EXPLORATIONS

Chapter 6

Biological Models with Differential Equations

In this chapter, you will explore several models representing the growth (or decline) of a biological population. Most of the models of a single population have a closed-form solution. Most of the models involving several interacting populations do not have a closed-form solution and must be studied numerically.

Exponential and Logistic Growth

The simplest model for the behavior of a biological population is the *exponential growth model* (Malthus, 1798) considered in Chapter 2.

$$\frac{dP}{dt} = kP, \quad P(t_0) = P_0 \qquad \text{[Exponential Growth]}$$

The solution to this separable differential equation is widely studied in precalculus and calculus.

$$P(t) = P_0 \, e^{k(t-t_0)}$$

For growing populations, the positive constant k is often interpreted in terms of the time T_2 needed to *double* the population.

$$k = \frac{\ln 2}{T_2}$$

This same model predicts radioactive decay with a negative constant k. In terms of the *halflife* $T_{1/2}$, the constant is as follows:

$$k = -\frac{\ln 2}{T_{1/2}}$$

Biologists move on to more complicated models when a simpler model no longer matches reality closely enough. The exponential growth model predicts unbounded growth over a long period of time. In natural environments, populations tend to stay bounded.

The *logistic growth model* (Verhulst, 1838) replaces the constant k by a variable expression to represent competition for limited resources as the population grows.

$$\frac{dP}{dt} = r\left(1 - \frac{P}{M}\right)P, \qquad P(t_0) = P_0 \qquad \text{[Logistic Growth]}$$

This separable equation can be solved easily by using partial fractions.

$$P(t) = P_0\, e^{r(t-t_0)}\left(\frac{M}{M + P_0\left\{e^{r(t-t_0)} - 1\right\}}\right) = M\left(\frac{P_0}{P_0 + \left\{M - P_0\right\}e^{-r(t-t_0)}}\right)$$

In the first form above, you can see that the solution behaves very much like exponential growth when P_0 is small compared to M and t is near t_0, because the term in the large parentheses is approximately one. The positive constant r is called the *intrinsic growth rate*.

The second form of the solution given above (which is algebraically equivalent to the first) helps you to see that the limiting population as $t \to \infty$ will always be M, called the *carrying capacity*. In addition, for a situation such as a forest fire or clear-cut logging where the carrying capacity M might be instantaneously reduced to a level below the initial population P_0, the model predicts decline from the larger P_0 to the smaller M.

Given the explicit formulas for the solutions of the exponential and logistic growth models, you do not need to numerically solve these differential equations in the **DifEq** graphing mode. On the TI-86, press [2nd] [MODE] and select the **Func** graphing mode. These models are so important that they have also been included as regression choices for a statistical fit in the [STAT] menu.

Exponential regression is easy to do and quite common. Logistic regression is much harder to do computationally (and may fail to converge in extreme cases).

Example 1: Exponential and Logistic Regression

Fit exponential and logistic growth models to the U. S. Census data and predict the U. S. population in the year 2020.

1790	3,929,214	1850	23,191,876	1910	91,972,266	1970	203,235,298
1800	5,308,483	1860	31,443,321	1920	105,710,620	1980	226,545,805
1810	7,239,881	1870	39,818,449	1930	122,775,046	1990	248,709,873
1820	9,638,453	1880	50,155,783	1940	131,669,275		
1830	12,866,020	1890	62,974,714	1950	150,697,361		
1840	17,069,453	1900	75,994,575	1960	179,323,175		

Solution

Enter the data in the default statistical lists **xStat** and **yStat**. There are several ways to do this, but the following instructions work in all cases.

1. On the home screen, press [2nd] [CATLG-VARS] [F1] (**CATLG**) and the letter **S** to locate the command **SetLEdit**.
2. Press [ENTER] to paste the command **SetLEdit** into the home screen and press [ENTER] again to make sure that the list editor has the default setting with only lists **xStat**, **yStat**, and **fStat**.
3. Press [2nd] [STAT] [F2] (**EDIT**) to enter the interactive list editor. If any of these lists contains data from previous statistical work, move the cursor to the heading at the top of the non-empty column, and press [CLEAR] [ENTER] to clear out the old column of numbers.
4. The easiest way to enter the dates (with increment 10 years) is to move with the cursor to highlight the column heading **xStat**, and press [ENTER] to make the entry line active. Then type on this entry line **seq** (J, J, 1790, 1990, 10), [ENTER]. Alternately, you may just type the dates, just as you must type the corresponding populations in the column headed **yStat**. (Figure 6.1)

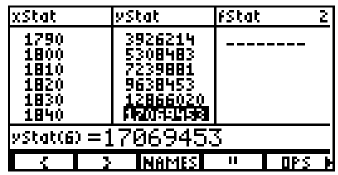

Figure 6.1

5. After you have finished entering the U. S. population census data, press [2nd] [QUIT] to move to the home screen and press [2nd] [STAT] [F1] (**CALC**) to display the regression option in the menu. Select [F5] (**ExpR**) and follow this command with the list names **xStat**, **yStat** ([2nd] [LIST] [F3] (**NAMES**)). (Figure 6.2)

Figure 6.2

6. Press [ENTER] to compute the regression coefficients. (Figure 6.3)

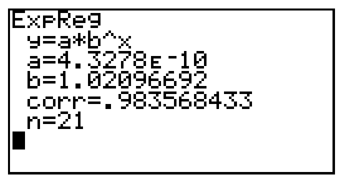

Figure 6.3

7. To view the resulting exponential function and the original data in the same plot, press [GRAPH] [F1] (**y(x)=**) and paste **RegEq** into **y1=** by pressing [2nd] [CATLG-VARS] [MORE] [MORE] [F4] (**STAT**). Use [▲] or [▼] to select **RegEq**. (Figure 6.4)

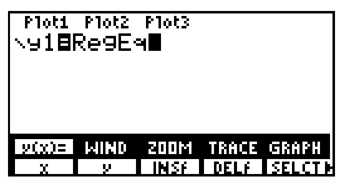

Figure 6.4

8. Press [2nd] [STAT] [F3] (**PLOT**) to display the screen shown in Figure 6.5. Select [F1] (**PLOT1**).

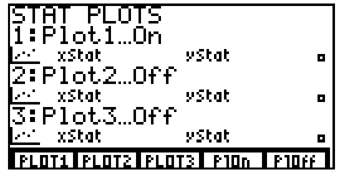

Figure 6.5

9. Verify that the settings match those in Figure 6.6.

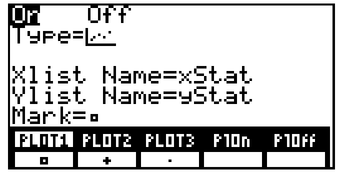

Figure 6.6

10. Press [GRAPH] [F2] (**WIND**) and use the window settings shown in Figure 6.7.

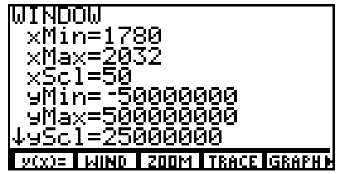

Figure 6.7

11. Press [F5] (**GRAPH**) followed by [F4] (**TRACE**) and trace to check the values of data points and the regression equation. (Figures 6.8 and 6.9)

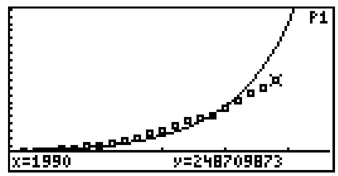

Figure 6.8

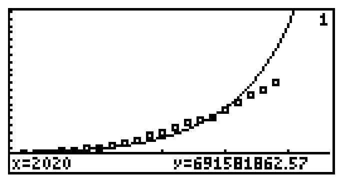

Figure 6.9

12. If you calculate a logistic regression instead by pressing [2nd] [QUIT] [2nd] [STAT] [F1] (**CALC**) [MORE] [F3] (**LgstR**), you get the more reasonable predictions. Note that the command in Figure 6.10 results in an error message (for a singular matrix).

Figure 6.10

Press [F5] (**QUIT**) to get out of the error state. Divide **xStat** by 1,000 and store this back in **xStat**. Divide **yStat** by 1,000,000 and store this back in **yStat.** (Figure 6.11)

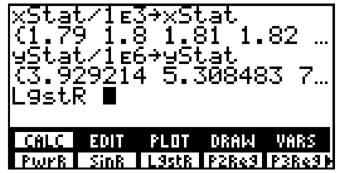

Figure 6.11

Now the command **LgstR** has no trouble. (Figure 6.12)

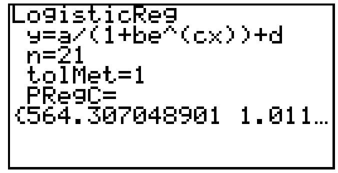

Figure 6.12

13. You will need to re-interpret input and output for the resulting regression equation. (Figures 6.13 through 6.15)

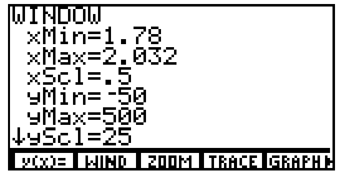

Figure 6.13

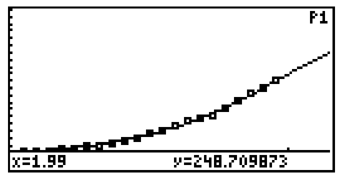

Figure 6.14

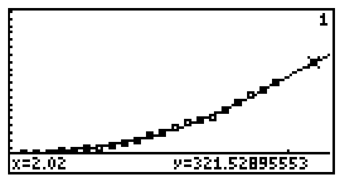

Figure 6.15

Translating the regression coefficients

$$a\,b^{x} = (4.3278\text{ E}-10)\,(1.02096692)^{x}$$

into the notation above, the exponential fit is equivalent to

$$t_0 = 1790, \quad P_0 = 5{,}850{,}029.71265, \quad k = 0.020750139049\,.$$

The graph of the exponential regression does not look very close, particularly for the most recent decades, and the prediction for the year 2020 using this model is 691,581,863. The logistic regression used by the TI-86 is slightly more general than ours (with one more parameter d). The form

$$\frac{a}{\left(1+b\,e^{c\,x}\right)}+d=\frac{564.307048901}{1+1.0117815236\text{ E15 }e^{-17.2958207603\,x}}+(-14.559252573)$$

does not directly translate into our notation. The long-term prediction of this more general model (carrying capacity) is $a + d = 549.747796328$. (You need to multiply this by 1,000,000 to convert to population). The graph of the logistic regression looks much better, and the prediction for the year 2020 is equivalent to a more reasonable 321,528,956. Actually, neither does an outstanding job of modeling the whole data set. Things like the U. S. Civil War, major waves of immigration, and world wars have a one-time impact that is not reflected in the assumptions of the model. Some of the exercises will explore using a subset of the data for a more accurate short-term prediction.

There are still deficiencies in the logistic growth model. No matter how small the population may be, the model predicts positive growth (positive derivative). This does not match what has happened in nature when a species such as the carrier pigeon was hunted so extensively that it dropped below a certain critical population. Such low populations have moved to extinction rather than growing, even when the hunting stopped. Population models that reflect this are said to exhibit *critical depensation*. In Example 2, you will compare a critical depensation model to a similar logistic model.

Example 2: Logistic Growth Models and Critical Depensation

Compare the following two population differential equation models.

$$\frac{dP}{dt}=3.2\left(1-\frac{P}{10}\right)P \qquad \text{[Logistic Growth]}$$

$$\frac{dR}{dt}=\begin{cases}4\,(R-2)\,R, & \text{if } 0\le R<2,\\ 5\left(1-\dfrac{R}{10}\right)(R-2), & \text{if } 2\le R\end{cases} \qquad \text{[Critical Depensation]}$$

Solution

On the TI-86, these two models become the following:

Q'1=3.2*(1-*Q*1/10)**Q*1 [Logistic Growth]

Q'2=(4*(*Q*2-2)**Q*2)(*Q*2<2)+(5*(1-*Q*2/10)*(*Q*2-2))(*Q*2≥2) [Critical Depensation]

It is inefficient (but convenient) to have both equations in the calculator at the same time. Even when you select only one of the equations, the TI-86 thinks these form a system that must be simultaneously solved.

1. Change the calculator to **DifEq** mode and type in the two equations in the differential equation editor. Make sure that **FldOff** is selected in the format screen.

2. Set the window to **tMin**=0, **tMax**=10, **tStep**= .1, **tPlot**=0, **xMin**=⁻2, **xMax**=14, **xScl**=1, **yMin**=⁻4, **yMax**=11, **yScl**=1, **difTol**=.005.

3. To see the general features of the logistic growth differential equation, select axes **x** = Q1 and **y**= Q'1, and enter initial conditions **QI1**= .1, **QI2**= .1.

4. Press [F5] (**GRAPH**) to display the plot of **Q'1(t)** versus **Q1(t)** in Figure 6.16. This plot is quite common in biology texts.

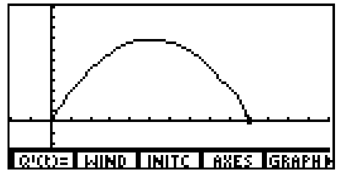

Figure 6.16

5. Change the axes to **x**=Q2 and **y**=Q'2 and change the initial conditions to **QI1**={1.99, 2.01}, **QI2**={1.99, 2.01} to see how the critical depensation differential equation differs. (Figure 6.17) Press [CLEAR] to eliminate the menus and view more of the plot.

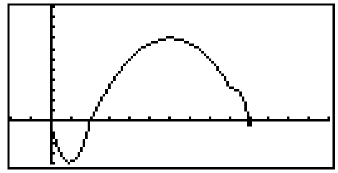

Figure 6.17

   Figures 6.16 and 6.17 are examples of what is sometimes called a *phase diagram*. Note that you have chosen to plot the solution function along the x-axis and the derivative of the solution along the y-axis. Both are examples of *autonomous* differential equations (where the time variable does not appear explicitly in the differential equation). The initial conditions were simply chosen so that you could see a fairly complete phase diagram. In Figure 6.17, you see that *dQ1/dt* is always positive for 0 < **Q1** < 10. In Figure 6.17, you see that *dQ2/dt* is negative for 0 < **Q2** < 2, giving the decline to extinction feature.

6. You can compare solutions by plotting both **Q1** and **Q2** for different initial conditions. Change the axes to **x**=t and **y**= Q and change the window to reduce **tMax** and **xMax** to 3 and set **xMin**= 0. Select various initial conditions for both **QI1** and **QI2**. In Figures 6.18 and 6.19, **Q1** is the "upper" curve in thick style.

Figure 6.18

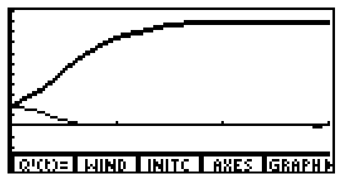

Figure 6.19

In Example 2, you have entered two equations in the differential equation editor, but the two have nothing to do with one another. The equations in such a system are uncoupled. The numerical routines of the TI-86 have no way to know this. The numerical methods implemented for the differential equations mode, however, are nicely configured to handle truly coupled systems of first order differential equations. Many biology problems naturally give a such a coupled system.

In the next example, you will briefly look at some typical models. The *Exercises* will explore additional models.

Example 3: The Predator-Prey Model

Consider the system usually described as a *predator-prey model* (Volterra, 1931),

$$\frac{dx}{dt} = 0.2x - 0.7xy$$

$$\frac{dy}{dt} = -0.4y + 0.5xy$$

where you can think of the function $x(t)$ as representing a population of rabbits that naturally grow at a rate proportional to their population (that is, exponential growth in the absence of predators) and the function $y(t)$ as representing a population of foxes that naturally decline (that is, exponential decay in the absence of prey). The term xy in both equations is proportional to the number of likely encounters of the two population in a certain environment. Encounters are detrimental to the rabbits and beneficial to the foxes.

Solution

1. You can study this system in **DifEq** mode. Enter the system of differential equations, with **x** = Q1 and **y** = Q2 in the differential equation editor (**Q'(t)=** screen). Make sure that there are no initial conditions set.

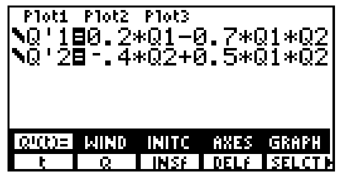

Figure 6.20

2. Select the settings in Figures 6.21 through 6.24.

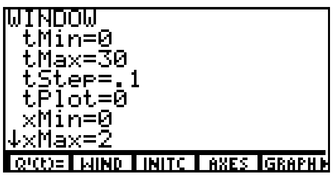

Figure 6.21

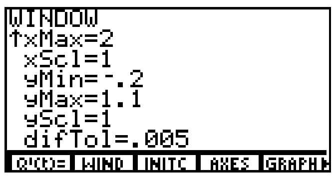

Figure 6.22

Figure 6.23

Figure 6.24

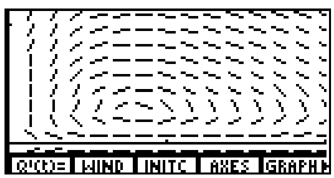

Figure 6.25

3. Press [GRAPH] [MORE] [F5] (**EXPLR**) to interactively select initial values for **x**(0) (**QI1**) and **y**(0) (**QI2**). (Figures 6.26 through 6.28)

Normally, these models have periodic solutions, which lead to closed loops in the figures at the right. If you use Euler's method or if you set **difTol** too large, the loops may not close because of numerical approximation errors. Also, if you change the nature of the model (as you will do in the Exercises), the analytic solution may no longer be periodic (closed loops).

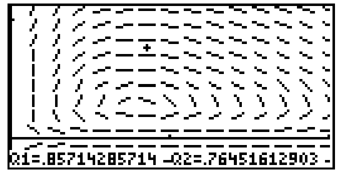

Figure 6.26

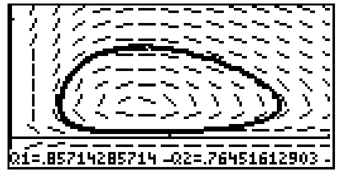

Figure 6.27

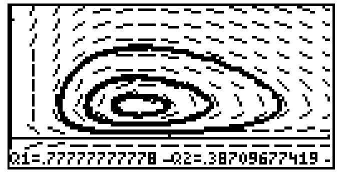

Figure 6.28

When two similar species live in the same habitat and compete for the same resources, then they might be modeled by the following system of equations.

$$\frac{dP}{dt} = r\,P\left(\frac{M - P - aQ}{M}\right), \quad \frac{dQ}{dt} = s\,Q\left(\frac{N - Q - bP}{N}\right)$$

This model for competitive species was proposed by Lotka and Volterra and studied by Gause, 1934. Notice that each reduces to a logistic equation in the absence of the other population (for example, when $Q = 0$ or $P = 0$). Thus r is the intrinsic growth rate, and M is the carrying capacity for P alone. Similarly, s is the intrinsic growth rate, and N is the carrying capacity for Q alone. The parameters a and b describe how one population is detrimental to the other. Here one species may "win out" over the other (although which species wins depends upon the magnitudes of the parameters). In the next example, the first population "wins."

Example 4: A Model for Competitive Species

Study the direction field and explore various solutions for the following:

$$\frac{dP}{dt} = 2\,P\left(\frac{8 - P - 1.5\,Q}{8}\right) \quad \text{and} \quad \frac{dQ}{dt} = 1.7\,Q\left(\frac{4 - Q - 0.8\,P}{4}\right)$$

Solution

Let **Q1** be P and **Q2** be Q. On the calculator, differential equations become the following.

Q'1(t)=2*Q1*(8-Q1-1.5*Q2)/8

Q'2(t)=1.7*Q2*(4-Q2-0.8*Q1)/4

1. Enter the equations and set the axes for **x** = Q1 and **y** = Q2. A nice viewing window for the direction field is **xMax** = 10, **xMin** = 0, **yMax** = 6, and **yMin** = ⁻1. The direction field seems to be headed for the ultimate state where **Q2**=0 and **Q1**=8, its carrying capacity (but you are not sure about the direction for solutions). (Figure 6.29)

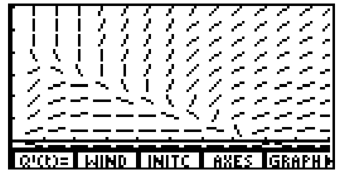

Figure 6.29

2. Using the **EXPLR** feature, watch several solutions as they progress from **t** = 0 to **t** = 5 based upon the graphical initial condition you select for the two populations. You see that the solutions move from your starting point to the limit **Q1**=8, **Q2**=0 as Figure 6.30 is created.

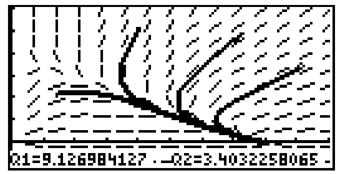

Figure 6.30

Example 5: The SIR Model

The *SIR* model from epidemiology gives us a chance to look at three populations involved in a non-fatal epidemic (such as the flu): the susceptible class S, the infected class I, and the removed (or recovered) class R.

$$\frac{dS}{dt} = -k\,S\,I, \qquad \frac{dI}{dt} = k\,S\,I - rI, \qquad \frac{dR}{dt} = rI$$

Here $S + I + R = N$, the total population in the considered region. You assume that N is constant for the time interval under consideration, so $dN/dt = 0$. Individuals leave the susceptible class (to become infected) at a rate proportional to the product of S times I in the model, and k is this proportionality constant. Individuals join the recovered class at a rate proportional to the size of the infected class in the model, and r is this proportionality constant. Then the differential equation for I is completely determined by the fact that $I = N - S - R$ and $dI/dt = dN/dt - dS/dt - dR/dt$. It is known that you need only consider the first two equations (since R is always the rest of the population N). To see a plot of all three, you will include the third equation as well.

Plot the solutions for the following *SIR* model (already in calculator format), where S is Q1, I is Q2, and R is Q3, and the constants of proportionality and the initial conditions are given.

Q'1(t)=⁻0.1*Q1*Q2 **Q'2(t)**=0.1*Q1*Q2-0.7*Q2 **Q'3(t)**=0.7*Q2

QI1=98 **QI2**=2 **QI3**= 0

Solution

1. Make sure **FldOff** is selected on the format screen. Enter the equations and the given initial conditions.
2. Set the viewing window to **tMin**=0, **tMax**=5, **tStep**=.1, **tPlot**=0, **xMin**=0, **xMax**=5, **xScl**=1, **yMin**=0, **yMax**=100, **yScl**=10, and **difTol**=.005.
3. Set the axes to show all three solutions with **x=t** and **y=Q.**
4. Change the style of the second and third equations so that you can tell which is which in Figures 6.31 and 6.32.

Figure 6.31

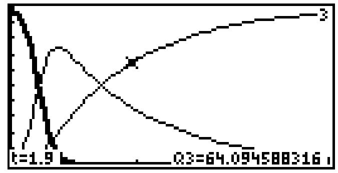

Figure 6.32

Exercises

1. Considering the data in Example 1, do both an exponential and a logistic regression using only the data from the 1790 through 1860 census counts. Use the regression models to predict the population in 1870 and 1880. Compare what these models predict to the actual counts in 1870 and 1880, and explain how the Civil War might have affected the actual population.

2. Using the data in Example 1, do both an exponential and a logistic regression using only the data from the 1950 through 1990 census counts. Then use the regression models to predict the population in 2020 and compare the results to those in Example 1.

3. Explore the critical depensation model in Example 2 alone. Plot the slope field for this equation and use the **EXPLR** feature to graphically fill in several solutions for the equation. Verify that if the initial population is less than 2, the population becomes extinct while if the initial population is greater than 2, the population tends to the reach the level 10. What happens if the initial population is exactly 2?

4. Change the constant 0.2 in the first equation of Example 3 to the values 0.05, 0.1, 0.15, and 0.3. Describe what effect this parameter has on the shape of the closed solution curve.

5. Replace the first equation in Example 3 with

$$\frac{dx}{dt} = 0.2x\left(1 - \frac{x}{2}\right) - 0.7xy\,,$$

   which is simply replacing an exponential part of the original with a logistic part. Keep the second equation the same. Look at the direction field and explore several solutions. Do you think the solutions still cycle as in Example 3?

6. Change the constant b from 0.8 to 0.3 in the second equation of the competitive species model in Example 4. Leave all other constants the same. Explore the direction field and plot several solutions interactively with the **EXPLR** feature. What will tend to happen in the long run (that is, who wins)?

7. In the *SIR* model in Example 5, the constant r might be considered as fixed (for example, if the recovery rate from the infection or disease is not affected by medication). Health officials can lower the constant k by initiating a vigorous campaign to warn people about minimizing contact with the infected population and urging good hygiene practices.

   In Example 5, determine the effect of reducing $k = 0.1$ to 0.07 while keeping all other constants and initial conditions fixed.