Growth

Stefano Allesina

What is ecology?

Ecology is the study of the relationships between **living organisms**, and their **physical environment**.

It is **highly interdisciplinary** (genetics, evolutionary biology, physics and chemistry, geography, ethology, demography, sociology).

It studies living systems at different scales:

- **Individuals** (metabolism, behavior, life-history)
- **Populations** (conspecifics living in the same habitat)
- **Metapopulations** (populations connected by migration/dispersal)
- **Communities** (interacting populations of different species)
- **Ecosystems** (including their physical and chemical characteristics)

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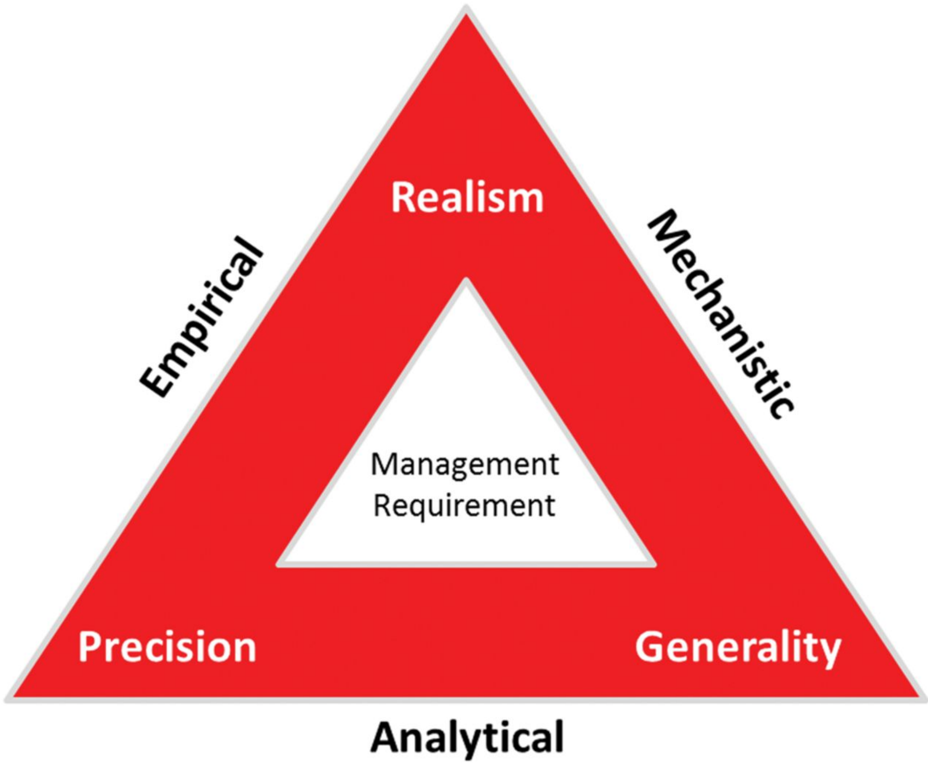
Complex adaptive systems

Ecological systems are prototypical **Complex Adaptive Systems**

- **Complex:** dynamic; composed of many interacting agents; network structure; nonlinear interactions.
- **Adaptive:** respond to change; adapt to new conditions; evolve.

Modeling complex systems



Dickey-Collas et al. ICES Journal of Marine Science, 2014

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Organization of the class

- **4.5 weeks**
- Each week, we pick **a theme**
- We explore **data**, **concepts**, and **mathematical models** on the theme
- We stress **ecological thinking**

You can find all the material (slides, data, code, papers) on the website for the class

github.com/StefanoAllesina/Bios20150 (https://github.com/StefanoAllesina/Bios20150)

If the title of a slide ends with the symbol Δ, then the data is available on the website. Similarly Π stands for papers, and χ for code.

How many people can the Earth support?

I was ever of opinion, that the honest man who married and brought up a large family, did more service than he who continued single, and only talked of population.

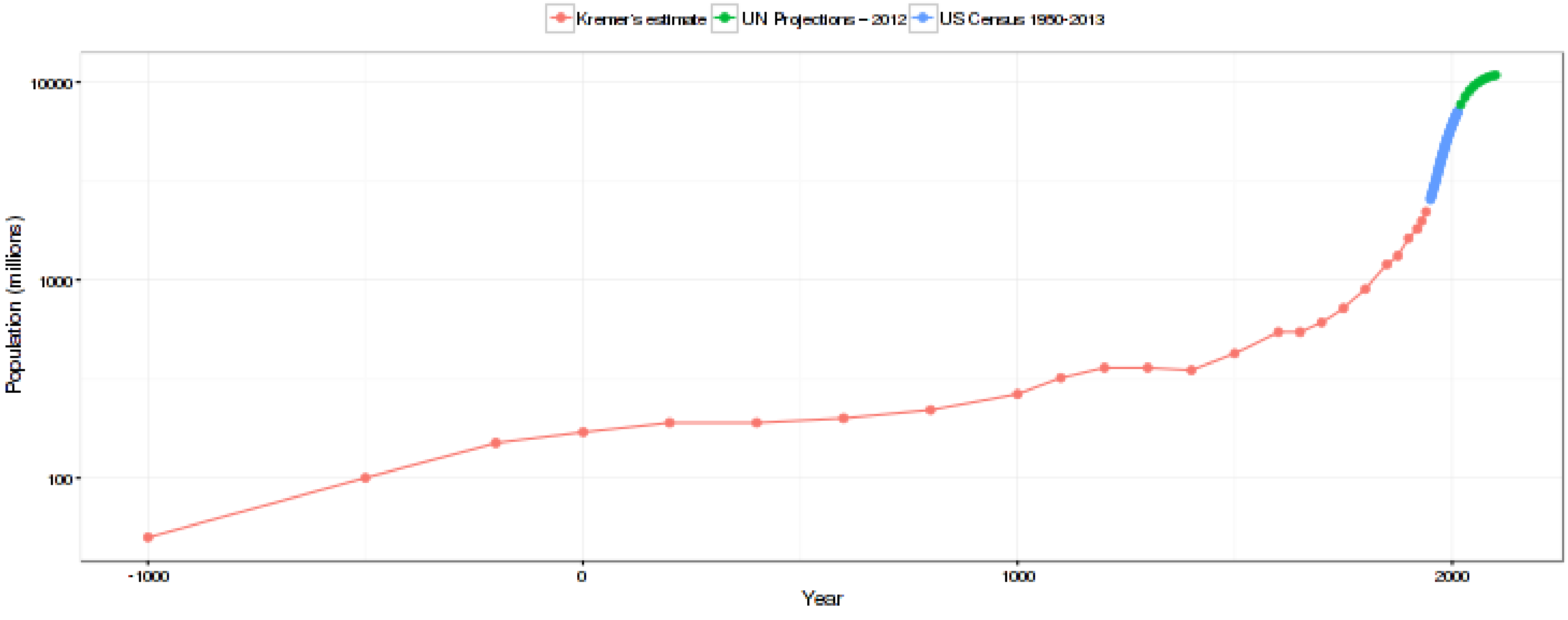
The Vicar of Wakefield (1776) by Oliver Goldsmith

Human growth: historical time series Δ

Years

-1,000 2,100

-1,000 -690 -380 -70 240 550 860 1,170 1,480 1,790 2,100



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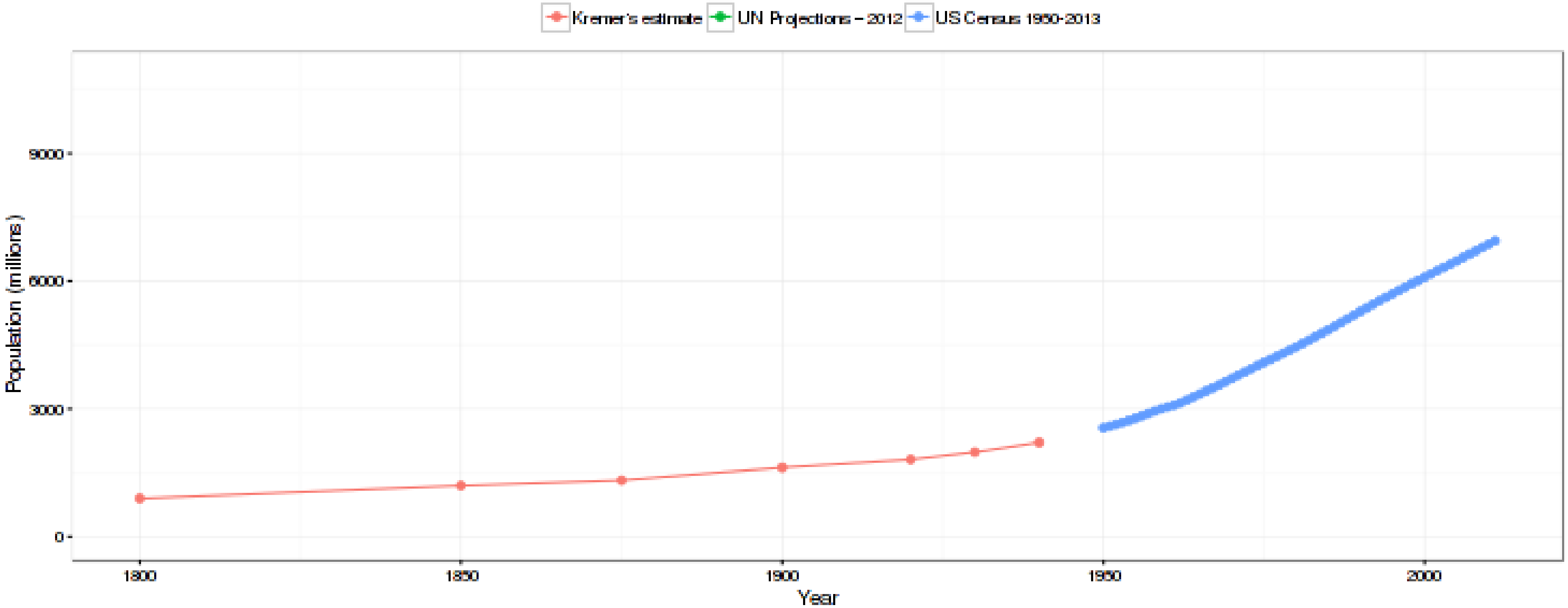
Why do we care? Δ



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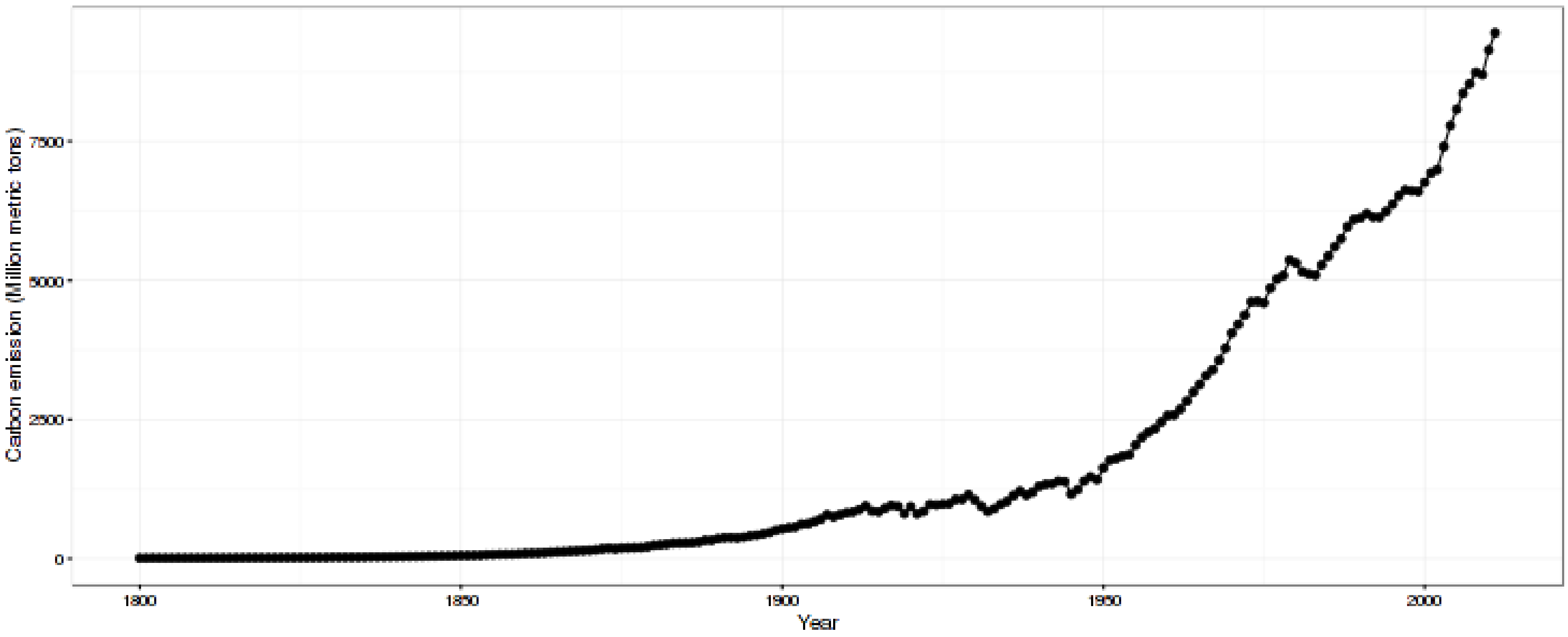
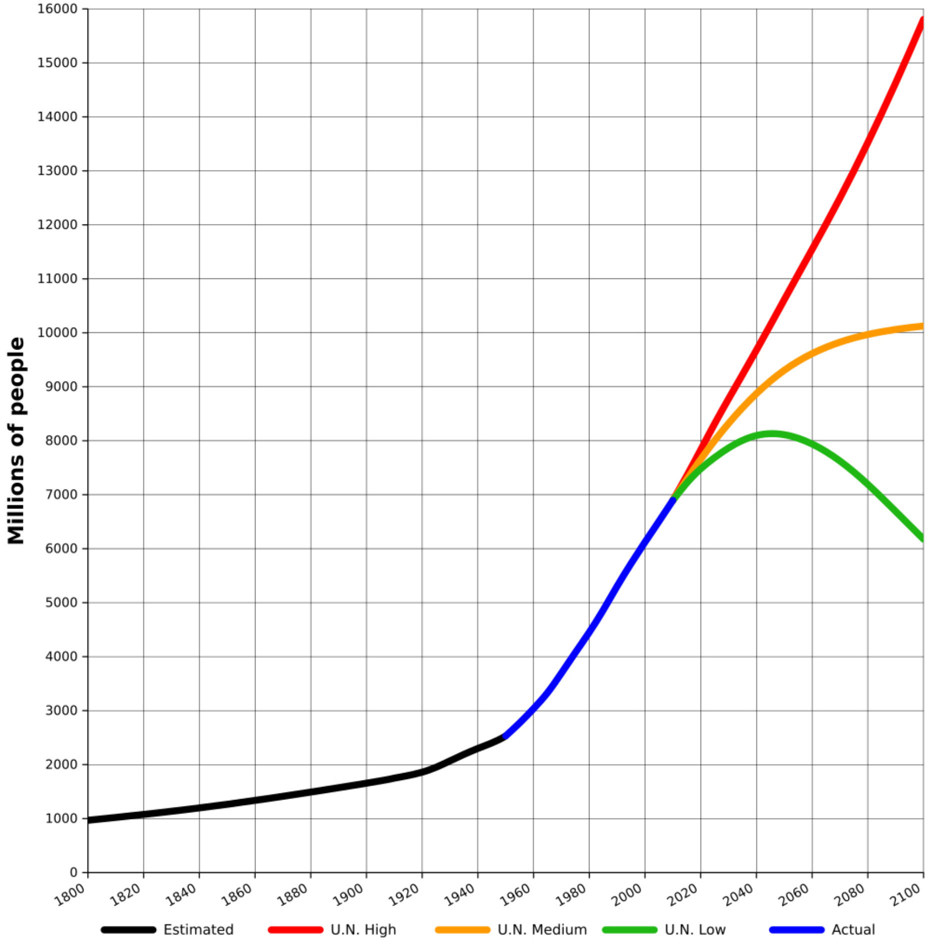
Why do we care? Δ



Estimates for 2100



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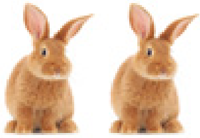
Fibonacci

Leonardo Pisano (a.k.a. Fibonacci) was the son of a trader from Pisa. In 1192, he followed his father to Bejaia, Algeria, where he studied the number systems the Arabs had brought from India. This is the decimal system we use today.

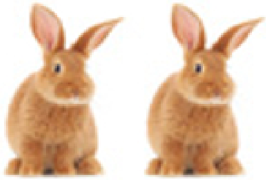
In 1202 he published the *Liber Abaci* where he introduced the number system that rapidly spread through Europe. The book contains a problem on the growth of the growth of rabbits, giving raise to the famous Fibonacci's sequence.

Rabbits

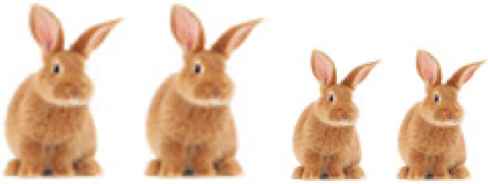
Take a couple of rabbits.



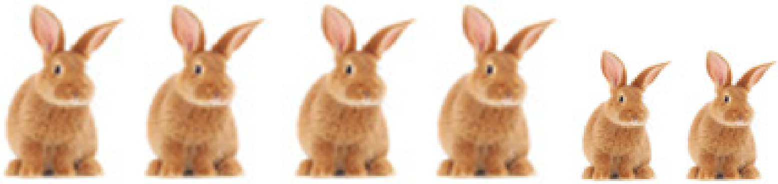
They're fully grown in one month.



The next month they reproduce: a new pair of rabbits!



They reproduce again, while their offspring matures:



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Many rabbits! χ

In a few years, the Earth would be scorched by hordes of rabbits!

$N_t = N_{t-1} + N_{t-2}$

```
##        [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11] [,12]
## Months    1    2    3    4    5    6    7    8    9    10    11    12
## Pairs     1    1    2    3    5    8   13   21   34    55    89   144
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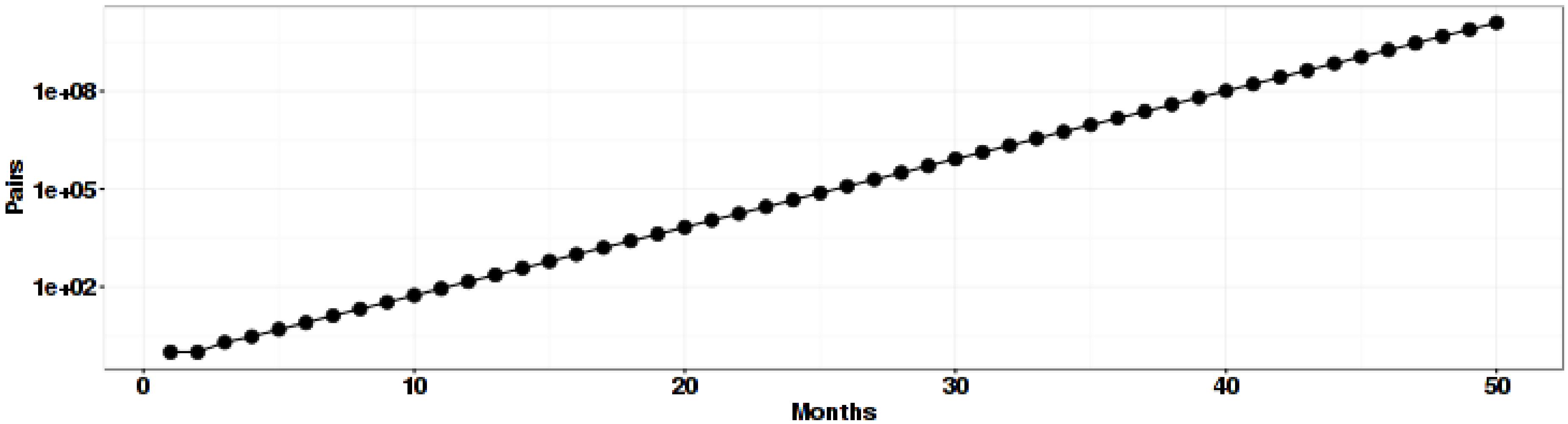

Geometric growth

The Swiss mathematician Euler (1707-1783) has left an indelible mark on science, publishing fundamental works in a number of mathematical disciplines. He became interested in the growth of populations because of what he read (and believed) in the Bible:

These three were the sons of Noah; and from these the whole earth was peopled (Genesis 9:19)

How long would it take to the sons of Noah to "people" the Earth? Euler considered the following model:

$$N_t = (1 + x)N_{t-1}$$

x is called the *annual growth rate* of the population. Starting from a certain population size (i.e., knowing N_0), we can project forward:

$$N_1 = (1 + x)N_0$$

$$N_2 = (1 + x)N_1 = (1 + x)^2 N_0$$

$$N_3 = (1 + x)N_2 = (1 + x)^3 N_0$$

$$\dots$$

Geometric growth

In his treatise *Introduction to the Analysis of the Infinite* (1748), Euler wrote:

Since after the Flood all men descended from a population of six, if we suppose that the population after two hundred years was 1,000,000, we would like to find the annual rate of growth.

Mathematically, you want to solve for x:

$$N_{200} = (1+x)^{200} N_0$$

$$10^6 = (1+x)^{200} 6$$

This looks very easy to solve, but it is not, if you don't have a calculator! Euler exploited a very recent invention, the table of logarithms (introduced by Napier in 1614):

$$\log_{10}(10^6) = \log_{10}((1+x)^{200} 6)$$

$$(6 - log_{10}(6))/200 = \log_{10}(1+x)$$

yielding $x \approx 0.0619$, meaning about 6.2% per year. Not an unrealistic result according to Euler, who concluded:

For this reason, it is quite ridiculous for the incredulous to object that in such a short space of time the whole earth could not be populated beginning with a single man

Geometric growth?

Interestingly, Euler repeated his calculation projecting forward of 400 years (instead of 200), and found that it would lead to more that 166 billion humans. He noted:

However, the whole earth would never be able to sustain that population.

Hold this thought, as we're going to explore it later.

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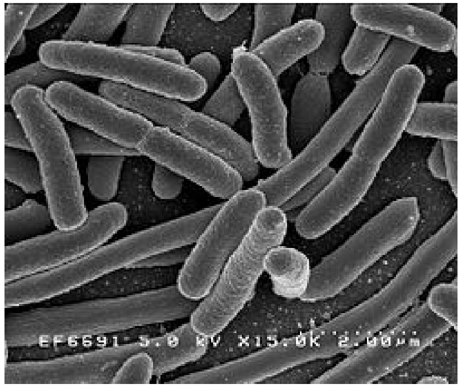
Just how fast is geometric growth?

Meet *Escherichia coli*, a Gram-negative bacterium that lives in your intestine (and in many other places). Some strains of *E. coli* can cause serious food poisoning.



Under ideal conditions, it can reproduce every 20 minutes (72 times per day). Each cell weighs about 10^{-15} kg.

We can write an equation for the mass of a population of *E. coli*, starting with a single bacterium, at time d days:

$$M_d = M_0 2^{72d}$$

and project forward

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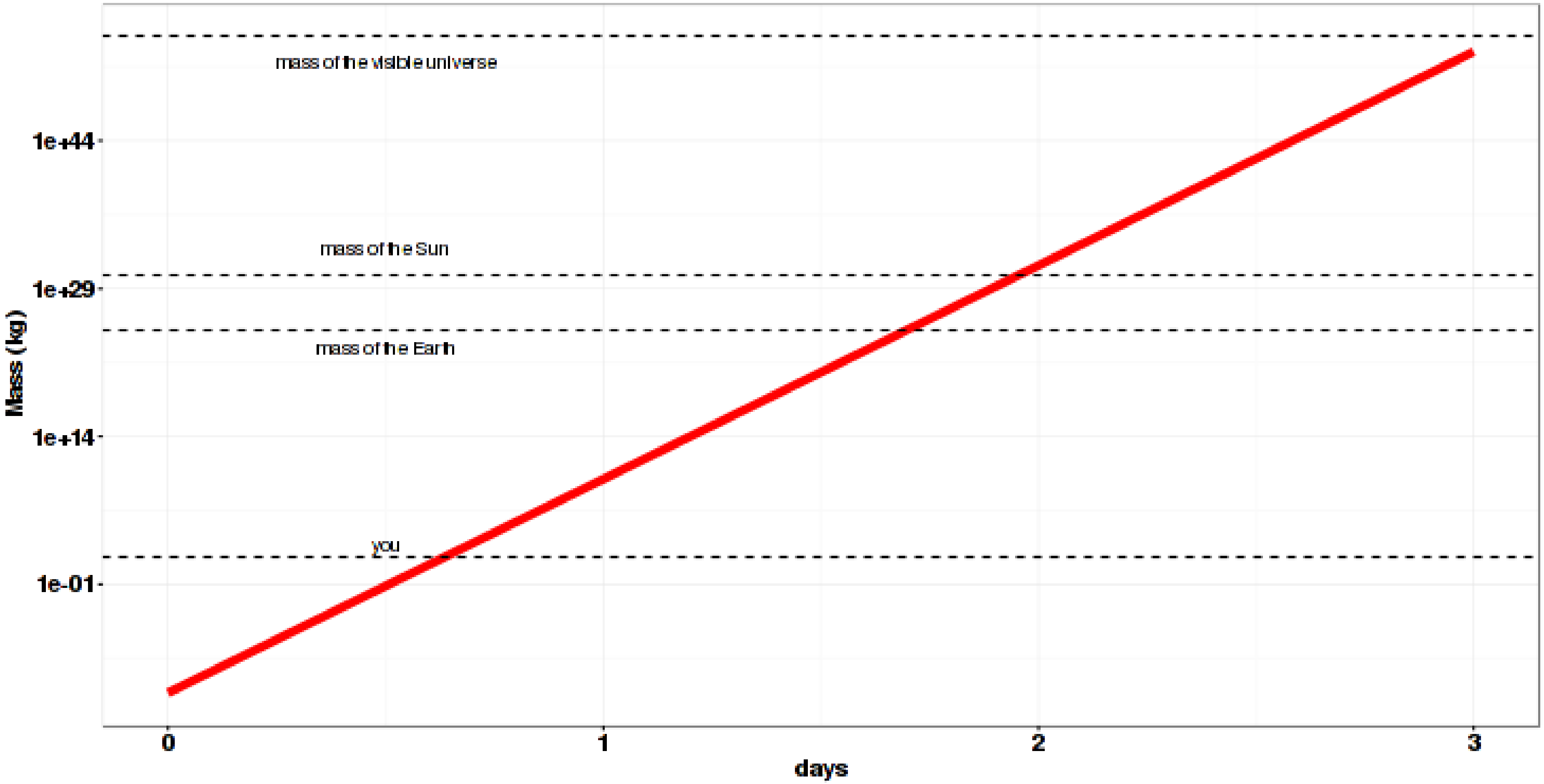
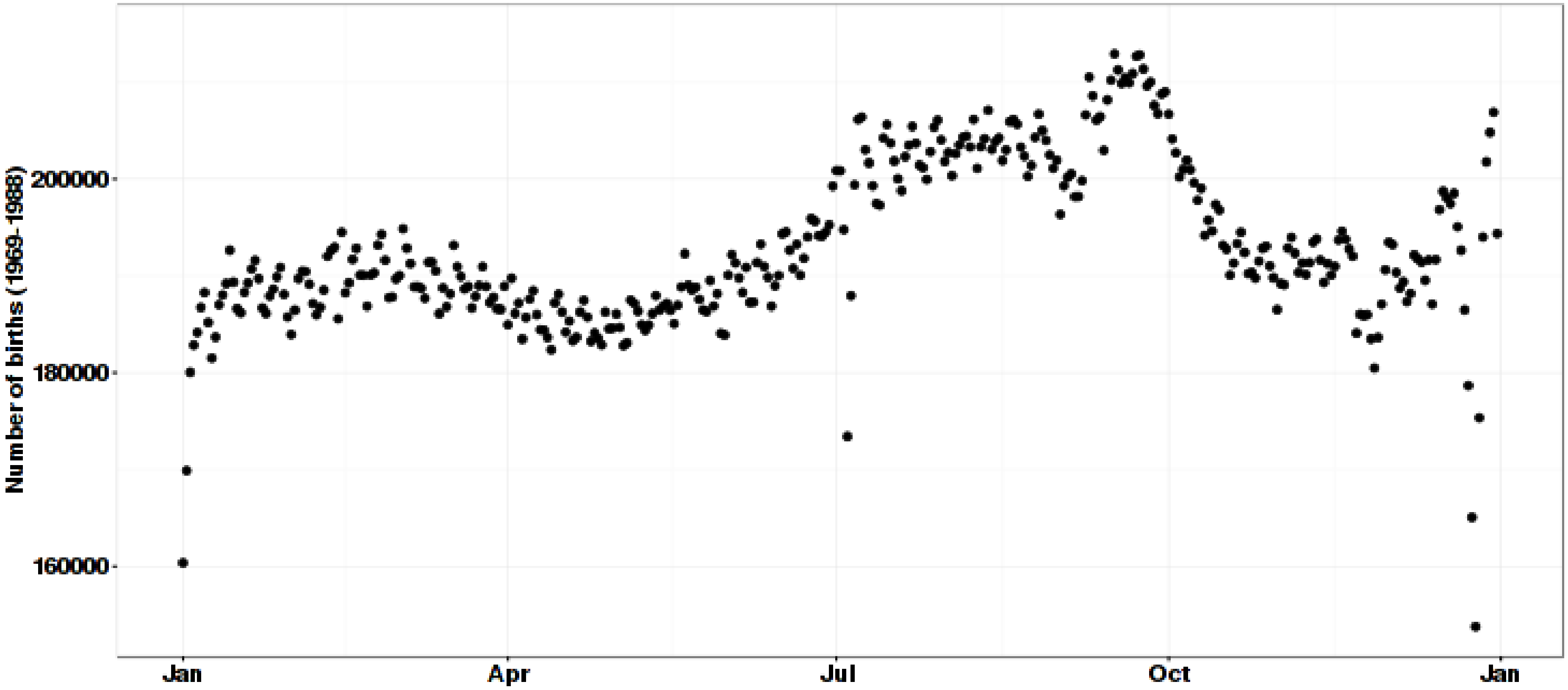
E. coli colony growth χ



Synchronized births Π

- Reproduction is synchronized in many animals and plants.
- Besides obvious seasonal effects, there might be more subtle causes leading to clustering in births (see Ims, 1990).
- These include phenological (e.g., pollinators hatch when plants are flowering), ecological (e.g., escape predators), and sociobiological (e.g., cooperative breeders).
- One of the most amazing cases is that of the banded mongoose (*Mungos mungo*): within a group, 64% of the births happen in the same night! (The reason for this is not very romantic: read Hodge *et al.* 2010).

Births by day in US 1969-88 (50 states and DC) Δ



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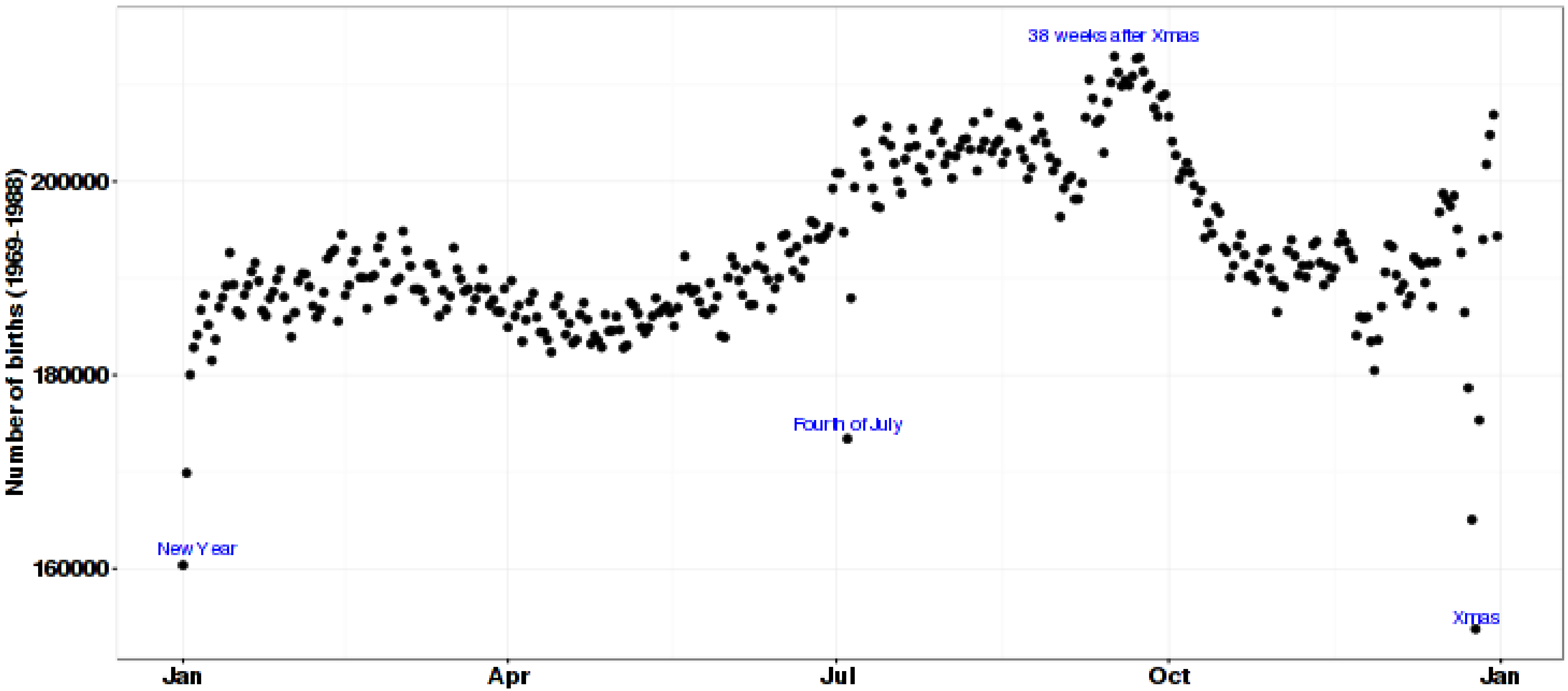
Births by day in US 1969-88 (50 states and DC) Δ



From discrete to continuous growth

$X(t + \Delta t) = X(t)(1 + r\Delta t)$

$X(t + \Delta t) - X(t) = r\Delta t X(t)$

$$\frac{X(t + \Delta t) - X(t)}{\Delta t} = rX(t)$$

Take the limit $\Delta t \to 0$:

$$\frac{dX(t)}{dt} = rX(t)$$

Exponential growth

Define initial population $X(0) = X_0$.

We model the **growth rate** of the population as:

$$\frac{dX(t)}{dt} = rX(t)$$

Meaning:

- $\frac{dX(t)}{dt}$ growth rate of population at time t. [units: Kg / time]
- $X(t)$ biomass (alternatively number of individuals, density per square Km, etc.) at time t. [units: Kg]
- r intrinsic growth rate [units: 1 / time]. $r > 0$ means the population grows, $r < 0$ shrinks, $r = 0$ is constant.

Solution:

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

- e is Euler's number $2.71828182845904523536028747135 2\ldots$

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Doubling time

How long before the population doubles in size?

$X(\tau) = 2X(0)$

$X(\tau) = X(0)e^{r\tau} = 2X(0)$

Independent of $X(0) > 0$!

$e^{r\tau} = 2$

$r\tau = \log(2)$

$\tau = \frac{log(2)}{r} = \frac{0.301029995...}{r}$

Thus, if $r = 0.01$, then the population doubles every 30 years or so; $r = 0.05$, every 6 years; and so on.

Halving time and carbon dating

Unstable atoms release energy through radioactive decay. This process is random, and, at the level of the single atom, cannot be predicted. However, we can measure statistically the rate at which atoms decay. The Carbon isotope $^{14}\mathrm{C}$ is formed in the athmosphere when cosmic rays strike Nitrogen atoms:

$$n + {}^{14}_{7}\mathrm{N} \rightarrow {}^{14}_{6}\mathrm{C} + p$$

Radioactive carbon forms CO_2 that is used by plants. Animals eat plants, etc. so that it is widely distributed in the biosphere. When an organism dies, it stops acquiring ${}^{14}_{6}\mathrm{C}$. In the athmosphere/living organisms, there are about 1.5 atoms of $^{14}\mathrm{C}$ for every 10^{12} of $^{12}\mathrm{C}$. The radioactive carbon loses an electron, and changes a proton into a neutron by emitting an electron antineutrino, resulting in Nitrogen.

$${}^{14}_{6}\mathrm{C} \rightarrow {}^{14}_{7}\mathrm{N} + e^{-} + \bar{\nu}_e$$

In about 5730 years, half of the radioactive carbon has decayed. Hence, $r = -log(2)/5730 = -0.00012096809$. If a tissue has only 0.75 parts of $^{14}\mathrm{C}$ for every 10^{12} of $^{12}\mathrm{C}$, the tissue is 5730 years old. A proportion of of $0.25/10^{12}$ would yield 34380 years, and so forth.

This method was proposed by Willard Libby (UofC) and collaborators in 1949. They were awarded the Nobel prize in 1960.

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Exercise: Date a the Shroud of Turin

"The Shroud of Turin, which many people believe was used to wrap Christ's body, bears detailed front and back images of a man who appears to have suffered whipping and crucifixion. It was first displayed at Lirey in France in the 1350s and subsequently passed into the hands of the Dukes of Savoy. After many journeys the shroud was finally brought to Turin in 1578 where, in 1694, it was placed in the royal chapel of Turin Cathedral in a specially designed shrine." (Damon *et al. Nature*, 1988)

In 1988, three laboratories analyzed the sample. They found that it had lost about 8% of its $^{14}\mathrm{C}$. Can you date the Shroud?

You can use the forumla $N(t) = N(0)e^{-0.000121t}$ to find the answer.

First law of ecology Π

If left unchecked, populations will grow/decay very fast!

Example: rabbits (again)

- Lore has it, Thomas Austin released 24 rabbits in his property near Victoria (Australia) in 1859.
- By 1886, the population had covered Victoria and New South Wales.
- In the 1920s, they were billions.
- Efforts to contain rabbits included building three rabbit-proof fences (failed), releasing the virus for mixomatosis and rabbit haemorrhagic disease. Read Bergstrom *et al.* 2009 for a detailed account on Macquarie Island in Tasmania.

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Limits to growth

Thomas R. Malthus (anonymously) published in 1978 a book entitled *An Essay on the Principle of Population, as It Affects the Future Improvement of Society, With Remarks on the Speculations of Mr Godwin, Mr Condorcet and Other Writers*.

The central idea of the book is that human populations will grow until they reach the limit of starvation. This negative view of progress inspired subsequent work (esp. Darwin), and elicited strong reactions (esp. Marx).

[…] the power of population is indefinitely greater than the power in the earth to produce subsistence for man. Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will shew the immensity of the first power in comparison of the second. By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal. This implies a strong and constantly operating check on population from the difficulty of subsistence. This difficulty must fall somewhere; and must necessarily be severely felt by a large portion of mankind.

In the second edition, titled *An Essay on the Principle of Population, or a View of its Past and Present Effects on Human Happiness, With an Enquiry Into Our Prospects Respecting the Future Removal or Mitigation of the Evils Which It Occasions* Malthus expanded on the possible ways to keep populations in check, including war, famine, abortion, economic factors, and delayed marriage.

Logistic growth

Inspired by Malthus, the Belgian mathematician Pierre-Francois Verhulst noted that there must be a limit to geometric growth, which can only be achieved in very special cases:

We shall not insist on the hypothesis of geometric progression, given that it can hold only in very special circumstances; for example, when a fertile territory of almost unlimited size happens to be inhabited by people with an advanced civilization, as was the case for the first American colonies.

He wrote a simple ordinary differential equation to describe the slowing down of growth at high population values:

$$\frac{dX(t)}{dt} = rX(t)\left(1 - \frac{X(t)}{K}\right)$$

This is now known as **logistic growth**, with r representing the intrinsic growth rate of the population when at low abundance, and K being the carrying capacity.

Logistic growth: behavior χ

Initial density X(0)

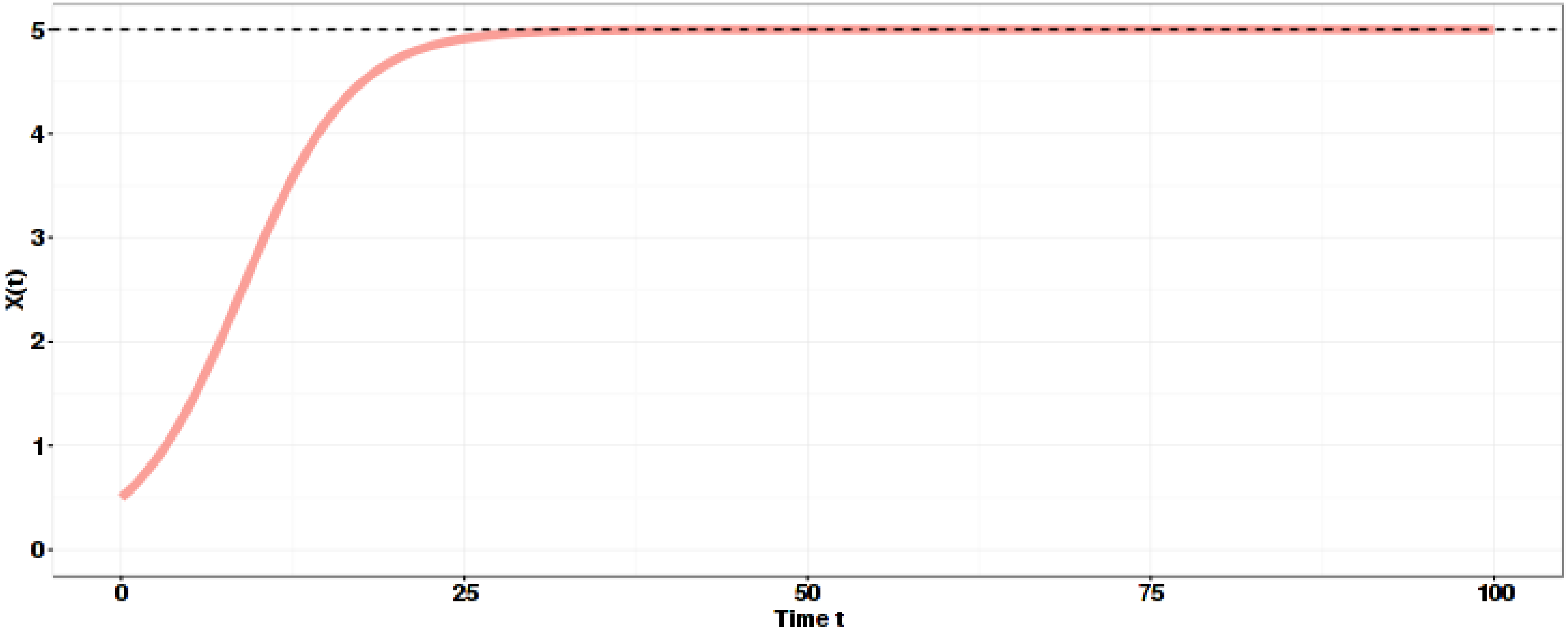
0.5

Intrinsic growth r

0.25

Carrying capacity K

5



You can estimate parameters from data

You can solve the equation:

$$X(t) = \frac{X(0)e^{rt}}{1 + X(0)(e^{rt} - 1)/K}$$

Take the population at three equally spaced points: X_0, X_1, X_2, each at T time units apart. Then:

$$K = X_1 \frac{X_0 X_1 + X_1 X_2 - 2X_0 X_2}{X_1^2 - X_0 X_2}$$

and

$$r = \frac{1}{T} \log\left(\frac{1/X_0 - 1/K}{1/X_1 - 1/K}\right)$$

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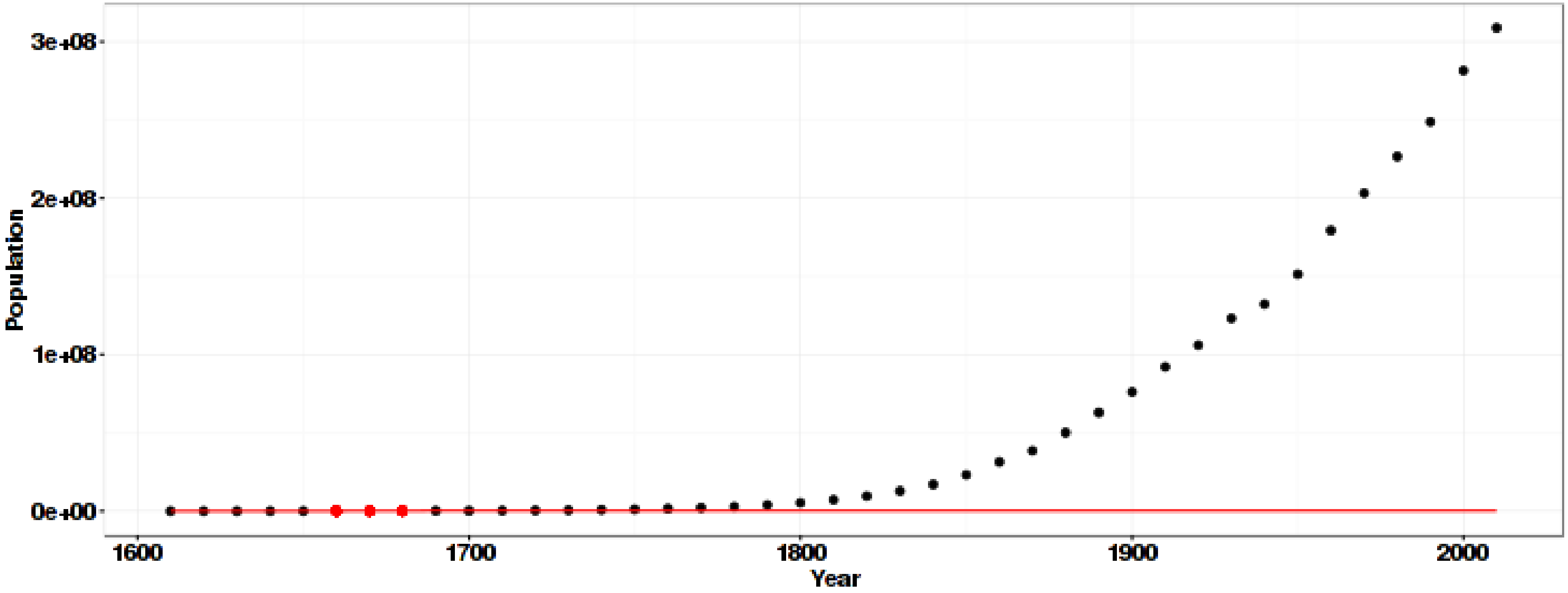
Example: US Population Δ

Starting date

1660

T

10



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Interesting cases

$$\frac{dX(t)}{dt} = rX(t)\left(1 - \frac{X(t)}{K}\right)$$

When $X \approx 0$, then we can approximate:

$$\frac{dX(t)}{dt} = rX(t) - \frac{rX(t)^2}{K} \approx rX(t)$$

…exponential growth!

When $X \approx K$, then the growth rate is close to zero (equilibrium, or steady-state).

When $X > K$, then the growth is negative.

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Equilibria χ

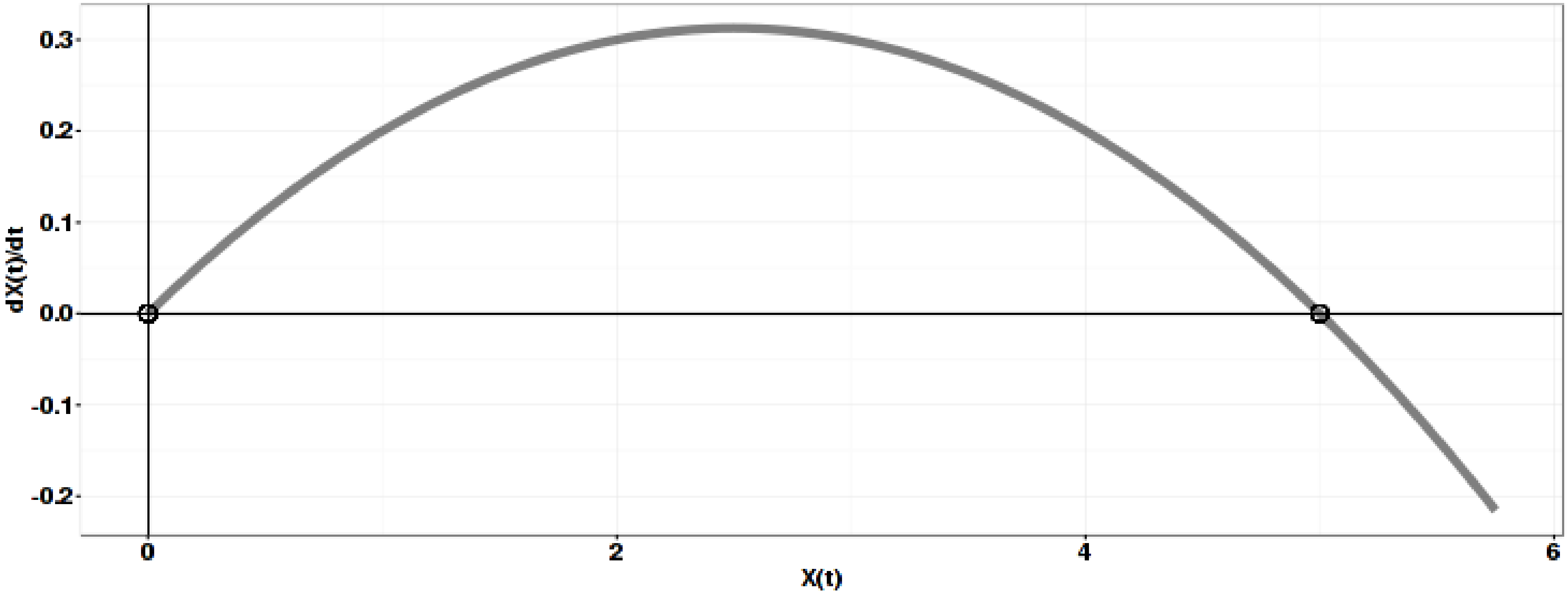
For which values of $X(t)$ does $\dfrac{dX(t)}{dt} = 0$?

Intrinsic growth r

0.25

Carrying capacity K

5



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Stability χ

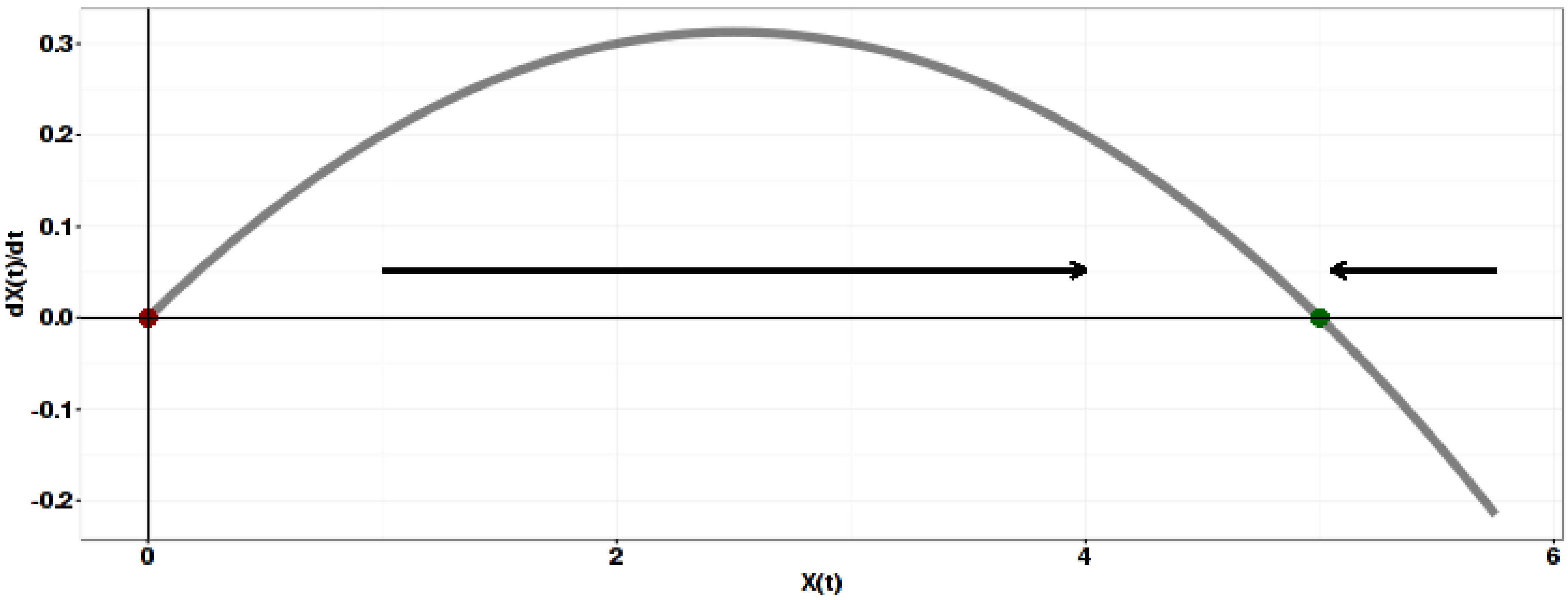
Will the population go back to the equilibrium if perturbed?

Intrinsic growth r

0.25

Carrying capacity K

5



What's carrying capacity?

Carrying capacity is the **maximum population size an environment can sustain indefinitely**.

- Limited resources (food, water, space)
- Crowding and interference

Overshooting the carrying capacity can have devastating effects:

- 1944: St Matthew Island, Bering Sea. 29 reindeers introduced.
- 1957: $>$ 1000 reindeers on the island. Individuals healthy; small patches overgrazed.
- 1963: $>$ 6000; thin and showing signs of stress; large overgrazed patches.
- 1966: only 42 survivors; no males; extinction within one generation.

Intra-specific competition

Intra-specific competition is a special case of density-dependent growth: the per-capita growth rate depends on the density of the population.

In the typical differential equations used to describe population growth, density-dependence appears as a non-linear term.

Exponential growth:

$$\frac{dX(t)}{dt} = rX(t)$$

per-capita growth: $\frac{1}{X(t)}\frac{dX(t)}{dt} = r$ No density-dependence.

Logistic growth:

$$\frac{dX(t)}{dt} = rX(t)\left(1 - \frac{X(t)}{K}\right) = rX(t) - \frac{rX(t)^2}{K}$$

per-capita growth: $\frac{1}{X(t)}\frac{dX(t)}{dt} = r - \frac{rX(t)}{K}$ Negative density dependence.

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Second law of ecology

No population is left unchecked for a long time
(but it could be long enough to cause great damage)

USFWS

Population structure

- So far, we've considered populations in which each individual has the same probability of reproducing dying.
- Of course, that's not the case at all.
- To make more accurate and realistic models, we need to model populations divided into classes of age/size.

Halley's life tables

Edmond Halley was an astronomer, mathematician, and polymath. He was instrumental in encouraging Newton to publish his *Principia* (Halley also funded the publication). Halley's comet is named after him (last time seen in 1986, will be back in 2061).

Halley also published the first *life table* in the 1693 article *"An estimate of the degrees of the mortality of mankind, drawn from curious tables of the births and funerals at the city of Breslaw, with an attempt to ascertain the price of annuities upon lives"*.

This contribution marks the beginning of life insurance!

The data he analyzed was collected by Caspar Neumann, a theologian living in Breslau (now Wroclaw, Poland), who gathered it from parochial registries reporting births and deaths.

Halley noticed that the number of births was close to the number of deaths in a given year. Halley assumed the population to be at **steady state**: the population aged P_k and the number of deaths at age k, are constant. The number of newborns P_0 is also constant. Then:

$$P_{k+1} = P_k - D_k$$

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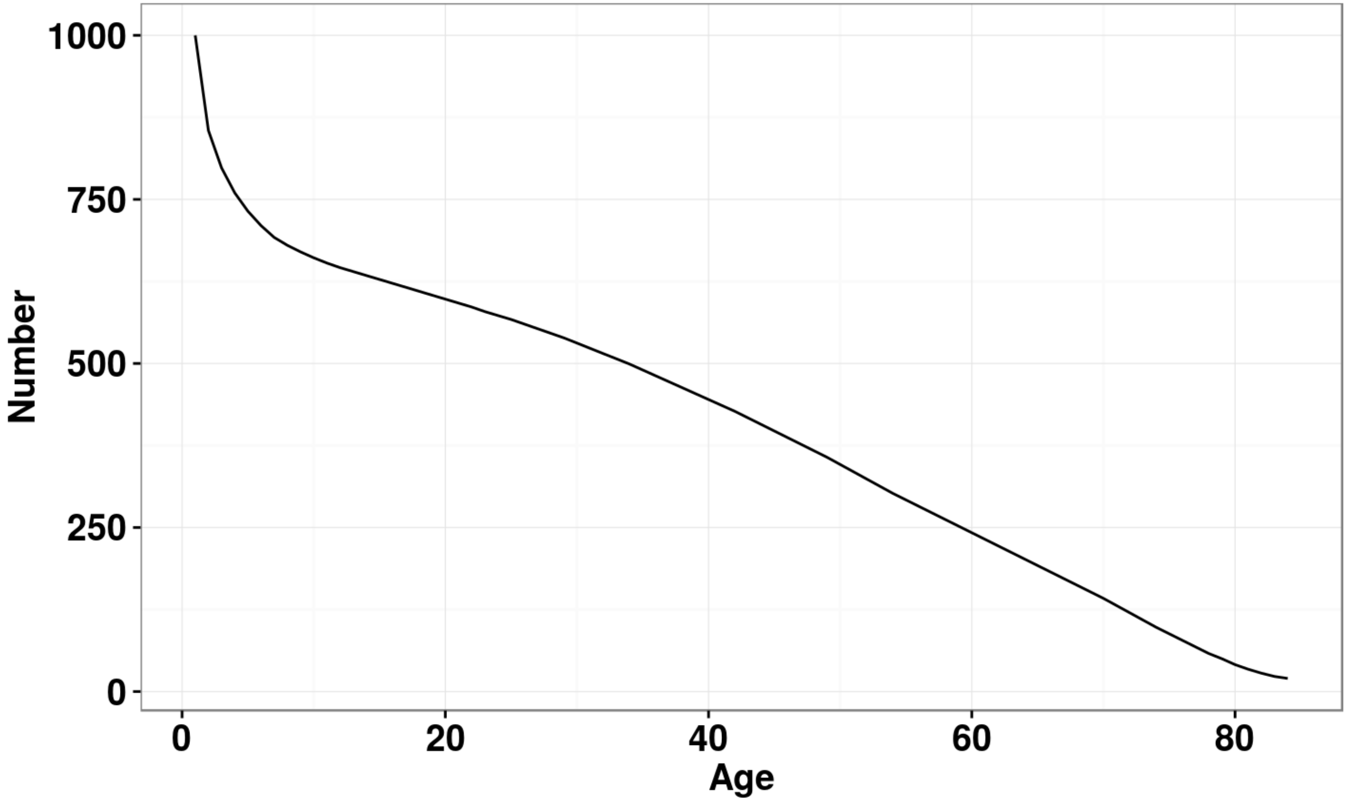
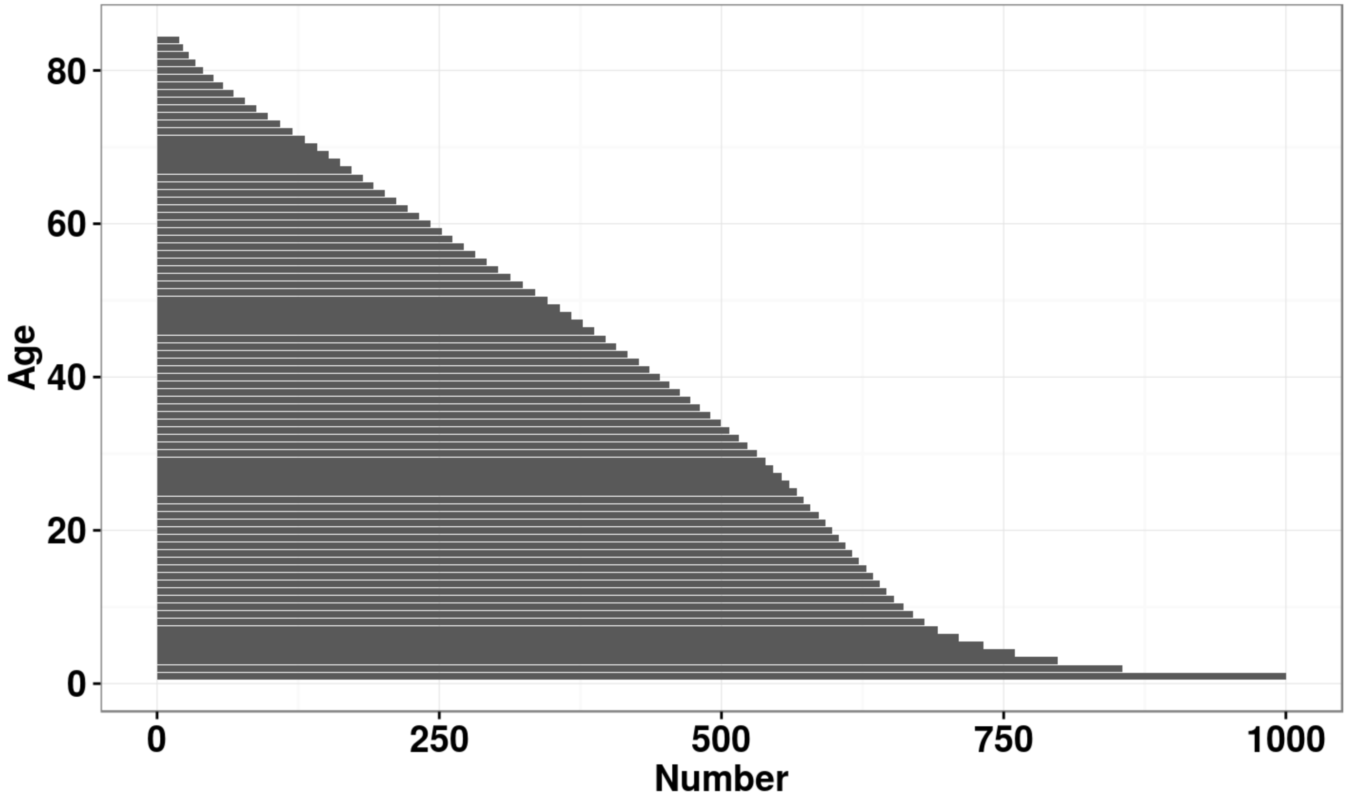
Halley's data: life table of Breslau Δ

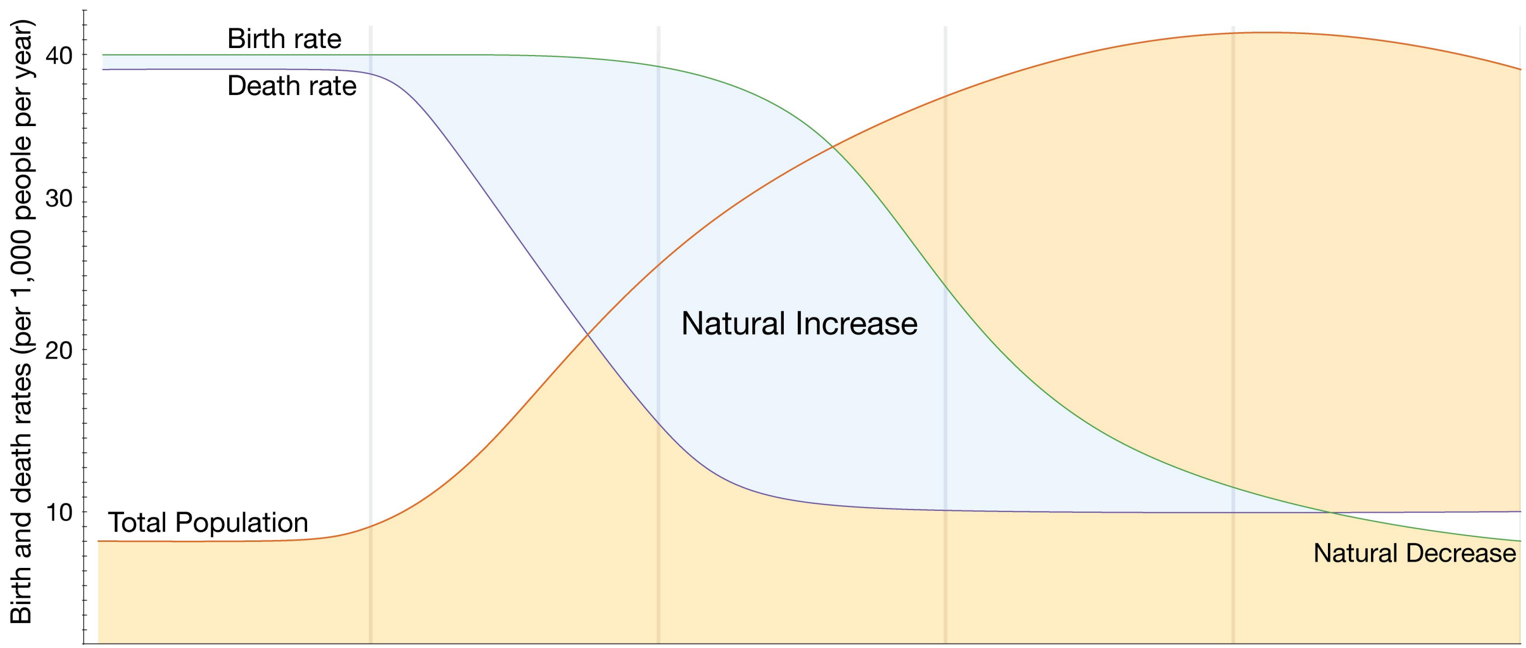


Population pyramid of Breslau Δ



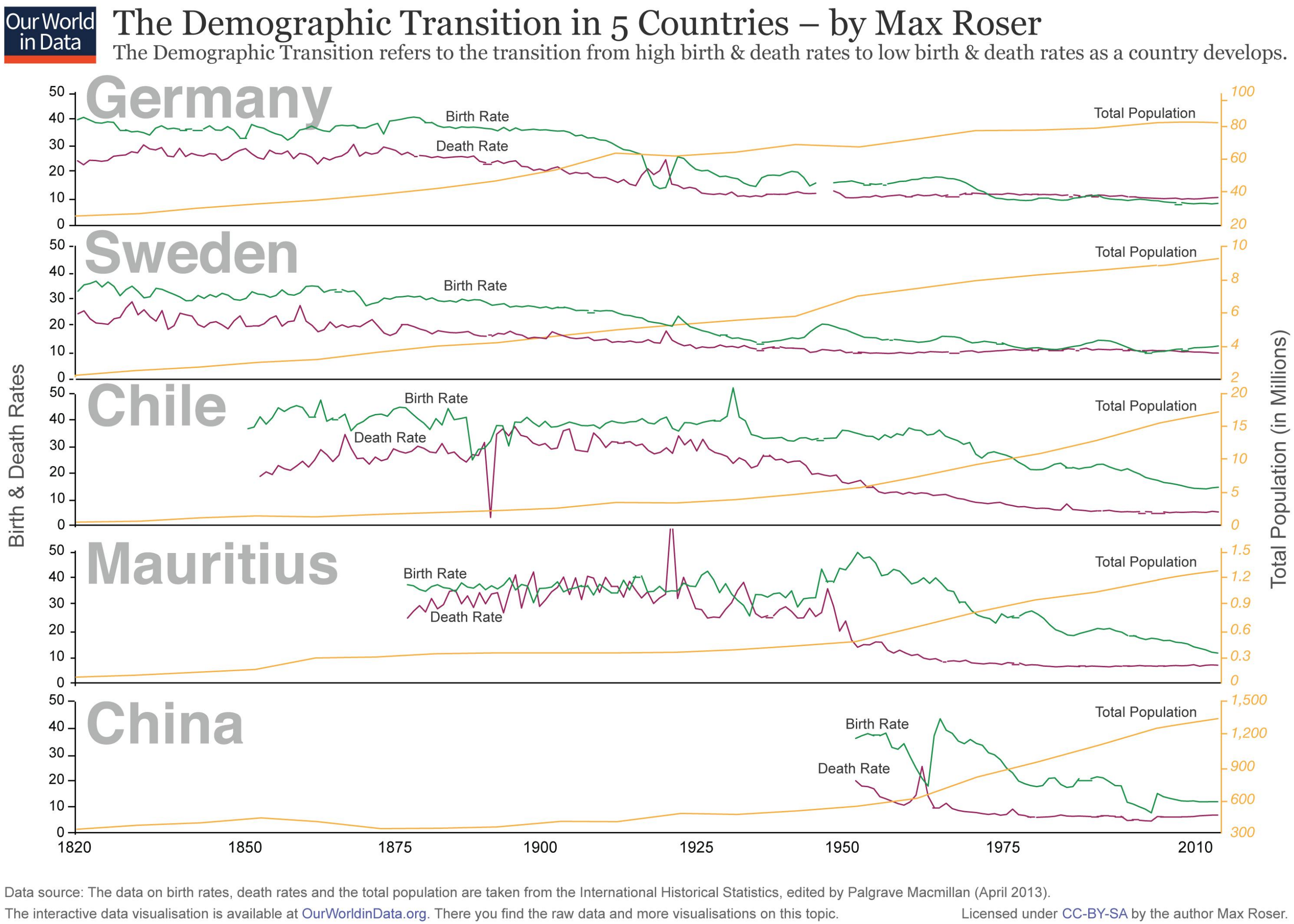
Demographic transition

Our World in Data



	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Birth rate	*High*	*High*	*Falling*	*Low*	*Very low*
Death rate	*High*	*Falls rapidly*	*Falls more slowly*	*Low*	*Low*
Natural increase	*Stable or slow increase*	*Very rapid increase*	*Increase slows down*	*Stable or slow increase*	*Stable or slow decrease*

Demographic transition



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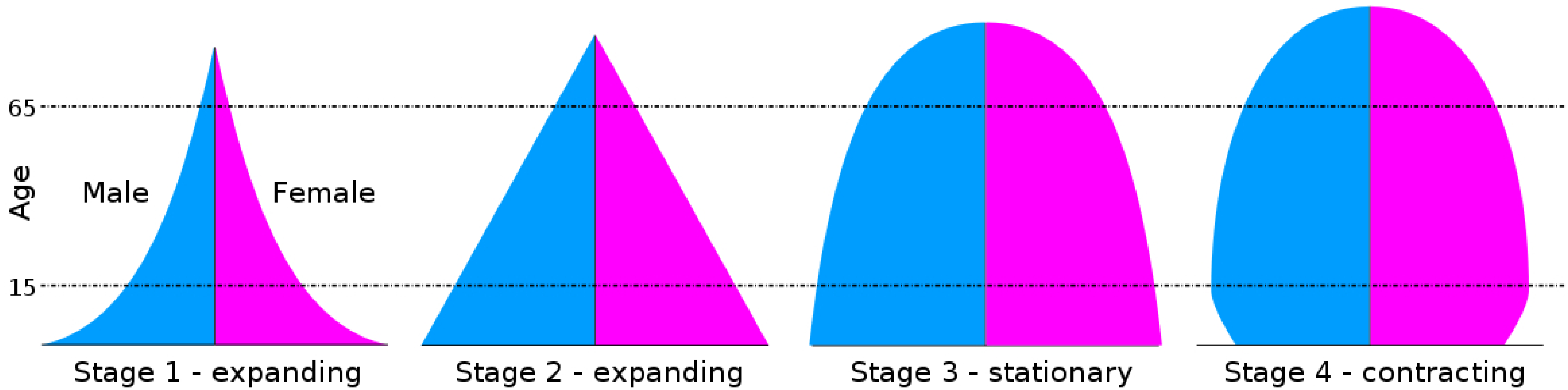
Demographic transition and pyramids



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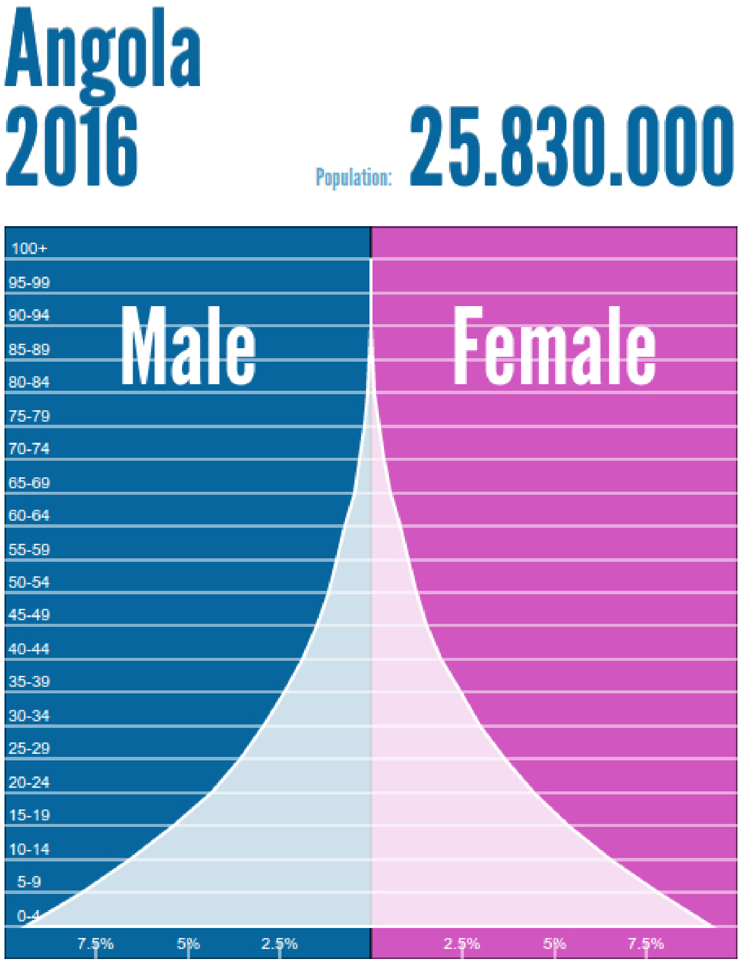
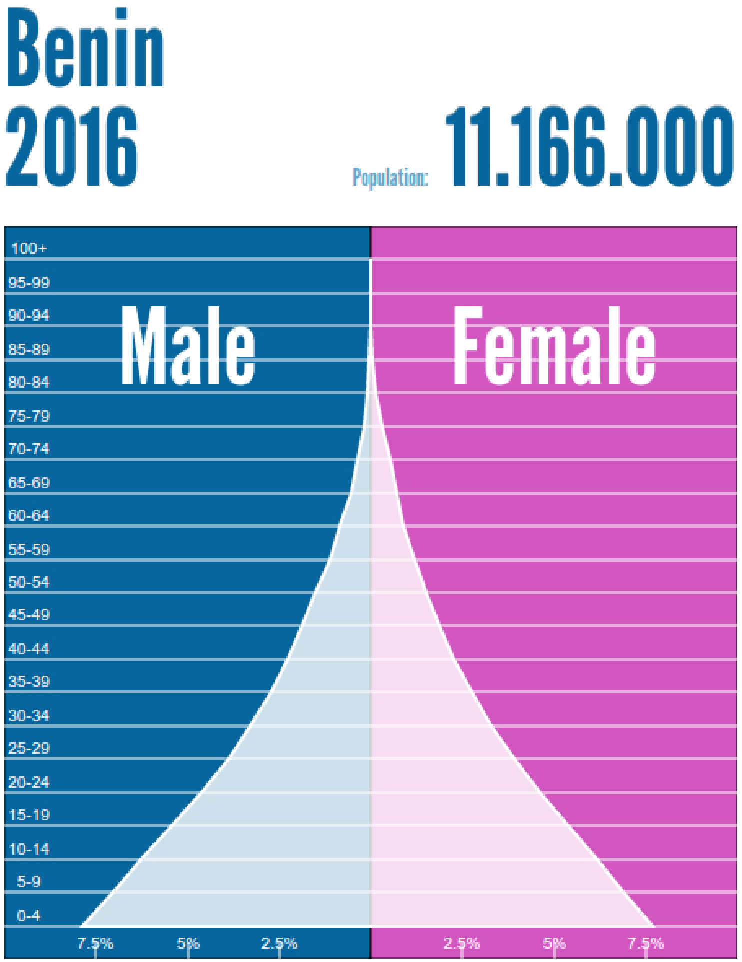
Stage 1


Angola
2016
Population: 25.830.000
Male
Female
100+
95-99
90-94
85-89
80-84
75-79
70-74
65-69
60-64
55-59
50-54
45-49
40-44
35-39
30-34
25-29
20-24
15-19
10-14
5-9
0-4
7.5%
5%
2.5%
2.5%
5%
7.5%


Benin
2016
Population: 11.166.000
Male
Female
100+
95-99
90-94
85-89
80-84
75-79
70-74
65-69
60-64
55-59
50-54
45-49
40-44
35-39
30-34
25-29
20-24
15-19
10-14
5-9
0-4
7.5%
5%
2.5%
2.5%
5%
7.5%

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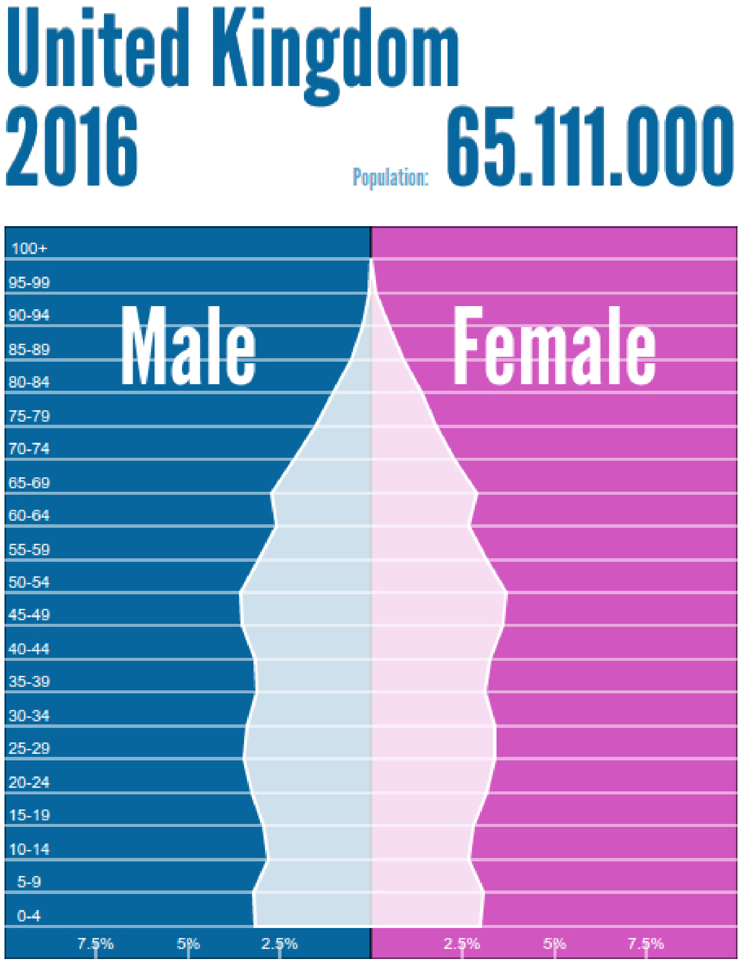
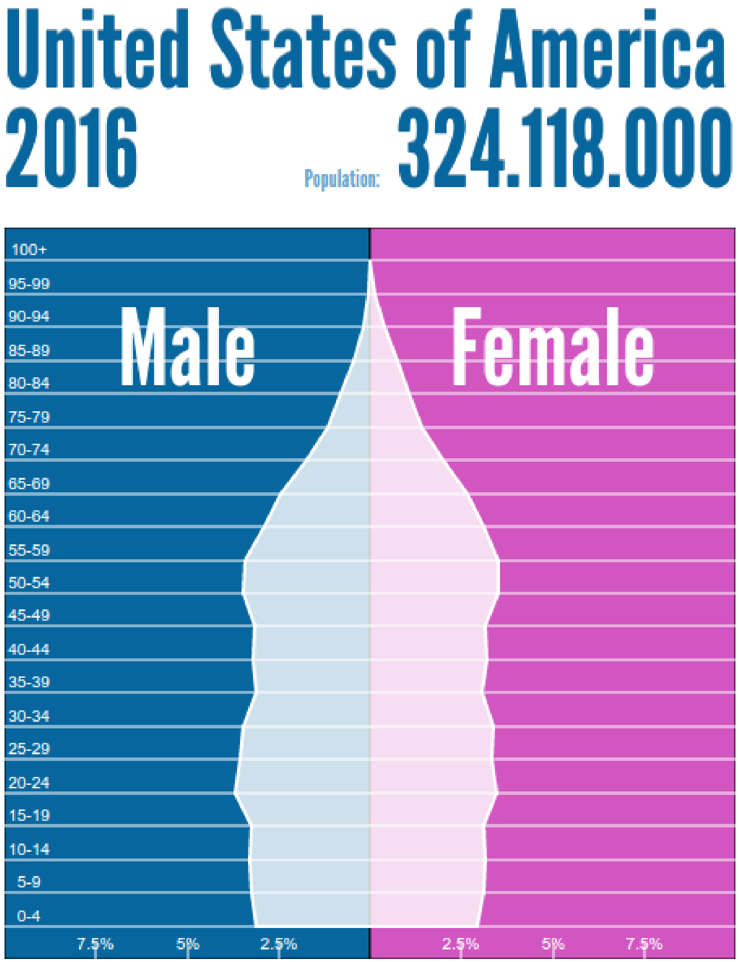
Stage 4


United Kingdom
2016
Population: 65.111.000
Male
Female
100+
95-99
90-94
85-89
80-84
75-79
70-74
65-69
60-64
55-59
50-54
45-49
40-44
35-39
30-34
25-29
20-24
15-19
10-14
5-9
0-4
7.5%
5%
2.5%
2.5%
5%
7.5%


United States of America
2016
Population: 324.118.000
Male
Female
100+
95-99
90-94
85-89
80-84
75-79
70-74
65-69
60-64
55-59
50-54
45-49
40-44
35-39
30-34
25-29
20-24
15-19
10-14
5-9
0-4
7.5%
5%
2.5%
2.5%
5%
7.5%

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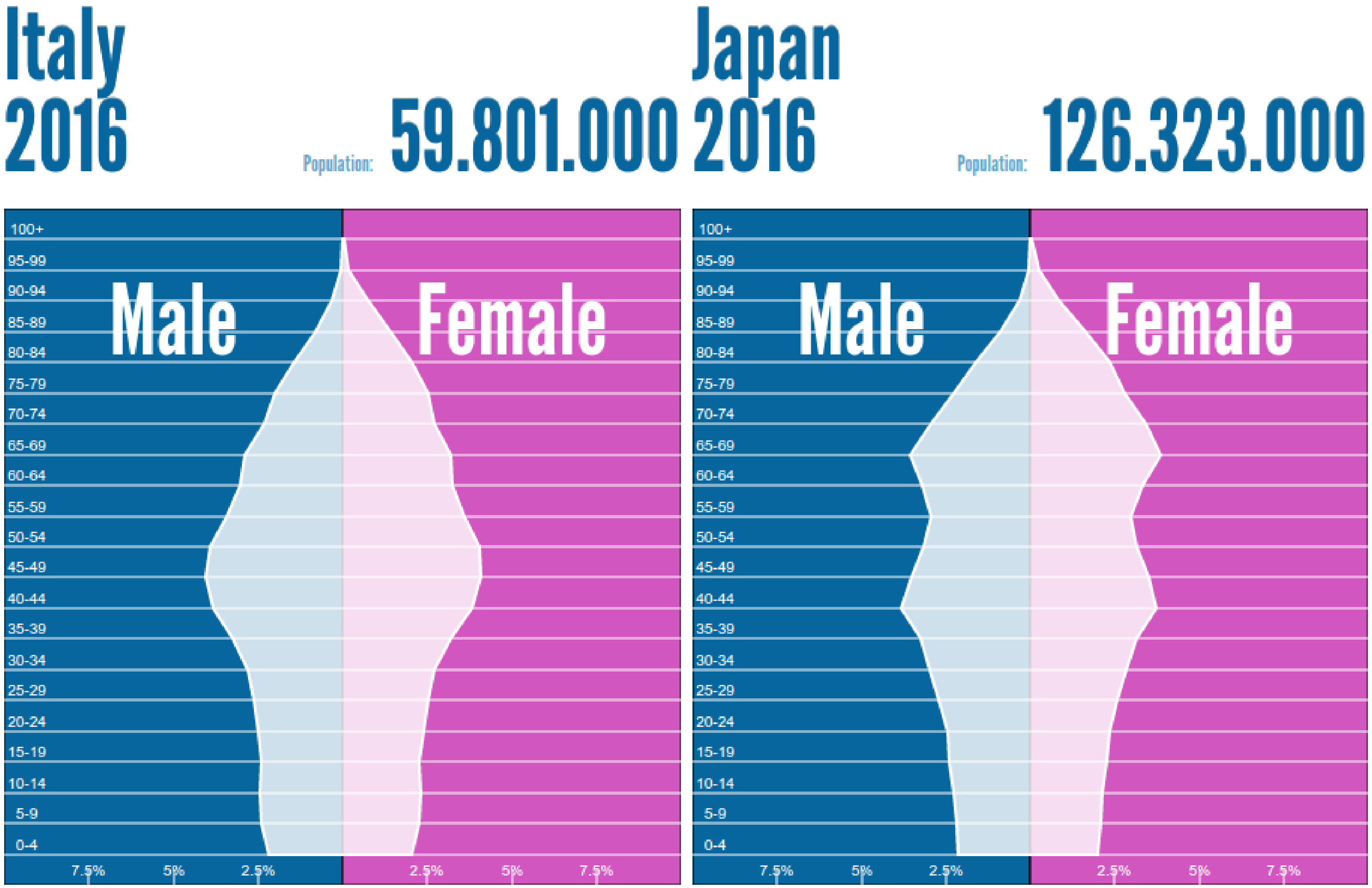
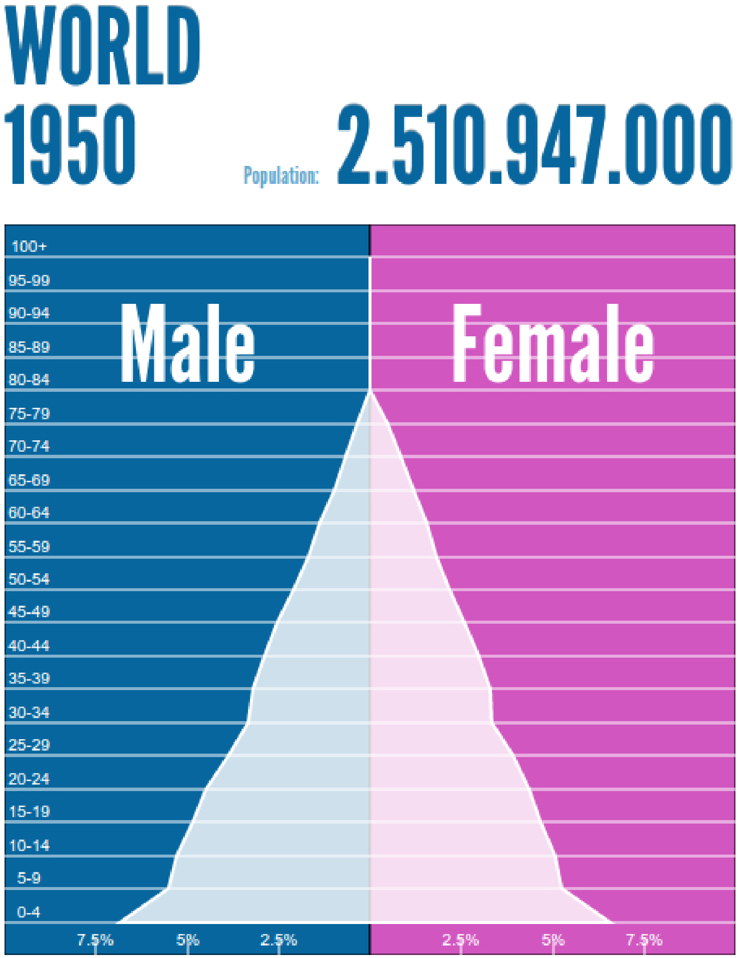
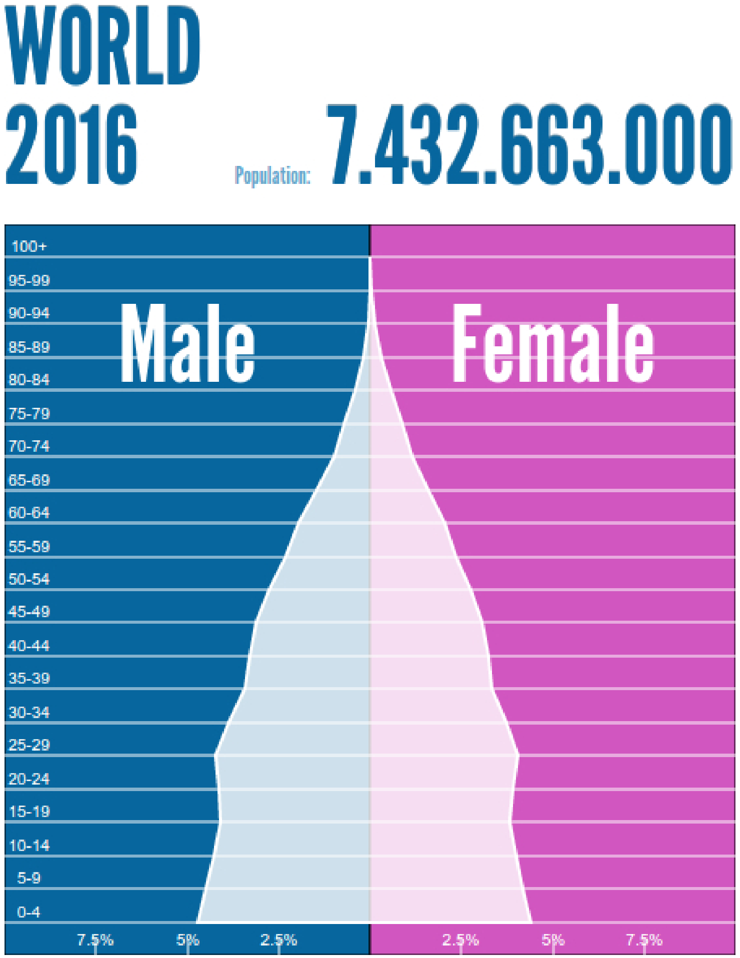
Stage 5


Italy
2016
Population: 59.801.000
Japan
2016
Population: 126.323.000
Male
Female
Male
Female
100+
95-99
90-94
85-89
80-84
75-79
70-74
65-69
60-64
55-59
50-54
45-49
40-44
35-39
30-34
25-29
20-24
15-19
10-14
5-9
0-4
7.5%
5%
2.5%
2.5%
5%
7.5%

World then and now





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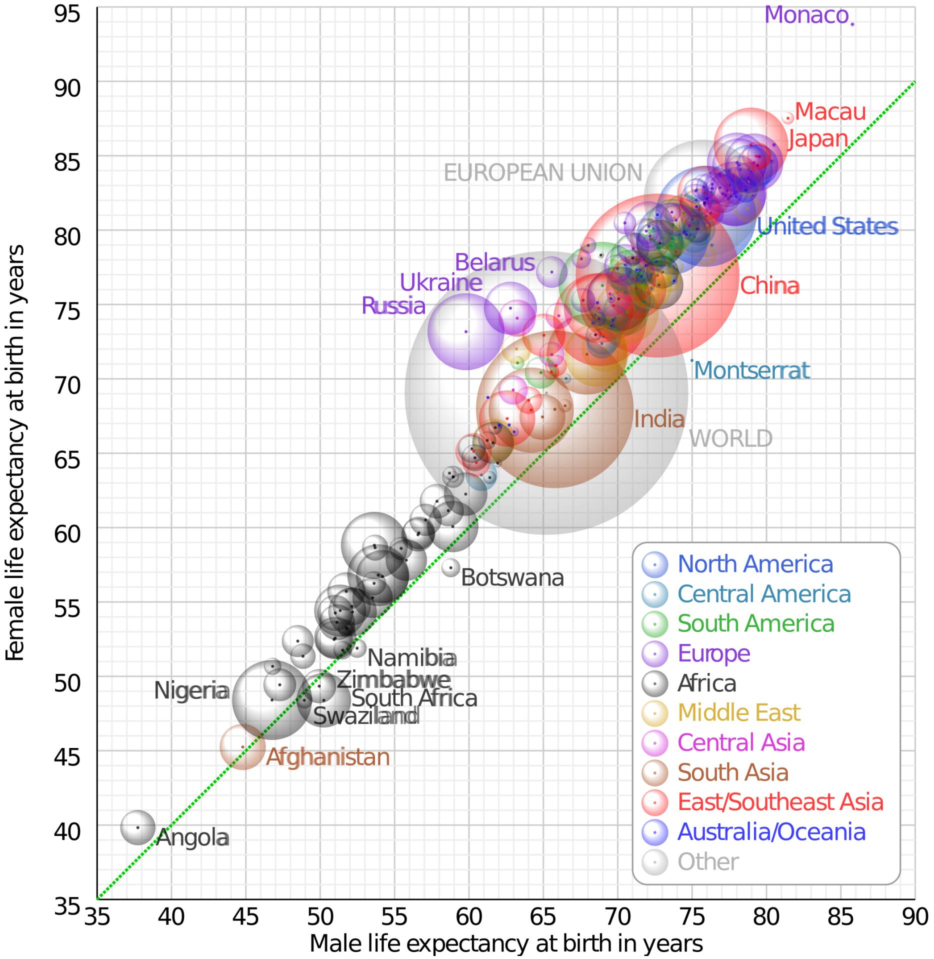
Life expectancy Men/Women



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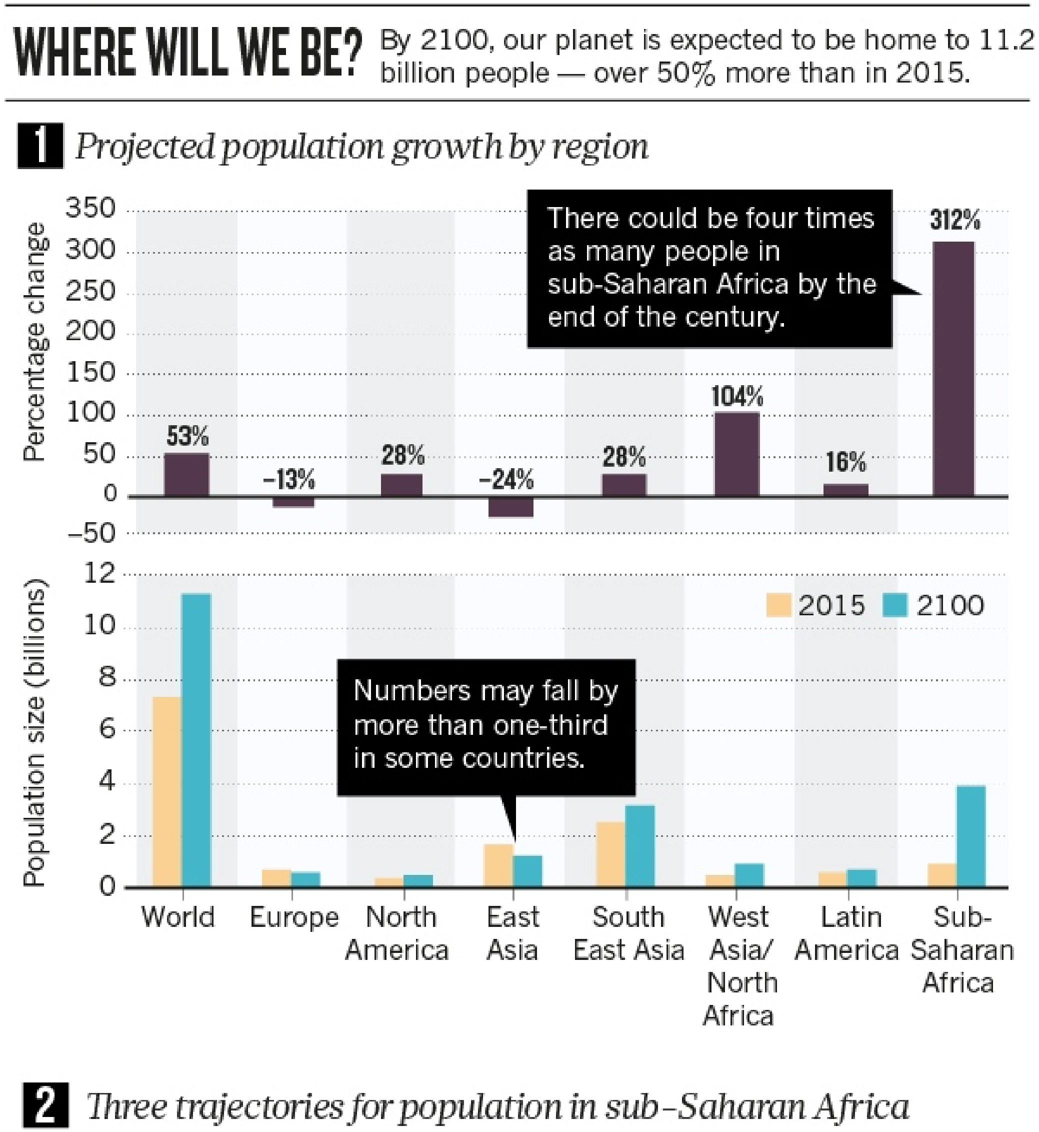
Projected growth II



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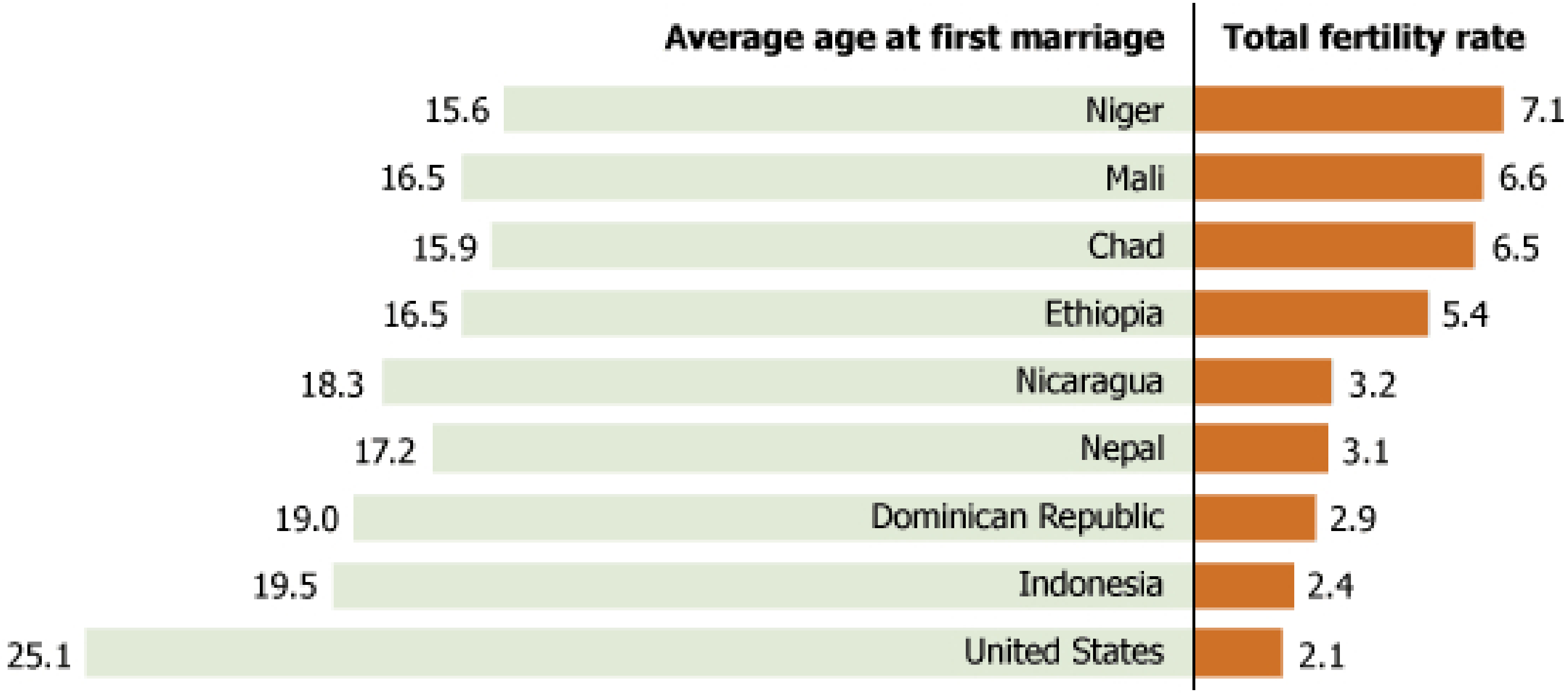
Fertility and family planning

- One of the main responses to rapid growth has been setting up voluntary family-planning programs
- In the developing world, 74M unwanted pregnancies per year. About 40% of total pregnancies. About half result in induced abortion.

Age at first marriage and total fertility



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927, 2B; 1960, 3B; 1974, 4B; 1987, 5B; 1999, 6B; 2011,

ly if unchecked (geometric, exponential).

tic).

by changing the environment and through

on, going from high mortality and high natality, to

are still high see the rapid rise of population

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