Lecture 6

Models of Single Populations

Interest in how populations tend to grow was stimulated in the late 18th century when Thomas Malthus (1766-1834) published "An Essay on the Principle of Population as it Affects the Future Improvement of Society." In his book Malthus put forth an exponential growth model for human population and concluded that eventually the population would exceed the capacity to grow an adequate food supply. Although the assumptions of the Malthusian model leave out factors important to population growth (so the model has proven to be inaccurate for technologically developed countries), nevertheless it is instructive to examine this model as a basis for later refinement.

General Compartmental Model

We can consider this problem as a compartmental model, with the compartment being the "world", "town", "organization", "ocean", etc.
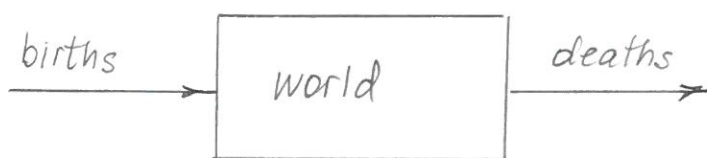
[Input-output compartmental diagram for a population]

This compartmental sketch leads to a word equation describing a changing population,

$$\left\{ \begin{array}{c} \text{rate of change} \\ \text{of population size} \end{array} \right\} = \left\{ \begin{array}{c} \text{rate of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{c} \text{rate of} \\ \text{deaths} \end{array} \right\}$$

Model Assumptions

- We assume that each individual in the population has an equal chance of giving birth and an equal chance of dying within a given time interval. It thus makes sense to talk about a per-capita birth rate β per unit time, per member of the population, and a per-capita death rate α. It follows,

We assume that the populations are sufficiently large so that we can ignore random differences between individuals.

- We assume that births and deaths are continuous in time.

- We assume that per-capita birth and death rates are constant in time.

- In the model development, we ignore immigration and emigration, which can be included later.

Formulating the Differential Equation

Let us suppose a population whose initial value is x_0, with constant per-capita birth rate β, and constant per-capita death rate α. Our aim is to predict the population size at any time t, $X(t)$.

We assume that the population can only change due to births or deaths, neglecting here any immigration or emigration. Also, we assume that this change in population at any time is proportional to the size of the population at that size.

Since the per-capita birth rate β is assumed constant, the overall birth rate at any time is the per-capita birth rate multiplied by the current population size. Similarly, the overall death rate is the per-capita death rate multiplied by the population size.

$$\left\{ \begin{array}{c} \text{rate of} \\ \text{births} \end{array} \right\} = \beta \left[\frac{1}{time} \right] X(t) \left[individuals \right] = \left[\frac{individuals}{time} \right]$$

$$\left\{ \begin{array}{c} \text{rate of} \\ \text{deaths} \end{array} \right\} = \alpha \left[\frac{1}{time} \right] X(t) \left[individuals \right] = \left[\frac{individuals}{time} \right]$$

Substituting into the model, we obtain

$$\boxed{\frac{dX}{dt} = \beta X - \alpha X}$$

We need one initial condition to ensure a unique solution: $X(0) = x_0$.

Solving the Differential Equation

Let $r = \beta - \alpha = \dfrac{\frac{dX}{dt}}{X}$ be the per-capita growth rate or the reproduction rate for the population, then

$$\begin{cases} \dfrac{dX}{dt} = rX \\[2mm] X(0) = x_0 \end{cases}$$

Malthusian Model

$$\Rightarrow \quad \boxed{X(t) = x_0 e^{rt}} \quad , \text{ if } r > 0 \; X \nearrow \text{ (growth)}$$
$$\qquad\qquad\qquad (1) \qquad\qquad r < 0 \; X \searrow \text{ (decay)}$$

Interpretation of Parameters

From the rate of deaths we can approximate the number of deaths by multiplying the rate of deaths by the length of the time interval. This approximation would be better if the time interval were short:

$$\left\{ \begin{array}{l} \text{number of deaths} \\ \text{in time interval } \Delta t \end{array} \right\} \approx \alpha X(t) \Delta t$$

Let us now suppose that x_1 people will die in time t_1, that is, t_1 is the average life expectancy. Then, let $X(t) = x_1$ and $\Delta t = t_1$ so that we have

$$x_1 \approx \alpha x_1 \Delta t_1 \quad \Rightarrow \quad \alpha \approx \frac{1}{t_1}$$

giving an estimate for α as the reciprocal of the average life expectancy.

For human populations, in developed countries, typically the per-capita death rate is quoted as

$$\alpha \approx 0.007 \left[\frac{1}{\text{year}} \right] \text{ or } 7 \text{ death per } 1,000 \text{ persons per year}$$

This approximates an average life expectancy of

$$\frac{1}{\alpha} = \frac{1}{0.007} = 140 \text{ years}$$

This value is too high for humans, but neverless is of the correct order of magnitude compared with true measured average life expectancy of humans, which is 70-80 years. The reason for the discrepancy is due to the fact that the real age distribution does not approximately follow an exponential distribution; instead, the population tends to fall rapidly at older ages. An exponential distribution is the natural distribution for compartment models. For many animal populations, with shorter lifespans and greater probability of dying at younger ages, the reciprocal of the per-capita death rate is usually a more accurate approximation of the average life expectancy.

Using the model we can predict the time taken for the population size to double.

$$X(t+T) = 2X(t) \quad, \quad T = ?$$

$$\frac{X(t+T)}{X(t)} = 2 = \frac{x_0 e^{r(t+T)}}{x_0 e^{rt}} = e^{rT} \implies \boxed{T = \frac{\ln 2}{r}}$$

Model Validation

Since $\ln\left(\frac{X(t)}{x_0}\right) = rt$, our model predicts that if we plot $\ln\left(\frac{X(t)}{x_0}\right)$ versus t, a straight line passing through the origin with slope r should result. However, if we plot the population data for the United States for several years, the model does not fit very well, especially in the later years. In fact, the 1970 cencus for the population of the United States was 203,211,926, and in 1950 it was 150,697,000. Substituting these values into Equation (1) and dividing the first result by the second gives

$$\frac{203,211,926}{150,697,000} = e^{r(1970-1950)} \implies r = \left(\frac{1}{20}\right)\ln\left(\frac{203,211,926}{150,697,000}\right) \approx 0.015$$

That is, during the 20-year period from 1950 to 1970, population in the United States was increasing at the average rate of 1.5% per year. We can use this information together with Equation (1) to predict the population for 1980. In this case,

$$t_0 = 1970, \quad x_0 = 203,211,926, \quad \text{and} \quad k = 0.015 \quad \text{yields}$$

$$X(1980) = 203,211,926\, e^{0.015(1980-1970)} = 236,098,574$$

The 1980 census for the population of the United States was 226,505,000 (rounded to the nearest thousand). Thus, our prediction is off the mark by roughly 4%.

$$\frac{236,098,574 - 226,505,000}{226,505,000} \times 100\% \approx 4.2\%$$

We can probably live with that magnitude error, but let's look into the distant future. Our model predicts that the population of the United States will be 28,688 billion in the year 2300:

$$X(2300) = 203,211,926 \cdot e^{0.015(2300-1970)} \approx 2.8688 \cdot 10^{10} = 28,688 \cdot 10^{6},$$

a population that exceeds current estimates of the maximum sustainable population of the entire planet! We are forced to conclude that our model is unreasonable over a long run.

Some populations do grow exponentially provided that the population is not too large. However, in most populations individual members eventually compete with one another for food, living space, and other natural resources. Let's refine our Malthusian model of population growth to reflect this competition.

Density - Dependent Growth.

If populations are observed over long periods they often appear to reach a limit, or to stabilise. We modify the exponential growth model to account for competition or limited resources and to include the stabilising effect observed in populations.

Background

As a population grows, individuals eventually will compete for the limited resources available. In principle, this competition means that a given environment can support only a limited number of individuals K, which is called the carrying capacity for the population. Technically, it is the population size for which the per-capita birth rate is equal to the per-capita death rate, excluding external factors such as harvesting or interaction with another population.

We need to extend the model to include an additional death rate due to the resource limitations, and thus curb the exponential growth and allow the population to stabilise.

Formulating the Differential Equation (Refining the Model)

Instead of assuming a constant per-capita death rate, we allow the per-capita death rate to increase as the population increaseas, as can be observed in some populations. We can model this behavior by assuming a linear dependence of the per-capita death rate on the population size,

$$\left\{ \begin{matrix} \text{per-capita} \\ \text{death rate} \end{matrix} \right\} = \alpha + \gamma X(t),$$

where $\alpha > 0$ is the per-capita death rate due to natural attrition, and $\gamma > 0$ is the per-capita dependence of deaths on the population size. Note that as $X \to 0$, the per-capita death rate tends to α, while for increasing population size the per-capita death rate increases.

This linear form is the simplest for a population dependent per-capita death rate that increases with increasing population size. The overall death rate is thus given by multiplying the per-capita death rate by the population size, so that

$$\left\{\begin{array}{l} \text{rate of} \\ \text{deaths} \end{array}\right\} = (\alpha + \gamma \bar{X})X = \alpha X + \gamma X^2.$$

The word equation

$$\left\{\begin{array}{l} \text{rate of change} \\ \text{in population} \end{array}\right\} = \left\{\begin{array}{l} \text{rate of} \\ \text{births} \end{array}\right\} - \left\{\begin{array}{l} \text{rate of} \\ \text{deaths} \end{array}\right\}$$

then translates to

$$\frac{dX}{dt} = \beta X - \alpha X - \gamma X^2.$$

Writing $r = \beta - \alpha$, which is the reproduction rate, we obtain the model for density-dependent growth,

(2)
$$\boxed{\frac{dX}{dt} = rX - \gamma X^2}$$
(Bernoulli's eq., autonomous)

An alternative formulation of this equation comes from splitting the death rate into a normal death rate and an extra death rate due to members of the population competing with each other for limited resources. Thus we can write

$$\left\{\begin{array}{l} \text{rate of change} \\ \text{in population} \end{array}\right\} = \underbrace{\left\{\begin{array}{l} \text{rate of} \\ \text{births} \end{array}\right\} - \left\{\begin{array}{l} \text{normal rate} \\ \text{of deaths} \end{array}\right\}}_{(\beta X - \alpha X) = (\beta - \alpha)X = rX} - \underbrace{\left\{\begin{array}{l} \text{rate of} \\ \text{deaths by crowding} \end{array}\right\}}_{\gamma X^2,\ \gamma > 0.}$$

For extra deaths by crowding, we assume that the per-capita death rate increases with population size. If we assume that it is proportional to the population size and thus given by γX, then the extra overall death rate is the extra per-capita death rate multiplied by the current population size.

$$\gamma \left[\frac{1}{\text{time·members}}\right] X [\text{members}] \; X [\text{members}] = \left[\frac{\text{members}}{\text{time}}\right]$$

Without actually solving the differential equation, we can infer how the solution would behave. The population has an initial value x_0. The derivative
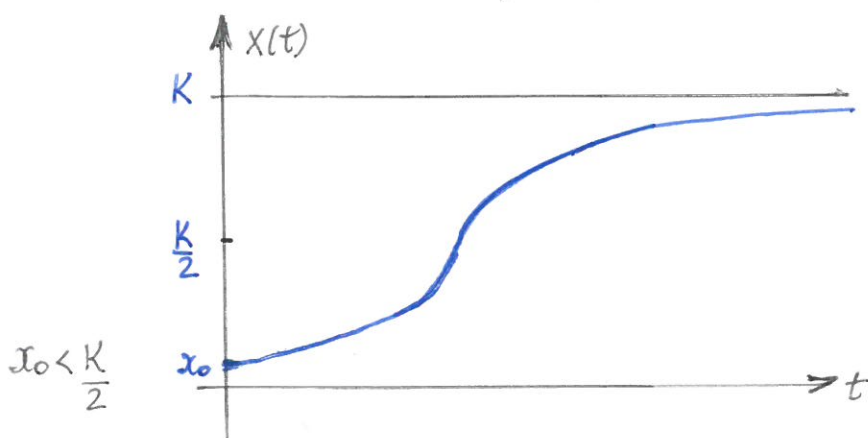
$$\frac{dX}{dt} = rX\left(1 - \frac{\gamma}{r}X\right) = rX\left(1 - \frac{X}{r/\gamma}\right) = rX\left(1 - \frac{X}{K}\right)$$

$K := r/\gamma$ (carrying capacity)

$$\frac{dX}{dt} > 0 \quad \text{if} \quad X < K, \quad X \text{ increases}$$

Moreover, $\dfrac{d^2X}{dt^2} = \dfrac{d}{dt}\left(rX - \gamma X^2\right) = r\dfrac{dX}{dt} - 2\gamma X\dfrac{dX}{dt} =$

$$= \frac{dX}{dt}\left(r - 2\gamma X\right) \implies X'' = 0 \quad \text{when} \quad X = \frac{1}{2}\frac{r}{\gamma} = \frac{1}{2}K$$

↙ Inflection points.

In words, when the population X reaches half of K, the growth dX/dt is most rapid ($X' > 0$, $X'' > 0$) and then starts to diminish toward zero ($X' > 0$, $X'' < 0$)

$x_0 < \dfrac{K}{2}$

The Logistic Equation

With $K = r/\gamma$, the differential equation (2) becomes

$$\frac{dX}{dt} = rX - \frac{r}{K}X^2,$$

which can be written as

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

This model leads to a nonlinear differential equation.
It is the logistic equation and is also referred to as
the limited growth model or the density-dependent model.
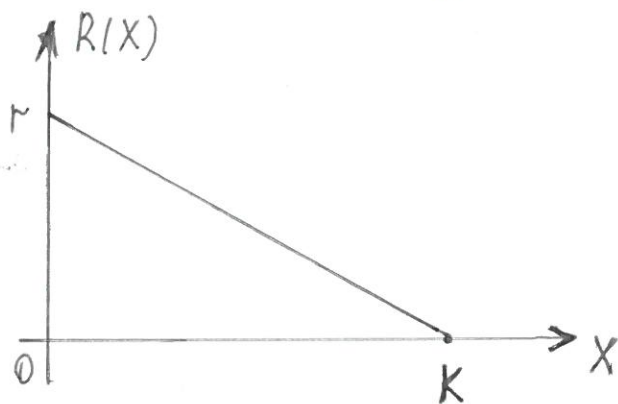We consider only $r>0$ and $k>0$ to ensure positive population
values.

Interpretation of the parameters

We can write a general differential equation for population
growth as

$$\frac{dX}{dt} = R(X)X,$$

where $R(X)$ represents a population dependent per-capita
growth rate. For the logistic equation we identify $R(X)$ as
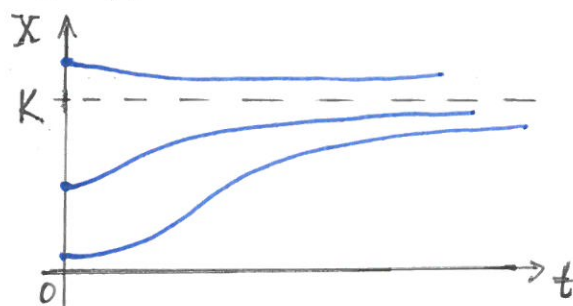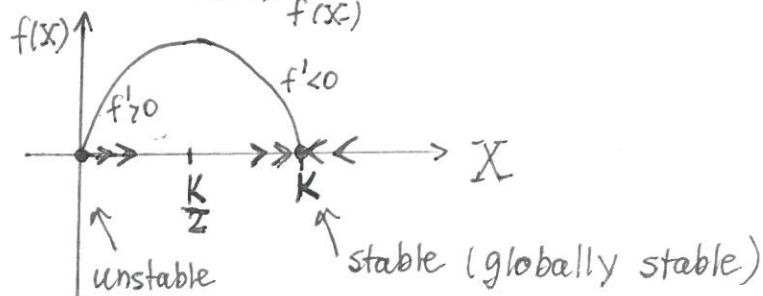
$$R(X) = r\left(1 - \frac{X}{K}\right).$$

If $R<0 \Rightarrow X>K \Rightarrow X \searrow K$.

[The simplest assumption for a population dependent per-capita
growth rate is a straight line].

Equilibrium Solutions and Stability

Equilibrium solutions are

$$\frac{dX}{dt} = 0 = \underbrace{rX\left(1 - \frac{X}{K}\right)}_{f(x)} \quad \Rightarrow \quad X=0 \quad \& \quad X=K$$

$f'>0$ $f'<0$

unstable   stable (globally stable)

Analytic Solution

Solve the initial-value problem

$$\begin{cases} \dfrac{dX}{dt} = rX\left(1 - \dfrac{X}{K}\right) = \dfrac{rX(K-X)}{K} & \text{D.E.} \\[2mm] X(0) = x_0 & \text{I.C.} \end{cases}$$

Separating the variables

$$\frac{K\,dX}{X(K-X)} = r\,dt$$

Partial Fraction Decomposition:

$$\frac{K}{X(K-X)} = \frac{A}{X} + \frac{B}{K-X} = \frac{A(K-X)+BX}{X(K-X)} = \frac{X(B-A)+AK}{X(K-X)} \Rightarrow$$

$$X^1: \quad B-A=0 \Rightarrow A=B$$

$$X^0: \quad AK = K \quad \Rightarrow A=1 \Rightarrow B=1$$

$$\int \frac{K\,dX}{X(K-X)} = \int \left(\frac{1}{X} + \frac{1}{K-X}\right) dX = \ln X - \ln|K-X| = \ln\left|\frac{X}{K-X}\right|$$

Therefore, $\quad \ln\left|\dfrac{X}{K-X}\right| = rt + C \Rightarrow \left|\dfrac{X}{K-X}\right| = e^C e^{rt}$ or

$$\frac{X}{K-X} = Ce^{rt} \qquad \frac{X(0)}{K-X(0)} = C \Rightarrow C = \frac{x_0}{K-x_0} \Rightarrow$$

$$X = \frac{x_0}{K-x_0}e^{rt}(K-X) \Longleftrightarrow X\left(1 + \frac{x_0}{K-x_0}e^{rt}\right) = \frac{Kx_0e^{rt}}{K-x_0} \Longleftrightarrow$$

$$X = \frac{\frac{Kx_0}{K-x_0}e^{rt}}{\left(1 + \frac{x_0}{K-x_0}e^{rt}\right)} \cdot \frac{e^{-rt}}{e^{-rt}} = \frac{\frac{Kx_0}{K-x_0}}{\left(\frac{x_0}{K-x_0} + e^{-rt}\right)} = \frac{\frac{Kx_0}{K-x_0}}{\frac{x_0}{K-x_0}\left(1 + \frac{(K-x_0)}{x_0}e^{-rt}\right)}$$

$$\boxed{X = \frac{Kx_0}{x_0 + (K-x_0)e^{-rt}}}$$

$$\lim_{t\to\infty} \frac{Kx_0}{x_0 + (K-x_0)e^{-rt}} = \frac{Kx_0}{x_0 + (K-x_0)\cdot 0} = K$$

(Horizontal Asymptote)

One advantage of recognizing that the maximum rate of growth occurs at $x = K/2$ is that the information can be used to estimate K. In a situation where the modeler is satisfied that the growth involved is essentially logistic, if the point of maximum rate of growth has been reached, then $K/2$ can be estimated.
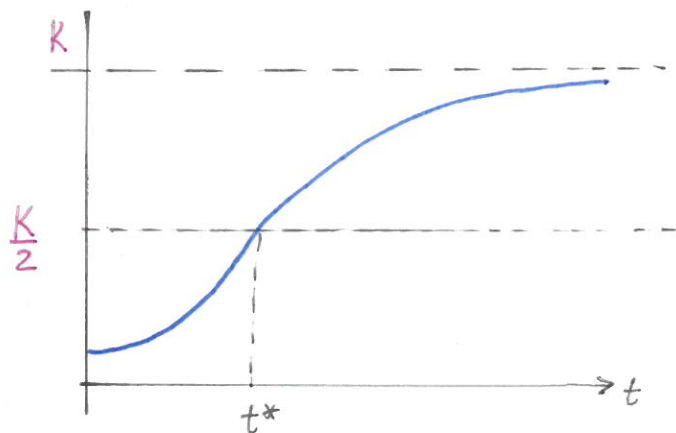
With the logistic model developed above we have incorporated an instantaneous reaction to the environment. That is, increased pressure on the resources produces an immediate response from the system in terms of, for example, more deaths. This is often not realistic in that the response usually takes effect after some time delay, or time lag. Vegetation needs time to recover and changed environmental conditions, which may lead to increased birth rates, will take time to appear in the numbers of an adult population. This leads us to model that includes a time delay resulting from a multitude of sources, such as maturation times, food supply, resources, or crowding — each a measurable quantity. If the time lag is small compared with the natural response time $(1/r)$, then there is a tendency to overcompensate, which may produce oscillatory behavior. (Sec. 3.7 & 3.8)