5 Population Models

Lisa: What happens when we're overrun by lizards?
Pr. Skinner: No problem. We simply release wave after wave of Chinese needle snakes. They'll wipe out the lizards.
Lisa: But aren't the snakes even worse?
Pr. Skinner: Yes, but we're prepared for that. We've lined up a fabulous type of gorilla that thrives on snake meat.
Lisa: But then we're stuck with gorillas!
Pr. Skinner: No, that's the beautiful part. When wintertime rolls around, the gorillas simply freeze to death.

From: *The Simpsons*

5.1 The Malthus Model

In 1798 Thomas Malthus, an English economist and philosopher, published *An Essay on the Principle of Population*. In this essay he asserted, based on evidence from the population growth of the European settlements in North America, that in a favorable and unrestricted environment human population would tend to double every 25 years. The food supply, he took as self-evident, could only be expected to increase by a fixed amount in the same time period. In due course this imbalance would result in an abundance of “misery and vice”, leading perhaps to some catastrophic demographic collapse.

Can we provide some simple biological mechanism that leads to Malthus’ assertion that reproducing populations double in size in a fixed time period? The process of using mathematical tools to derive results about complex systems from simpler assumptions is called *mathematical modeling*. This approach has the advantage of making explicit the ingredients that we think are responsible for the observed phenomena. We can then examine these assumptions in new situations or in controlled experiments to assess their importance.

The first assumption we make for what we call the Malthusian model is that the population of organisms under consideration is large and reproduces uniformly throughout the year (or whatever time period is appropriate). This assumption allows us to use differential equations. For organisms with more regulated life cycles, (many types of insects for instance), this is not valid and different mathematical techniques are needed. These will be considered in Chapter 17.

Our second assumption relates to the per capita birth and death rates, r_b and r_d. These are defined as the number of births (resp. deaths) per individual in a unit of time. For example, if a population started with a size $N = 1{,}000{,}000$ and there were 3,000 births during a year (which we take as our unit of time), then the per capita birth rate would be $\frac{3{,}000}{1{,}000{,}000} = .003$. Roughly speaking, this number means that in the course of a year each existing organism creates on average .003 new organisms. In discussing human demography, most people find it more meaningful to multiply the per capita birth rate by 1000, giving the birth rate per 1000 people. In the example above, this would be 3. The table below lists the birth and death rates per 1000 people (as of 1997) in various countries.

Country	Birth Rate per 1000	Death Rate per 1000
Albania	21.35	7.45
Cambodia	41.63	16.49
Italy	9.13	10.18
Mexico	25.49	4.91
United States	14.4	8.8
Source: *CIA World Factbook* (1998) at http://www.odci.gov/cia/publications/pubs.html		

Table 5.1

We assume that in the time period under consideration the birth and death rates remain constant. We can use this and the first assumption to formulate a description of the instantaneous rate at which the population grows. Namely, let us denote by $N = N(t)$ the population at time *t*. We want an expression for the change in the population over a short time interval Δt. This is given by

$$N(t+\Delta t) - N(t) = \text{\# of births} - \text{\# of deaths}.$$

Since r_b is the per capita birth rate, the number of births occurring in a population of size N in unit time is given (approximately) by $r_b N$ and so in the short time interval Δt the assumption of uniform distribution of births implies that the number of births will be $(\Delta t)r_b N$. (For example, if $\Delta t = .1$ there would be only 1/10 of the births in that time interval than in the entire year.) Similarly, the number of deaths will be $(\Delta t)r_d N$. Hence,

$$N(t+\Delta t) - N(t) \approx (\Delta t)r_b N - (\Delta t)r_d N = (\Delta t)rN,$$

where $r = r_b - r_d$ is called the *intrinsic growth rate* or *natural growth rate*. Now divide both sides of the last equation by Δt and take the limit as $\Delta t \to 0$. On the left side we obtain the limit of the difference quotient for $N(t)$, which is just $\frac{dN}{dt}$. We have then a differential equation for population growth, which we call the Malthusian model:

$$\frac{dN}{dt} = rN \tag{5.1}$$

This is the same equation we studied in the section of chapter 2 devoted to money. In that setup each dollar actually created an additional $r\%$ dollars in interest. Our population model behaves mathematically as if the change in the population was due to each individual contributing the same small percent increase (or decrease). We know from our previous work (see Chapter 2, example 2.9) that the solutions of (5.1) are $N(t) = N_0 e^{rt}$, where $N_0 = N(0)$ denotes the initial population.

The graph below depicts several solutions with the same initial value N_0, but with different values of r. Note that when r is negative the value of N tends towards zero, a situation fulfilling Malthus' scenario for an overpopulated earth.

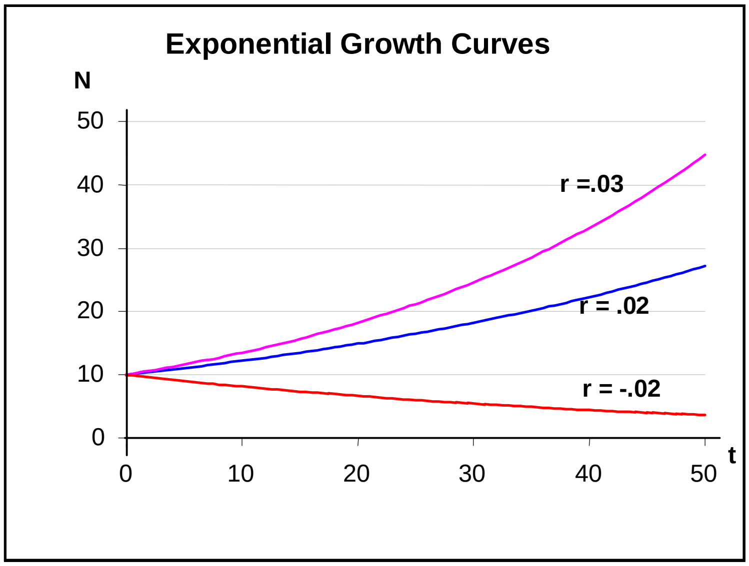


Figure 5.1

Example 5.1: Given that the present population of the U.S. is 270 million, and assuming the Malthusian model, what will be the population in 50 years?

Solution:

Based on the birth and death rates presented in Table 5.1 above, the intrinsic U.S. growth rate per 1000 is $14.4-8.8=5.6$. Thus the value of r is .0056. The growth function is $N(t)=270e^{.0056t}$. Letting t=50 gives $N(50)=270e^{.28}\approx 357$ million.■

As in our discussion of money in Chapter 2, we can now easily find the value of the *doubling time*, a number which Malthus and most subsequent demographers use to characterize exponential growth. Recall from Chapter 2 that this is the time t_2 required for the population N to double in size. We found its value to be

$$t_2=\frac{\ln 2}{r} \tag{5.2}$$

Example 5.2: What is the doubling time for the U.S. population, based on the data in Table 5.1?

Solution:

Since $r = .0056$ we have $t_2 = \frac{\ln 2}{.0056} \approx 124$ years. Actually the doubling time is considerably less because we have ignored migration to the U.S. See exercise 2 on page 11.■

5.2 A Harvesting Model

Mathematical models are most interesting when they indicate some unexpected effect. In particular, when two opposing processes are operating, mathematics often enables one to understand the net outcome. Suppose a species is reproducing with exponential growth. What will happen to the population if a fixed number of individuals are removed each year (harvested), in addition to the usual loss due to deaths. We will see that mathematically we arrive at a situation identical to the payment of an annuity that was discussed in the exercises of Chapter 2. However, we make no use of that discussion in what follows.

To analyze the harvesting scenario described above we need to derive an appropriate differential equation. We can proceed as we did for Malthus' equation, condensing the steps now that we are familiar with the arguments. To be specific, suppose the natural growth rate $r = .02$ and 50 individuals are harvested uniformly each year. In time Δt the change in the population due to the natural growth factor will be $(\Delta t)rN = (\Delta t).02N$. However, opposing this will be the decrease in the population due to the harvesting. We assumed this was 50 per year. Therefore, in time Δt the number removed is $50(\Delta t)$. Thus, the overall change in the population $\Delta N \approx (\Delta t)(.02N - 50)$. Dividing by Δt and taking the limit as $\Delta t \to 0$ gives the following differential equation:

$$\frac{dN}{dt} = .02N - 50 \tag{5.3}$$

We need to consider the initial values N_0. Let's consider two examples, $N(0) = 1000$ and $N(0) = 3000$. Using numerical methods to solve the equations in these cases we obtain the solutions shown in Figure 5.2.

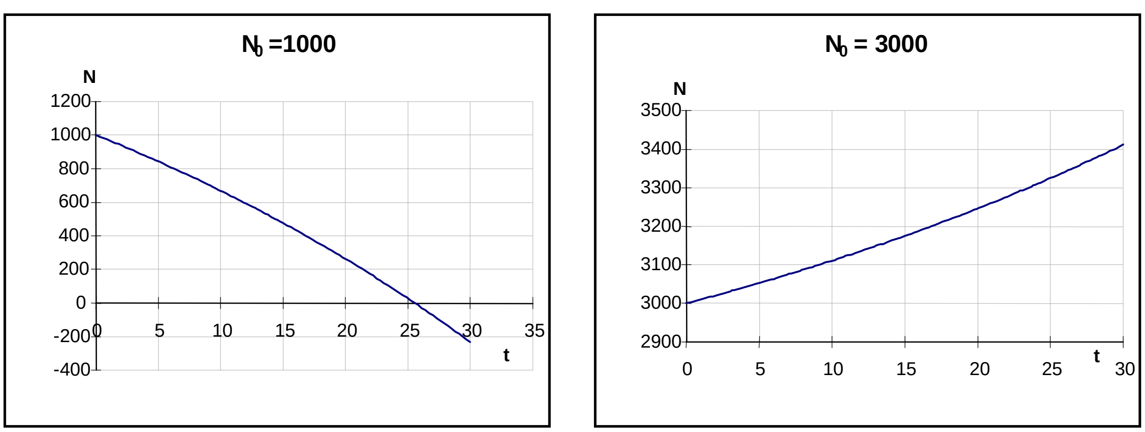


Figure 5.2

It certainly appears that when $N_0 = 1000$ the population decreases, eventually (for $t \approx 25$) reaching a value of zero, after which the mathematical solution ceases to have a real meaning. On the other hand, the solution that begins at $N_0 = 3000$ seems to grow without bound. We can use the qualitative theory developed in chapter 4 to confirm these features of the solution.

Example 5.3: Use qualitative methods to analyze the solutions of the differential equations (5.3) with initial conditions $N_0 = 1000$ and $N_0 = 3000$.

Solution:

- Find the equilibrium or steady state solutions. Letting $g(N) = .02N - 50$ denote the right side of (5.3), the steady state solution is obtained by solving the equation $g(N) = 0$. This gives $N = 2500$.
- Plot the graph of $g(N)$ vs. N. This is a straight line of slope .02 and horizontal intercept equal to the steady state value 2500 found above. See Figure 5.3.

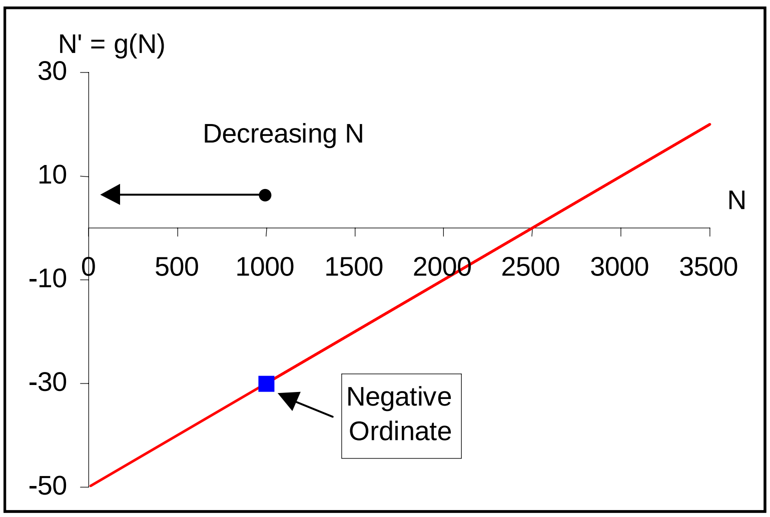


Figure 5.3

With an initial value of $N_0 = 1000$, the ordinate N' on the graph is negative so the solution $N(t)$ will steadily decrease. The value of N will eventually reach zero, indicating that the population becomes extinct. The harvesting level of 50 is too large to be sustained when the initial population is only 1000. The concavity of the solution graph $N = N(t)$ can also be predicted from Figure 5.3. Recall from Chapter 4 that the sign of $g(N)g'(N)$ determines the concavity. When $N = 1000$, $g(N) < 0$ and $g'(N) = .02$ is a positive constant (the slope of the line). Therefore, $g(N)g'(N) < 0$ and the graph of $N(t)$ will be concave down, as indicated in left panel of Figure 5.2. The reader should carry out the similar reasoning needed to obtain the solution curve $N(t)$ when $N_0 = 3000$. ■

Example 5.4: What is the maximum harvest that could be sustained with an initial population of size $N_0 = 1000$?

Solution:

The intrinsic growth rate is 0.02 per capita per year so that in one year a population of size 1000 would be expected to produce 20 new members. We would therefore expect that a harvest of 20 or less could be sustained, but not one exceeding 20. If the harvest level is 20, then the differential equation for the growth of the population becomes

$$\frac{dN}{dt} = .02N - 20 \tag{5.4}$$

The steady state solution for this equation is $N = 1000$, so an initial population of $N_0 = 1000$ will stay at that level indefinitely. Note, though, that in this case $N_0 = 1000$ is an unstable equilibrium (give the arguments). Why does this imply that setting the harvest at the maximum level is not a good policy? ■

5.3 The Logistic Model

Malthus assumed rather arbitrarily that if the productive capacity of the environment was currently C_0 then, after a certain number of years, this might rise to $2C_0$ and then to $3C_0$ after the same period had passed, etc. Thus, if the initial capacity were C_0, after k such periods the capacity would have increased to kC_0. During the same time population would have grown according to a law of the form $N_0 A^k$, where A is a constant greater than one (see Exercise 4). The productive capacity available per person is the ratio $kC_0 / N_0 A^k = const \times k / A^k$ and the ratio k / A^k approaches 0 as k approaches infinity, (for example with $k = 100$ we have $100/2^{100} \approx 7.8 \times 10^{-29}$). Thus the amount of sustenance available per person would drop to zero, producing widespread famine and death.

There are two ways out of the Malthusian dilemma. One is the possibility that the carrying capacity of the environment increases more rapidly than is postulated above. This has certainly been the case over the two hundred years since the publication of Malthus' Essay. Just to present some recent data, consider the growth of world population and grain production in the period 1970 to 1996:

World Population & Grain Production 1970 to 1996			
	1970	1980	1996
World Population, *millions*	3706	4455	5767
% increase		20.2%	29.5%
Grain, *millions of metric tons*	1171	1535	2044
% increase		31.1%	33.2%
Source: *Handbook of International Economic Statistics 1997*			
http://www.odci.gov/cia/publications/hies97			

Table 5.2

As the table shows, over each time period, the percentage growth in the grain production exceeded the corresponding increase in population, although perhaps ominously the two appear to be converging. The longer-term historical record is more difficult to analyze, primarily because of a lack of good statistics, particularly regarding crop production. Nonetheless, the earth is finite and eventually an exponentially growing population would cover every square inch, so that regardless of how productive we are in the "short run", a Malthusian growth curve must eventually lead to disaster.

There is, however, an alternative "soft landing." Namely, the population might keep increasing, but at a slower and slower rate (See Exercise 5 for whether this is suggested by the data in Table 5.2). Such a scenario was first described mathematically in the 1830s by P.F. Verhulst and was rediscovered a hundred years later by R. Pearl and L.J. Reed. It is possible to derive Verhulst's model from some simple biological principles as we did for Malthus' equation. We prefer a simpler approach. The Malthus equation (5.1) can be rewritten as

$$\frac{1}{N}\frac{dN}{dt} = r\,.$$

On the left side we have the rate of change of population $\frac{dN}{dt}$ divided by N, in other words, the per capita rate of change. The Malthus equation asserts that this per capita rate is constant. Suppose though that this rate is not constant, but decreases as the population increases. This is referred to as *a density dependent growth rate*. There are many ways to describe this mathematically. The simplest and the one used by Verhulst is to assume that for some constant K

$$\frac{1}{N}\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right).$$

Notice that when N is small compared with K, the term $(1 - N/K)$ will be close to one and the per capita growth rate will be nearly r. As N approaches K the ratio N/K approaches one and therefore $(1 - N/K)$ and the per capita growth rate will be close to zero. We rewrite the equation in its standard form; it is usually referred to as the *logistic equation*.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \qquad (5.5)$$

What do the solutions of (5.5) look like? Consider, for example, taking $r = .02$, $K = 50$ and initial value $N_0 = 10$. The differential equation is then $N' = .02N(1 - N/50)$, which has steady state solutions $N = 0$ and $N = 50$. Numerical methods yield the following solution curve for t in the interval [0, 300]:

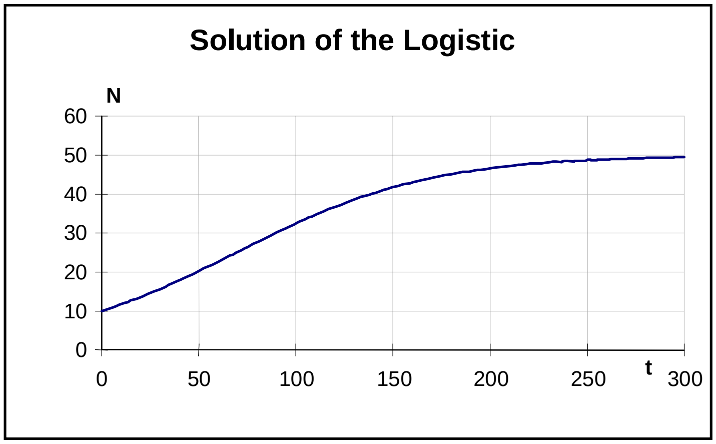


Figure 5.4

The solution rises with increasing slope from its initial value of $N_0 = 10$. Around $N \approx 25$ the curve turns concave down, that is the slope starts to decrease, approaching zero. The value of N rises simultaneously towards an asymptotic limit of 50. This behavior is quite typical of the logistic equation. Qualitative methods allow us to analyze the general case, where the numerical values of the population parameters r and K are not specified.

Example 5.5: Use qualitative methods to analyze solutions of the logistic equation (5.5).

Solution:

- *Equilibrium solutions*: $g(N) = rN(1 - N/K) = 0$ implies $N = 0$ or $N = K$.

- *Stability analysis*: To analyze the stability consider the graph of $N' = g(N)$ vs. N. Assuming r and K are both positive, this is a downward facing parabola having intercepts at $N = 0$ and $N = K$.

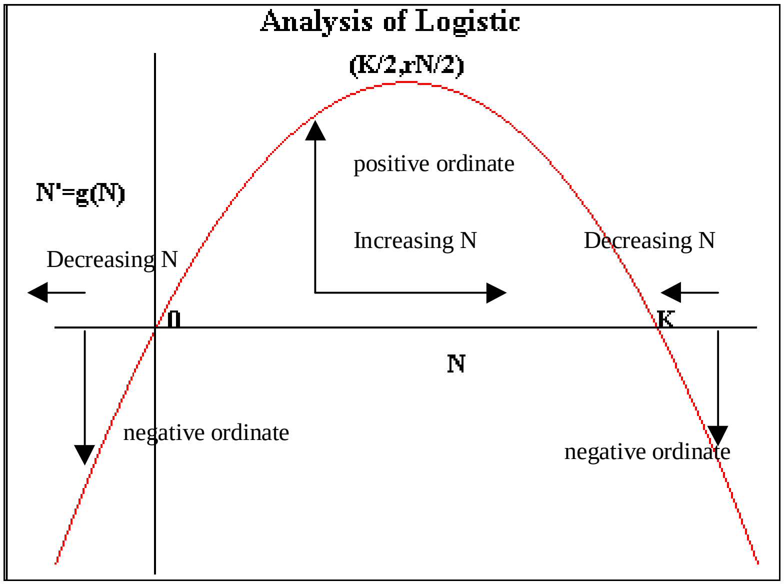


Figure 5.5

From Figure 5.5 we see that K is a stable equilibrium solution, and 0 is unstable. Any solution with initial value between 0 and K will tend towards K (so will a solution with initial value larger than K, though these are of less practical significance). As we know from the theory of qualitative solutions, a solution will possess an inflection point if it passes through a value of N for which $g'(N) = 0$. Since $g(N) = rN - \frac{rN^2}{K}$, the derivative $g'(N) = r - \frac{2rN}{K} = 0$ for $N = K/2$. At this population size N is increasing at its greatest rate (why?). A family of solutions is shown below:

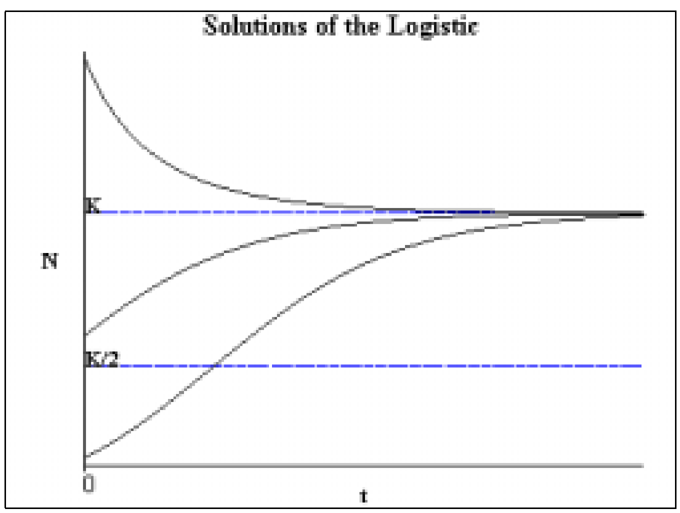


Figure 5.6

■

The constant K is called the *carrying capacity of the environment*, because according to this model any initial positive population size will tend towards K. The constant r is called the *intrinsic growth rate*, because when $N \approx 0$ the term $(1 - N/K)$ in (5.5) can be disregarded and the differential equation is approximately the same as $N' = rN$. In this case the population grows exponentially until it reaches a size large enough for the factor $(1 - N/K)$ to begin to suppress the growth rate.

Although under well-controlled laboratory conditions the logistic growth pattern has been experimentally confirmed for certain microbial populations (yeast for example), its applicability to human populations has not been demonstrated. When Reed and Pearl rediscovered the logistic equation they were quite impressed with how well it was able to model the growth of the U.S. population from the first census in 1790 to 1940. In fact, using a variation of the method of least squares that we will discuss later, we can find values of r and K for which the solution of the logistic differential equation provides a suitable fit to the data. For the period 1790 to 1940 we find that $r = .0315$ and $K = 189$ million. The predicted population values, obtained using the latter values for r and K in the differential equation (5.5) with initial condition $N_0 = 3.9$ million (the U.S. population in 1790), and the actual census data are shown on the left in Figure 5.7, below. Human events, however, did not quite follow the mathematical script. Following the post-World War II baby boom and a resurgence in immigration, the predicted population limit of 189 million was exceeded around 1960.

Using a similar technique we can try to fit a logistic curve to the population growth curve from 1790 to 1990. This time we obtain an estimate that $r = .0285$ and $K = 304$ million. However, when we plot the logistic curve against the actual population data for this period, we see that the fit is not nearly as impressive as it was using the more restricted data up to 1940. It remains to be seen whether the predicted limit will correctly describe the future growth of the U.S. population.

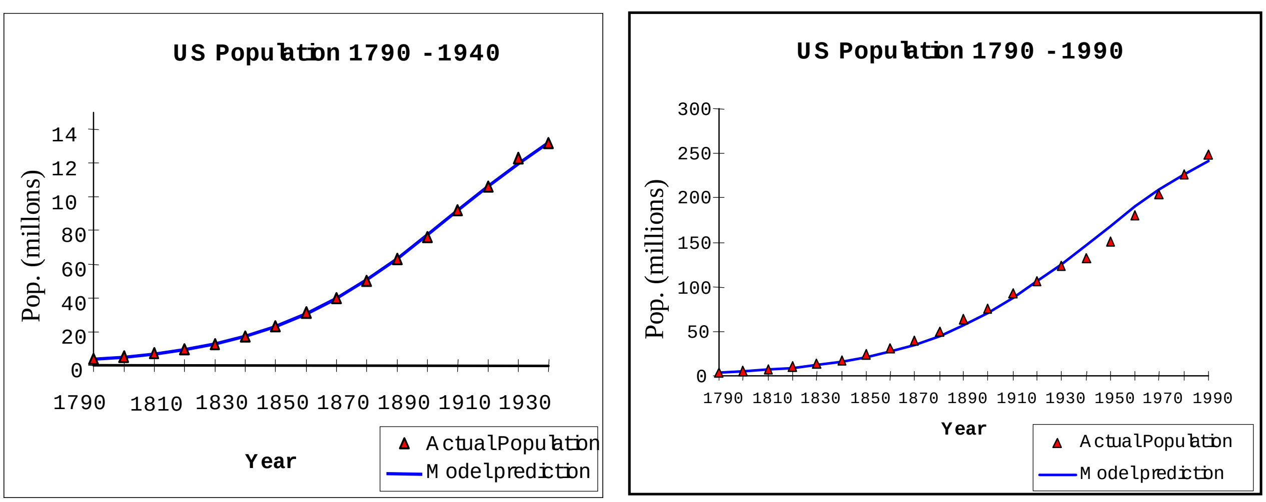


Figure 5.7

5.4 Summary

Differential equations can be used to describe the growth of biological populations in which reproduction occurs more or less continuously over time. Assuming constant per capita birth and death rates, we are led to the ***Malthusian model***, $N' = rN$. This model predicts exponential growth for positive growth rates r and eventual extinction for $r < 0$. Since exponential growth is not a sustainable state in the long-term, modelers have sought simple, and perhaps plausible, schemes that would avoid such an outcome. A reasonable hypothesis is to assume that the increasing density of a growing population leads to a reduction in the per capita growth rate. The ***logistic model***, $N' = rN\left(1 - \frac{K}{N}\right)$, provides one realization of this principle. In this model, the population N, rather than growing exponentially, approaches a limiting value, K, the carrying capacity.

For economic reasons, populations may be subjected to ***harvesting***. Various harvesting scenarios can be modeled by modifying the assumed natural growth equation. For example, a constant yield, h, culled from an exponentially growing population N, leads to the model $N' = rN - h$. Other examples, as well as related conservation models, can be found in the exercises.

5.5 Exercises

1. a) Using the data in Table 5.1 solve the Malthus equation (5.1) for the population of Italy, using as the initial population in 1997 the value N_0 = 57 million.

   b) Assuming the same trend in the population continues, what will be the population of Italy in 2050?

   c) What is the percent decrease in the population of Italy in one year?

2. According to the *World Factbook* cited above, the current net migration rate into the U.S. is approximately 3.1 per 1000 persons per year. Recalculate the doubling time taking this into account.

3. Given that the 1997 populations of Mexico and the U.S. are 97.5 and 268 million respectively, assuming the Malthus model and the growth rates in Table 5.1, when will the populations of the two countries be equal and what will be their common size?

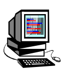
4. If the size of a population follows an exponential growth equation, $N = N_0 e^{rt}$, show that in any time period Δt the population is multiplied by the factor $A = e^{r(\Delta t)}$. Using this result, show that in k consecutive periods of length Δt, the population grows by the factor A^k.

5. a) Table 5.2 shows that in the 10-year period from 1970 to 1980 the world population increased from 3.71 billion to 4.45 billion. Assuming the population growth in those years

was governed by an equation $\frac{dN}{dt} = rN$, determine the value of r, the annual growth rate. Express the answer as annual increase per 1000 persons.

b) Repeat the calculation in part a) using the data from 1980 to 1996. Does the result support the contention that the world's population growth rate is decreasing?

6. a) Use separation of variables to find the exact solution of (5.3) when $N_0 = 1000$. Using the answer, find how long it will take for N to equal 125. (Note: The calculus will be simpler if you rewrite the equation as $\frac{dN}{dt} = .02(N - 2500)$ and divide by $(N - 2500)$ when separating the variables.)



b) Using the program *ode.xls* (and the modified Euler method), solve the differential equation (5.3) numerically and determine with the software how long it will take before N reaches 125.

c) Suppose when the population reaches a size of 125, a ban on harvesting is imposed. Assuming the growth rate of the species remains the same as in a), how long will it take for the population to recover to its original size of 1000? You can use either exact formulas or the program *ode.xls* to find the answer.

7. A local fishing site contains an estimated 50,000 fish, with a natural population growth rate of 5% per year. The annual catch by local fisherman depletes this population by about 3,000 fish per year.

a) Set up a differential equation that models the growth of the fish population, taking into account the effect of fishing. State as clearly as you can what physical assumptions about the fish population this model is based on.

b) Using qualitative analysis sketch a graph of the population vs. time. Explain briefly how this graph is obtained.

c) Based on your answer in b) can the current annual catch be sustained indefinitely? Confirm the result by finding the exact solution of the equation in a). (In regard to solving the equation, see the note to 6a).)

8. a) Suppose an endangered species has a natural growth rate equation $\frac{dN}{dt} = -.02N$, so that eventually the population will become extinct. If breeding programs are able to introduce 100 new members to the wild stock each year (with the additions made uniformly throughout the year), explain why the population growth will be modeled by the equation

$$\frac{dN}{dt} = -.02N + 100 \tag{5.6}$$

b) Using qualitative methods determine the steady state solution for (5.6). Is it stable or unstable?

c) If the current population size is $N_0 = 1000$, make a sketch of the solution of (5.6) and in particular indicate what will happen to the population as $t \to \infty$. Justify your answer.

9. a) The growth of a population follows a logistic differential equation with $r = .02$ and $K = 300$. Sketch curves of the population $N(t)$ for initial values $N_0 = 100$ and $N_0 = 200$.

b) For each of the initial conditions described in a) determine for what population size the growth rate $\dfrac{dN}{dt}$ is a maximum.

10. The logistic model assumes that the carrying capacity K is a constant. Suppose however that a growing population actually causes the carrying capacity to increase, a result possibly of cultural innovation. For example, suppose that K has the form $K = K_0 + c\sqrt{N}$, where K_0 is the intrinsic carrying capacity and c is a positive constant. Note that the per capita increase in the carrying capacity is $c\sqrt{N}/N = c/\sqrt{N}$, which decreases as N increases, an instance of the economic law of diminishing returns. Thus we take as our model the modified logisitic

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K_0 + c\sqrt{N}}\right) \tag{5.7}$$

a) With the values $r = .02$, $K_0 = 300$, $c = 2$, and $N_0 = 100$, use the file *ode.xls* to examine numerically the behavior of (5.7) as $t \to \infty$. In particular, using the numerical solution estimate the value of the steady state solution. How does the result differ from that obtained in exercise 9 with the pure logistic and $K = 300$? Does the answer make sense?

b) Use qualitative methods to find an exact expression for the steady state solution that you estimated in a). (Hint: You should obtain a quadratic equation in the variable $u = \sqrt{N}$.)

11. Using the file *ode.xls*, numerically solve the logistic differential equation for the U.S. population growth from 1790 to 1940 using the values $r = .0315$ and $K = 189$ with $N_0 = 3.929$. (We are assuming that $t = 0$ corresponds to 1790.) Compare the population estimates for the years 1800, 1810, …, 1940 with the actual census figures given in the data file *us_pop.xls*.

12. a) The logistic differential equation (5.5) can actually be solved explicitly using separation of variables. Verify that for any constant C formula (5.8) below gives a solution.

$$N(t) = \frac{K}{1 + Ce^{-rt}} \tag{5.8}$$

b) Show that if $N_0 = N(0)$ then the value of C in (5.8) is given by $\dfrac{K}{N_0} - 1$.

c) In our discussion of the logistic we showed that when the population starts out below its carrying capacity the rate of increase of the population reaches a maximum when the population size reaches half the carrying capacity. Show using (5.8) that this occurs for $t = \frac{\ln C}{r}$.

d) Using the U.S. census data from 1790 to 1940 and the logistic model described in exercise 11, determine the year in which the U.S. population should have reached half its carrying capacity.

13. A population of size $N_0 = 2000$ is living in an ecosystem in which its growth is governed by a logistic equation with $r = .03$ and $K = 2200$. Suppose a sudden environmental change causes a 30% drop in the carrying capacity. Set up a revised logistic model and determine the long term effect on the size of the population. Include a sketch showing the graph of the population $N(t)$.

14. a) A differential equation of the same type as (5.6) also arises in problems of physiology, so-called compartment models. For example, suppose that the body excretes or metabolizes 30% of a certain antibiotic each hour. If a patient is given a continuous intravenous dosage of 75 mg/hr, explain why the amount y (in mg) of antibiotic in the patient's blood satisfies the differential equation

$$\frac{dy}{dt} = -.3y + 75 \tag{5.9}$$

b) Using (5.9), find the limiting value of the amount of antibiotic in the patient's blood. Justify your answer using qualitative methods. (Note: You should take $y(0) = 0$. Why?)

c) Suppose the antibiotic is fed from liter bags that contain 500 mg of antibiotic. (The bags are replaced when they are empty.) At what rate r in ml/hr should the drip rate be set so that in the long term the patient will have a steady level of 250 mg of antibiotic in his blood?

15. The logistic model illustrates density dependent per capita growth. Some biological models of tumor growth (*Gompertz model*) seem best described by time dependent per unit growth. If V denotes the volume of a solid tumor at time t, suppose the growth rate dV/dt is given by

$$\frac{dV}{dt} = 2e^{-t}V \tag{5.10}$$

Note that as t increases the per volume rate of increase V'/V decreases. (The latter ratio can also be thought of as approximately the relative rate of increase, $\Delta V/V$, in unit time. We can say, not implausibly, that as the tumor grows its volume increases by smaller and smaller percentages).

a) Qualitative methods cannot be used to analyze (5.10) as written. (Why?) Use separation of variables to solve (5.10) with the initial condition $V_0 = .25$. What is the limiting volume of the tumor as $t \to \infty$?

b) Using *ode.xls* and the modified Euler method numerically solve the differential equation (5.10) with initial condition $V_0 = .25$. As a check on your work in a) plot the solution you found there along with the numerical solution.

16. a) A more realistic harvesting model than the one we considered in section 5.2 assumes that the natural population obeys a logistic differential equation. Suppose a population with a natural rate of increase of $r = .03$ and a natural carrying capacity of $K = 1000$ is subject to harvesting of 5 units per year. What differential equation will govern the growth rate?

b) Using the program *ode.xls* (and the modified Euler method) solve the differential equation in a), and determine the long-term behavior of the population if its initial size is

i) 150 ii) 500 iii) 1000.

c) In cases when the population tends towards zero, determine approximately how long it takes for the population to reach zero. You should include a printout of a relevant graph in each case.

d) Using the qualitative theory of differential equations, find the equilibrium values for the differential equation you derived in a). Use your analysis to confirm the results of the computer analysis in parts b) and c). (Hint: When computing the equilibrium values you will find the numerical work easier if you multiply the coefficients in the relevant quadratic equation by 1000.)

17. a) As we discussed in section 5.2 it may be economically desirable to set the harvesting level so that each year we withdraw the total natural increase in the population during that year. This would tend to keep the population at a fixed size and so we could continue with this harvesting level, which is known as the *sustainable yield*. Suppose the population without harvesting is governed by a differential equation

$$\frac{dN}{dt} = g(N),$$

and the population at $t = 0$ is N_0. Explain, either intuitively or by reference to an appropriate differential equation, why the sustainable yield is $g(N_0)$.

b) Use the result in a) to show that the maximum sustainable yield occurs for an initial population size satisfying $g'(N_0) = 0$. Referring to the model in problem 16a), find the population size, N_0 that gives the maximum sustainable yield and the size of this yield. Explain <u>using stability arguments</u> why it might not be desirable to actually harvest this amount.