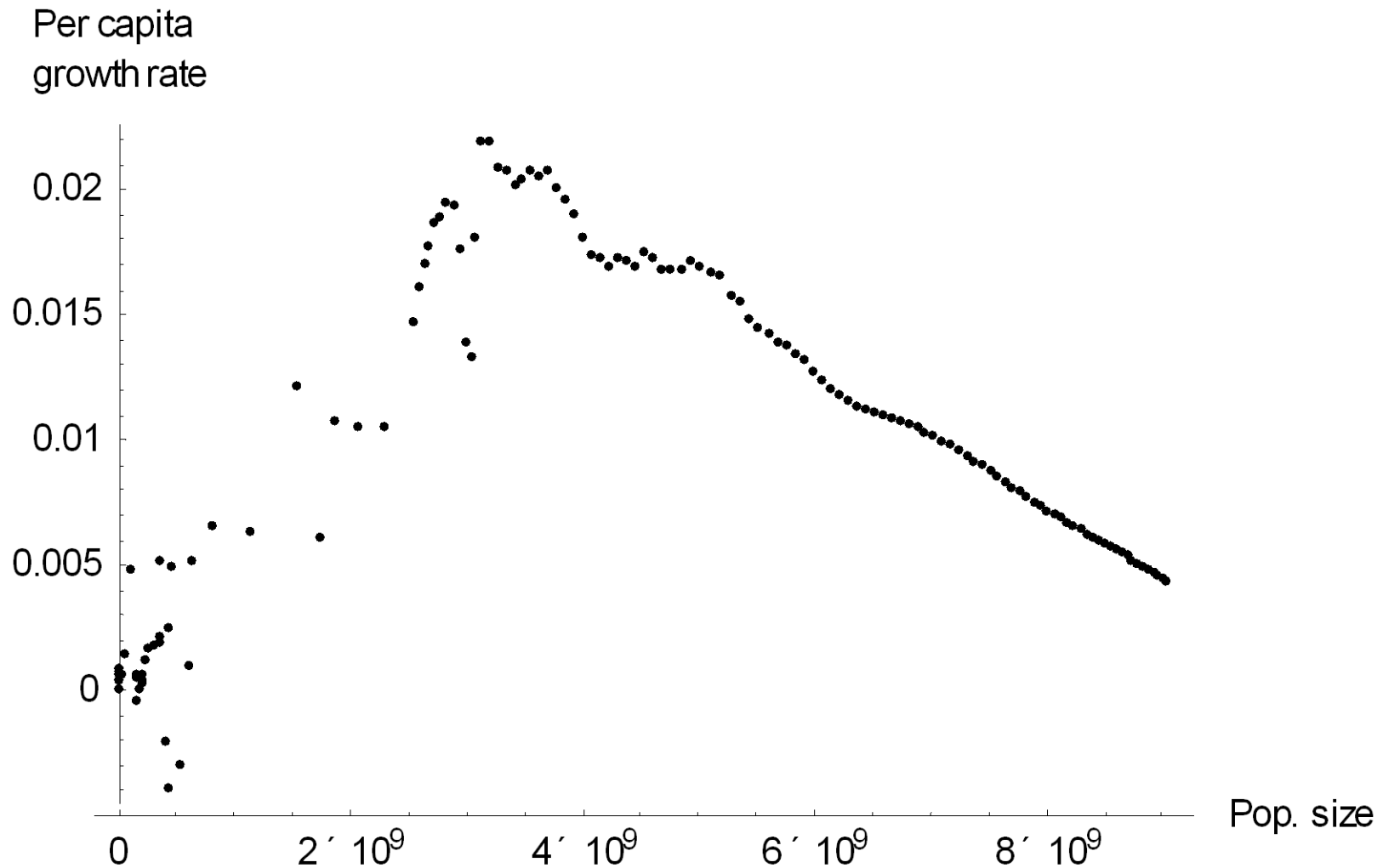
Absorbancy (density)

Complex medium



Absorbancy (density)

Density Dependence Human population



Growth curve of yeast



Raymond Pearl
(1879-1940)

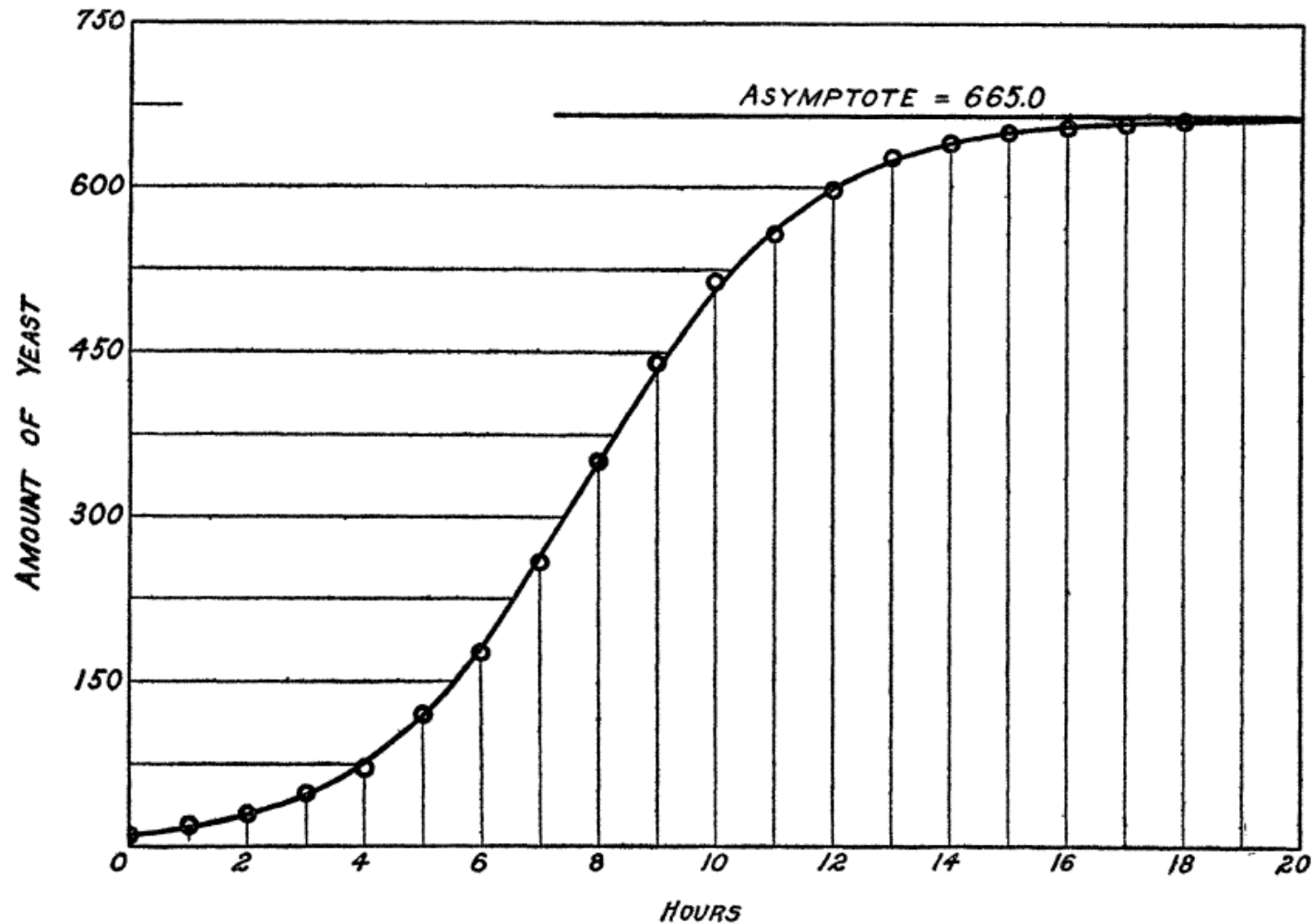
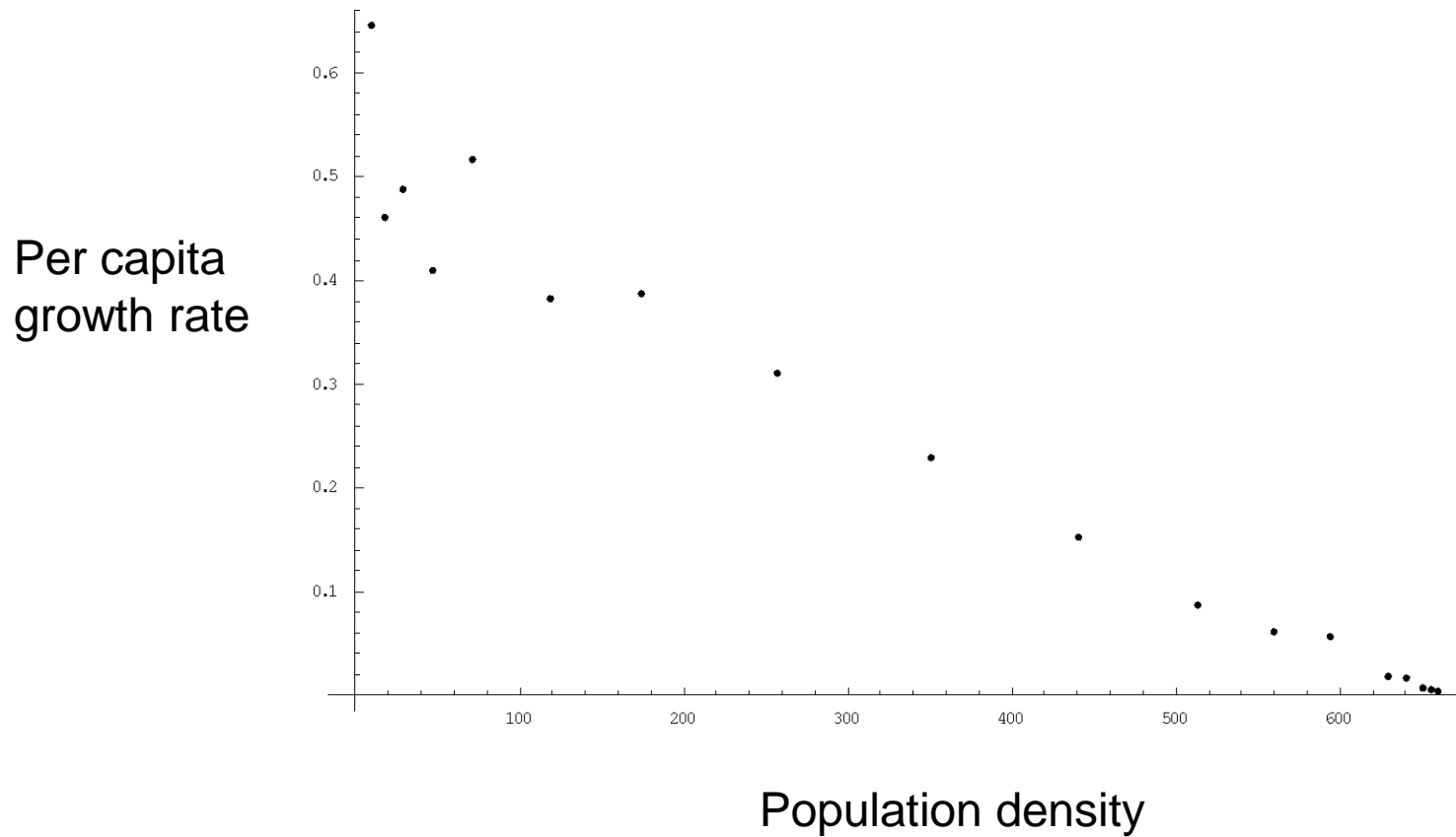


FIG. I. THE GROWTH OF A POPULATION OF YEAST CELLS

From R. Pearl (1927) Q. Rev. Biol. 2 532-548 using data from Carlson (1913) Biochem. Zeitschr. 57, 313-334

Growth curve of yeast

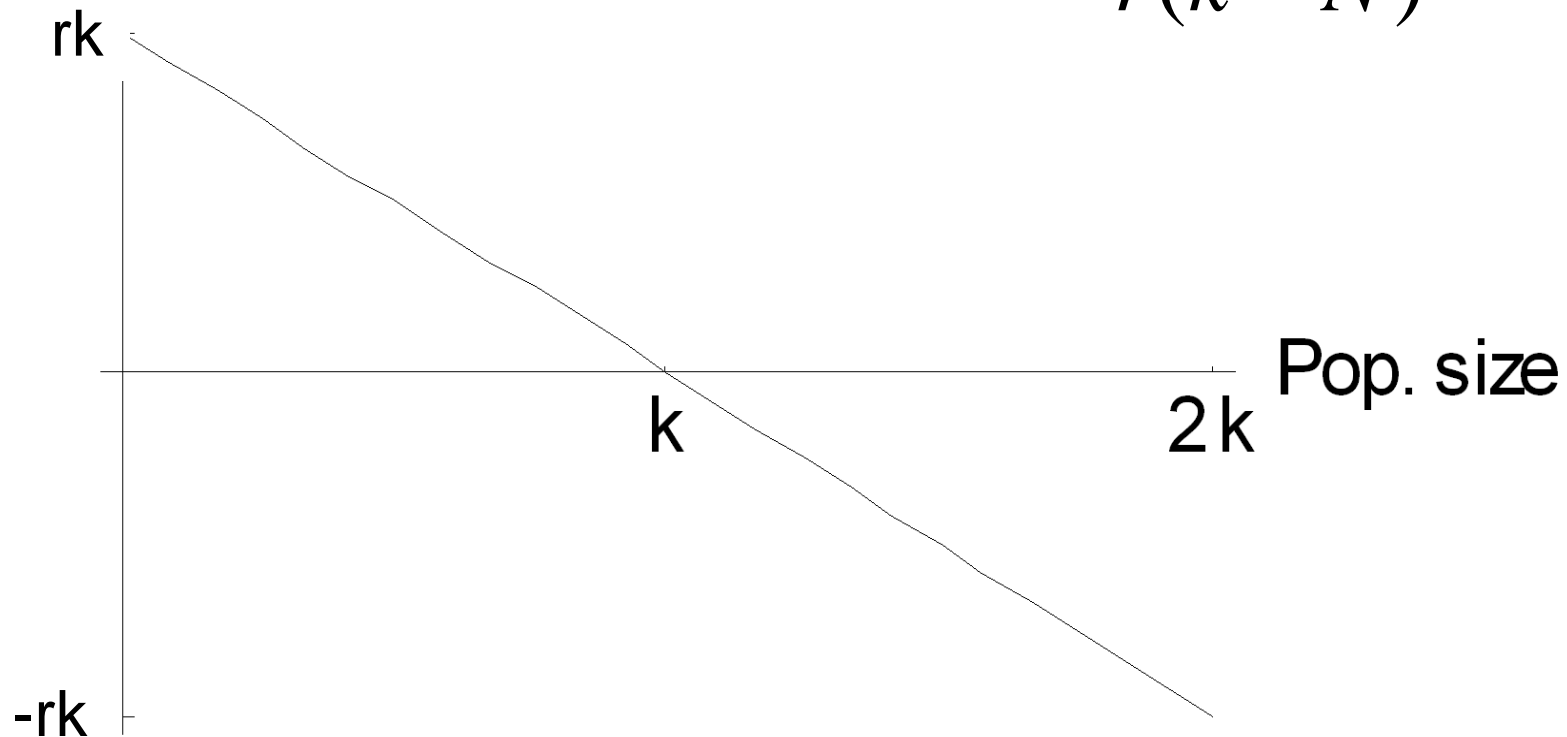


Logistic Growth

- The per capita growth rate depends on the population size
- To study the effects of a density dependent growth rate let's assume the growth rate decreases linearly with the population size

Logistic Growth

Per capita
growth rate



Logistic Growth

- We can write this as:

per capita growth rate is a function of N , in this case we use $r(k-N)$

- The population growth can be described as:

$$\frac{dN}{dt} = r(k - N)N$$

- The parameter k is the carrying capacity
- This is the logistic growth model
- Note: slightly different parametrisation from other texts

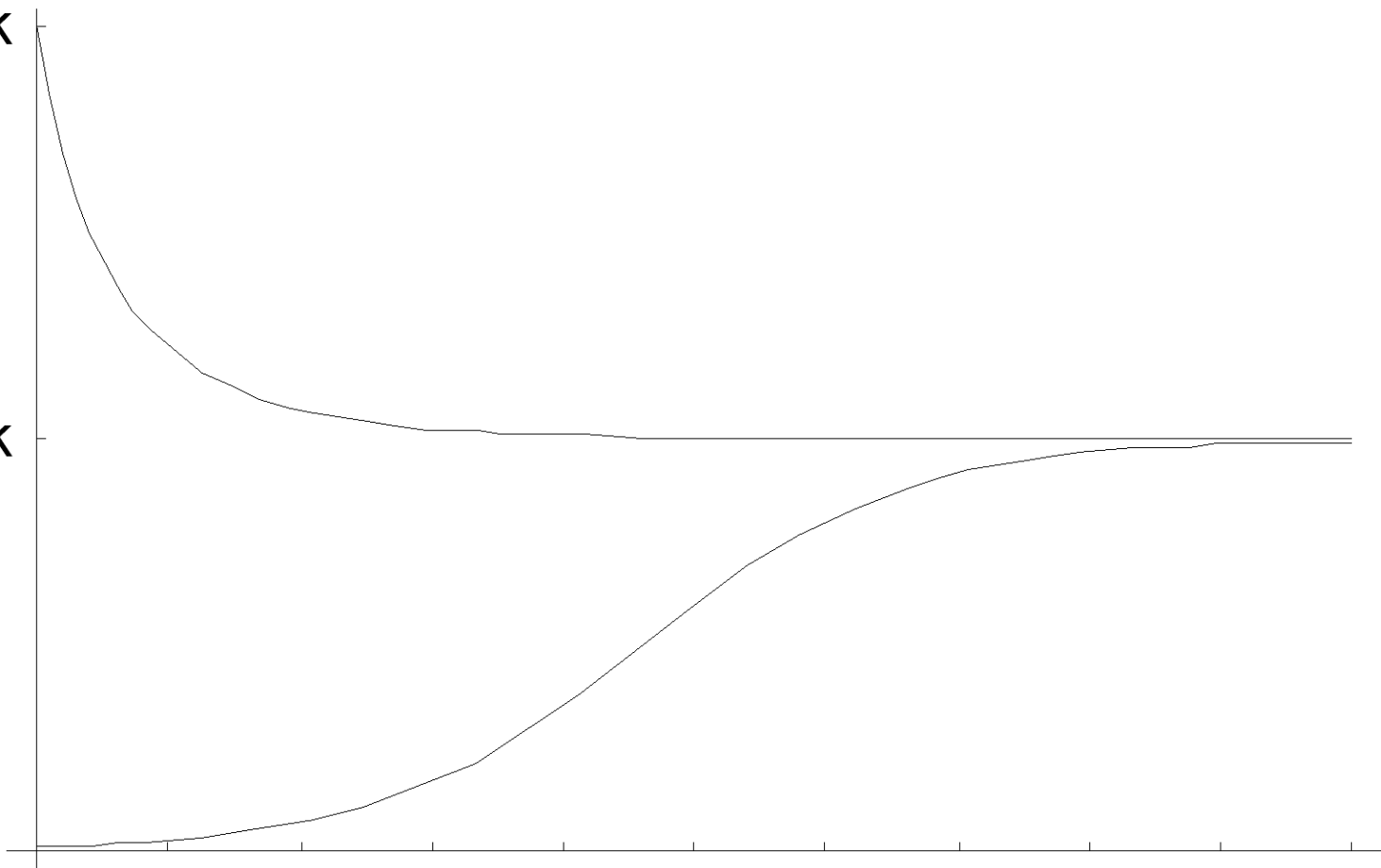
Logistic Growth

Pop. Size

$2k$

k

Time



Calculation of the equilibria

- To find the equilibria we solve

$$0 = r(k - N^*)N^*$$

- To give

$$N^* = 0 \quad \text{or} \quad N^* = k$$

Stability of the equilibria

- We study the dynamics close to the equilibrium N^*
- In general, if the dynamics are given by

$$\frac{dN}{dt} = F(N)$$

- Equilibrium:

$$0 = F(N^*)$$

Stability of the equilibria

- We can expand F in a Taylor series around N^*
$$F(N) = F(N^*) + (N - N^*)F'(N^*) + h.o.t$$
- And because we are studying the dynamics close to the equilibrium point (where $F(N^*) = 0$) this simplifies to:

$$F(N) = (N - N^*)F'(N^*) + h.o.t$$

- Using $x = N - N^*$, we can now write the linearised dynamics as:

$$\frac{dx}{dt} = xF'(N^*)$$

Stability of the equilibria

- For the logistic model this gives us as the linearised dynamics close to equilibrium:

$$\frac{dx}{dt} = r(k - 2N^*)x$$

Stability of $N^* = 0$

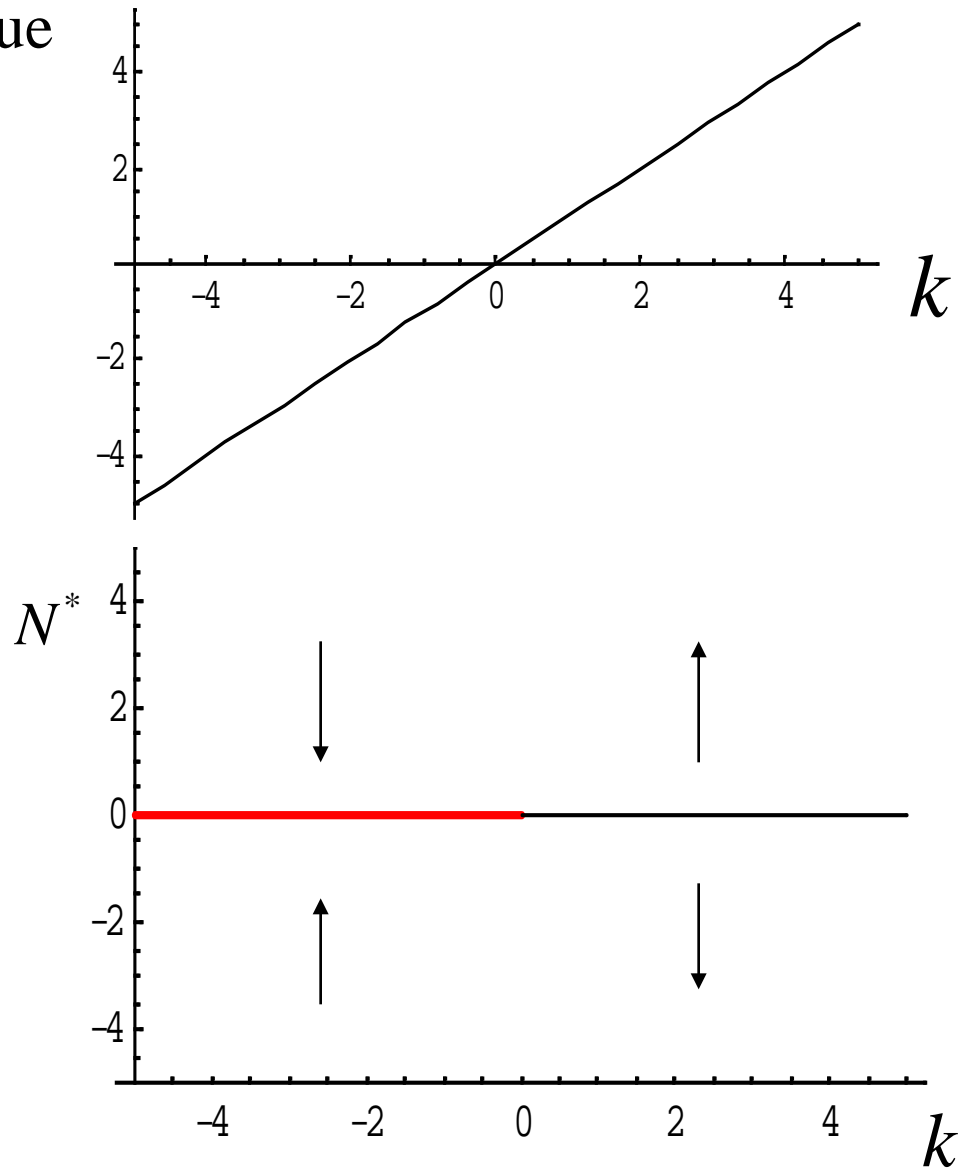
- The dynamics close to equilibrium are approximately:

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

- With solution $x(t) = x(0)e^{rkt}$
- The rate rk is called the eigenvalue
- The equilibrium is stable if $rk < 0$
and unstable if $rk > 0$

Stability of $N^* = 0$

Eigenvalue



Stability of $N^* = k$

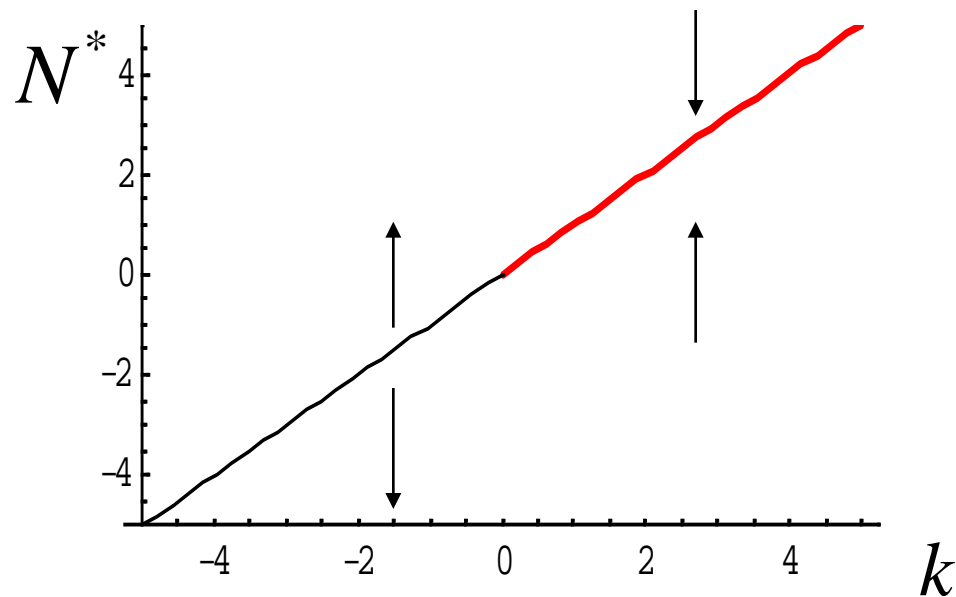
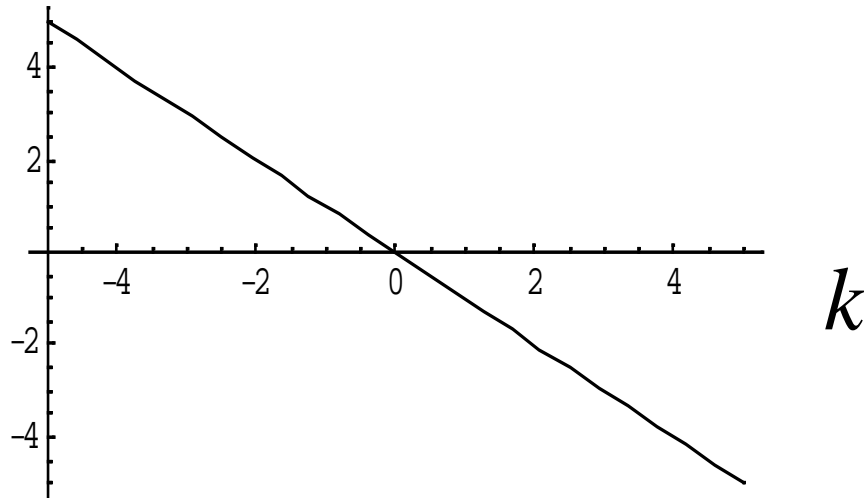
- The dynamics close to equilibrium are approximately:

$$\frac{dx}{dt} = -rkx$$

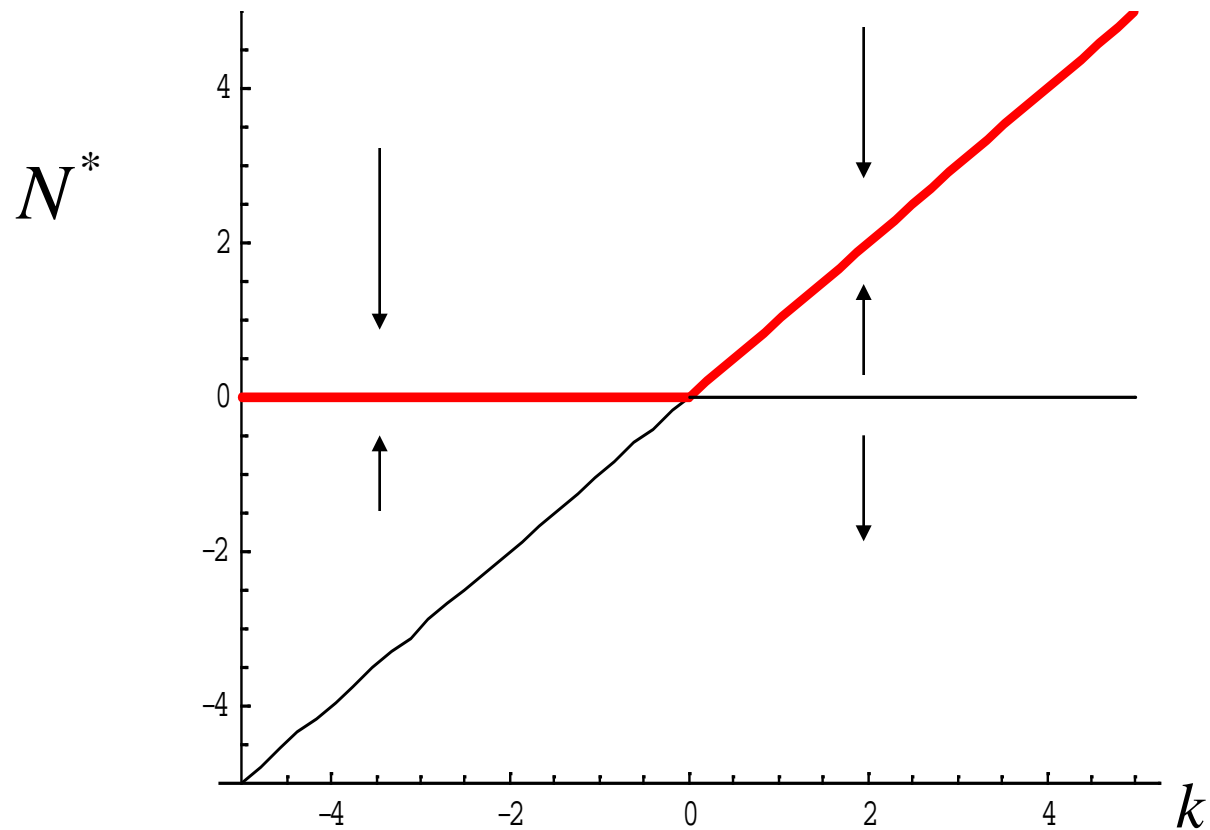
- The equilibrium is unstable if $rk < 0$
and stable if $rk > 0$

Stability of $N^* = k$

Eigenvalue



Bifurcation diagram



A transcritical bifurcation

Logistic growth

- But what does the logistic growth model really mean?
- The carrying capacity is often interpreted as a parameter of the system with a biological meaning
- Often the carrying capacity depends on life history parameters (pair approximations)

Pair approximations

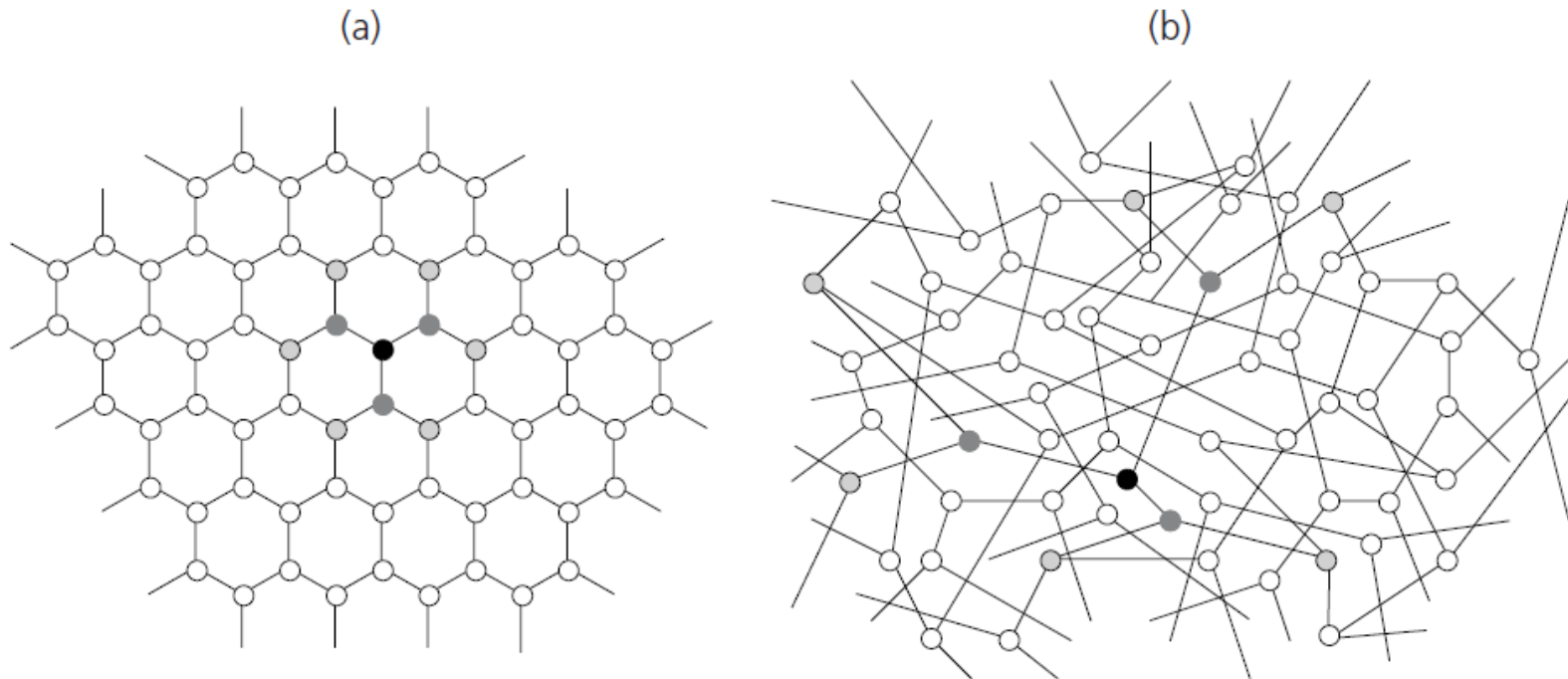


Figure 19.1 Examples of (a) a regular two-dimensional lattice and (b) a random network, both with a neighborhood size of three. In both graphs, a focal site (black) and its neighbors up to two links away (dark and light gray) are indicated.

Pair approximations

- More refined spatial model: count the pairs of sites occupied on a lattice.
- If the birth and death rates depend on global densities the logistic equation is recovered
- If the rates depend on the local densities, you need a much more complicated model (see e.g. van Baalen 2000) as you need to take local correlations into account.
- The carrying capacity now becomes a compound parameter which depends on the birth and death rates.

Another example: the metapopulation

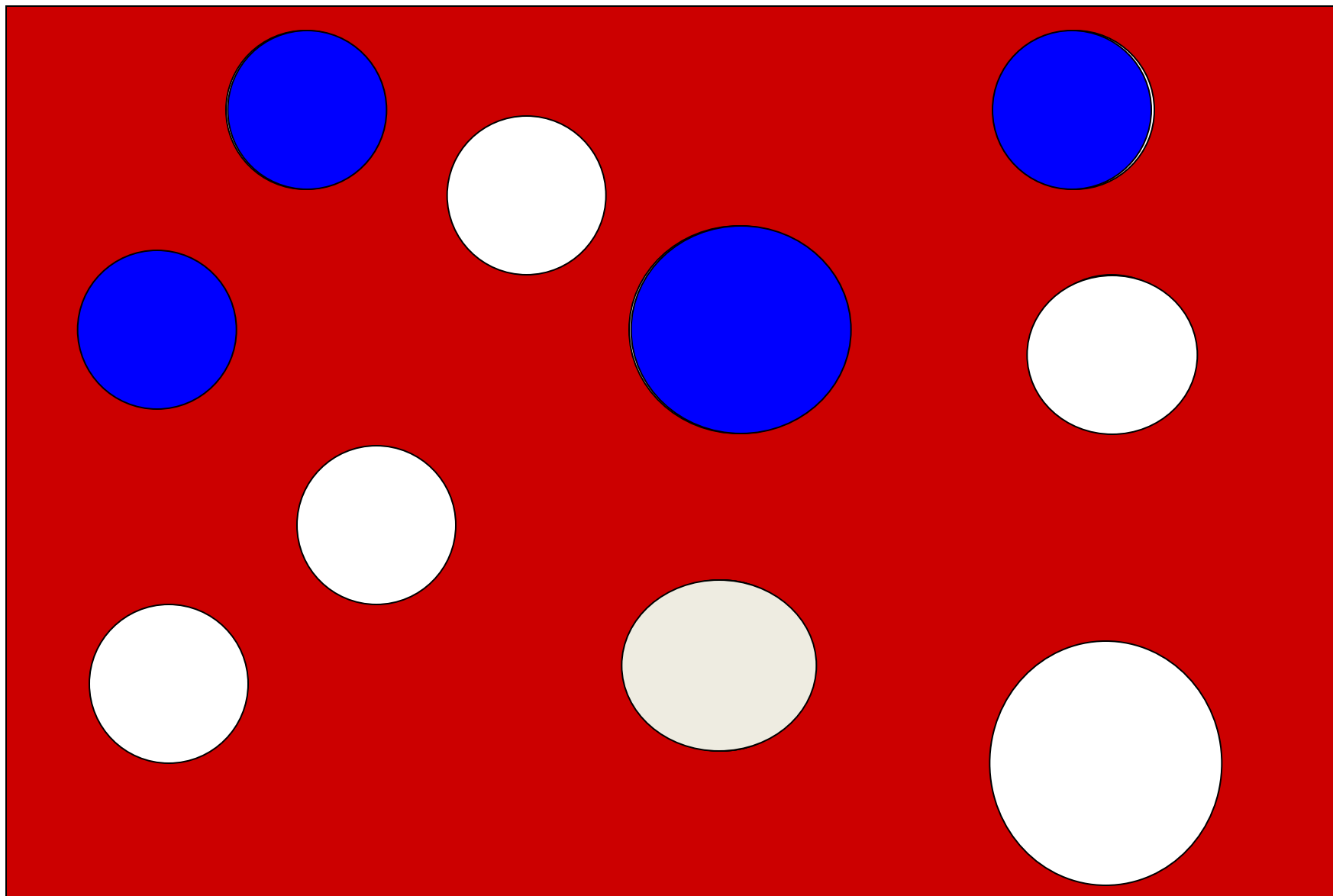
- The idea of a population of populations goes back to Andrewartha and Birch (1954) and Nicholson and Bailey (1934)
- Richard Levins coined the term in 1969
- The idea is related to McArthur and Wilson's island biogeography

The Metapopulation Concept

- Metapopulation:
A population of populations
- Small populations are prone to become extinct
- This can be due to external factors
- Or through chance fluctuations (demographic stochasticity)
- Regional persistence despite local extinction

Metapopulation Theory

- Major assumption of metapopulation theory:
- Local population dynamics are fast compared to the lifetime of a local population
- The local densities reach equilibrium quickly after colonisation
- All patches are the same



Metapopulation Theory

- The number of occupied patches, rather than the number of individuals is the variable of interest
- it is sufficient to know how many patches are occupied

p = fraction of patches occupied

Metapopulation Theory

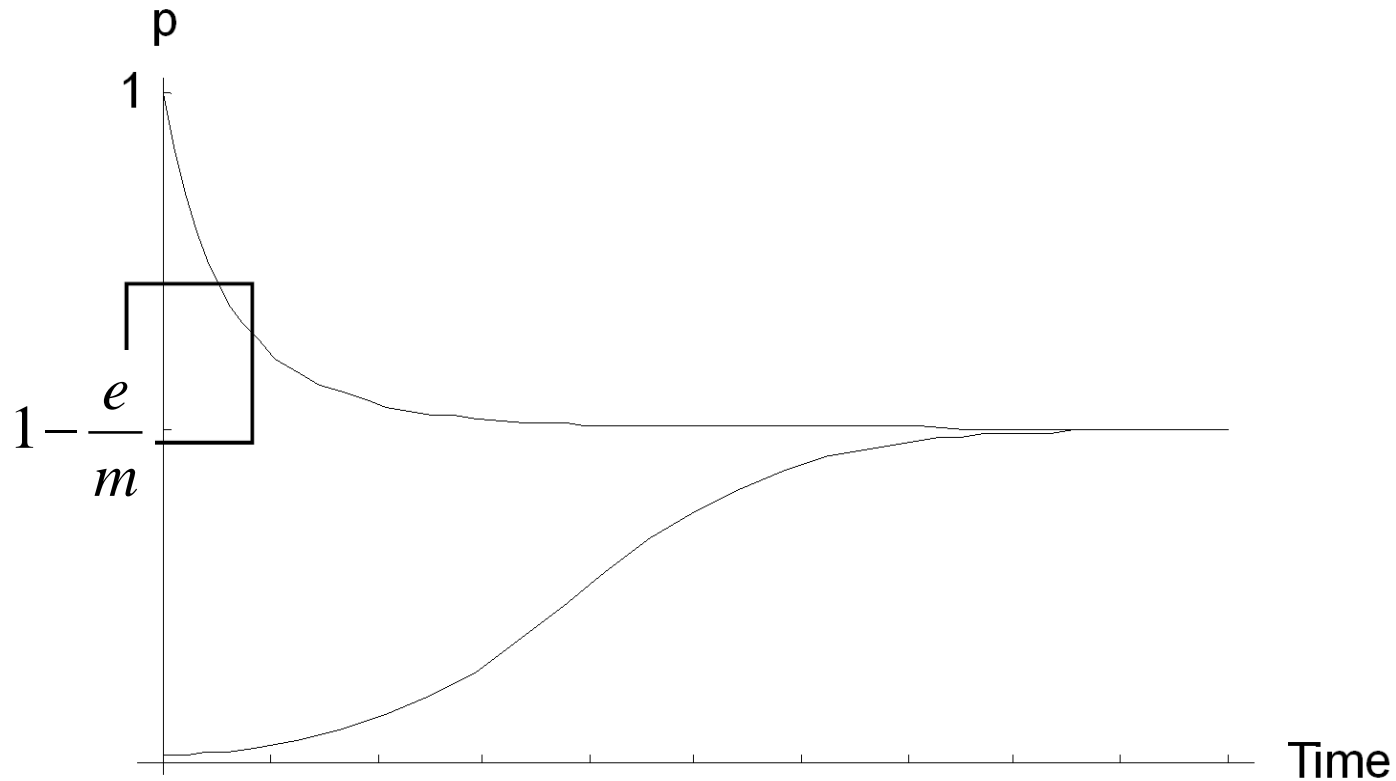
Every patch has a similar rate of sending out dispersers (mp), which need to find empty patches ($1-p$). Colonisation rate $mp(1-p)$

Extinction rate, e , nr of extinctions: ep

$$\frac{dp}{dt} = mp(1-p) - ep$$

Levins' metapopulation model

Metapopulation Theory



Solution to the Levins' model

Metapopulation Theory

- This is of course just the same as the logistic growth model

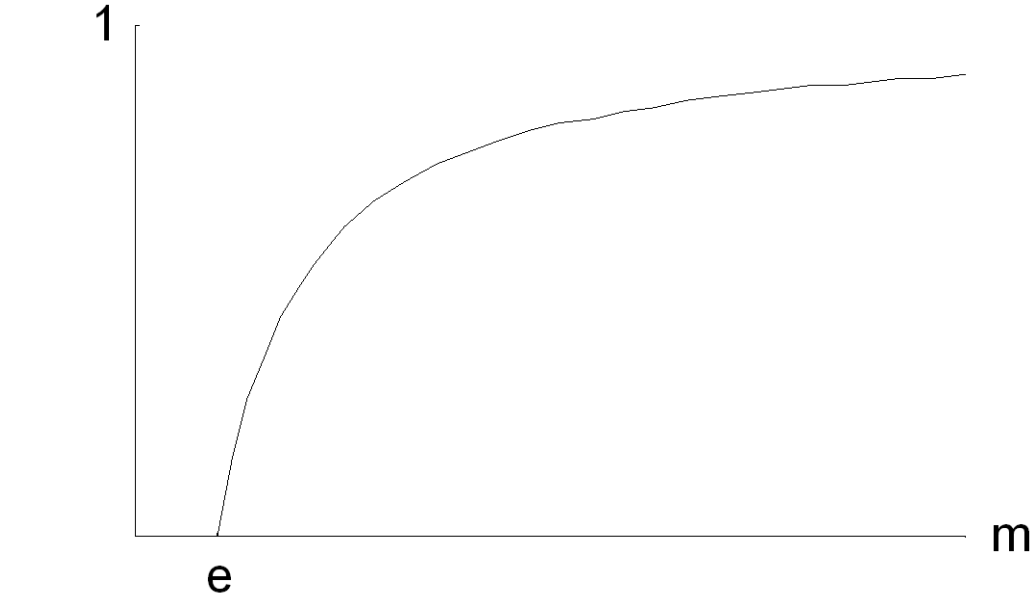
$$\frac{dp}{dt} = mp(1 - p) - ep$$

$$\frac{dp}{dt} = mp\left(1 - \frac{e}{m} - p\right)$$

$$\frac{dp}{dt} = mp(k - p) \quad \text{with} \quad k = 1 - \frac{e}{m}$$

Metapopulation Theory

- At equilibrium $p=1-e/m$



Metapopulation Theory

- Two observations:
- For the metapopulation to persist colonisation needs to exceed extinction
- There will always be unoccupied patches
- The carrying capacity depends on the colonisation and extinction rates

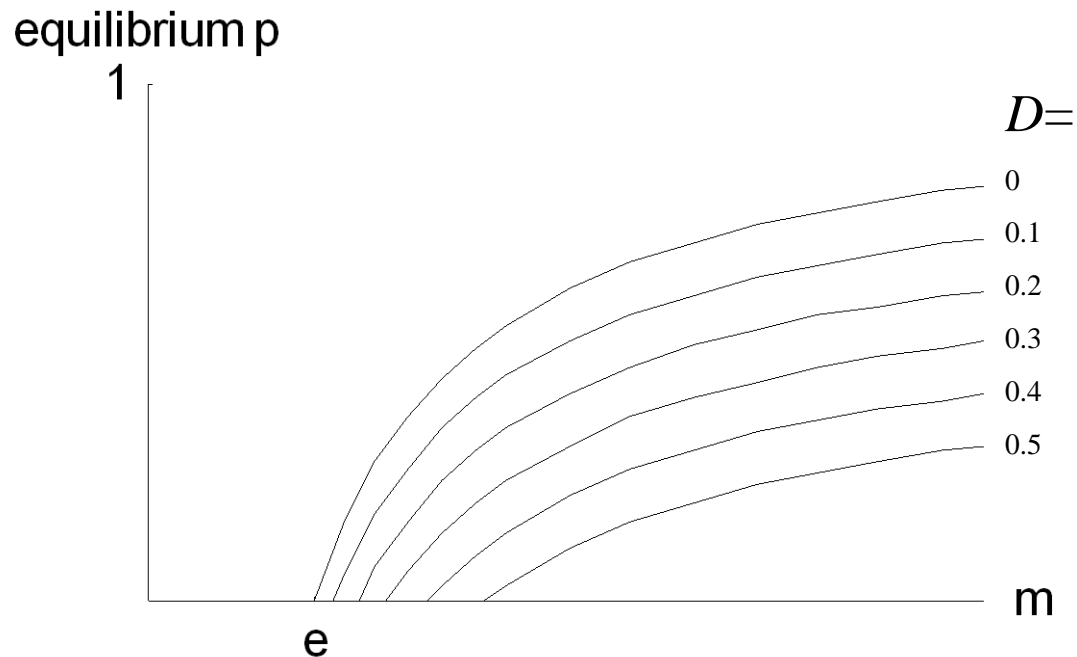
Habitat destruction

- Habitat destruction can easily be incorporated in metapopulation theory by assuming a fraction D cannot be colonised

$$\frac{dp}{dt} = mp(1 - D - p) - ep$$

Habitat destruction

- Equilibrium fraction ($1-D-e/m$) decreases with habitat destruction:



Metapopulations

- Note that in this respect the metapopulation model behaves fundamentally different from other models
- Normally, reducing the area, say halving it, halves the population size
- In a metapopulation taking 60% of the area will have the effect of subtracting 60% from the equilibrium population size, and this could actually cause extinction

The Spotted Owl Debate

- the metapopulation was used in the debate around the protection of the northern spotted owl (*Strix occidentalis caurina*) in the USA



The Spotted

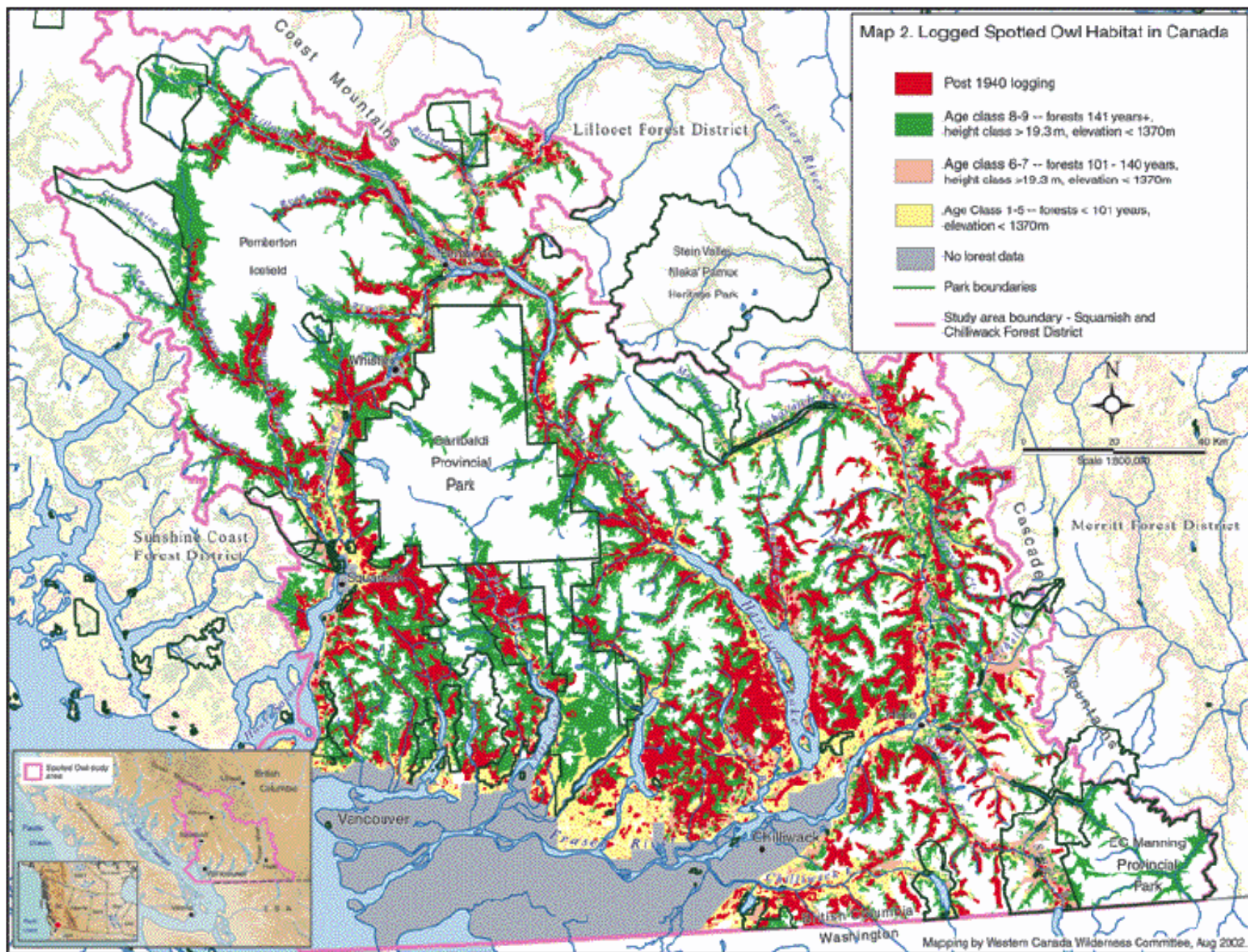
- The northern spotted brown owl lives in old woodland in the north western USA (California, Oregon) and Canada
- Increased logging of old forest is threatening the northern spotted owl



The Spotted Owl Debate

- Logging is important for the local economy
- By 1950 only 10-15% of the original old forest was left and the remaining forests were publicly owned
- Logging continued leading to habitat loss and habitat fragmentation

Map 2. Logged Spotted Owl Habitat in Canada



The Spotted Owl Debate

- The northern spotted owl was listed as threatened in Oregon under the “Endangered Species Act”
- This legally obliged the state to provide protection for this species, and its habitat
- It caused a conflict environmental groups and timber industry

The Spotted Owl Debate

- The spotted owl is an indicator species: a decline indicates that other species are possibly declining too
- To breed and reproduce it needs large territories (400-3200 ha) of old forest (>150 yrs)

The Spotted Owl Debate

- Young owls disperse and need to find new territories
- Not all territories are occupied at all times
- Territories fall empty and are reoccupied

The Spotted Owl Debate

- This was an important element of the debate:
- In order to protect the Spotted Owl, the Endangered Species Act states that the habitat has to be protected
- Metapopulation models were used in court to make this case
- Cutting down unoccupied territories can endanger the species, even if it doesn't endanger individuals

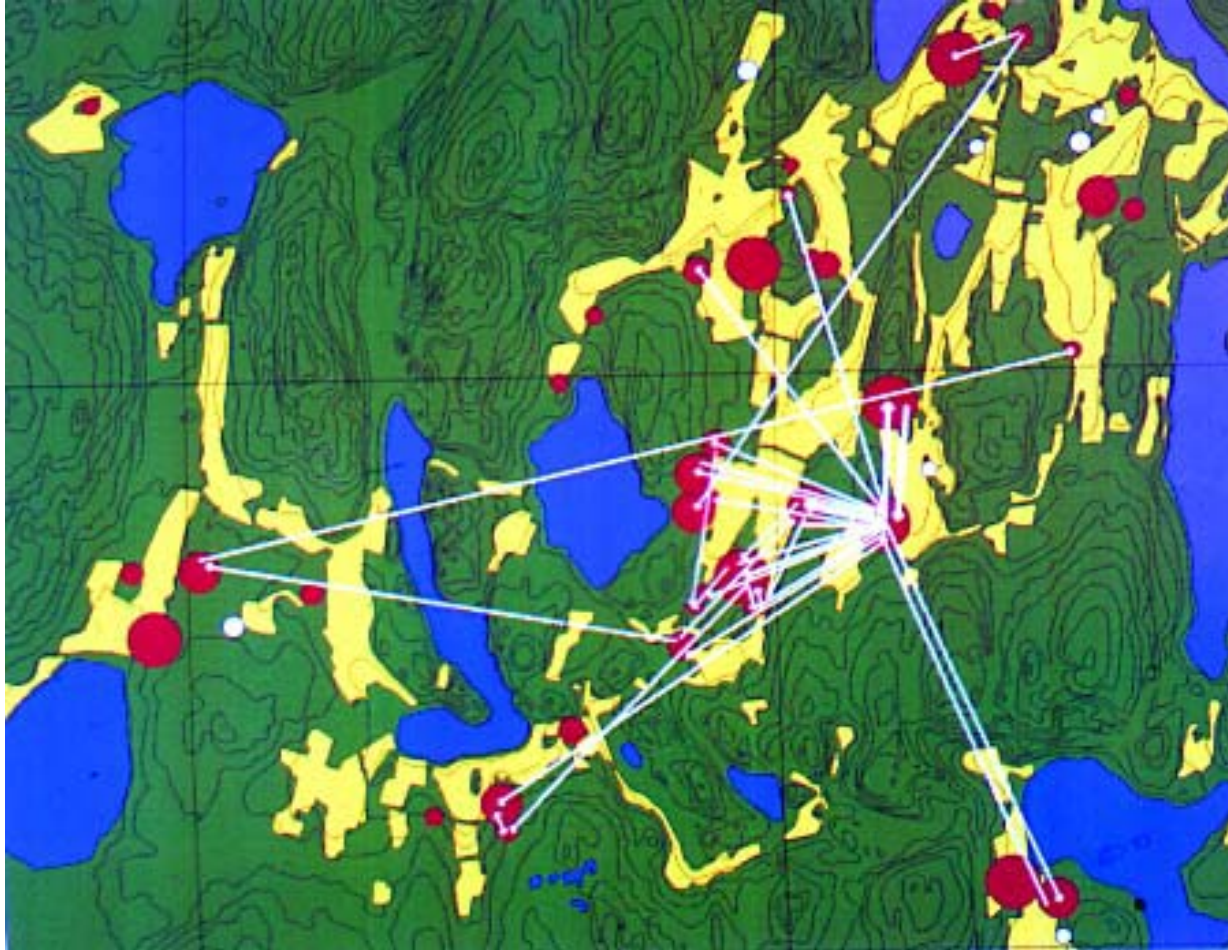
Examples of Metapopulations

Examples of metapopulations:

- A number of butterfly populations have a metapopulation structure (*Plebejus argus*, Glanville fritillary, bay checkerspot)
- *Daphnia* in rock pools
- Voles on islands

(see Hanski's books)

Examples of Metapopulations



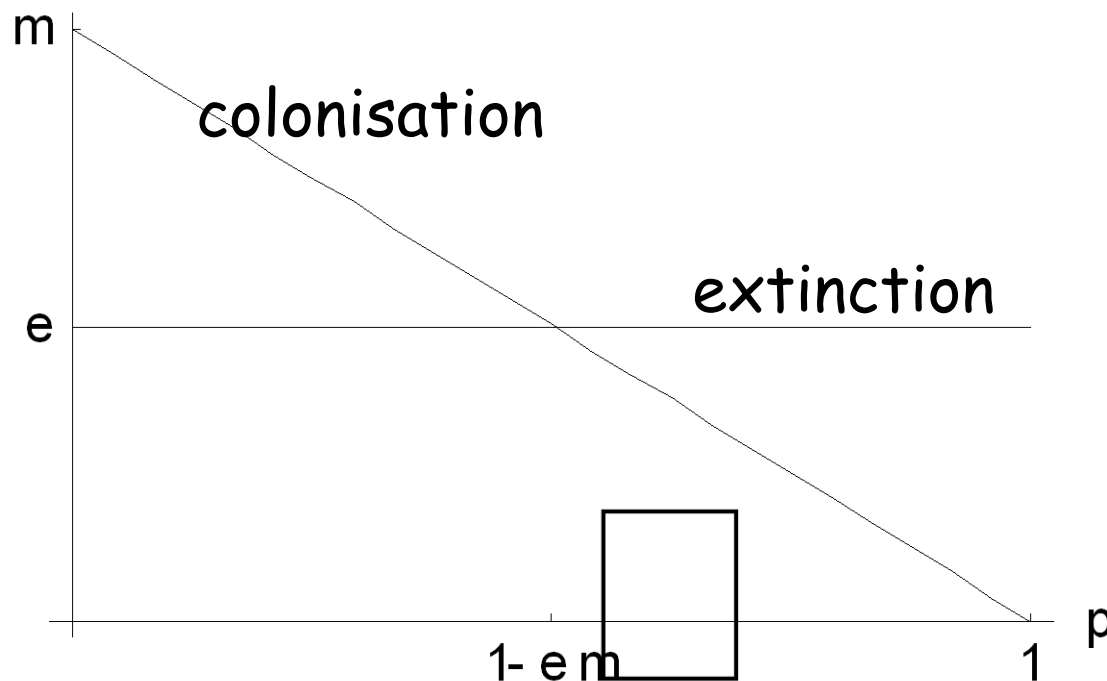
Glanville fritillary (*Melitaea cinxia*)

Metapopulations and carrying capacity

- What the metapopulation demonstrates is that the carrying capacity is not a simple parameter of the system
- It depends on other factors, such as birth and death rates, or the ability to colonise space.
- This has been generalised in other spatial models

Rescue effect

- The Levins' metapopulation assumes extinction rates are constant



Rescue effect

- Population numbers in a patch could depend on the number of patches occupied in the vicinity (immigration)
- The extinction rate will decrease if more patches are occupied.
- Hanski proposed $e=e_0 \exp(-ap)$

Rescue effect

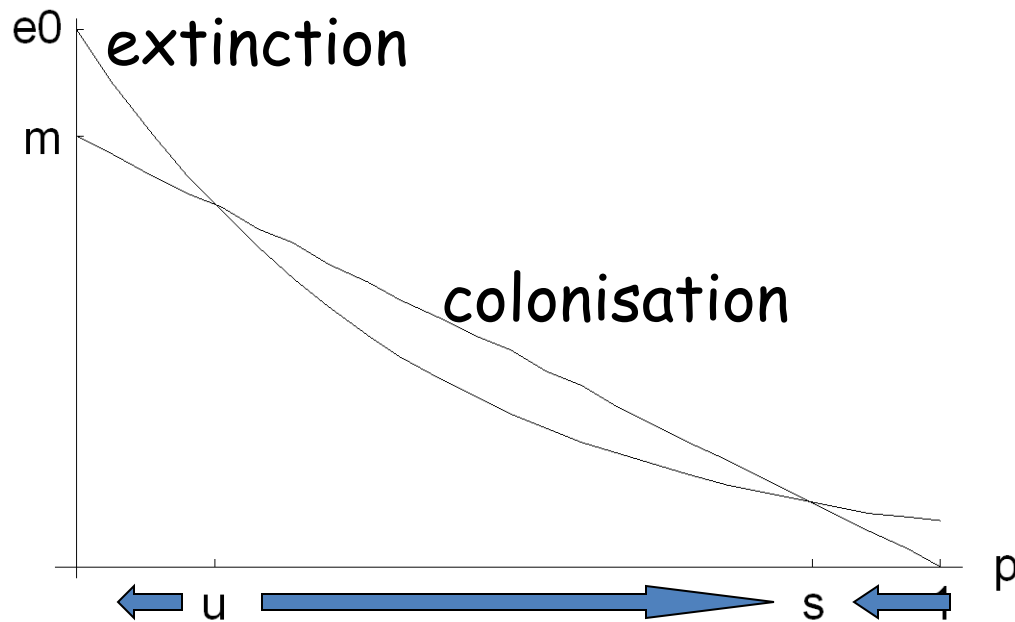
- The rescue effect can create alternative stable states, with the effect that the metapopulation becomes extinct if reduced below a threshold fraction

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Rescue effect

- If $e = e_0 \exp(-ap)$



Rescue effect

- The rescue effect can create alternative stable states, with the effect that the metapopulation becomes extinct if reduced below a threshold fraction

Learning outcomes

- Understand the exponential and logistic growth model
- Appreciate how to understand the qualitative outcomes of the model and how they depend on the parameters.
- Understand the metapopulation concept

Two modelling PhD studentships

Deadline 31/1/15.

How to dry seeds: developing a mathematical model for the seed drying process and predicting the quality of dried seeds?

Vincent Jansen, Prof. Michael Stumpf (IC) +

Team of seed specialists from RHUL and Syngenta

BBSRC DTP OR RHUL funded EU/UK residency criteria

<http://www.findaphd.com/search/projectdetails.aspx?PJID=50553>

Robustness and Evolutionary Dynamics of Biosynthetic Organisms in Biotechnology

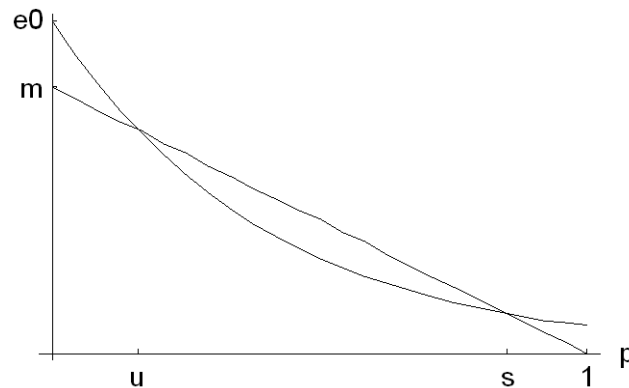
Michael Stumpf (RHUL) and Vincent Jansen. BBSRC funded

<http://www.findaphd.com/search/projectdetails.aspx?PJID=69619>

Rescue effect

- Model:

$$\frac{dp}{dt} = mp(1-p) - e_0 \exp(-ap)p$$

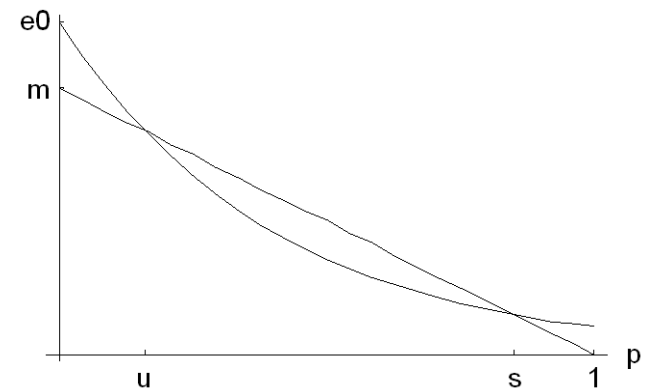


Rescue effect

- Equilibria:

$$\begin{cases} p^* = 0 \\ m(1 - p^*) = e_0 \exp(-ap^*) \end{cases}$$

- The last eqn is transcendental: we cannot solve it in closed form for p

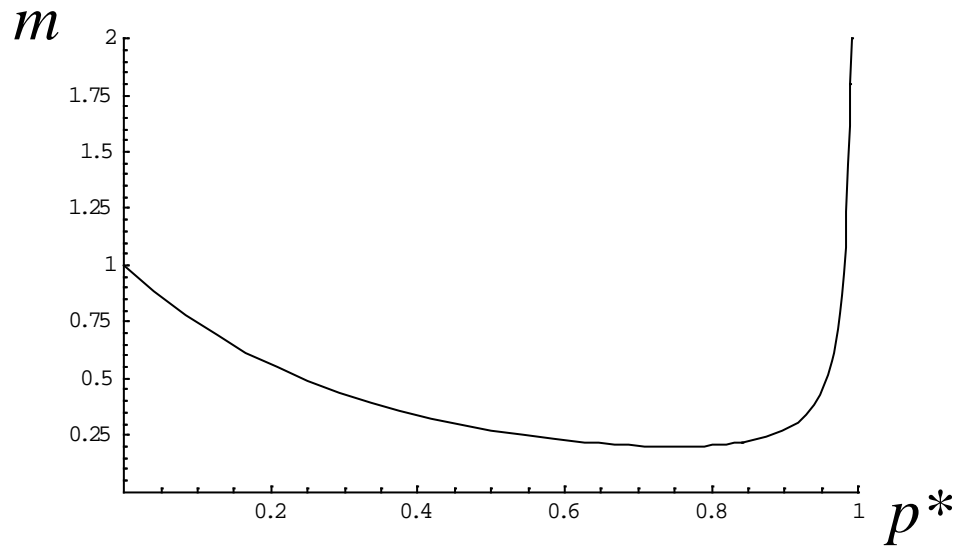


Rescue effect

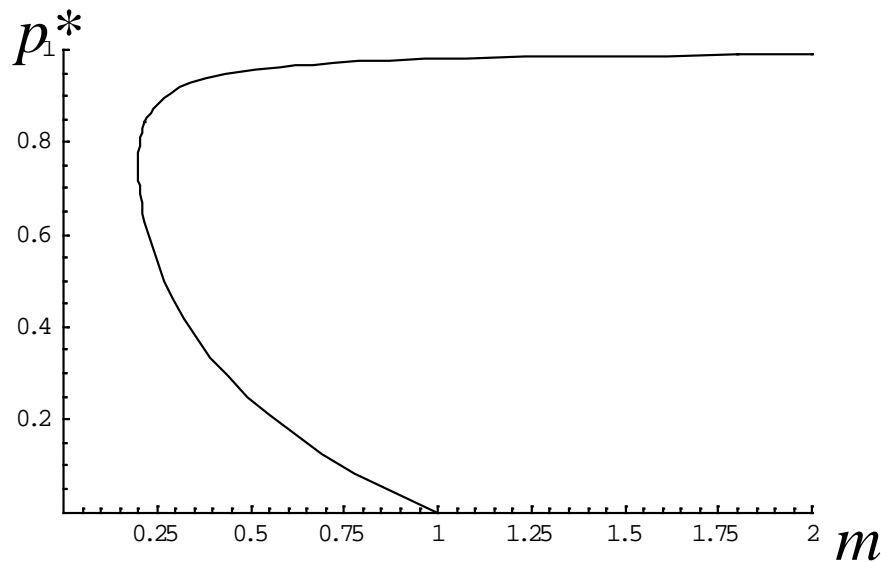
- We can employ a trick here. Even though we cannot solve it for p^* , we can solve it for m as

$$m = e_0 \frac{\exp(-ap^*)}{1 - p^*}$$

Rescue effect



$$m = e_0 \frac{\exp(-ap^*)}{1 - p^*}$$



Rescue effect

- Linearised model:

$$\begin{aligned}\frac{dx}{dt} &= x \left(m(1 - 2p^*) - e_0 \left(\exp(-ap^*) - a \exp(-ap^*) p^* \right) \right) \\ &= x \left(m(1 - 2p^*) - e_0 \exp(-ap^*) (1 - ap^*) \right) \\ &= mx \left(1 - 2p^* - (1 - p^*) (1 - ap^*) \right) \\ &= p^* mx (a(1 - p^*) - 1)\end{aligned}$$

Rescue effect

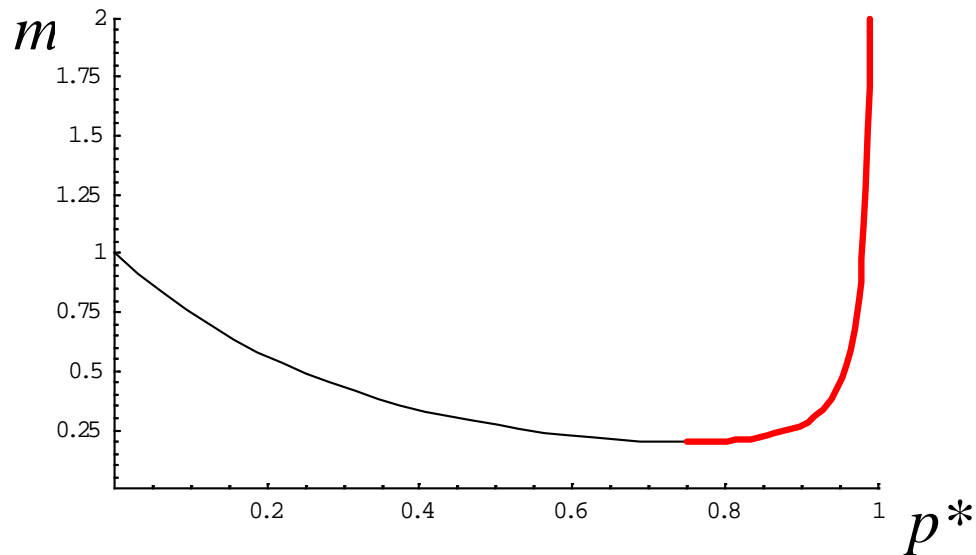
Now note that:

$$\begin{aligned}\frac{dm}{dp^*} &= -\frac{e_0 \exp(-ap^*)}{(1-p^*)^2} (a(1-p^*)-1) \\ &= \frac{m}{(1-p^*)} (a(1-p^*)-1)\end{aligned}$$

And hence:

$$\frac{dx}{dt} = -xp^*(1-p^*) \frac{dm}{dp^*}$$

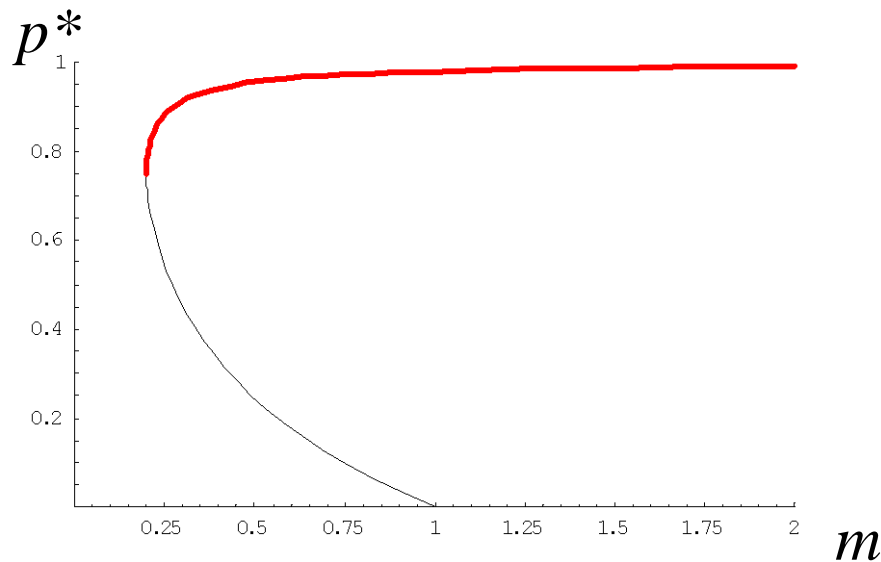
Rescue effect



$$m = e_0 \frac{\exp(-ap^*)}{1 - p^*}$$

Stable if

$$-p^*(1 - p^*) \frac{dm}{dp^*} < 0$$



Fibonacci's rabbits

Difference equation

$\{-1,1\},\{1,0\}$ (juvenile, adults)

Recurrence

$\{0,1\},\{1,1\}$

$-\lambda(1-\lambda)+1=0$

$\lambda=1/2\pm 1/2 \sqrt{5}$

*Fibonacci's rabbits, dying

Difference equation

$$\{\{-1,1,1\},\{1,-1,0\},\{0,1,-1\}\}$$

Recurrence

$$\{\{0,1,1\},\{1,0,0\},\{0,1,0\}\}$$

$$1 + \lambda - \lambda^3 = 0$$

No simple solution, but has one ev at approx

$$1.324 < 1/2 + 1/2 \sqrt{5}$$

Problem can be rewritten to Padova sequence:

$$x(t) = x(t-2) + x(t-3)$$

See

<http://matheminutes.blogspot.co.uk/2012/02/killing-fibonaccis-rabbits.html>