1 Mathematical models of the population growth

1.1 How many people can the Earth support? (Or a quick refresher on the least square method)

I would like to start with a very simple and yet interesting example of biological data that cry out for mathematical analysis. Consider the following numbers:

Year	1900	1920	1930	1940	1950	1955	1960	1965	1970	1975	1980	1985	1990	1995	2000
Population	1625	1813	1987	2213	2516	2752	3020	3336	3698	4079	4448	4851	5292	5700	6100

These numbers provide (quite accurate) estimates of the total Earth population during the 20th century (and I purposely did not include any data on the years after 2000). I can also represent them graphically, as follows.

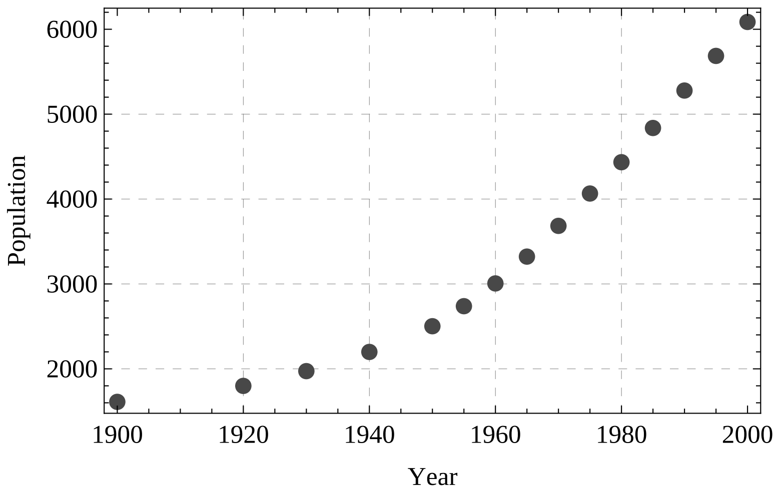

Figure 1: The total world population during the 20th century, millions versus years

Since not every year given a specific value it is very natural to ask the following question: Given the data, determine some function f, such that $f(t)$ gives the world population at the year t. I can fix the qualitative form of function f, e.g., straight line, parabola, exponent and so on, which depends on some free parameters, and determine, given the data, the "best" possible such function (i.e., determine the actual values of these parameters). This is called *approximation*, and this is what I will discuss in some detail.

Let $f(t, a_1, a_2, \ldots, a_m)$ be a family of functions of a specific form that depend on the parameters $a_1, \ldots, a_m$. To proceed I need to determine what it means "the best possible such function," because different choices are possible. It turns out that one that is working good is to minimize the sum of squares of deviations of f from the observed values x_j, $j = 0, \ldots, n$.

To make this general discussion precise, consider a specific example, e.g.,

$$f(t, a, b) = at + b,$$

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which is the equation of the straight line with parameters a, b. Also consider some abstract data set:

t_0	t_1	$\cdots$	t_n
x_0	x_1	$\cdots$	x_n

At each point t_j the square of the deviation is

$$(x_j - f(t_j, a, b))^2,$$

and therefore my ultimate task is to find the values of a and b that minimize the following sum

$$g(a, b) = \sum_{j=0}^{n} (x_j - f(t_j, a, b))^2 = \sum_{j=0}^{n} (x_j - at_j - b)^2.$$

To find the minimum of a function, I need to find two partial derivatives

$$\frac{\partial g}{\partial a}(a, b) = -2\sum_{j=0}^{n}(x_j - at_j - b)t_j = -2\Big(\sum_{j=0}^{n} x_j t_j - a\sum_{j=0}^{n} t_j^2 - b\sum_{j=0}^{n} t_j\Big),$$

$$\frac{\partial g}{\partial b}(a, b) = -2\sum_{j=0}^{n}(x_j - at_j - b) = -2\Big(\sum_{j=0}^{n} x_j - a\sum_{j=0}^{n} t_j - bn\Big),$$

and equal them to zero, which yields a linear algebraic system

$$a\sum_{j=0}^{n} t_j^2 + b\sum_{j=0}^{n} t_j = \sum_{j=0}^{n} x_j t_j,$$

$$a\sum_{j=0}^{n} t_j + bn = \sum_{j=0}^{n} x_j,$$

which can be readily solved for the unknown a and b.

For example for the data on the world population I find, after some calculations, that

$$f(t) = -90402 + 48t,$$

i.e., $a = 48$ and $b = -90402$. You can compare the data with the found best linear approximation in the figure below.

You may see that agreement is not very good, and probably the straight line should be replaced by something else. It can also be seen by calculating the value of

$$g(a, b) = 3060000.$$

It seems that a parabola would approximate the data better:

$$f(t, a, b, c) = at^2 + bt + c.$$

Indeed, repeating exactly the same calculations, I will find a system of three linear equations with three unknowns, which again can be solved by the standard methods. After some calculations (for which it is probably better to use a computer) I find

$$f(t) = 0.54t^2 - 2047t + 1954510.$$

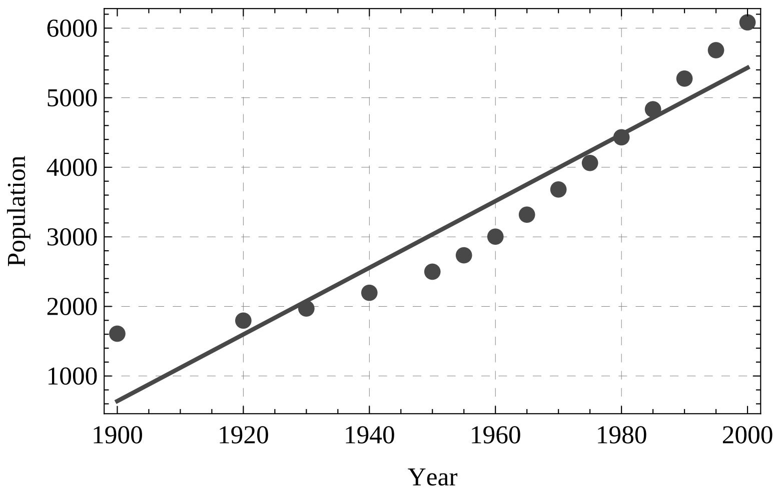

Figure 2: The total world population during the 20th century, millions versus years, and the best linear approximation $f(t) = 48t - 90402$

You can see in the figure that agreement now is quite good, moreover

$$g(a, b, c) = 47273,$$

which is significantly better than for the linear case. Now I can use the found formula to *interpolate* the data, e.g., find the value $f(1910) = 1652$. Did I solve my problem? Not really. First, the choice of parabola was quite arbitrary, maybe a cubic parabola would do better. Second, if I put $t = 0$ (*extrapolate*, i.e., go beyond the given range of the data), I get $f(0) = 1954510$ million people at the year 0 A.D., which is clearly a ridiculous estimate.

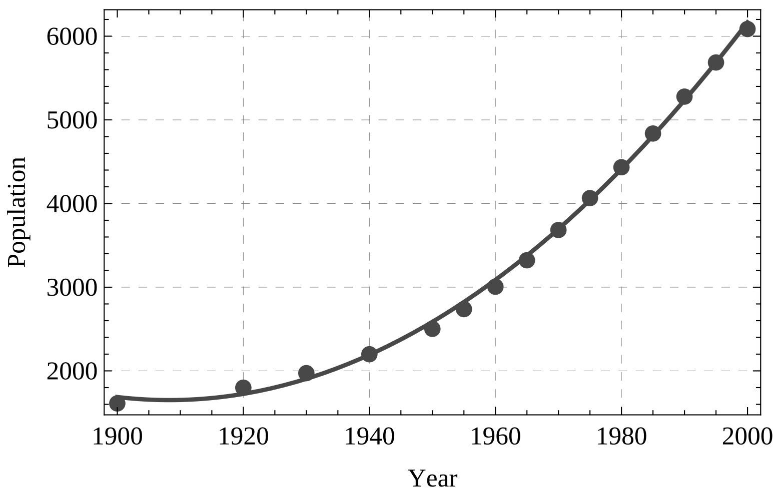

Figure 3: The total world population during the 20th century, millions versus years, and the best quadratic approximation $f(t) = 0.54t^2 - 2047 + 1954510$

At this point I would like to stop discussing the data (and the *method of least squares*, that is used to find a best possible f among a given family of functions depending on free parameters) and switch to the ordinary differential equations (ODE).

1.2 ODE models of population growth

The usual process of *mathematical modeling* goes in several stages: First, we start with the situation at hands and formulate the main features of the considered system (physical, chemical, biological, etc), which we would like to retain in our mathematical model. At the same stage we disregard many unimportant for us details. After this first stage we formulate a mathematical model, which is built on our simplifying assumptions. If we have the model, we can forget about the original system and perform an analysis of the obtained mathematical problem. Finally, the solutions to this model should be interpreted in terms of the original system. Of course, the whole process is usually much more involved, but the outlined above line of reasoning can be found in many real world modeling situations. I will present a great number of examples in this course.

As a very basic example of the modeling approach, let me introduce the so-called *Malthus equation*. A very simple biological process of a population growth is considered. Let $N(t)$ denote the number of individuals in a given population (for concreteness you can think of a population of bacteria) at the time moment t. In this course the variable t will almost exclusively denote *time*. Now I calculate how the population number changes during a short time interval h. I have

$$N(t+h) = N(t) + bhN(t) - dhN(t).$$

Here I used the fact that the total population at the moment $t+h$ can be found as the total population at the moment t plus the number of individuals born during time period h minus the number of died individuals during time period h. b and d are per capita *birth* and *death rates* respectively (i.e., the numbers of births and deaths per one individual per time unit respectively). From the last equality I find

$$\frac{N(t+h) - N(t)}{h} = (b-d)N(t).$$

Next, I *postulate* the existence of the derivative

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \lim_{h\to 0} \frac{N(t+h) - N(t)}{h},$$

assume for simplicity that both b and d are constant, and hence obtain an ordinary differential equation

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (b-d)N,$$

which is usually called in the biological context the *Malthus equation* (I will come back to Malthus). Finally, I rewrite the equation in the form

$$\dot{N} = mN, \quad N(0) = N_0, \tag{1.1}$$

where $N(t)$ is the population size at the time moment t, m is the parameter of the model, $m = b - d$. How did Malthus arrived at this mathematical model? Obviously, the process of the population growth or decline is very intricate, which is subject to many important factors, such as weather, temperature, diseases, religion and so on. Malthus stated his simplifying assumption that the population growth is "geometric," by this he meant that the population size increases in a geometric progression, which can be described as the relation $N(t+h) = wN(t)$, where w is the parameter of the geometric growth. In the terms of the continuous time, this means exactly the equation (1.1). So, he had a simplifying assumption, and his mathematical model — (1.1). Now I analyze the mathematical model, in this case I can simply solve it:

$$N(t) = N_0 e^{mt}, \tag{1.2}$$

which predicts the *exponential growth* if $m > 0$. At the same time Malthus argued that the goods increase in the world *linearly*. Exponential population growth plus linear increase of food and similar things together mean, by Malthus, a catastrophe. Here is what Malthus wrote

> A man who is born into a world already possessed, if he cannot get subsistence from his parents on whom he has a just demand, and if the society do not want his labour, has no claim of right to the smallest portion of food, and, in fact, has no business to be where he is. At nature's mighty feast there is no vacant cover for him. She tells him to be gone, and will quickly execute her own orders, if he does not work upon the compassion of some of her guests. If these guests get up and make room for him, other intruders immediately appear demanding the same favour. The report of a provision for all that come, fills the hall with numerous claimants. The order and harmony of the feast is disturbed, the plenty that before reigned is changed into scarcity; and the happiness of the guests is destroyed by the spectacle of misery and dependence in every part of the hall, and by the clamorous importunity of those, who are justly enraged at not finding the provision which they had been taught to expect. The guests learn too late their error, in counter-acting those strict orders to all intruders, issued by the great mistress of the feast, who, wishing that all guests should have plenty, and knowing she could not provide for unlimited numbers, humanely refused to admit fresh comers when her table was already full.
>
> Thomas Robert Malthus (13 February 1766 — 23 December 1834)
> *An Essay on the Principle of Population*, Second edition
> (this quotation was removed from the text in the subsequent editions)

It is interesting to note that actually Malthus was wrong. Ok, I hope that it is not surprising at this point that Malthus was wrong, given the number of the simplifying assumptions put in the model, but what I call "interesting" is that the human population actually grew faster than the exponential growth predicts. Consider this in some details.

First, I would like to see how my exponential function approximates the data I have. In my case I have, recall the least square method I used in the first subsection in this lecture,

$$f(t, a, b) = ae^{bt}.$$

However, (the student must convince himself that my statement is correct) the system for the partial derivatives

$$\frac{\partial g}{\partial a} = 0, \quad \frac{\partial g}{\partial b} = 0$$

is no longer linear! and hence cannot be easily solved without applying specific numerical procedures. One can avoid this obstacle by noticing that $\log f$ is a linear function of a and b:

$$\log f(t, a, b) = \log a + bt = A + bt.$$

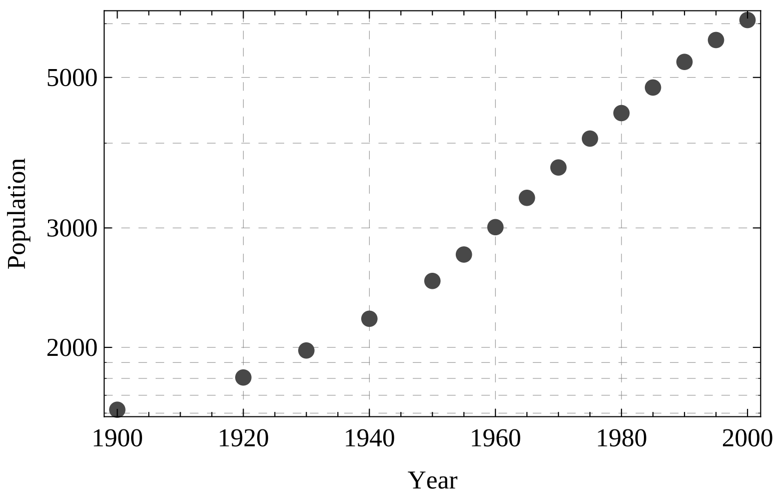

Figure 4: The total world population during the 20th century, millions versus years, in logarithmic coordinates

This transformation is also often useful for presenting the data in logarithmic coordinates, see the figure. Anyway, I find that

$$f(t, a, b) = 1.15 \times 10^{-9} e^{0.01462t}, \quad g(a, b) = 1600000,$$

which is better than the linear approximation but worth than the quadratic one, see the graphical comparison.

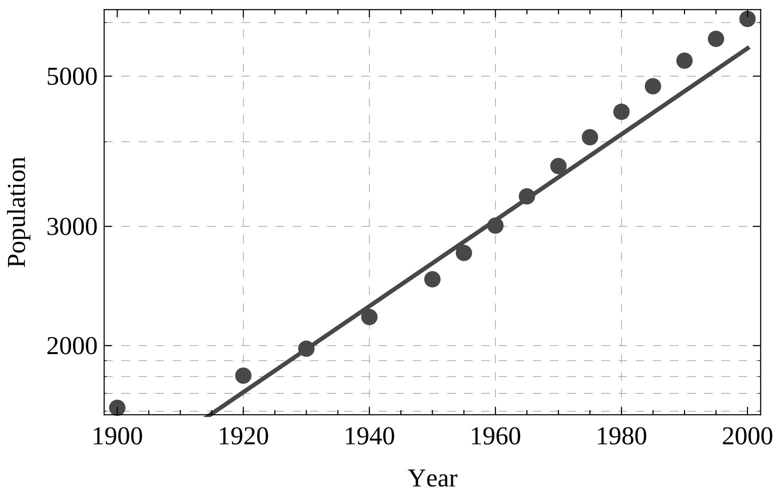

Figure 5: The total world population during the 20th century, millions versus years, and the best exponential approximation of the data, in logarithmic coordinates

If I consider available estimates of the world population for the last 2000 years, not just a century, the disagreement with the exponential function is even worth. Note that I again use the logarithmic coordinates to plot the population numbers. I.e., instead of $N(t)$ I actually plotted $\log N(t)$. If the

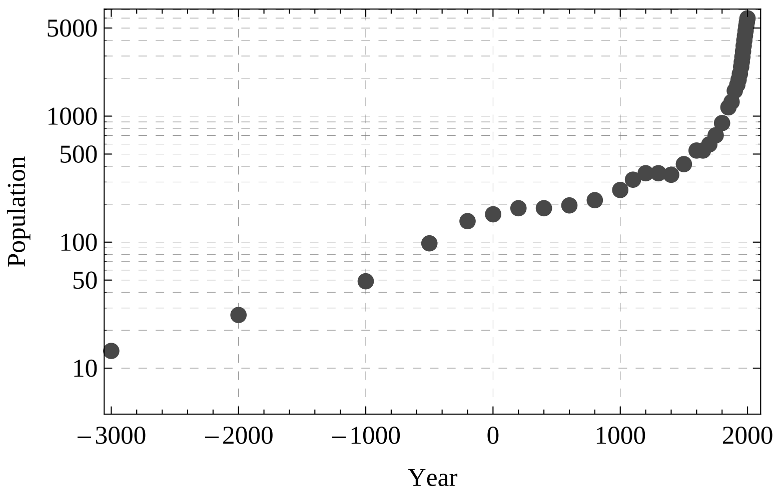

Figure 6: World population versus time, in millions, in logarithmic coordinates

population growth was exponential, given by $N(t) = N_0 e^{mt}$, then in the logarithmic coordinates I would get the straight line. It turns out actually that a much better fit can be obtained if I assume that the function N has the *hyperbolic* form

$$N(t) = \frac{C}{T - t}, \qquad (1.3)$$

where $C \approx 2 \times 10^{11}$, $T \approx 2026$ can be found by the same method of least squares (but here one must to solve a nonlinear system of equations). This formula is very precise if I consider only 400-500 years of the population estimates up to 1960. Note that when $t \to T$, the population *blows up.*

However, if I consider the population growth only during the last 100 years or so (the original data plus the last 15 years), I will see that the population actually stabilizes. And this conclusion

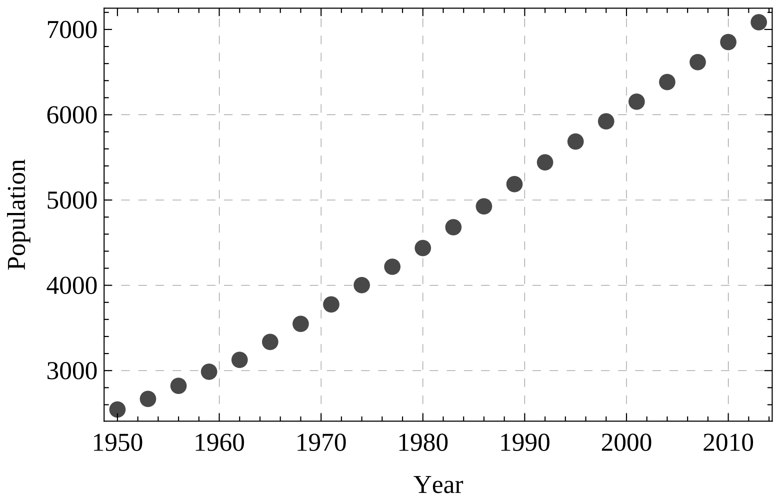

Figure 7: World population versus time, in millions, for the last 65 years

should be quite obvious from a common sense. Therefore, Malthus' interpretation of his mathematical model (1.1) and its solutions is clearly wrong; however, even from such a simple and unrealistic mathematical model can be made a very far reaching conclusion, which was made by Charles Darwin, who put together the underlying law of the geometric (or exponential) growth and clear impossibility of the infinite human population. Darwin wrote:

> In October 1838... I happened to read for amusement Malthus on Population... it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species.

Hence even very simple models can lead to very important and nontrivial conclusions!

The fact that no population can grow to infinity should be included in our mathematical models if we would like to consider predictions of the population size in the future times.

Very general, I can assume that the law of growth has the general form

$$\dot{N} = NF(N),$$

where $F(N)$ is some function, which has to be negative for sufficiently large values of N (do you see why it is important?). If this function is smooth enough, I can represent it with the help of the Taylor formula around $N = 0$:

$$F(N) = F(0) + \frac{F'(0)}{1!}N + \frac{F''(0)}{2!}N^2 + o(N^2).$$

Here the notation $f(N) = o(g(N))$ when means that

$$\lim_{N \to 0} \frac{f(N)}{g(N)} = 0,$$

and I also assume that this term is negligible when $N \to \infty$.

Note that if in the Taylor formula I keep only the constant term, I obtain exactly the Malthus equation

$$\dot{N} = mN,$$

where $m = F(0)$. If I keep two terms, I obtain the equation

$$\dot{N} = NF(N) = N\big(F(0) + F'(0)N\big) = mN\left(1 - \frac{N}{K}\right),$$

where I used another parametrization (do you see how $F(0)$ and $F'(0)$ are connected to m and K?), which is the *logistic equation*, and the parameter K is the *carrying capacity*. Therefore, I presented a mechanistic argument in favor of the logistic equation as the simplest first order differential equation describing the population growth apart of the Malthus equation. I hope that at this point you already know that, given $N(0) = N_0$, the logistic equation has the solution

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-mt}} \to K, \quad t \to \infty.$$

Again, using the available data and the method of the least squares, I can estimate the three parameters of the logistic curve, and find, e.g., that $K = 11740$, that is, the world population will stabilize at approximately 12 billion people, see the comparison of the data with the best logistic fit in the figure below.

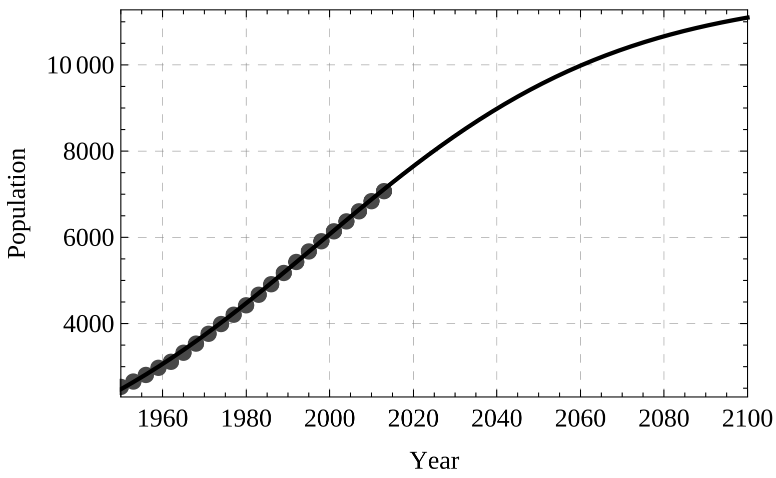

Figure 8: World population versus time, in millions, for the last 65 years and the best logistic fit together with prediction of the increase of the world population

There are a great number of different population models in the literature. To give just one more example, I can consider the model of the form

$$\dot{N} = mN\left(1 - \frac{N}{K} - \frac{b}{1+aN}\right),$$

where in addition to the usual logistic equation, another mortality term is added, and a and b are positive parameters. This last equation actually describes an important ecological phenomenon of *Allee's effect*, which states that the maximal per capita population growth occurs at some intermediate values of N, whereas for both large and small values of N it becomes smaller or even probably negative (for the large values we have, as we discussed, depletion of resources, and for small values of N you can think of the chance of finding a mate).

Anyway, I hope at this point it is clear that it would be beneficial to treat first order ODE, since they can describe, as a first approximation, the population growth. I will also use the mathematical theory of first order ODE (which is not very complex, let me put it this way) to introduce the language of nonlinear dynamics, which we will use throughout the course. Finally, you already noted that our models depend on parameters, and if the parameters change, sometimes sudden changes in the system behavior occur. These changes are called *bifurcations*, and I will also introduce some bifurcation analysis, which will be very handy the whole semester.