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

Single species models, stability, metapopulations

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Outline

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

Exponential Growth

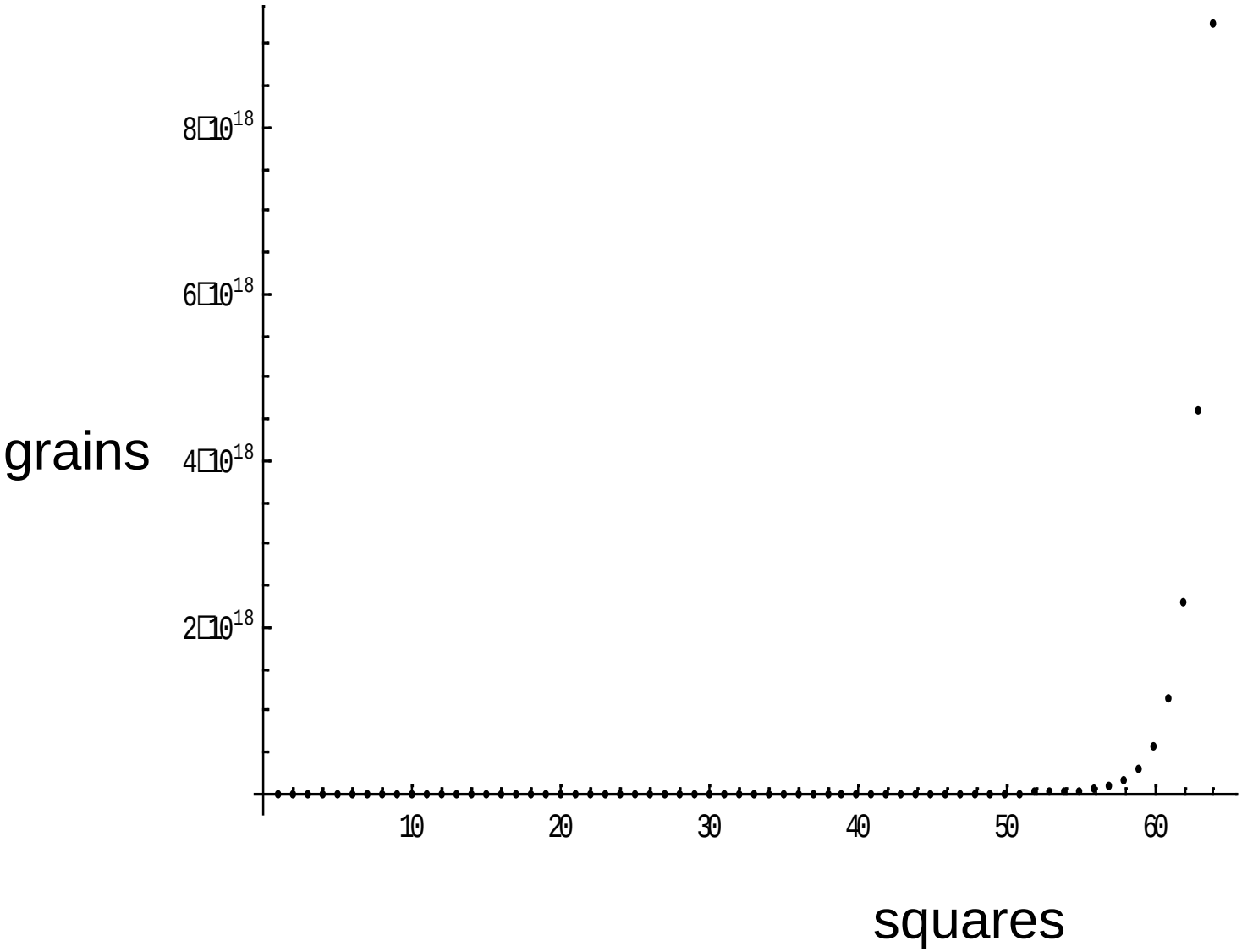
- The simplest model for growth is to assume that the net per capita growth is density independent

- 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 x 10^{11} metric tons, more than 500 times the current yearly global rice production!


grains
8□10^18
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4□10^18
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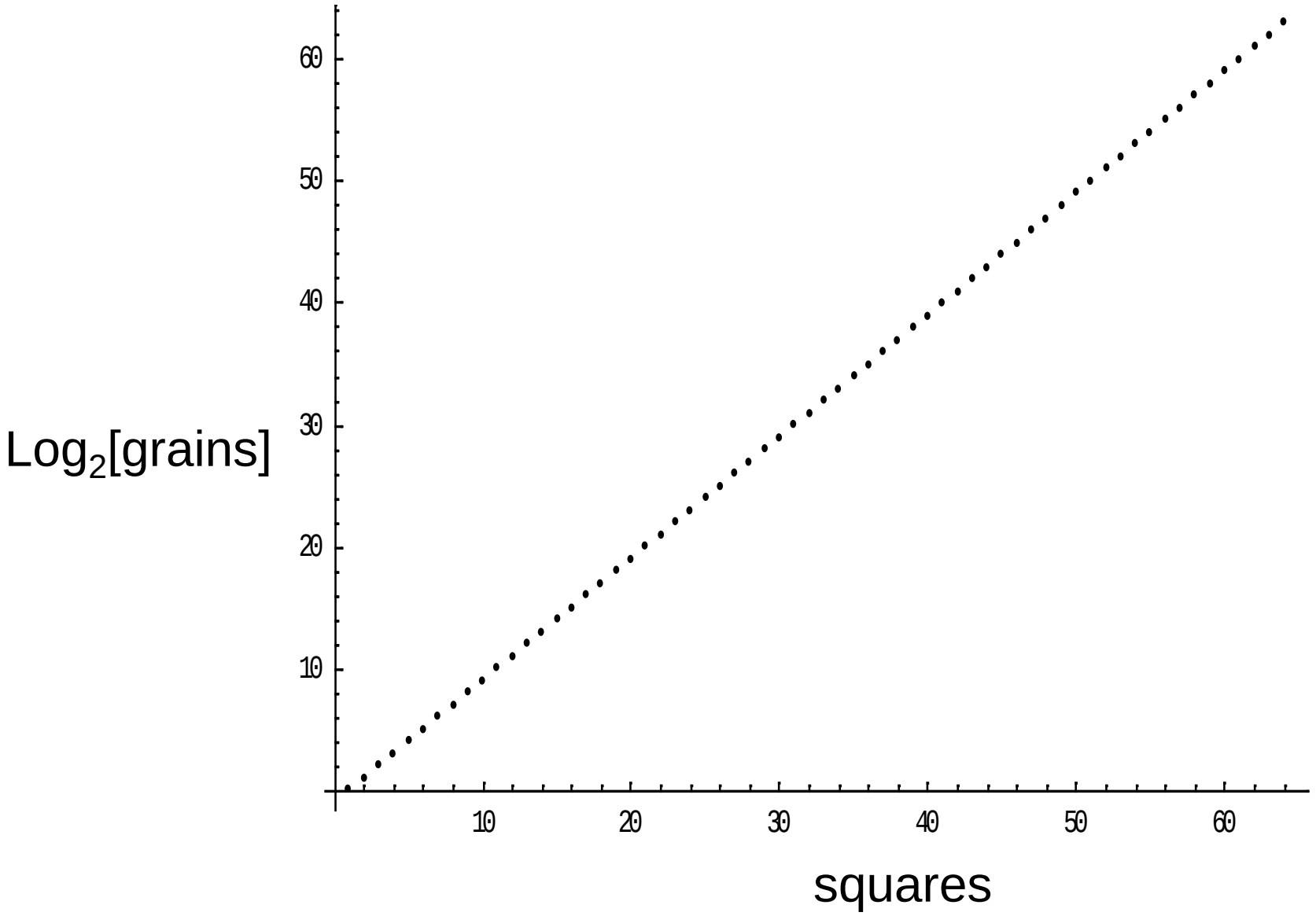
squares


Log2[grains]
60
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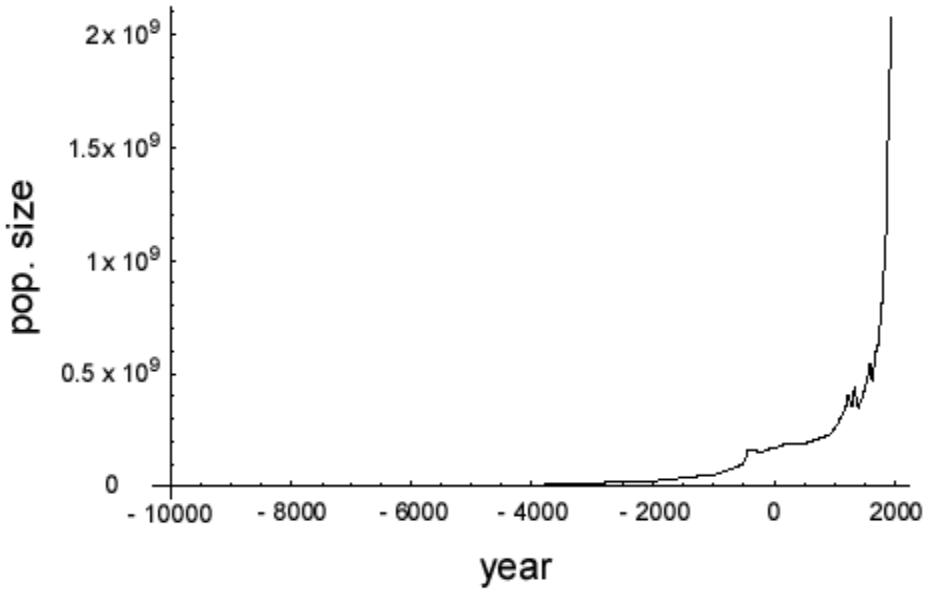
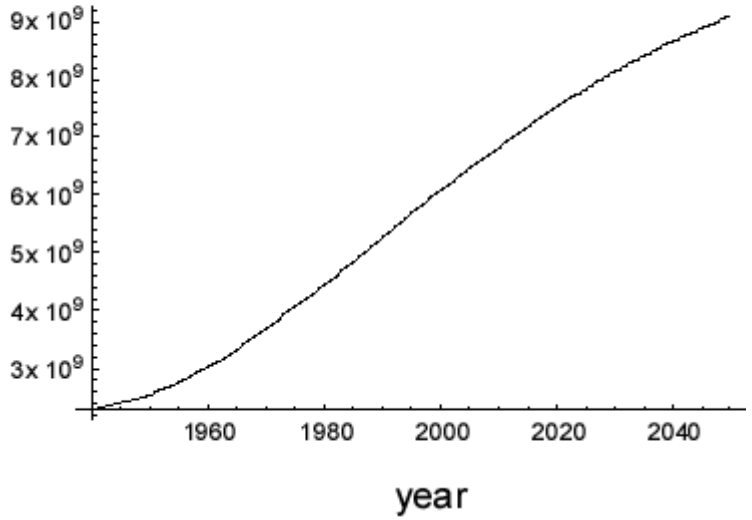
squares

Humans vs Bacteria:
the growth of the human population





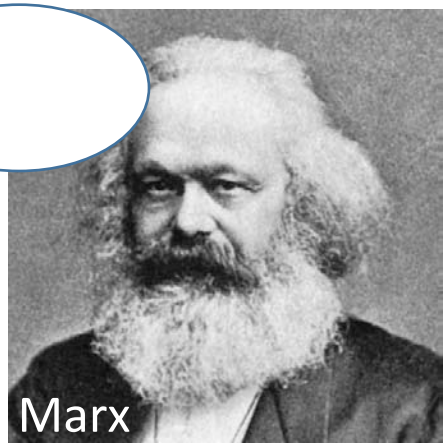
Humans vs Bacteria:

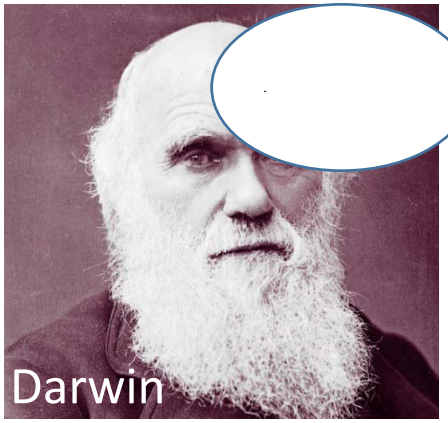
- Can we find any patterns in human population growth?

- Malthus wrote an essay (1789) in which he claims that the human population grows geometrically

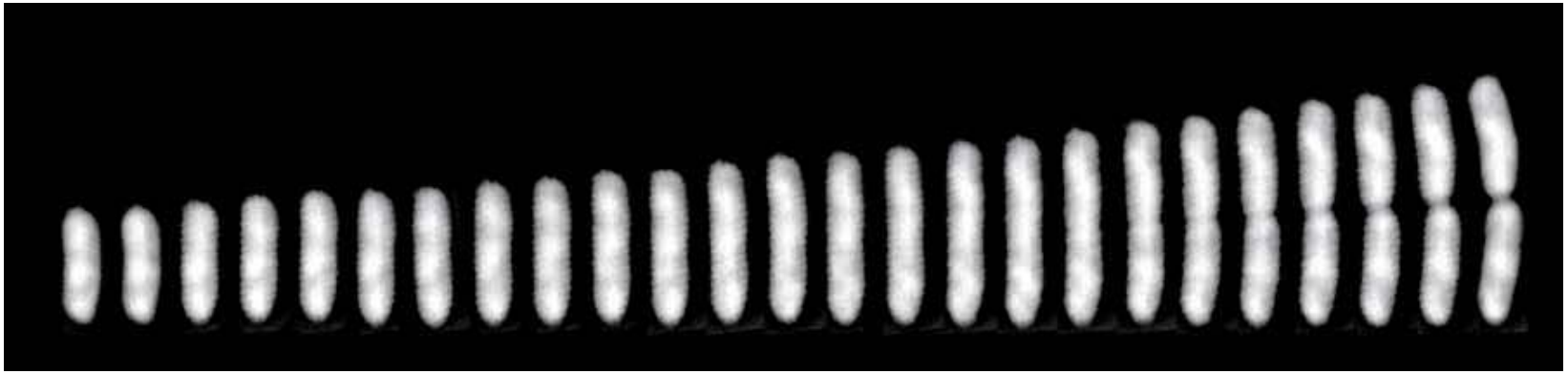
- The view that the human population grows in a similar fashion to a bacterial population has been very influential

The reverend Thomas Malthus


Marx


Darwin

Humans vs Bacteria: Bacterial growth

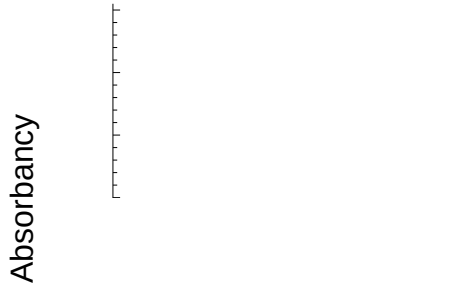


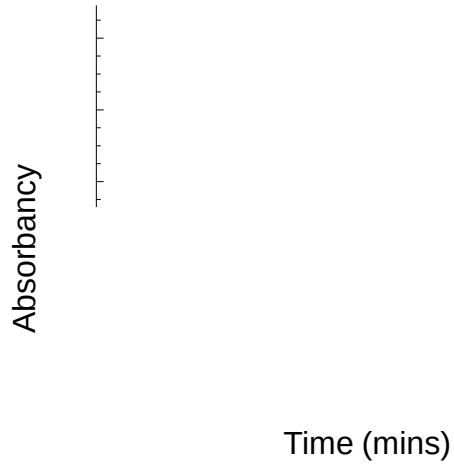
A single E. coli cell dividing

- 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

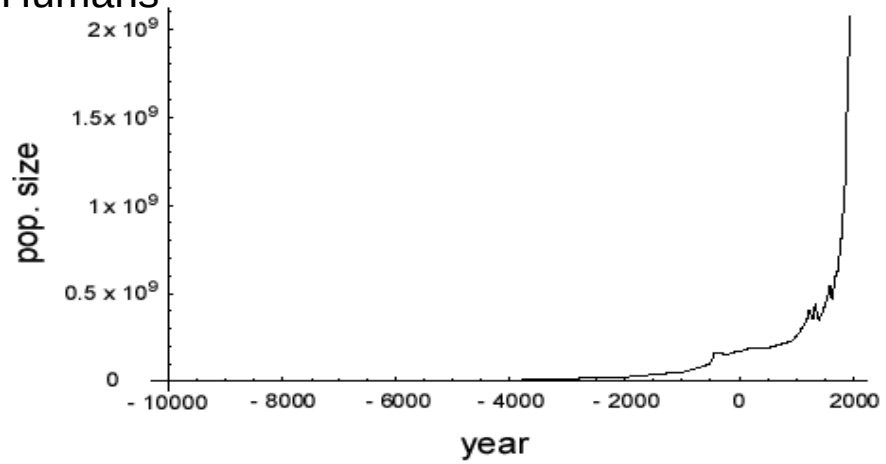


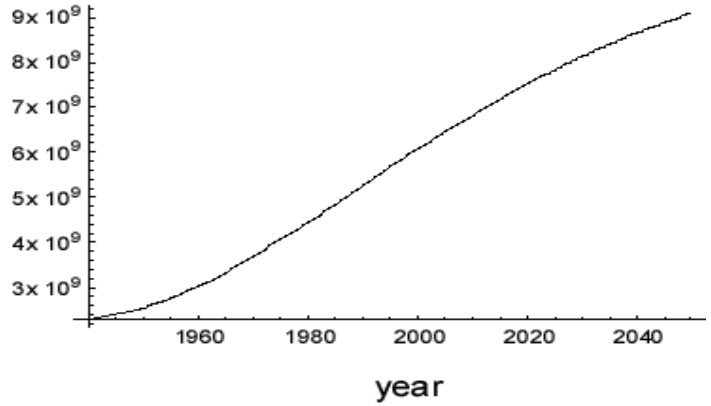


•http://biology.clc.uc.edu/fankhauser/labs/microbiology/growth_curve/growth_curve.htm

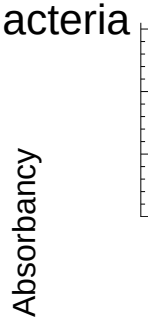
Humans vs Bacteria

Humans





Bacteria



Time (mins)

Time (mins)

Do human and bacterial populations grow in the same way?

Obviously the time scale is different

But are the growth curves the same or different?

To find out we will build a simple model for exponential (geometric) growth, and see if Malthus was right.

The reverend Thomas Malthus

Exponential Population Growth

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

  Births = $b\ N_t$

  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:

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

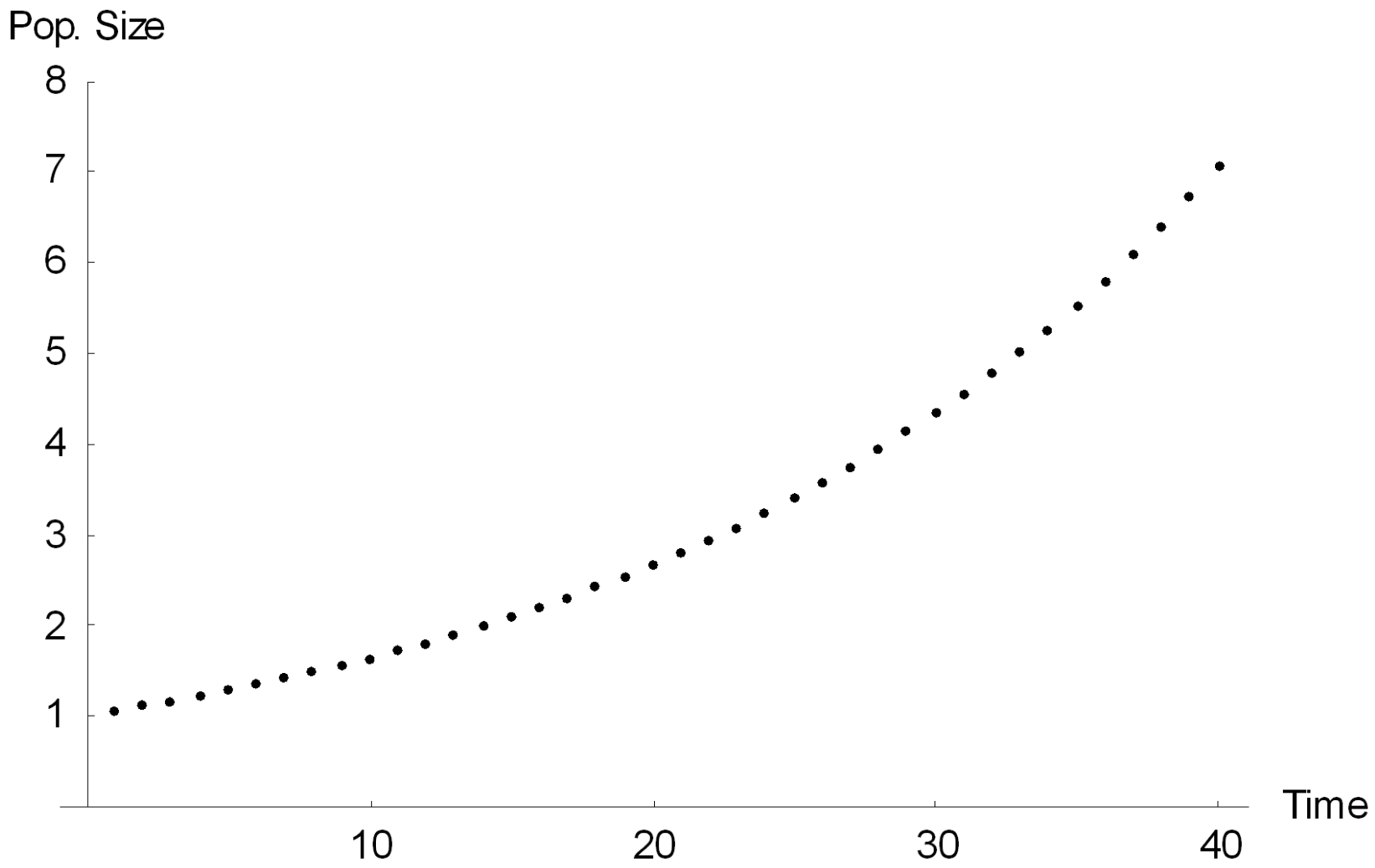
or

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

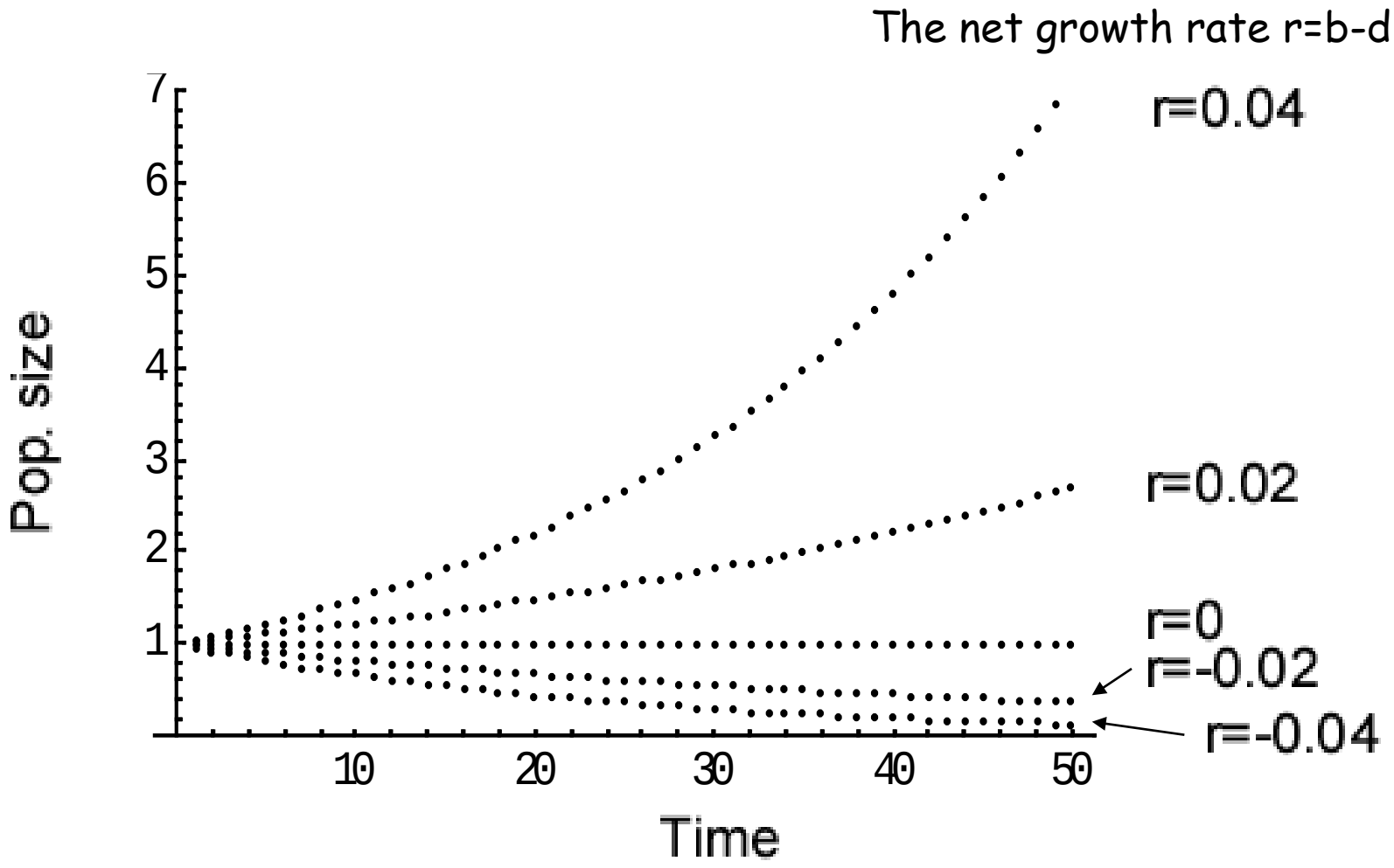
General solution:

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

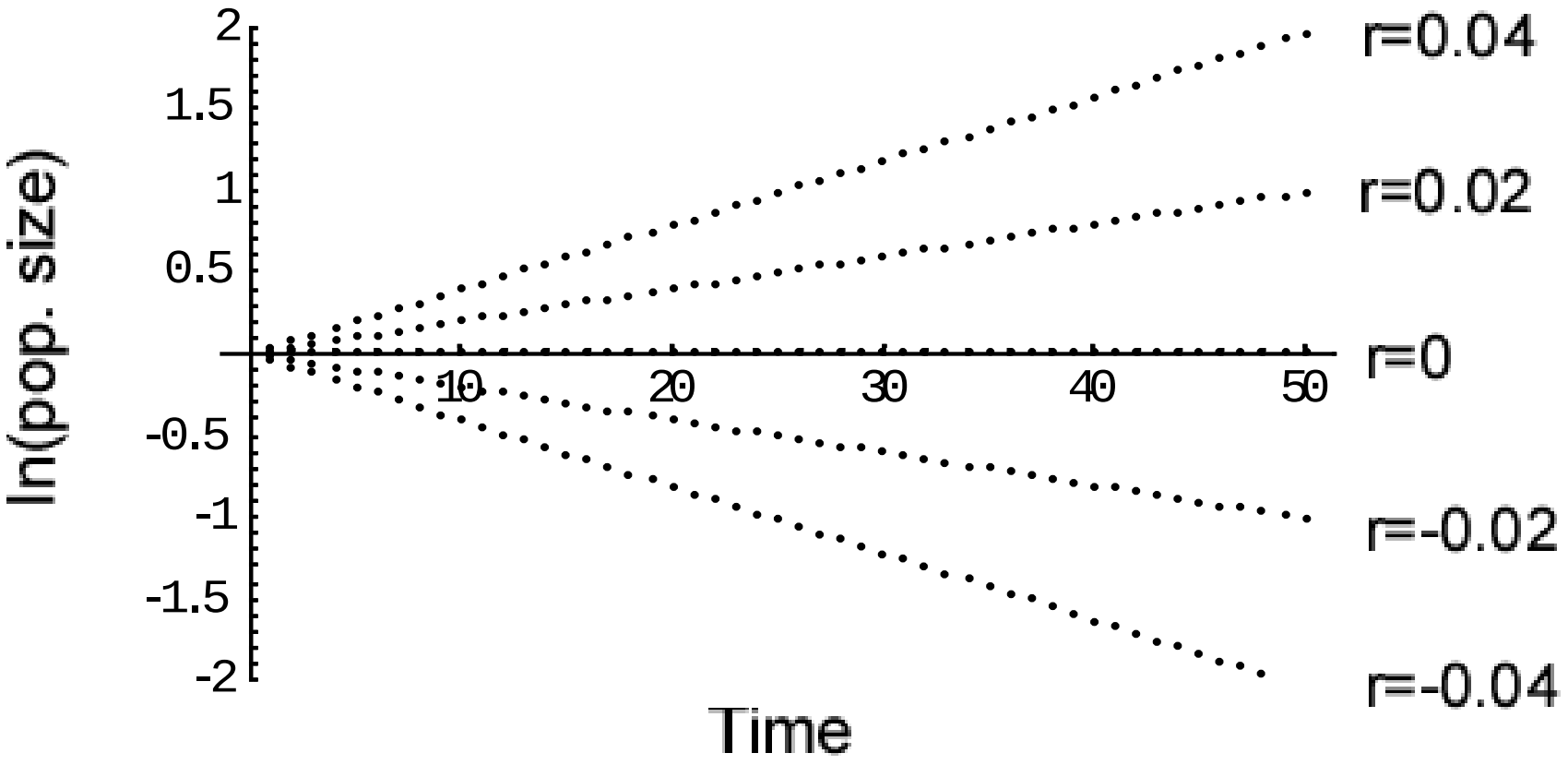
Exponential Growth



Exponential growth



Exponential growth



The Fibonacci sequence

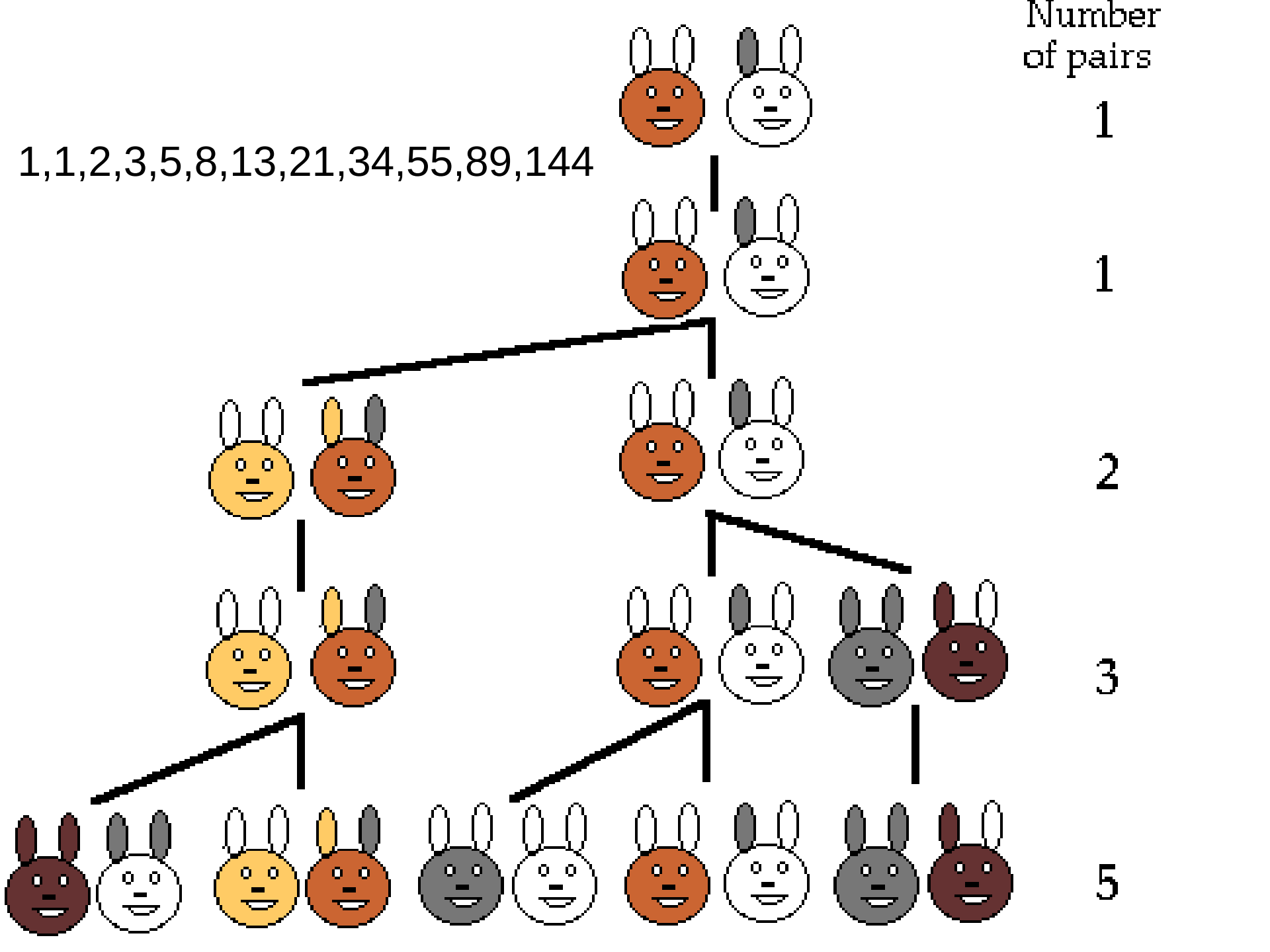
Leonardo of Pisa (Fibonacci)
(c. 1170 – c. 1250)

Page from the Liber Abaci, with the Fibonacci sequence

The Fibonacci sequence

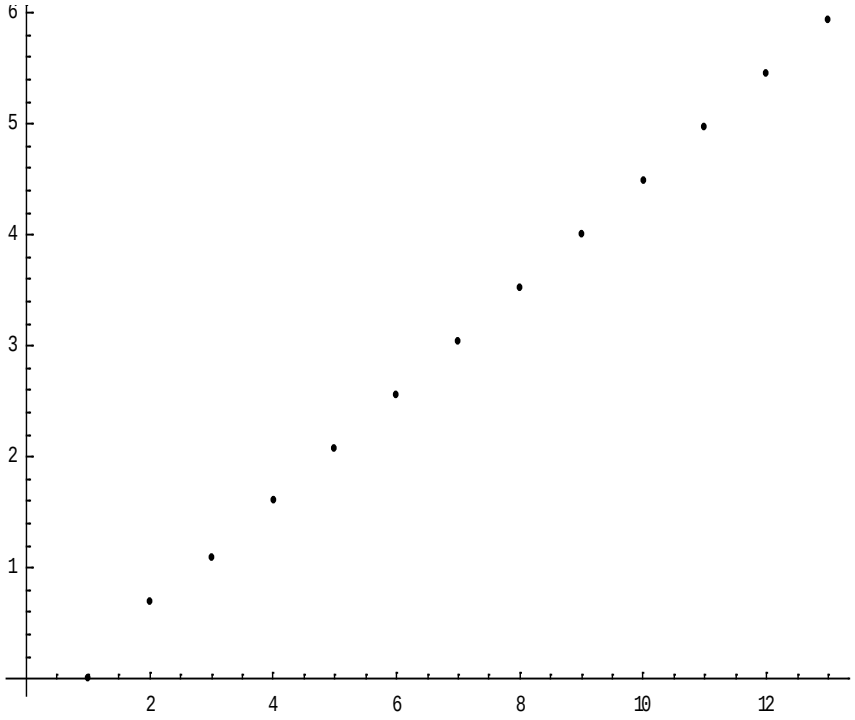
Leonardo of Pisa
(Fibonacci)
(c. 1170 – c. 1250)

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 ?


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

Fibonacci’s rabbits

ln[nr of rabbits]



time

Exponential growth (continuous time)

If we assume constant per capita birth and death rates:

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

Which can be rewritten as

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

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

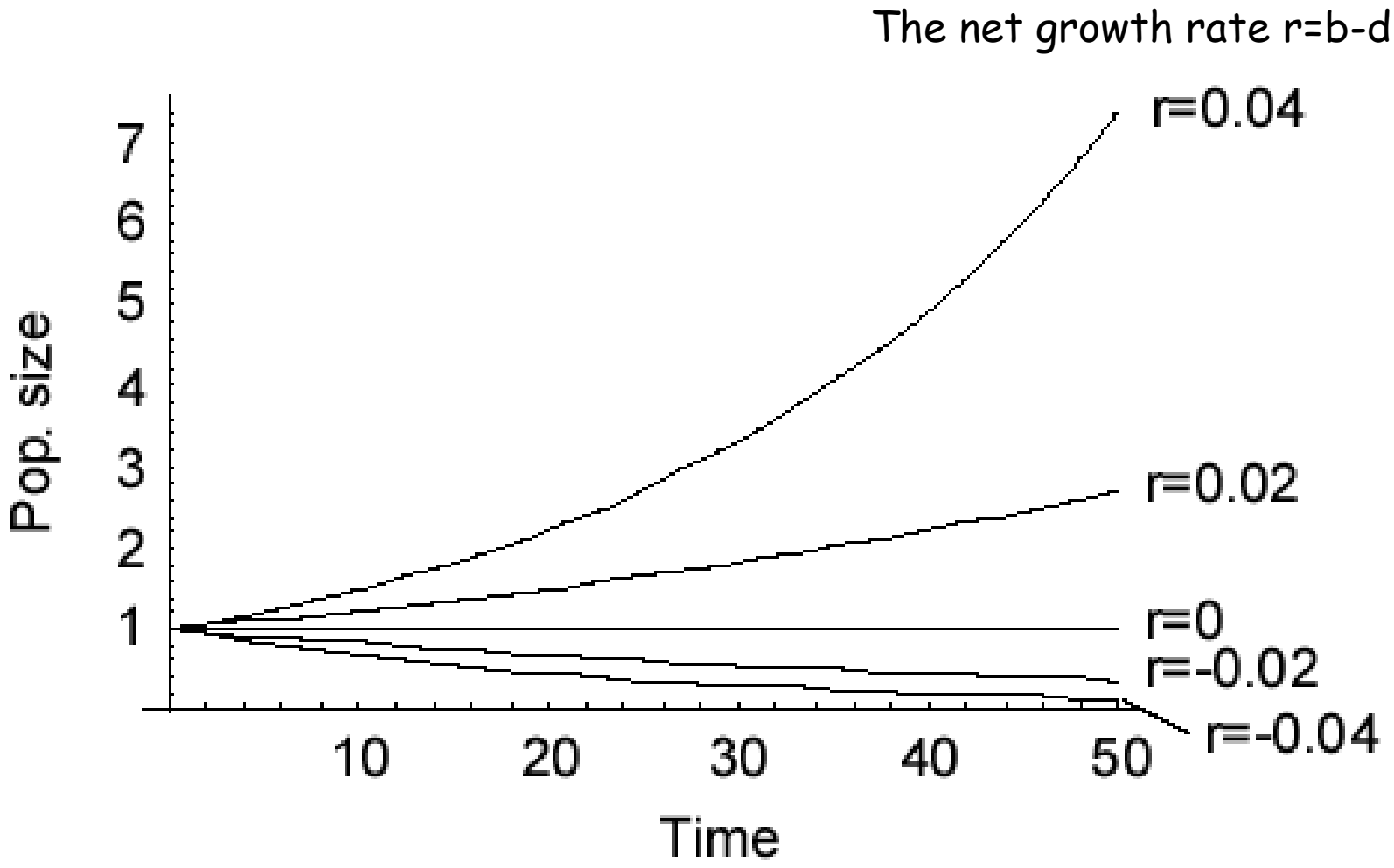
$$\frac{dN}{dt} = r\,N$$

Can be solved to give:

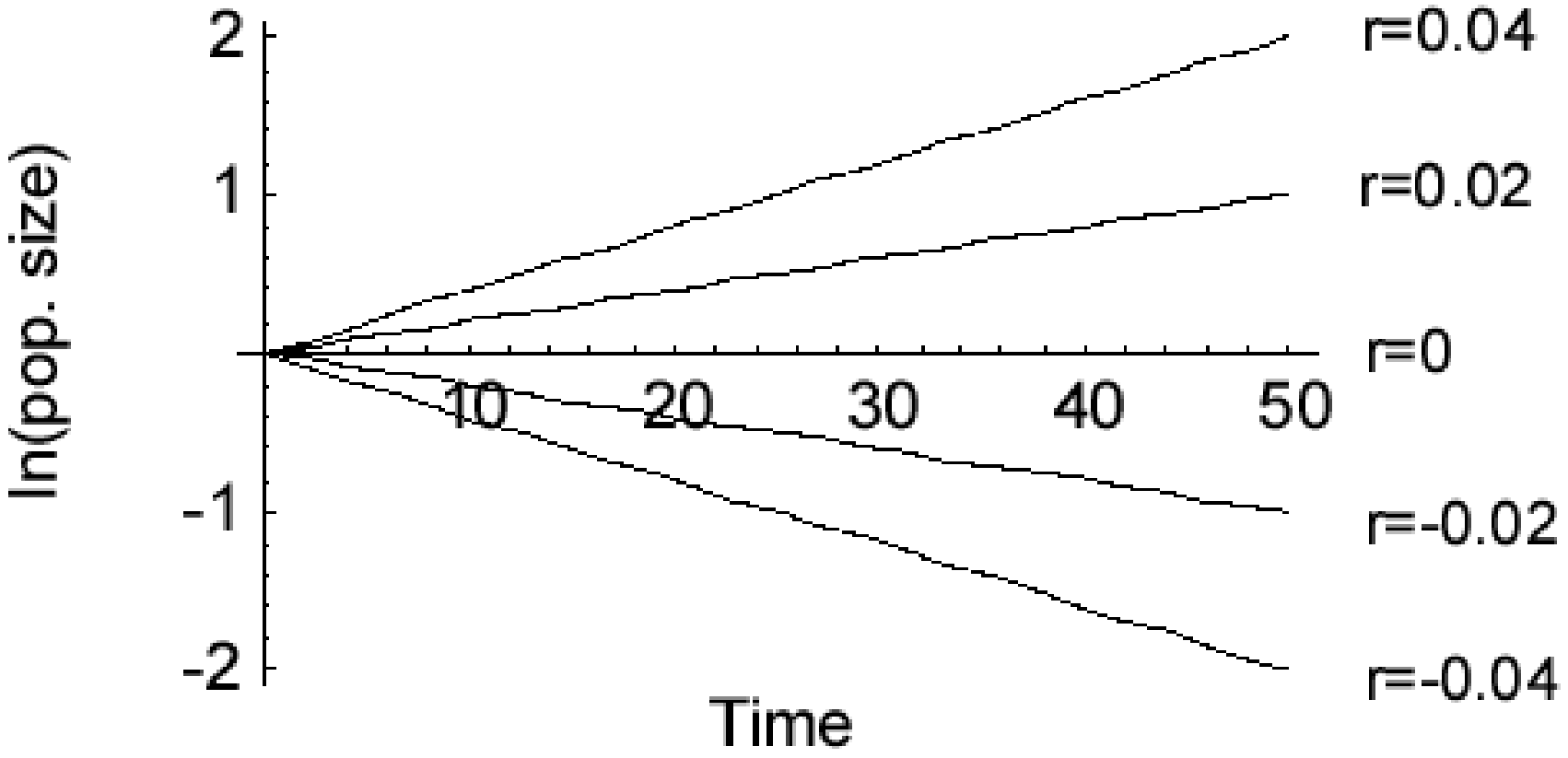
$$N(t) = N(0)e^{rt}$$

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

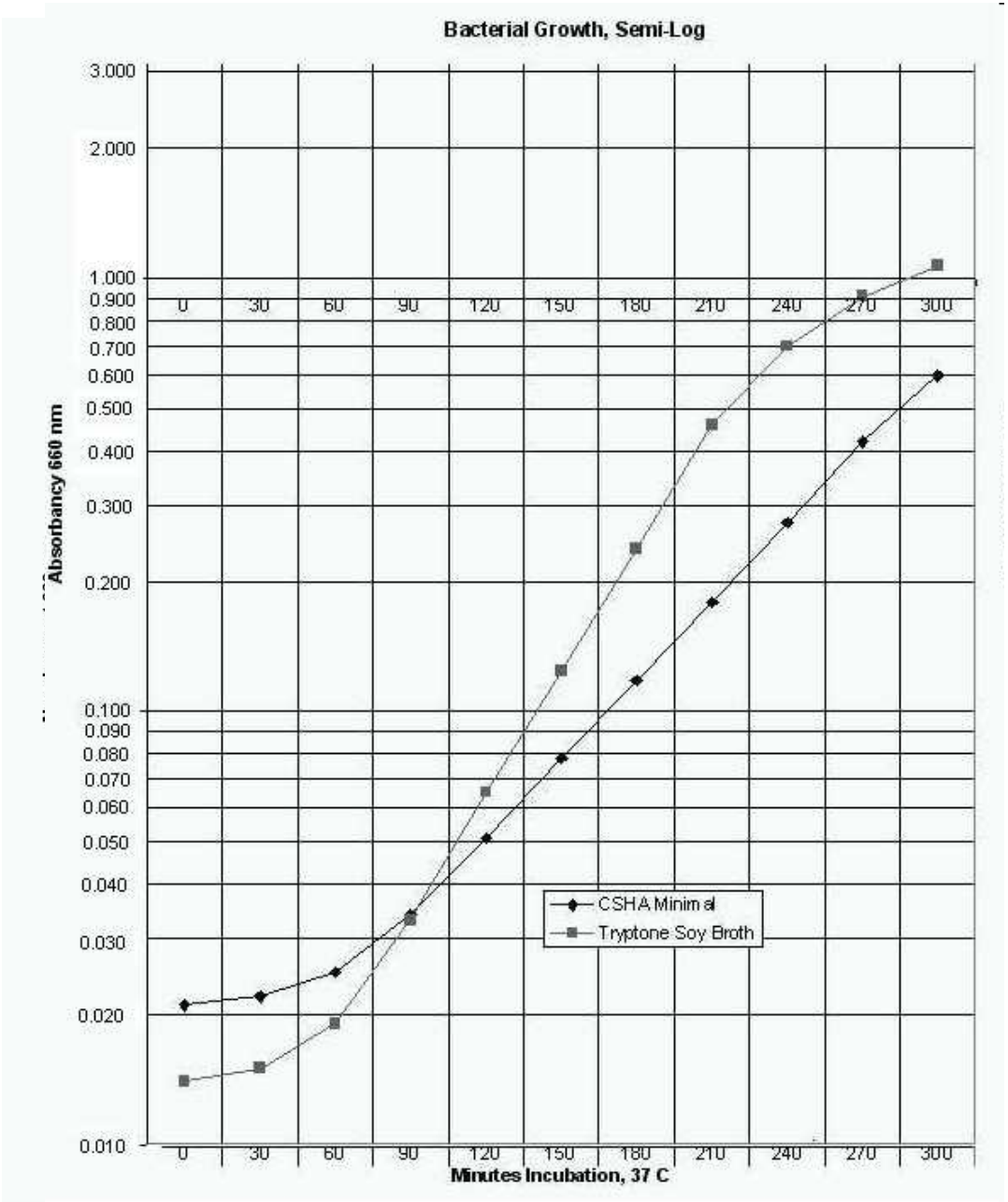


Humans vs Bacteria analysed

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

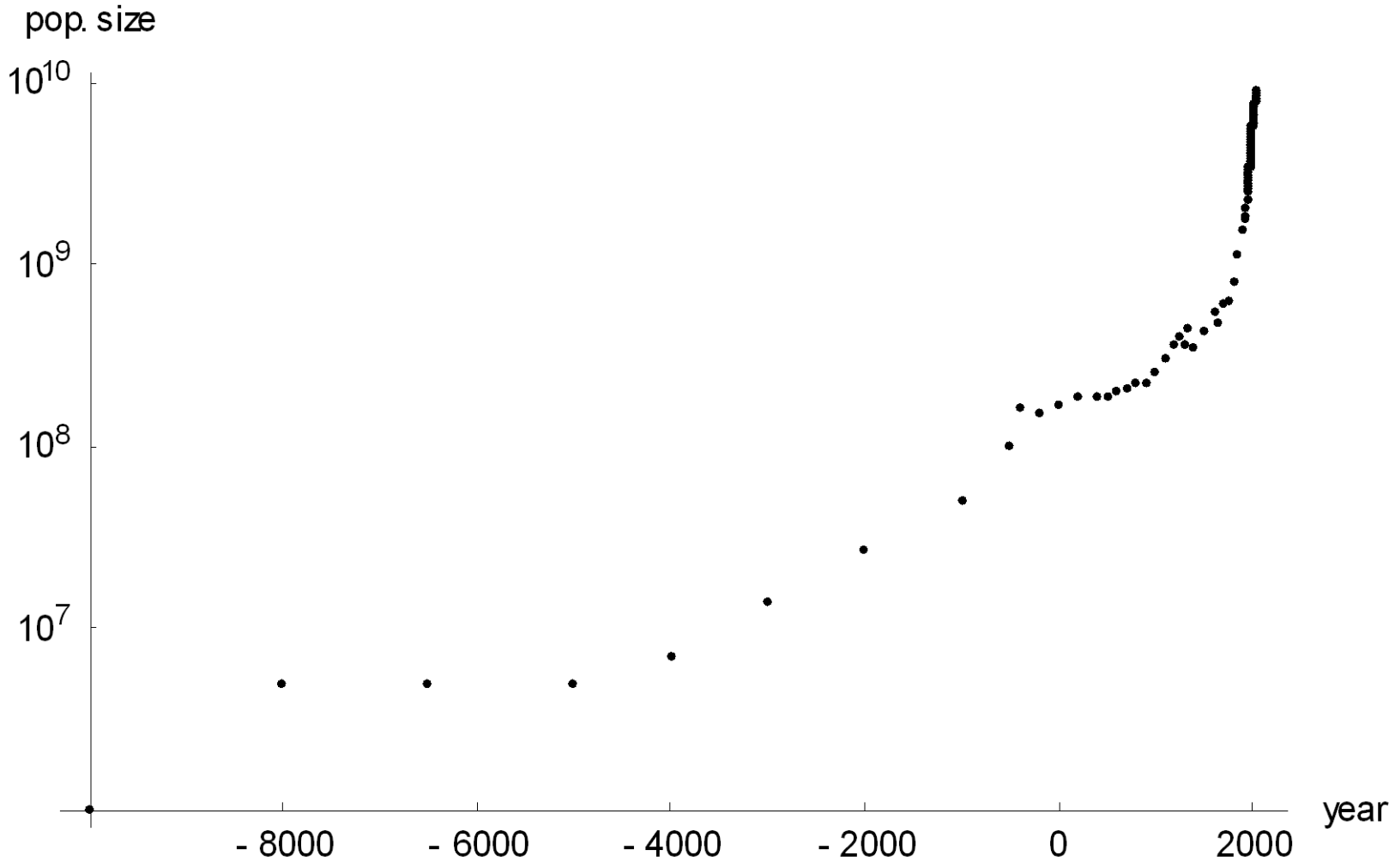
Example: Bacterial Growth

Escherichia coli grown on minimal salts vs complex media



•http://biology.clc.uc.edu/fankhauser/labs/microbiology/growth_curve/growth_curve.htm

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:

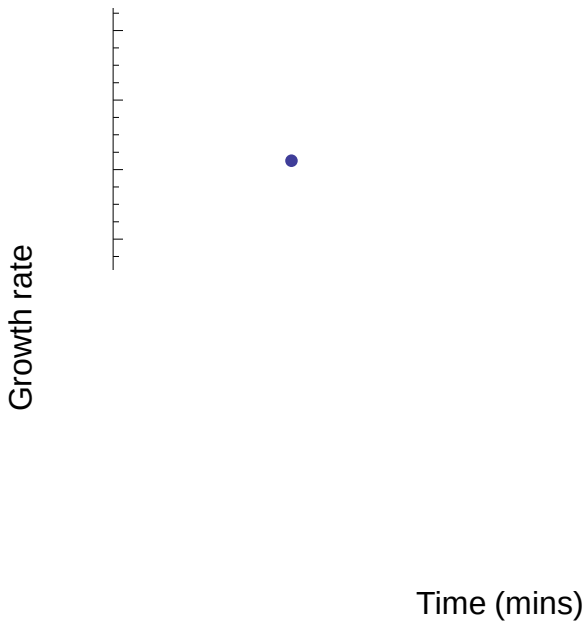
$$N(T) = N(0)e^{rT}$$

Solving for r we find

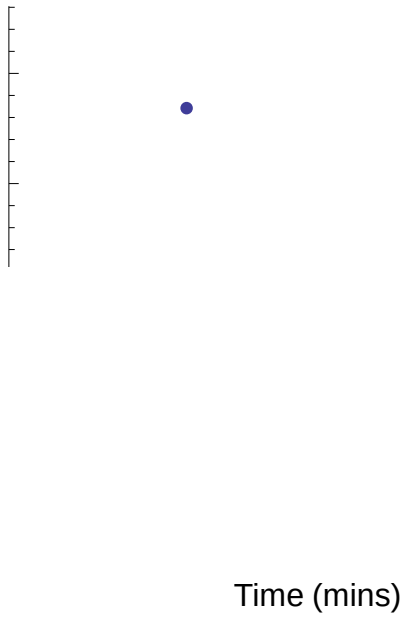
$$r = \frac{1}{T}\ln\frac{N(T)}{N(0)}$$

Are growth rates constant for bacteria?

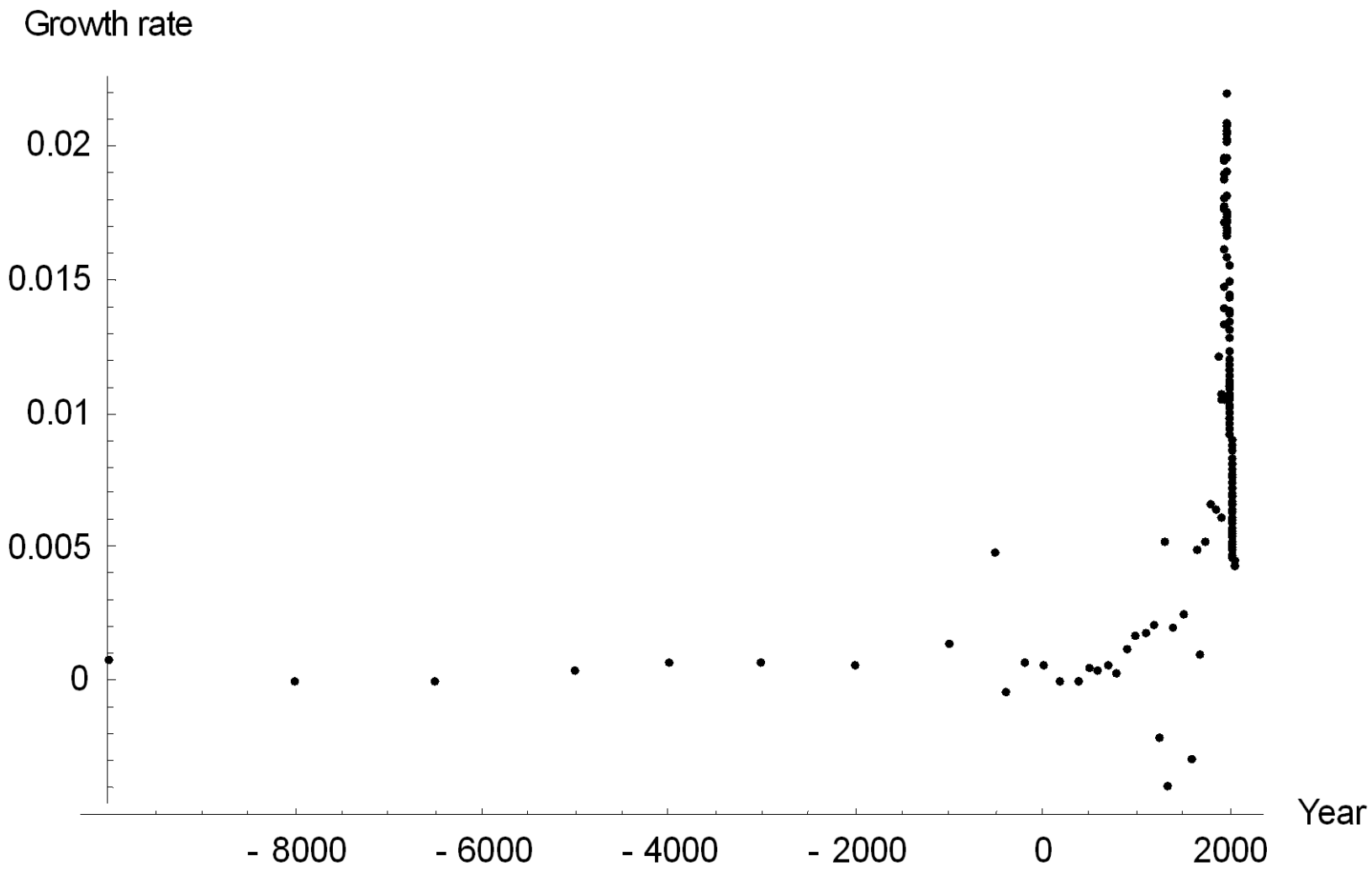
Simple medium



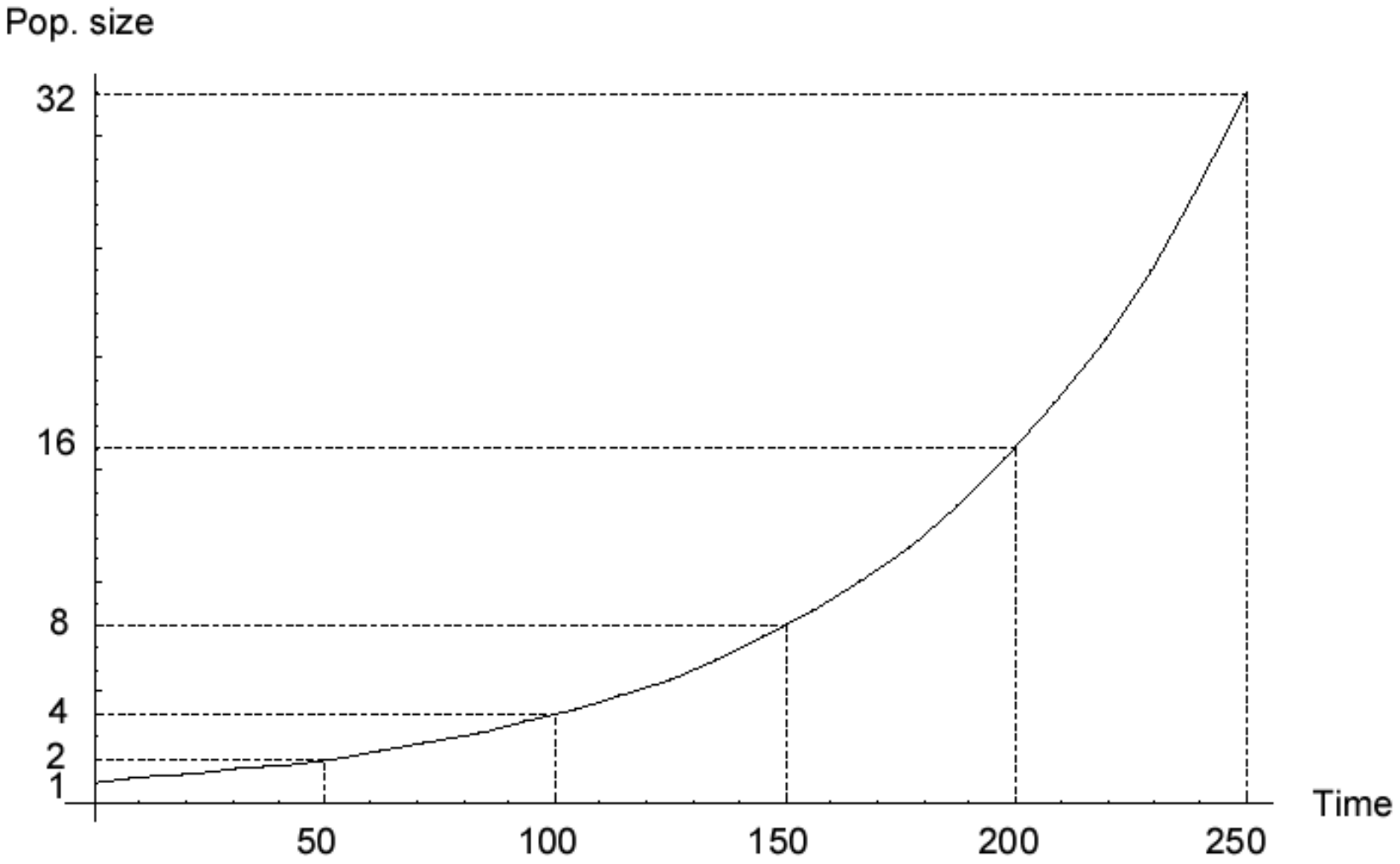
Complex medium



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 bacterial population is about 50 mins.

- For the human population it was, over the last 12000 years, approx. 900 years
- From 1950 until now it was approx. 35 years

Density Dependence

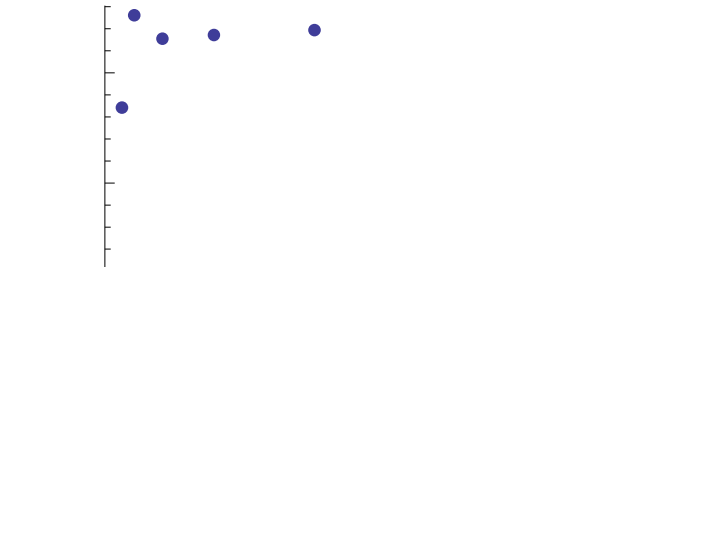
- For the exponential growth rate we assumed the per capita growth rate is independent of the population size

- Let’s see if that is correct

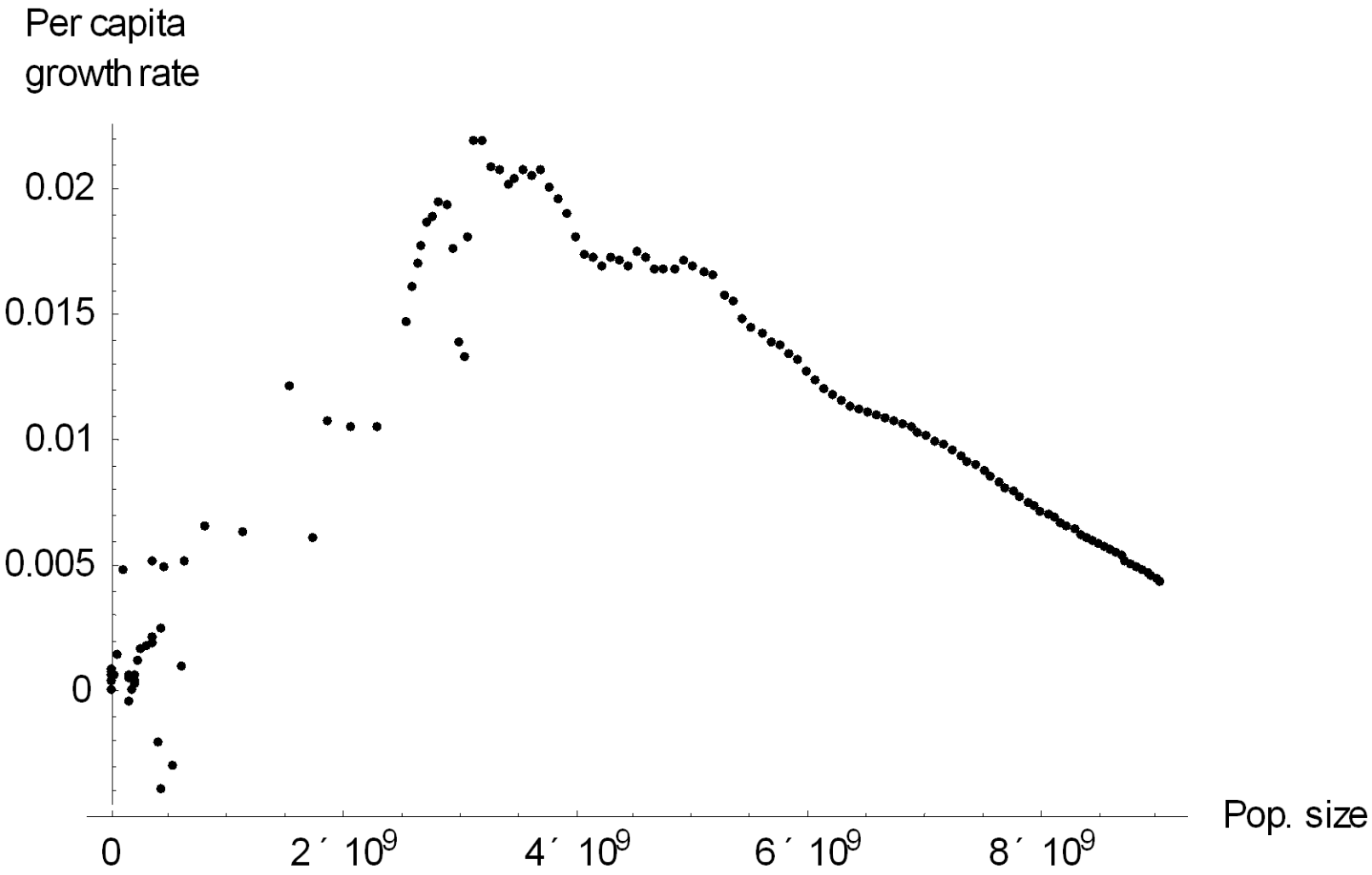
Are growth rates constant for bacteria?

Simple medium

Complex medium

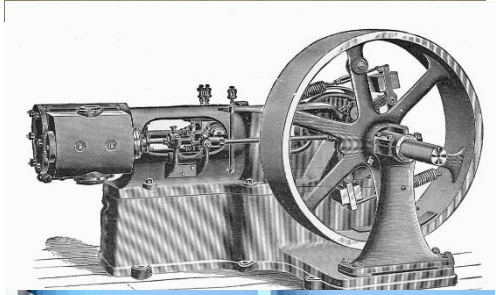


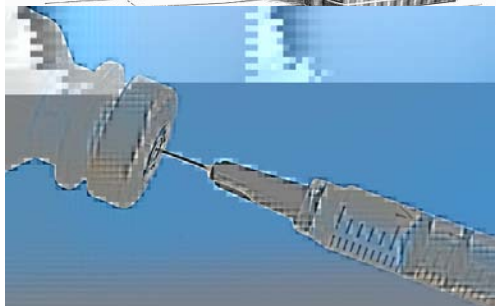
Density Dependence in the Human population



Density Dependence in the Human population

- For big populations the growth rate declines with size
- But initially the growth rate increased with sizes: the bigger the population got the better we did.
- This is where Malthus was wrong: humans are not like bacteria, and we have not ran out of resources yet





Growth curve of yeast

Raymond Pearl
(1879-1940)

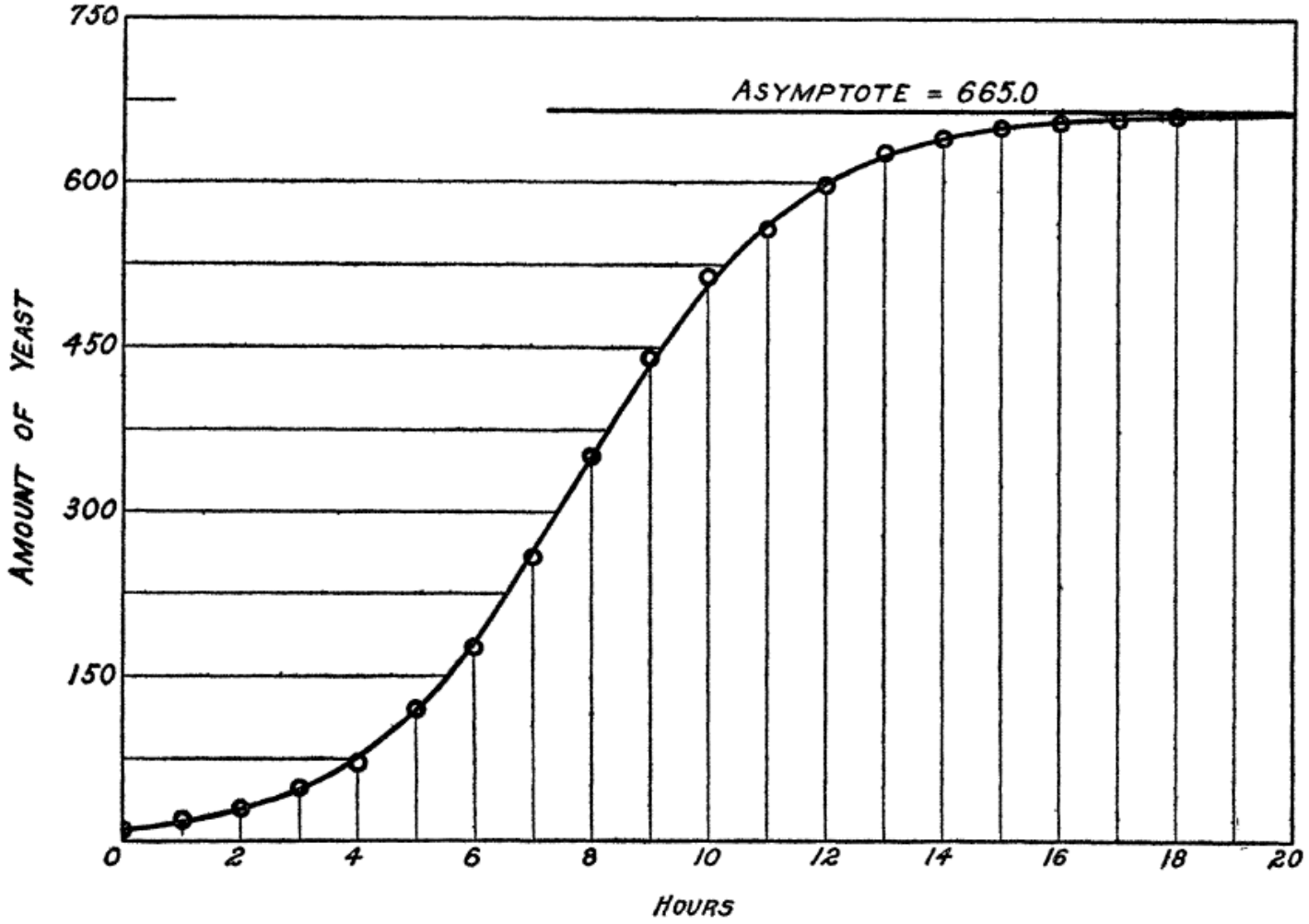
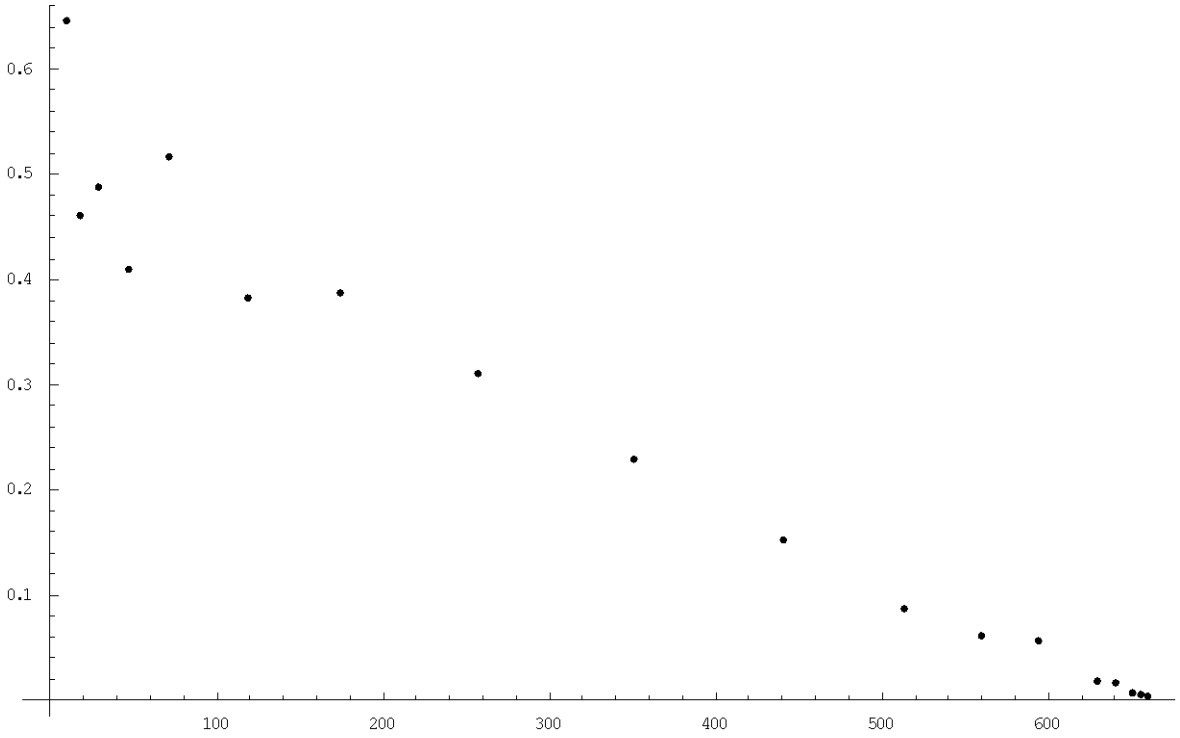


FIG. 1. THE GROWTH OF A POPULATION OF YEAST CELLS

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

Growth curve of yeast

Per capita growth rate



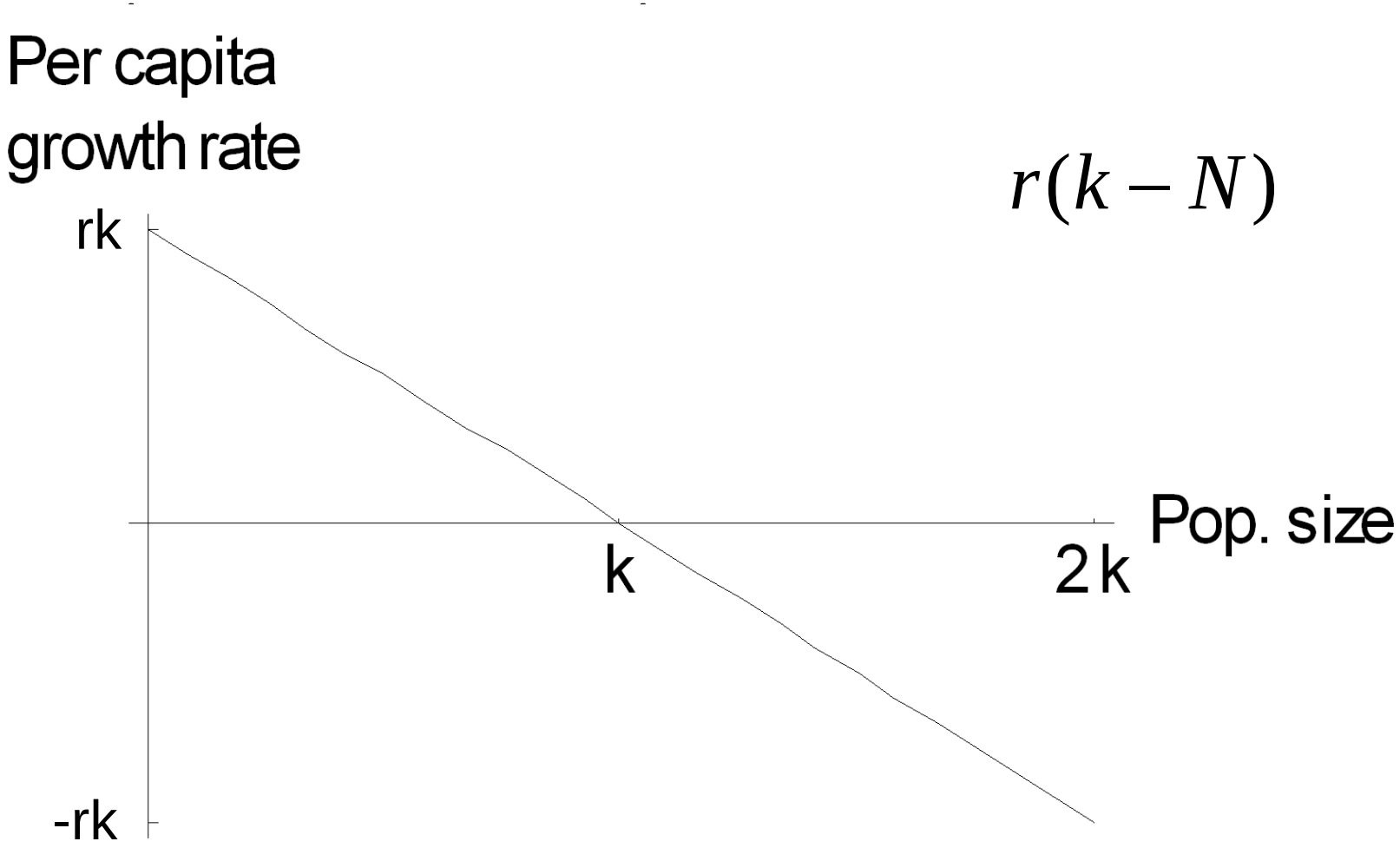
Population density

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



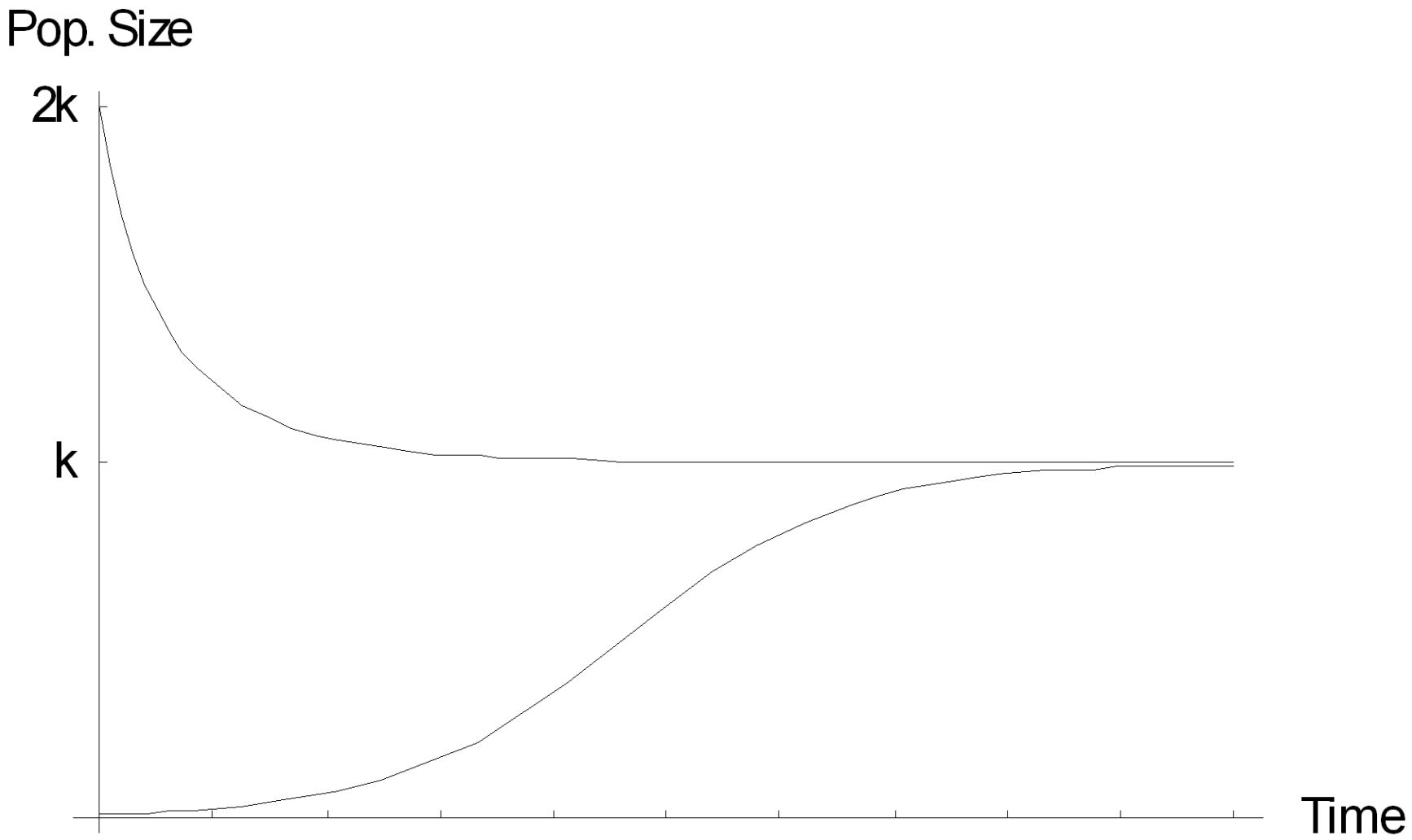
Logistic Growth

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



Calculation of the equilibria

- To find the equilibria we solve

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

- To give

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

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:

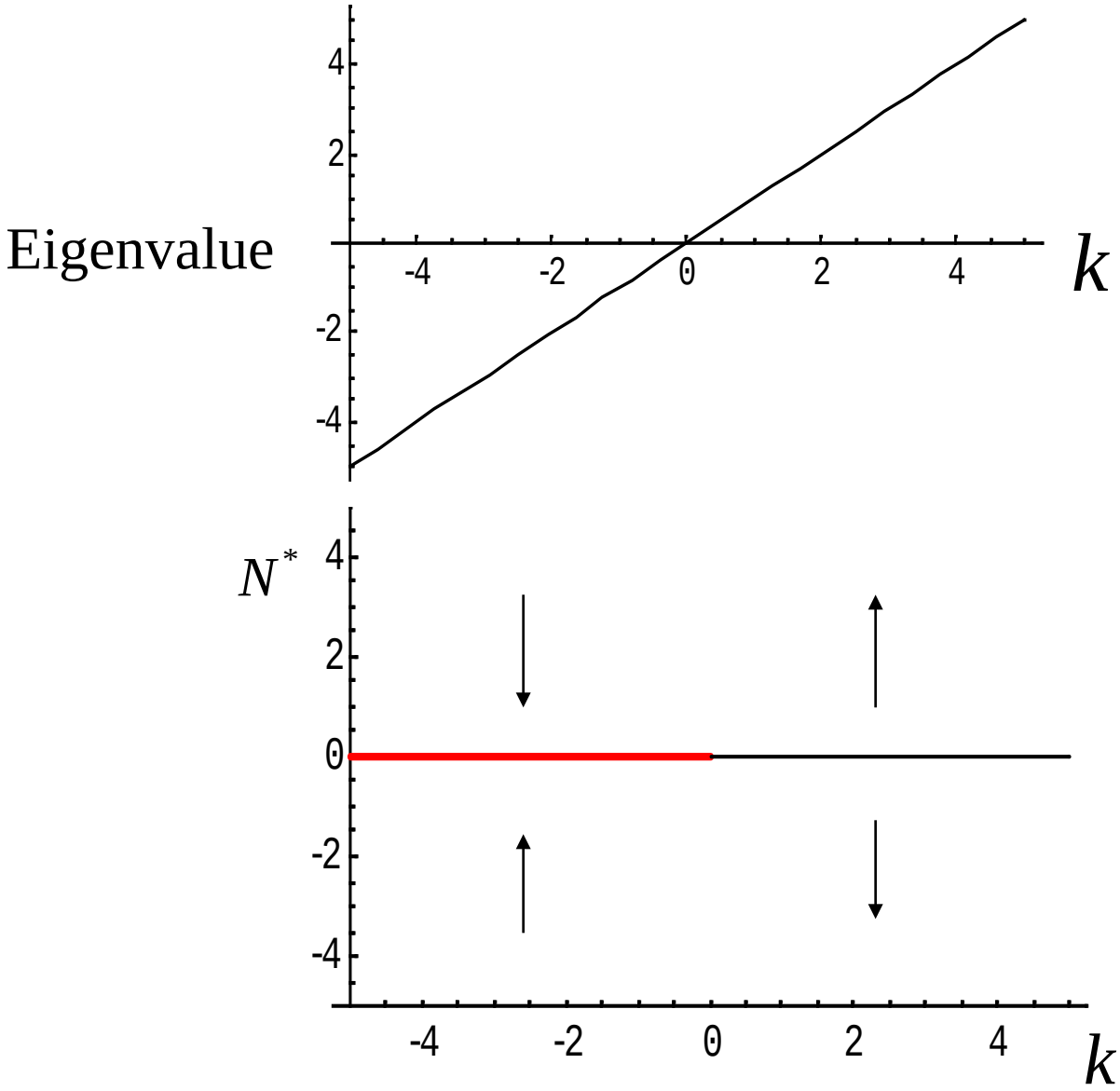
$$\frac{dx}{dt} = rkx$$

- 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 $N^* = 0$



Stability of $N^* = k$

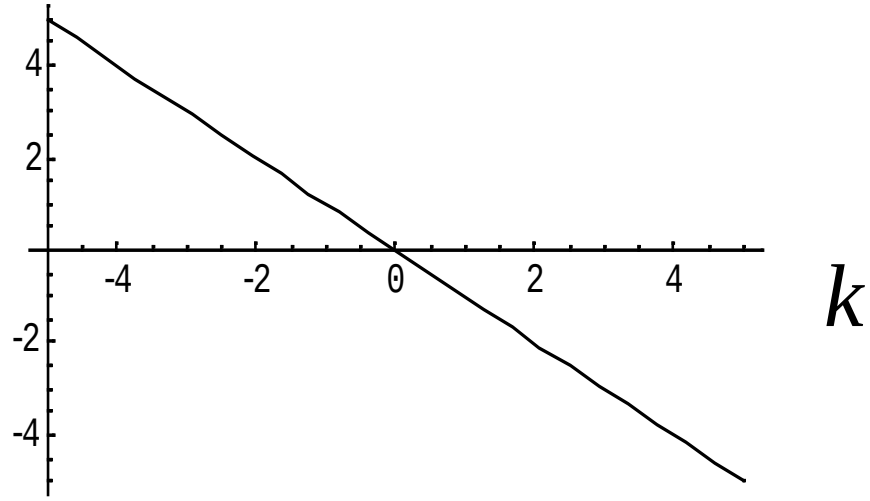
- The dynamics close to equilibrium are approximately:

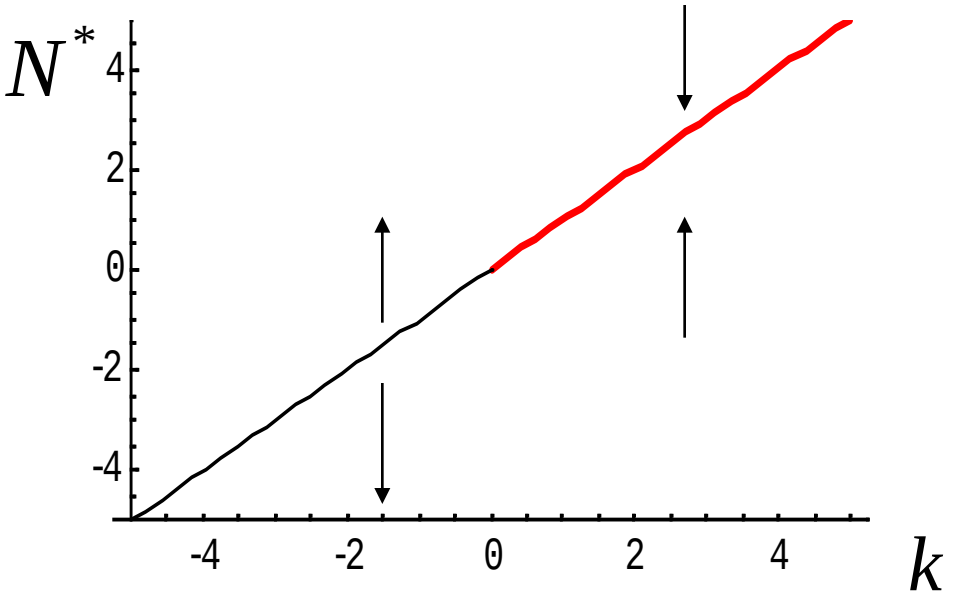
$$\frac{dx}{dt} = -rkx$$

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

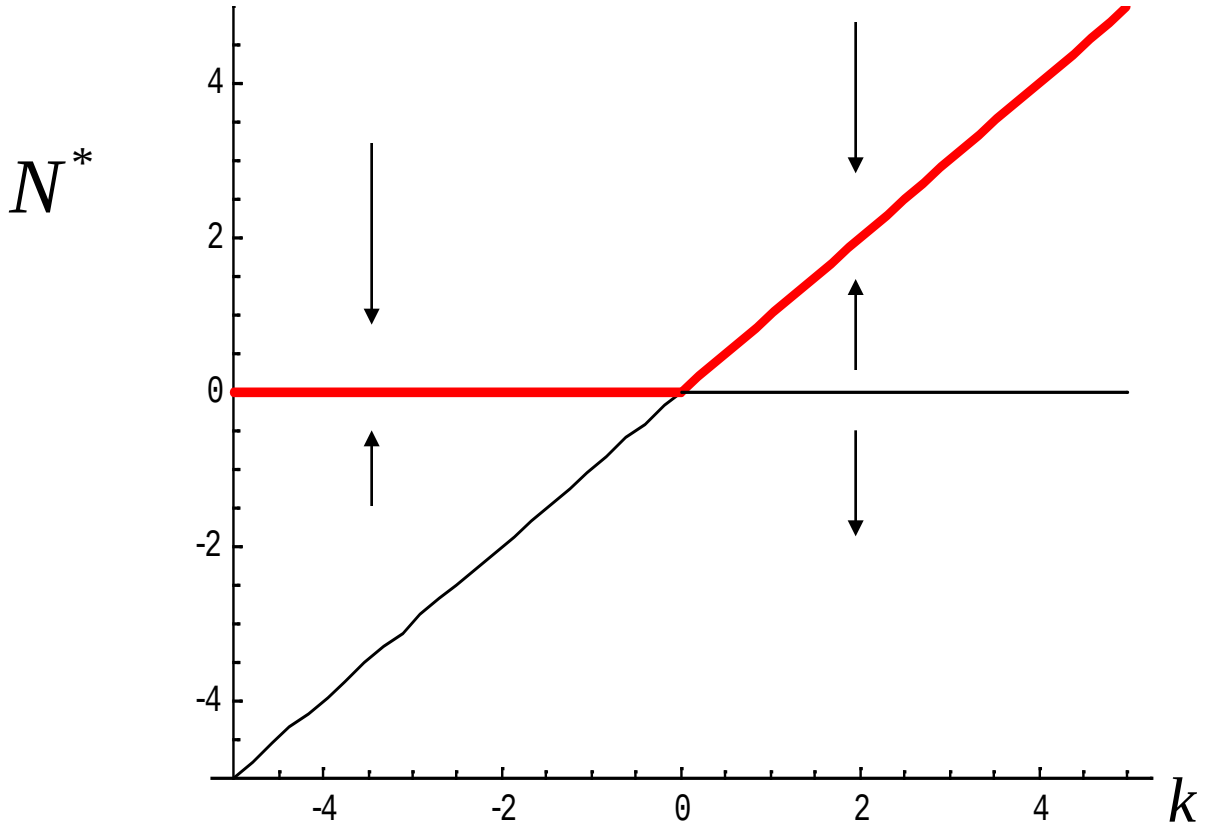
Stability of $N^* = k$

Eigenvalue





Bifurcation diagram



A transcritical bifurcation

Now do Practical 1: Make bifurcation diagram for the continuous logistic equation.

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

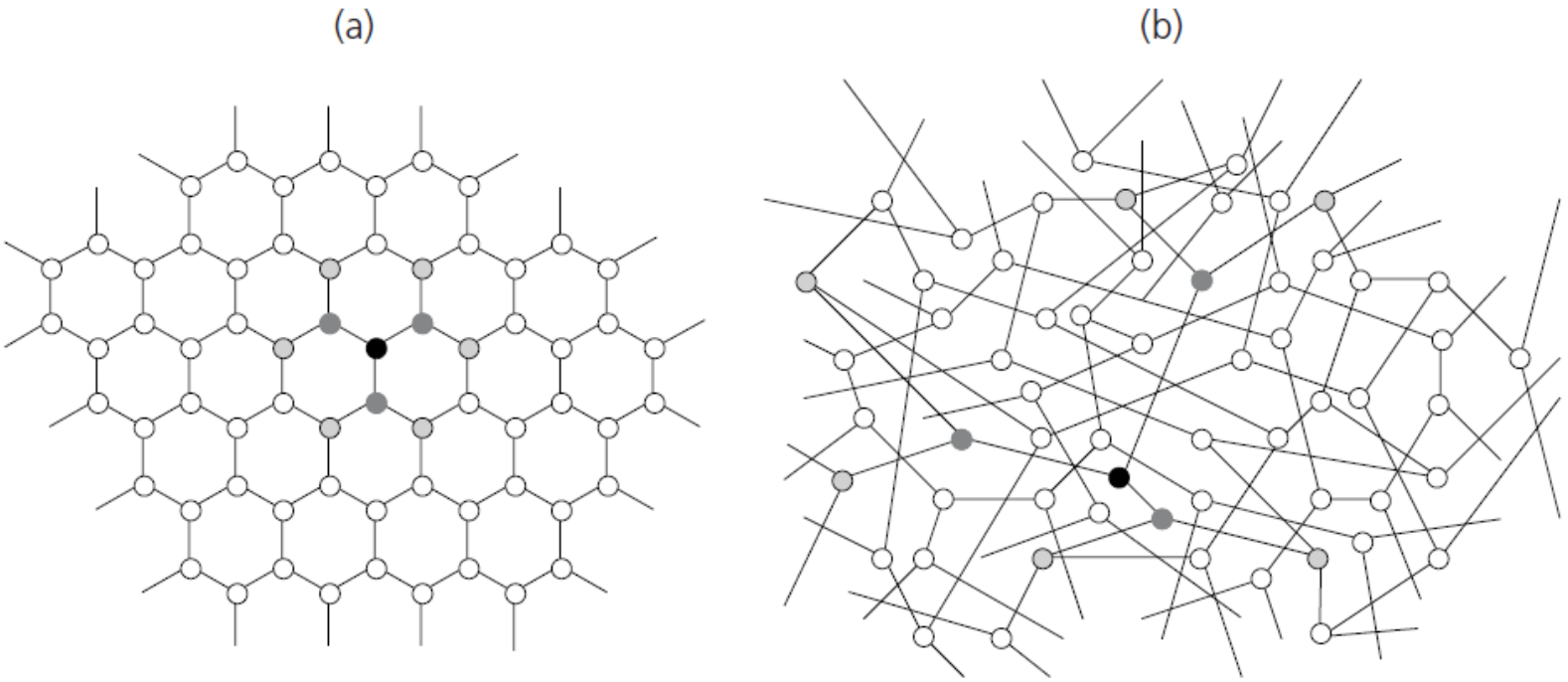


Figure 19.1 Examples of (a) a regular two-dimensional lattice and (b) a random network, both with a neighborhood size of three. In both graphs, a focal site (black) and its neighbors up to two links away (dark and light gray) are indicated.

From: van Baalen, M. (2000). Pair approximations for different spatial geometries. Pages 359-387 in: U. Dieckmann, R. Law, & J.A.J. Metz, Eds. The Geometry of Ecological Interactions: Simplifying Spatial Complexity. Cambridge University Press, Cambridge.

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

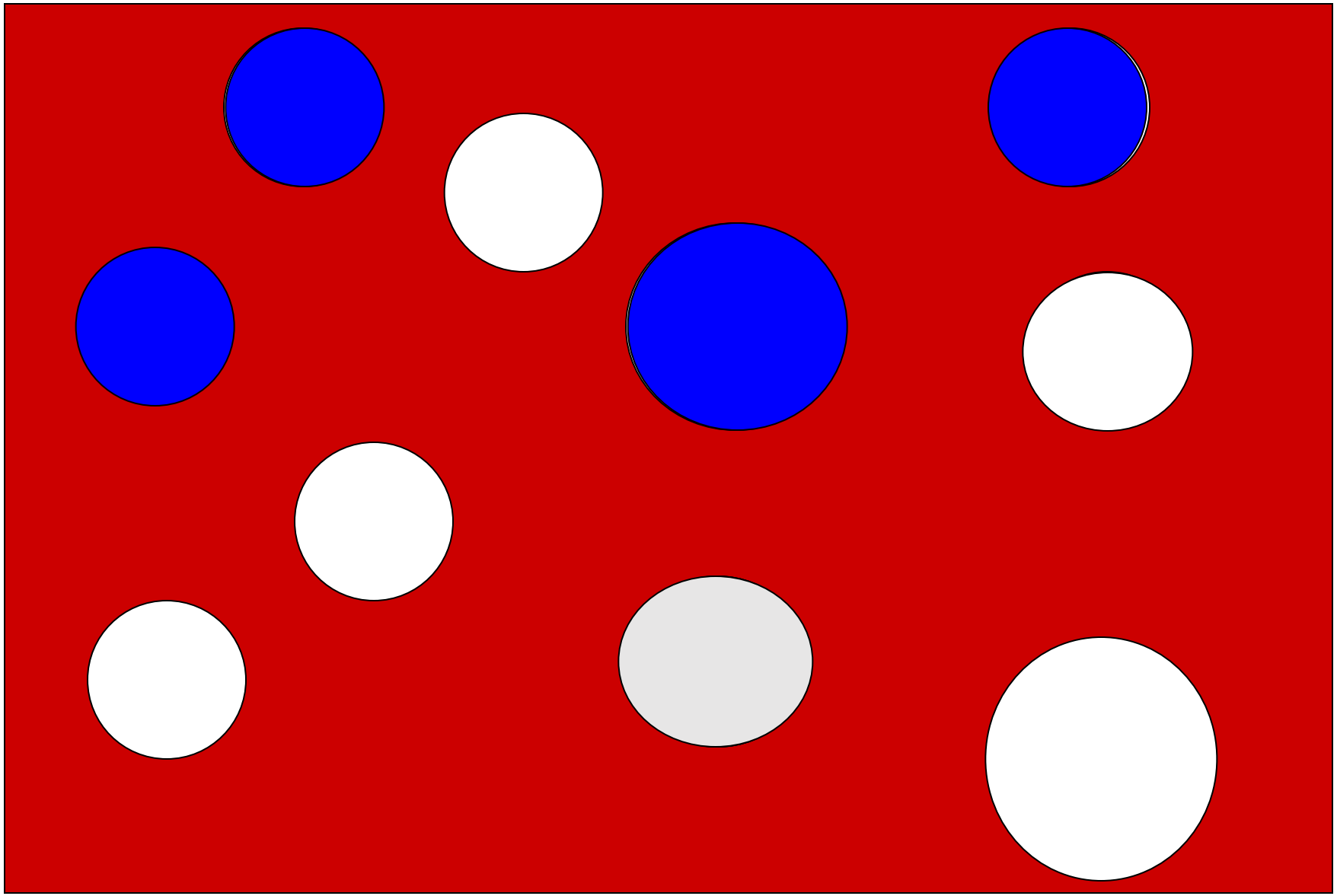
- Metapopulation:

  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

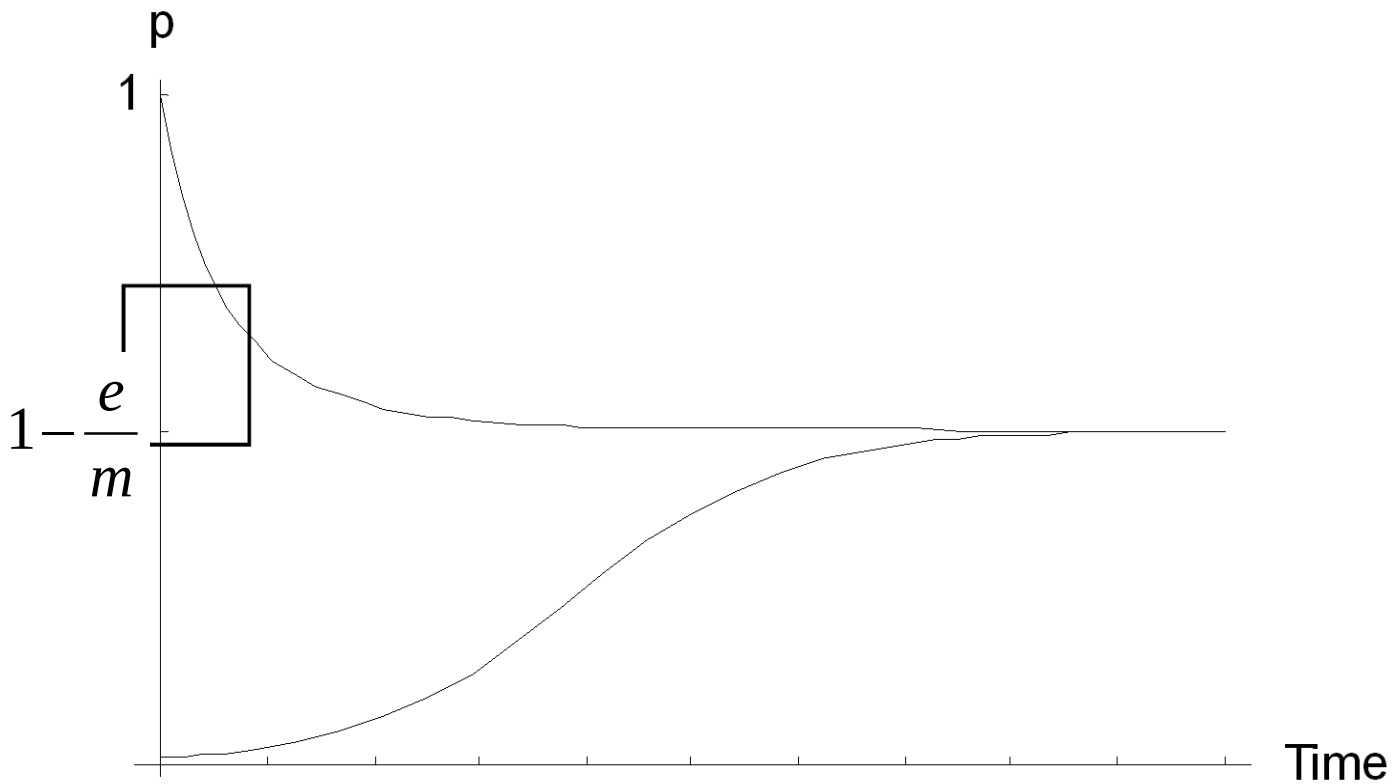
Every patch has a similar rate of sending out dispersers (*m p*), which need to find empty patches (*1-p*). Colonisation rate *m p* (*1-p*)

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

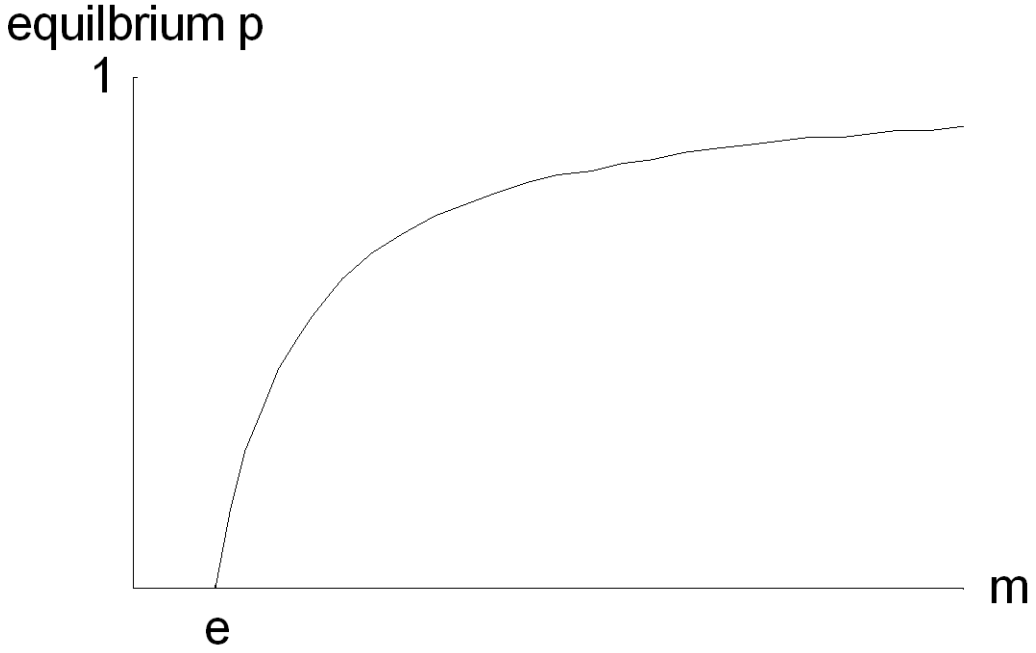
$$\frac{dp}{dt} = mp(1-p) - ep$$

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

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

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

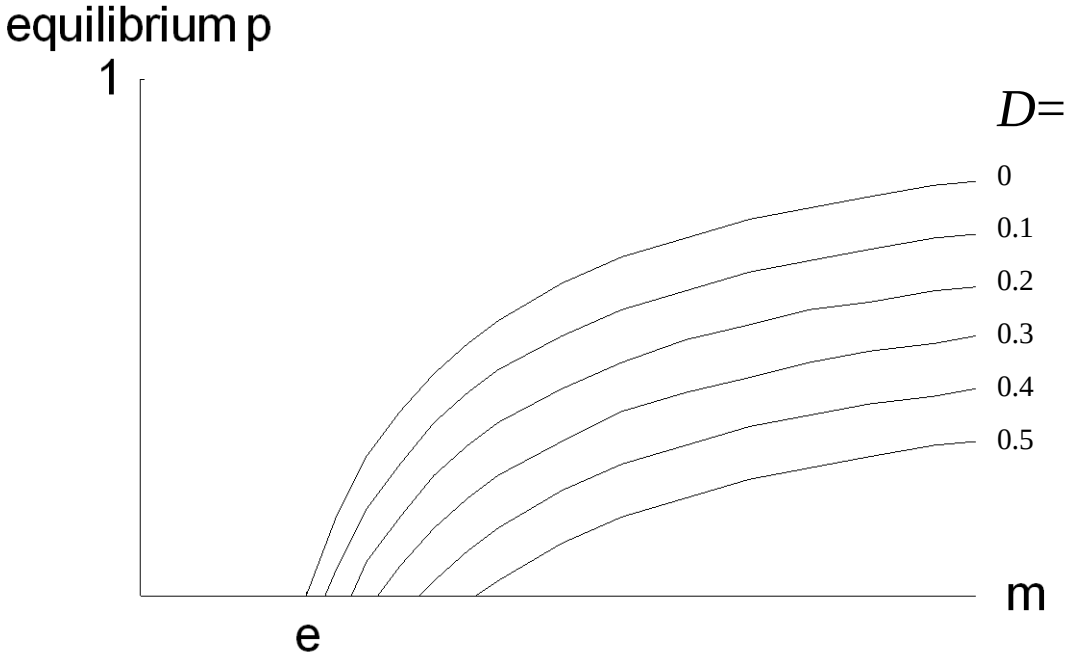
Habitat destruction

- 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 halfing 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

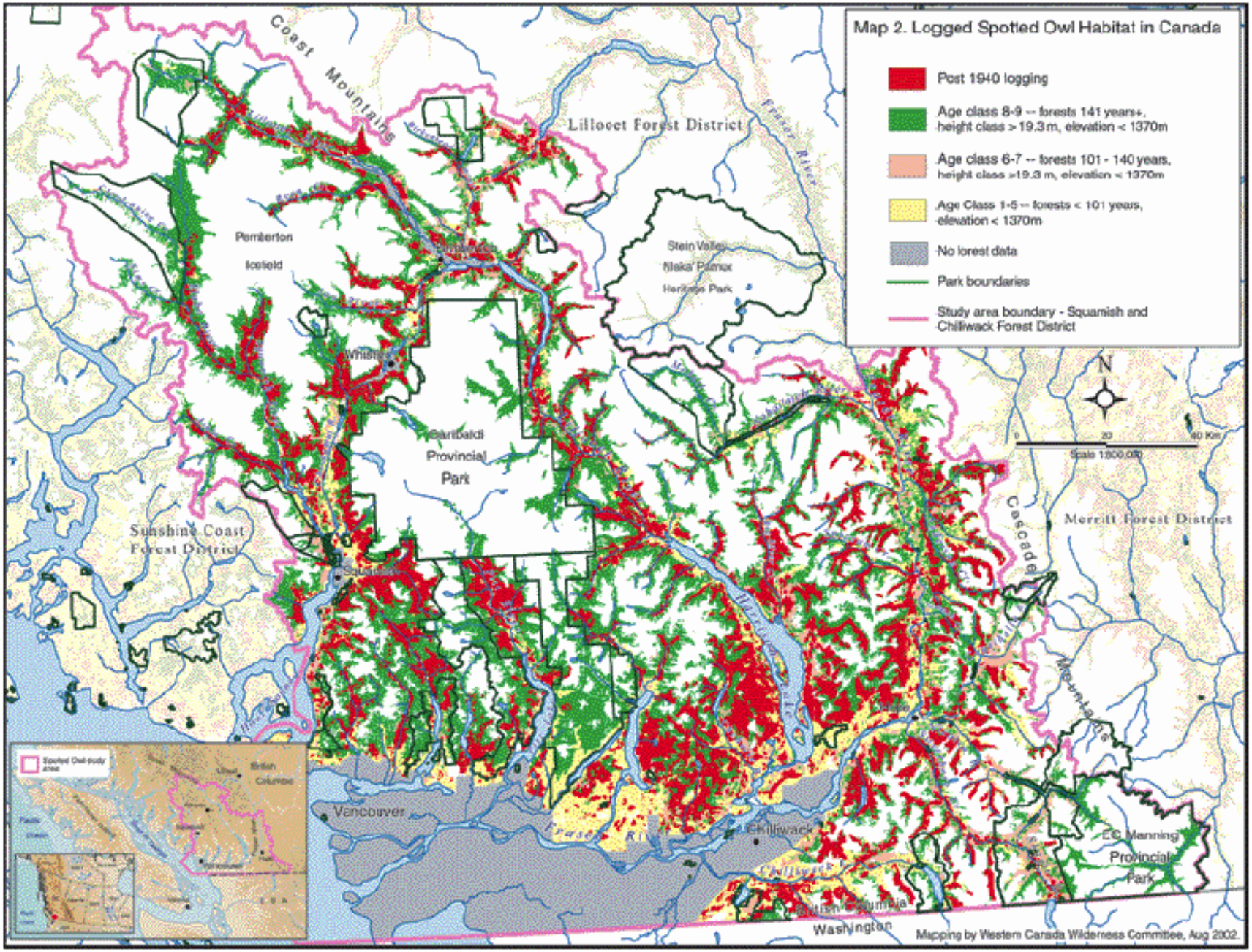
- the metapopulation was used in the debate around the protection of the northern spotted owl (*Strix occidentalis caurina*) in the USA

The Spotted Ow

- 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
Post 1940 logging
Age class 8-9 -- forests 141 years+, height class > 19.3m, elevation < 1370m
Age class 6-7 -- forests 101 - 140 years, height class >19.3 m, elevation < 1370m
Age Class 1-5 -- forests < 101 years, elevation < 1370m
No forest data
Park boundaries
Study area boundary - Squamish and Chilliwack Forest District
Coast Mountains
Lillooet Forest District
Fraser River
Pemberton Icefield
Stein Valley Nlaka' Pamux Heritage Park
Whistler
Garibaldi Provincial Park
Sunshine Coast Forest District
Squamish
Cascade Mountains
Merritt Forest District
Vancouver
Chilliwack
E.C. Manning Provincial Park
British Columbia
Washington
N
0 20 40 Km
Scale 1:800,000
Spotted Owl study area
Mapping by Western Canada Wilderness Committee, Aug 2002

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

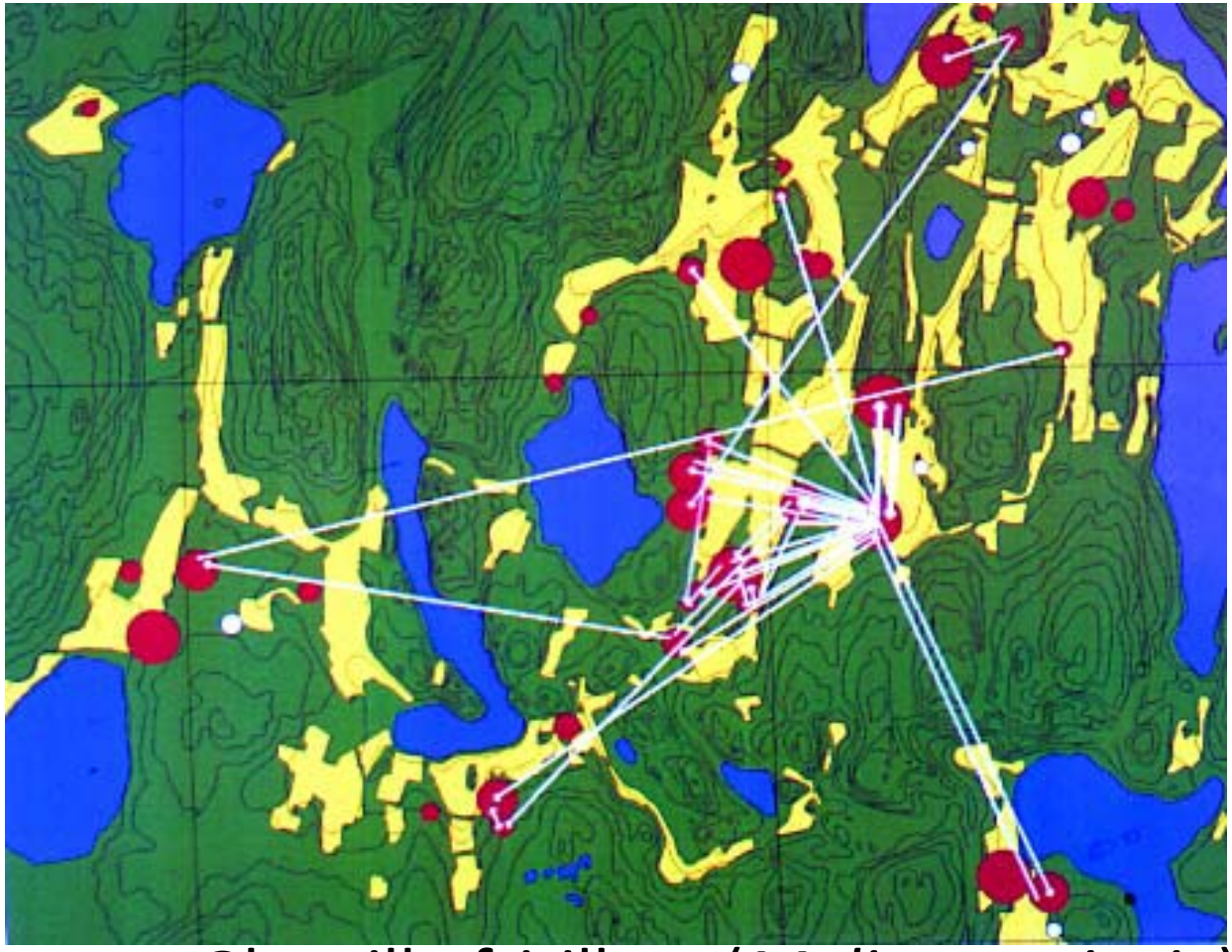
Examples of Metapopulations

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



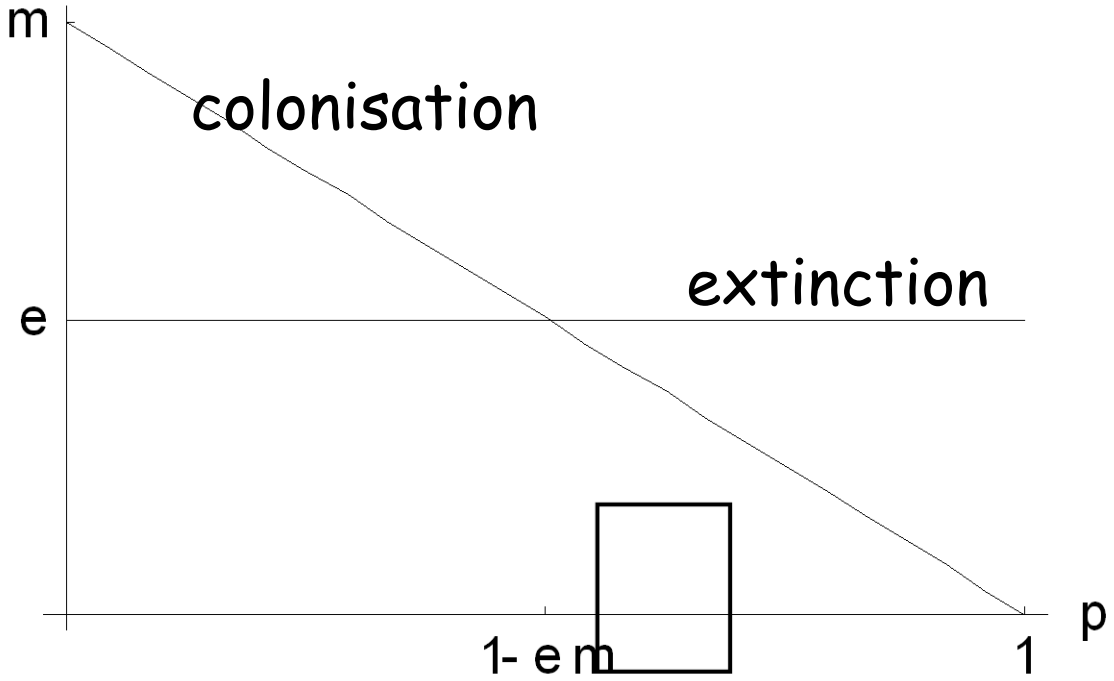
Glanville fritillary (*Melitaea cinxia*)

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

Rescue effect

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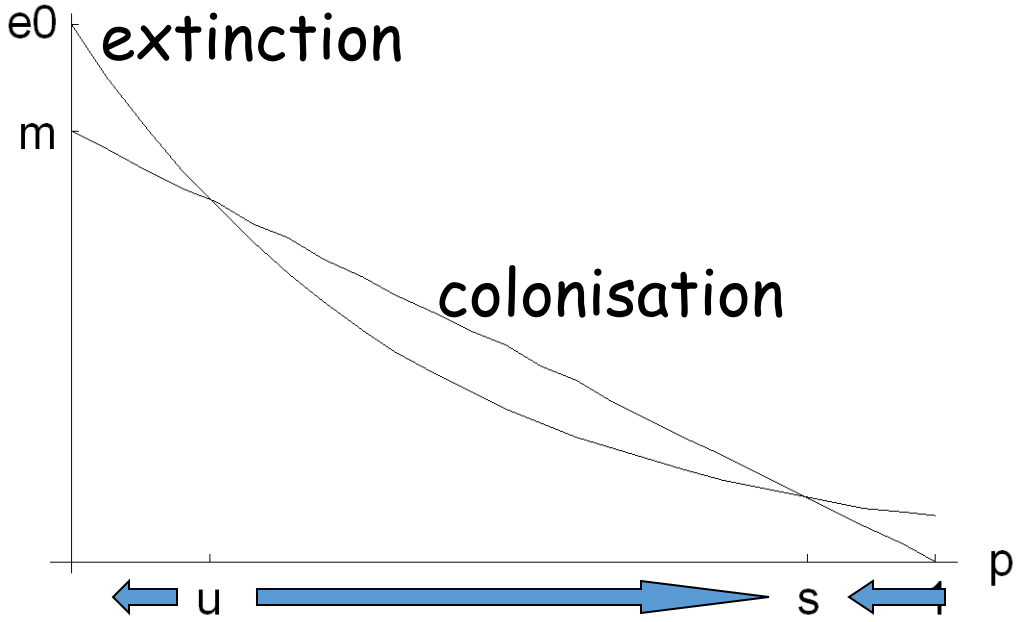
Rescue effect

- 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

- Do *Practical 1*, questions on metapopulation theory after the lectures.

Learning outcomes

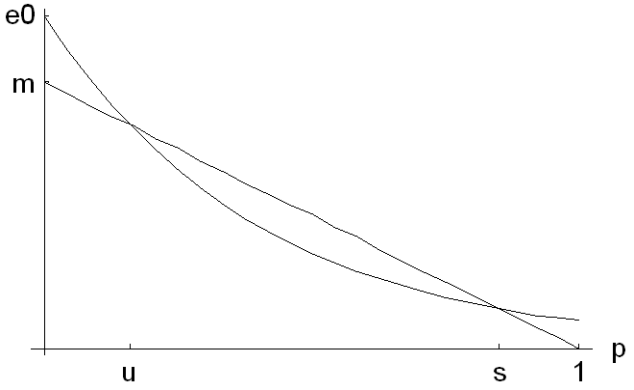
- Understand the exponential and logistic growth model
- Appreciate how to understand the qualitative outcomes of the model and how they depend on the parameters.
- Understand how the logistic model links to more detailed biological, e.g. metapopulation models

Rescue effect

- Equilibria:

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

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

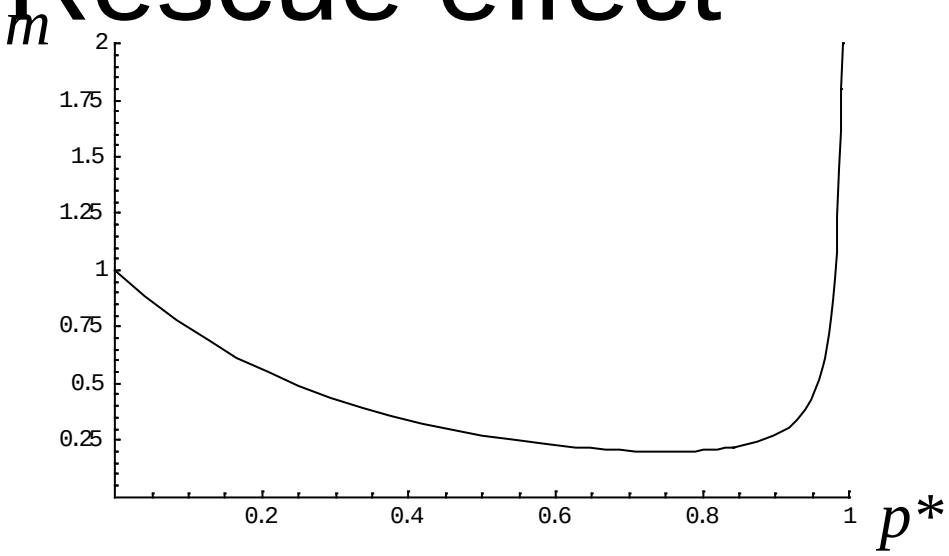


Rescue effect

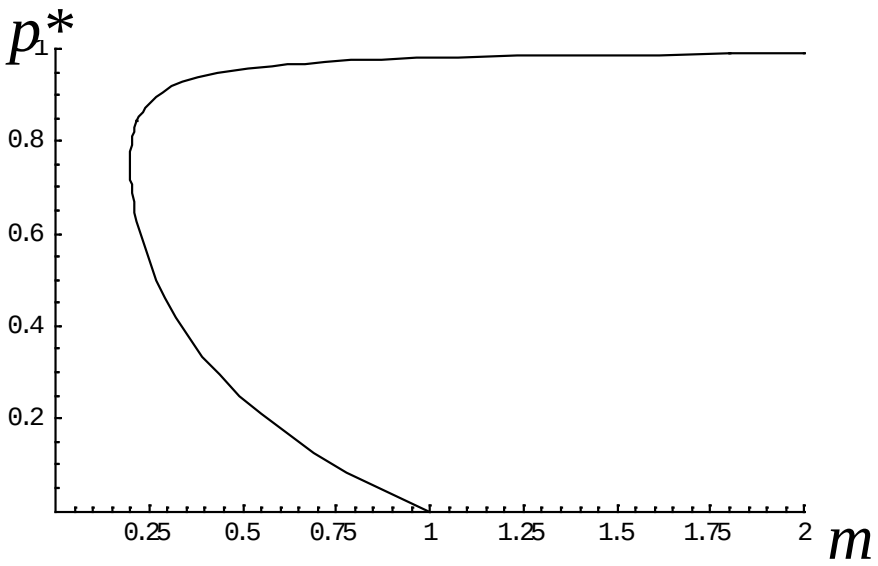
- We can employ a trick here. Even though we cannot solve it for *p**, we can solve it for *m* as

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

Rescue effect



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



Rescue effect

- Linearised model:

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

Rescue effect

Now note that:

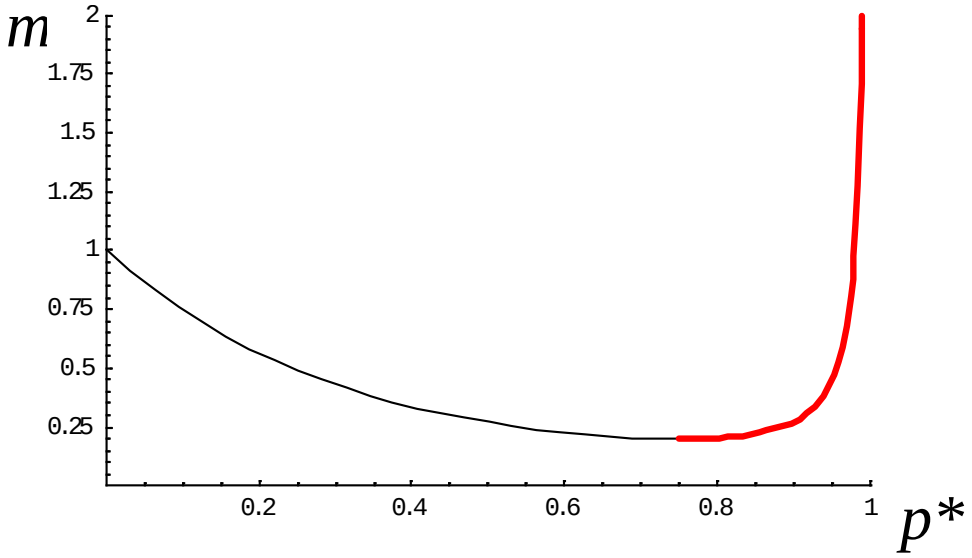
$$\frac{dm}{dp^*} = -\frac{e_0 \exp(-ap^*)}{\left(1-p^*\right)^2}\left(a\left(1-p^*\right)-1\right)$$

$$= \frac{m}{\left(1-p^*\right)}\left(a\left(1-p^*\right)-1\right)$$

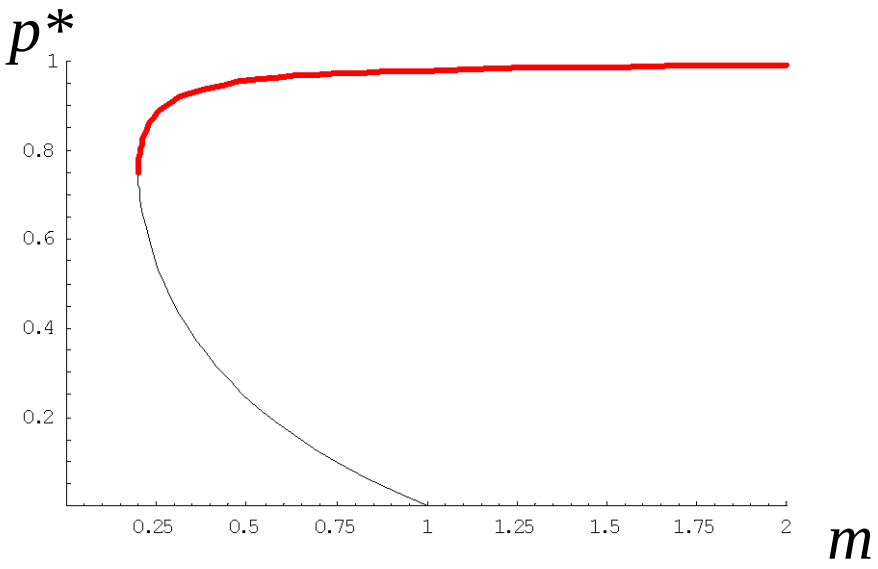
And hence:

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

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}}

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

$\lambda=1/2+-1/2$ 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+ λ- λ^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