Simple and not so simple population growth models in ODEs

Demography

demography, n.
Etymology: *Greek* $\delta\tilde{\eta}\mu o\zeta$ *people* + $-\gamma\rho\alpha\phi\iota\alpha$ *writing.*
That branch of anthropology which deals with the life-conditions of communities of people, as shown by statistics of births, deaths, diseases, etc.

Oxford English Dictionary

Objective – simple version

We are given a table with the population census at different time intervals between a date a and a date b, and want to get an expression for the population. This allows us to:

- compute a value for the population at any time between the date a and the date b (**interpolation**),
- predict a value for the population at a date before a or after b (**extrapolation**).

The US population from 1790 to 1910

Year	Population (millions)
1790	3.929
1800	5.308
1810	7.240
1820	9.638
1830	12.866
1840	17.069
1850	23.192

Year	Population (millions)
1860	31.443
1870	38.558
1880	50.156
1890	62.948
1900	75.995
1910	91.972

PLOT THE DATA !!! (here, to 1910)

Using MatLab (or Octave), create two vectors using commands such as

```
t=1790:10:1910;
```

Format is

Vector=Initial value:Step:Final value

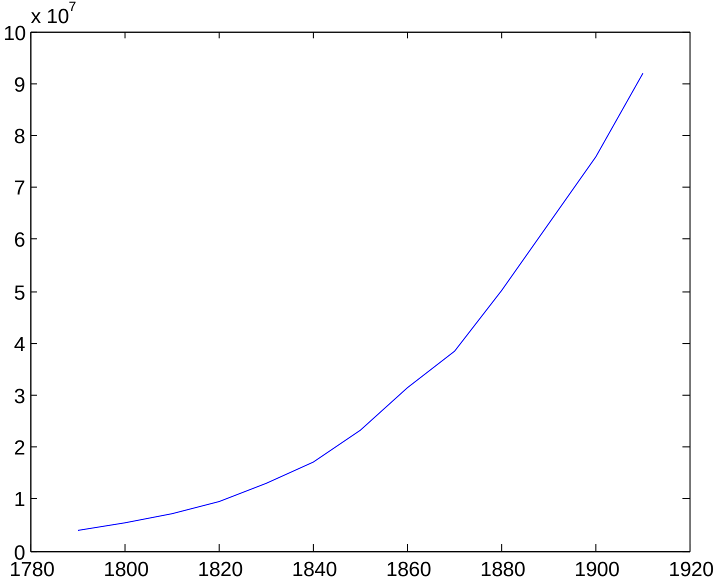
(semicolumn hides result of the command.)

```
P=[3929214,5308483,7239881,9638453,12866020,...
17069453,23191876,31443321,38558371,50155783,...
62947714,75994575,91972266];
```

Here, elements were just listed (... indicates that the line continues below).

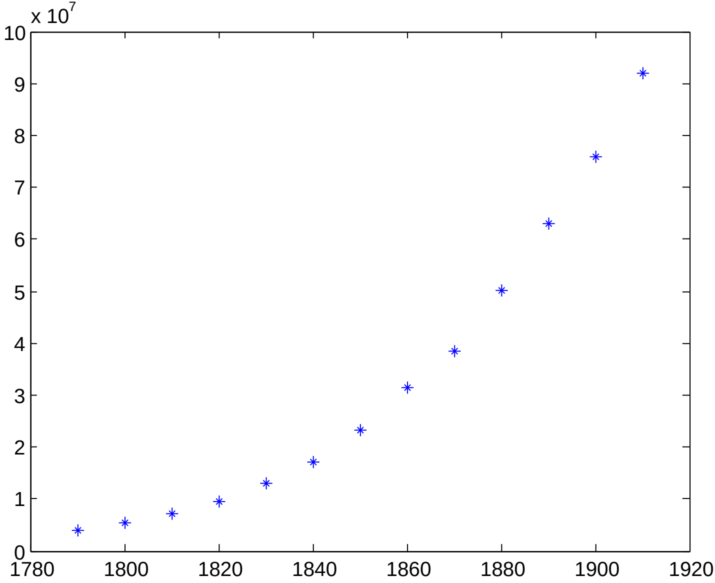
Then plot using

```
plot(t,P);
```



To get points instead of a line

```
plot(t,P,'*');
```



First idea

The curve looks like a piece of a parabola. So let us fit a curve of the form

$$P(t) = a + bt + ct^2.$$

To do this, we want to minimize

$$S = \sum_{k=1}^{13} (P(t_k) - P_k)^2,$$

where t_k are the known dates, P_k are the known populations, and $P(t_k) = a + bt_k + ct_k^2$.

We proceed as in the notes (but note that the role of a, b, c is reversed):

$$S = S(a, b, c) = \sum_{k=1}^{13} \left(a + bt_k + ct_k^2 - P_k\right)^2$$

is maximal if (necessary condition) $\partial S/\partial a = \partial S/\partial b = \partial S/\partial c = 0$, with

$$\frac{\partial S}{\partial a} = 2\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)$$

$$\frac{\partial S}{\partial b} = 2\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k$$

$$\frac{\partial S}{\partial c} = 2\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k^2$$

So we want

$$2\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k) = 0$$

$$2\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k = 0$$

$$2\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k^2 = 0,$$

that is

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k) = 0$$

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k = 0$$

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k^2 = 0.$$

Rearranging the system

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k) = 0$$

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k = 0$$

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2 - P_k)t_k^2 = 0,$$

we get

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2) = \sum_{k=1}^{13} P_k$$

$$\sum_{k=1}^{13}(at_k + bt_k^2 + ct_k^3) = \sum_{k=1}^{13} P_k t_k$$

$$\sum_{k=1}^{13}(at_k^2 + bt_k^3 + ct_k^4) = \sum_{k=1}^{13} P_k t_k^2.$$

$$\sum_{k=1}^{13}(a + bt_k + ct_k^2) = \sum_{k=1}^{13} P_k$$

$$\sum_{k=1}^{13}(at_k + bt_k^2 + ct_k^3) = \sum_{k=1}^{13} P_k t_k$$

$$\sum_{k=1}^{13}(at_k^2 + bt_k^3 + ct_k^4) = \sum_{k=1}^{13} P_k t_k^2,$$

after a bit of tidying up, takes the form

$$\left(\sum_{k=1}^{13} 1\right) a + \left(\sum_{k=1}^{13} t_k\right) b + \left(\sum_{k=1}^{13} t_k^2\right) c = \sum_{k=1}^{13} P_k$$

$$\left(\sum_{k=1}^{13} t_k\right) a + \left(\sum_{k=1}^{13} t_k^2\right) b + \left(\sum_{k=1}^{13} t_k^3\right) c = \sum_{k=1}^{13} P_k t_k$$

$$\left(\sum_{k=1}^{13} t_k^2\right) a + \left(\sum_{k=1}^{13} t_k^3\right) b + \left(\sum_{k=1}^{13} t_k^4\right) c = \sum_{k=1}^{13} P_k t_k^2.$$

So the aim is to solve the linear system

$$\begin{pmatrix} 13 & \sum_{k=1}^{13} t_k & \sum_{k=1}^{13} t_k^2 \\ \sum_{k=1}^{13} t_k & \sum_{k=1}^{13} t_k^2 & \sum_{k=1}^{13} t_k^3 \\ \sum_{k=1}^{13} t_k^2 & \sum_{k=1}^{13} t_k^3 & \sum_{k=1}^{13} t_k^4 \end{pmatrix} \begin{pmatrix} a \\ b \\ c \end{pmatrix} = \begin{pmatrix} \sum_{k=1}^{13} P_k \\ \sum_{k=1}^{13} P_k t_k \\ \sum_{k=1}^{13} P_k t_k^2 \end{pmatrix}$$

With MatLab (or Octave), getting the values is easy.

- To apply an operation to every element in a vector or matrix, prefix the operation with a dot, hence

  ```
  t.^2;
  ```

  gives, for example, the vector with every element t_k squared.
- Also, the function `sum` gives the sum of the entries of a vector or matrix.
- When entering a matrix or vector, separate entries on the same row by `,` and create a new row by using `;`.

Thus, to set up the problem in the form of solving $Ax = b$, we need to do the following:

```
format long g;
A=[13,sum(t),sum(t.^2);sum(t),sum(t.^2),sum(t.^3);...
sum(t.^2),sum(t.^3),sum(t.^4)];
b=[sum(P);sum(P.*t);sum(P.*(t.^2))];
```

The `format long g` command is used to force the display of digits (normally, what is shown is in "scientific" notation, not very informative here).

Then, solve the system using

```
A\b
```

We get the following output:

```
>> A\b
Warning: Matrix is close to singular or badly scaled.
         Results may be inaccurate. RCOND = 1.118391e-020.


ans =


        22233186177.8195
        -24720291.325476
        6872.99686313725
```

(note that here, Octave gives a solution that is not as good as this one, provided by MatLab).

Thus

$P(t) = 22233186177.8195 - 24720291.325476t + 6872.99686313725t^2$

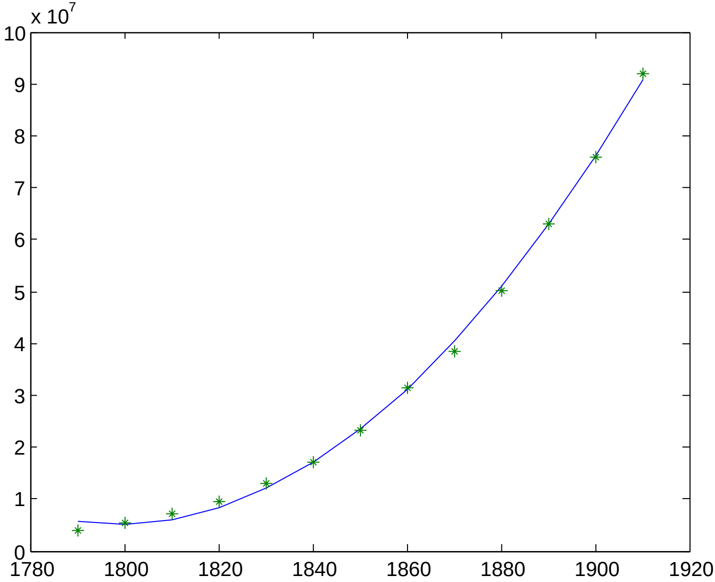
To see what this looks like,

```
plot(t,22233186177.8195-24720291.325476.*t...
+6872.99686313725.*t.^2);
```

(note the dots before multiplication and power, since we apply this function to every entry of t). In fact, to compare with original data:

```
plot(t,22233186177.8195-24720291.325476.*t...
+6872.99686313725.*t.^2,t,P,'*');
```

Our first guess, in pictures



Now we want to generate the table of values, to compare with the true values and thus compute the error. To do this, we can proceed directly:

```
computedP=22233186177.8195-24720291.325476.*t...
+6872.99686313725.*t.^2;
```

We get

```
computedP =

 Columns 1 through 4:

     5633954.39552689      5171628.52739334      6083902.03188705      8370774.90901184

 Columns 5 through 8:

     12032247.1587601      17068318.7811356      23478989.7761383      31264260.1437798

 Columns 9 through 12:

      40424129.884037      50958598.9969215      62867667.4824371      76151335.3405762

 Column 13:

     90809602.5713463
```

We can also create an **inline** function

```
f=inline('22233186177.8195-24720291.325476.*t+6872.99686313725.*t.^2')
f =

     Inline function:
     f(t) = 22233186177.8195-24720291.325476.*t+6872.99686313725.*t.^2
```

This function can then easily be used for a single value

```
octave:24> f(1880)
ans =      50958598.9969215
```

as well as for vectors..

(Recall that t has the dates; t in the definition of the function is a dummy variable, we could have used another letter-.)

```
octave:25> f(t)

ans =

 Columns 1 through 4:

     5633954.39552689      5171628.52739334      6083902.03188705      8370774.90901184

 Columns 5 through 8:

     12032247.1587601      17068318.7811356      23478989.7761383      31264260.1437798

 Columns 9 through 12:

      40424129.884037      50958598.9969215      62867667.4824371      76151335.3405762
12186176863781.4
 Column 13:

     90809602.5713463
```

Form the vector of errors, and compute sum of errors squared:

```
octave:26> E=f(t)-P;
octave:27> sum(E.^2)
ans =      12186176863781.4
```

Quite a large error (12,186,176,863,781.4), which is normal since we have used actual numbers, not thousands or millions of individuals, and we are taking the square of the error.

To present things legibly, one way is to put everything in a matrix..

```
M=[P;f(t);E;E./P];
```

This matrix will have each type of information as a row, so to display it in the form of a table, show its transpose, which is achieved using the function `transpose` or the operator ′.

```
M'
ans =
 3929214      5633954.39552689      1704740.39552689    0.433862954658
 5308483      5171628.52739334     -136854.472606659   -0.0257803354756
 7239881      6083902.03188705     -1155978.96811295    -0.159668227711
 9638453      8370774.90901184     -1267678.09098816    -0.131522983095
12866020      12032247.1587601     -833772.841239929   -0.0648042550252
17069453      17068318.7811356     -1134.21886444092  -6.644728828e-05
23191876      23478989.7761383      287113.776138306    0.0123799289086
31443321      31264260.1437798     -179060.856220245  -0.00569471832254
38558371       40424129.884037      1865758.88403702    0.0483879073635
50155783      50958598.9969215      802815.996921539    0.0160064492846
62947714      62867667.4824371     -80046.5175628662  -0.00127163502018
75994575      76151335.3405762      156760.340576172   0.00206278330494
91972266      90809602.5713463     -1162663.42865372    -0.012641456813
```

Now for the big question...

How does our formula do for present times?

```
f(2006)
ans =      301468584.066013
```

Actually, quite well: 301,468,584, compared to the 298,444,215 July 2006 estimate, overestimates the population by 3,024,369, a relative error of approximately 1%.

What is missing here?

What is missing here

A mechanistic interpretation of why the curve takes this shape

Thomas Robert Malthus (1766-1834) – England

- Born 1766 in Surrey, England
- 1798, Anglican country curate
- 1805, Professor of History and Political Economy at the East India Company College
- Died 1834 in Bath, England

Master work

An Essay on the Principle of Population (6 editions published from 1798 to 1826)

The way in which these effects are produced seems to be this. We will suppose the means of subsistence in any country just equal to the easy support of its inhabitants. The constant effort towards population... increases the number of people before the means of subsistence are increased. The food therefore which before supported seven millions must now be divided among seven millions and a half or eight millions. The poor consequently must live much worse, and many of them be reduced to severe distress. The number of labourers also being above the proportion of the work in the market, the price of labour must tend toward a decrease, while the price of provisions would at the same time tend to rise. The labourer therefore must work harder to earn the same as he did before. During this season of distress, the discouragements to marriage, and the difficulty of rearing a family are so great that population is at a stand.

In the mean time the cheapness of labour, the plenty of labourers, and the necessity of an increased industry amongst them, encourage cultivators to employ more labour upon their land, to turn up fresh soil, and to manure and improve more completely what is already in tillage, till ultimately the means of subsistence become in the same proportion to the population as at the period from which we set out. The situation of the labourer being then again tolerably comfortable, the restraints to population are in some degree loosened, and the same retrograde and progressive movements with respect to happiness are repeated.

Malthusian growth

For Malthus, there are two processes affecting the population: birth and death. Suppose

- birth at *per capita* rate b
- death at *per capita* rate d
- life duration has exponential distribution

then population at time t, $P(t)$, satisfies

$$\frac{d}{dt}P(t) = (b - d)P(t)$$

which we will write

$$P' = (b - d)P$$

Malthus:

$$P' = (b - d)P$$

Let $r = b - d$ be rate of change of the population and suppose that at time t_0, $P(t_0) = P_0$, then, of course,

$$P(t) = P_0 e^{r(t-t_0)}$$

Criticism of the work of Malthus

Almost impossible to come up with a list of people who did not like the work of Malthus: it is very long

Pierre François Verhulst

- Born 1804 in Brussels, Belgium
- 1835, professor of mathematics at the Université libre de Bruxelles
- 1840, École Royale Militaire
- Died 1849 in Brussels, Belgium

Master work

Notice sur la loi que la population suit dans son accroissement (1838)

PROCEEDINGS

OF THE

NATIONAL ACADEMY OF SCIENCES

Volume 6 JUNE 15, 1920 Number 6

ON THE RATE OF GROWTH OF THE POPULATION OF THE UNITED STATES SINCE 1790 AND ITS MATHEMATICAL REPRESENTATION[1]

BY RAYMOND PEARL AND LOWELL J. REED

DEPARTMENT OF BIOMETRY AND VITAL STATISTICS, JOHNS HOPKINS UNIVERSITY

Read before the Academy, April 26, 1920

The logistic curve

Pearl and Reed try

$$P(t) = \frac{be^{at}}{1 + ce^{at}}$$

or

$$P(t) = \frac{b}{e^{-at} + c}.$$

The logistic equation

The logistic curve is the solution to the ordinary differential equation

$$P' = rP\left(1 - \frac{P}{K}\right),$$

which is called the **logistic equation**. r is the **intrinsic growth rate**, K is the **carrying capacity**

Deriving the logistic equation

The idea is to represent a population with the following components:

- birth, at the **per capita** rate b,
- death, at the **per capita** rate d,
- competition of individuals with other individuals reduces their ability to survive, resulting in death.

This gives

$$P' = bP - dP - \text{competition}.$$

Accounting for competition

Competition describes the mortality that occurs when two individuals meet.

- In chemistry, if there is a concentration X of one product and Y of another product, then XY, called **mass action**, describes the number of interactions of molecules of the two products.
- Here, we assume that X and Y are of the same type (individuals). So there are P^2 contacts.
- These P^2 contacts lead to death of one of the individuals at the rate c.

Therefore, the **logistic** equation is

$$P' = bP - dP - cP^2.$$

Reinterpreting the logistic equation

The equation

$$P' = bP - dP - cP^2$$

is rewritten as

$$P' = (b - d)P - cP^2.$$

- $b - d$ represents the rate at which the population increases (or decreases) in the absence of competition. It is called the **intrinsic growth rate** of the population.
- c is the rate of **intraspecific** competition. The prefix **intra** refers to the fact that the competition is occurring between members of the same species, that is, within the species.

Another (..) interpretation of the logistic equation

We have

$$P' = (b - d)P - cP^2.$$

Factor out an P:

$$P' = \big((b - d) - cP\big)P.$$

This gives us another interpretation of the logistic equation. Writing

$$\frac{P'}{P} = (b - d) - cP,$$

we have P'/P, the **per capita growth rate** of P, given by a constant, $b - d$, minus a **density dependent inhibition** factor, cP.

Equivalent equations

$$
\begin{aligned}
P' &= (b-d)P - cP^2 \\
&= \big((b-d) - cP\big)P \\
&= \left(r - \frac{r}{r}cP\right)P, \quad \text{with } r = b-d \\
&= rP\left(1 - \frac{c}{r}P\right) \\
&= rP\left(1 - \frac{P}{K}\right),
\end{aligned}
$$

with

$$
\frac{c}{r} = \frac{1}{K},
$$

that is, $K = r/c$.

3 ways to tackle this equation

1. The equation is separable. [explicit method]
2. The equation is a Bernoulli equation. [explicit method]
3. Use qualitative analysis.

Studying the logistic equation qualitatively

We study

$$P' = rP\left(1 - \frac{P}{K}\right). \qquad \text{(ODE1)}$$

For this, write

$$f(P) = rP\left(1 - \frac{P}{K}\right).$$

Consider the initial value problem (IVP)

$$P' = f(P), \quad P(0) = P_0 > 0. \qquad \text{(IVP1)}$$

- f is C^1 (differentiable with continuous derivative) so solutions to (IVP1) exist and are unique.

Equilibria of (ODE1) are points such that $f(P) = 0$ (so that $P' = f(P) = 0$, meaning P does not vary). So we solve $f(P) = 0$ for P. We find two points:

- $P = 0$
- $P = K$.

By uniqueness of solutions to (IVP1), solutions cannot cross the lines $P(t) = 0$ and $P(t) = K$.

There are several cases.

- $P = 0$ for some t, then $P(t) = 0$ for all $t \geq 0$, by uniqueness of solutions.
- $P \in (0, K)$, then $rP > 0$ and $P/K < 1$ so $1 - P/K > 0$, which implies that $f(P) > 0$. As a consequence, $P(t)$ increases if $P \in (0, K)$.
- $P = K$, then $rP > 0$ but $P/K = 1$ so $1 - P/K = 0$, which implies that $f(P) = 0$. As a consequence, $P(t) = K$ for all $t \geq 0$, by uniqueness of solutions.
- $P > K$, the $rP > 0$ and $P/K > 1$, implying that $1 - P/K < 0$ and in turn, $f(P) < 0$. As a consequence, $P(t)$ decreases if $P \in (K, +\infty)$.

Therefore,

Theorem

Suppose that $P_0 > 0$. Then the solution $P(t)$ of (IVP1) *is such that*

$$\lim_{t \to \infty} P(t) = K,$$

so that K is the number of individuals that the environment can support, the **carrying capacity** *of the environment.*
If $P_0 = 0$, then $P(t) = 0$ for all $t \geq 0$.

Putting things together

- Malthus

$$P' = (b - d)P$$

- Verhulst

$$\begin{aligned} P' &= rP\left(1 - \frac{P}{K}\right) \\ &= (b - d)P - cP^2 \end{aligned}$$

$\Rightarrow$

$$P' = B(P) - D(P)$$

describes both models

$$P' = B(P) - D(P)$$

Malthus:

$$B(P) = bP$$

$$D(P) = dP$$

Verhulst:

$$B(P) = bP$$

$$D(P) = dP - cP^2$$

What type of hypotheses on B and D?

Warder Clyde Allee

- Born 1885 in Bloomingdale, Indiana
- 19101-1912, Assistant Professor of Zoology, University of Chicago
- 1912-1921, U of Illinois, Williams College, U. of Oklahoma, Lake Forest College and Woods Hole
- 1921-, University of Chicago
- 1950-, University of Florida at Gainesville
- Died 1955 in Gainesville, Florida

Master work

Principles of animal ecology (1949)

The Allee effect

For small populations, reproduction and survival increases with population density, whereas for large populations, increasing density reduces growth rate

Two types of effects:

- stong Allee effect: $\exists$ critical size/density below which the population declines and above which it increases
- weak Allee effect: $\nexists$ critical size/density but at lower densities, growth is increasing with densities

Allee effect

Write dynamics as

$$P' = G(P)$$

and assume $G(0) = G(K) = 0$. Population exhibits an Allee effect if there is $I \subset [0, K]$ such that

$$G(P) > G'(0)P$$

As P'/P is per capita growth rate, this means that on I,

$$\frac{P'}{P} = \frac{G(P)}{P} > G'(0)$$

Strong vs weak Allee effect

Strong Allee effect:

$$G'(0) < 0$$

i.e., per capita growth rate is negative in the limit of low density

Weak Allee effect:

$$G'(0) > 0$$

i.e., per capita growth rate is positive in the limit of low density

Strong Allee effect

$$P' = rP\left(\frac{P}{K_0} - 1\right)\left(1 - \frac{P}{K}\right)$$