

Population Ecology

An Introduction to Computer Simulations

Ruth Bernstein

University of Colorado, USA



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Preface

This text of computer simulations is designed to accompany an undergraduate college course in ecology, population biology, or conservation. The exercises allow the student to explore, by means of computer simulations, the effects of biotic and abiotic variables on population densities through time. They also provide basic modeling skills that can be applied elsewhere, as in term papers dealing with the conservation of endangered species or the control of pest species. Each exercise can be completed within approximately two hours. The text assumes no prior knowledge of MATLAB by either the student or the instructor.

This version of the text uses MATLAB Release 12 or 13 and Windows 98 or later; it is written for use in a laboratory, in which files are stored on a portable disk. I have assumed, here, that the portable disk is a floppy disk. If the disk is not a floppy, then the command `cd a:` needs to be changed, substituting the appropriate letter other than `a`. If the exercises are done on a student-owned computer, then the command `cd a:` should be omitted wherever it appears. Output is in the form of graphs with figure legends, in which the student demonstrates an understanding of the biological principles. The exercises on predation, optimal foraging, conserving an endangered species, and controlling a pest species can be used as class projects, in which the class is divided into groups with each group responsible for one aspect of the topic.

The exercises are presented in as simple a form as possible, in order that the student can concentrate on biological topics rather than on simulation procedures. New techniques and shortcuts are introduced gradually so as not to overwhelm the student with procedures in the first few weeks of the course. Commands are explained each time they are used for the first time and are defined in the glossary. In addition, the software

program can be used to define commands. To find an explanation of the term `dsolve`, for example, simply enter :“`help dsolve`.”

Three windows are typically used when carrying out the simulations: the command window, the command-history window, and the program window. The command window is the main window, in which most information is entered. It always displays the symbol `>>` in the left margin. The command-history window keeps a record of all commands that are entered. It can be used to search for errors and to transfer commands (by highlighting, right clicking, copying) to the command window (by pasting). The program window is used to write and store programs (called *m-files*) that will be applied more than once. The command window and the command-history window are opened by scrolling down “view” on the toolbar; the program window is opened by scrolling down “file” and then either “new, m-file” or “open” on the toolbar. Always clear both command windows (scroll down edit) between exercises when doing more than one exercise in a single sitting.

This text has been tested on several classes of undergraduates at the University of Colorado. Thus, if part of an exercise does not work, most likely it is because you have made a typing error. If you cannot find the error, it helps to print your commands and then review them carefully on the printed copy.

I am deeply indebted to Joan Roughgarden for this manual, both for the general concept of teaching population ecology by means of computer simulations and for specific techniques presented in her text, *Primer of Ecological Theory* (Prentice Hall, 1998). The advantage of using this approach to teach the dynamics of populations, as compared with either no simulations or simulations that use “canned” programs, is that students learn the logic of the classic models, how changes in the variables influence population densities, and how to develop their own models of population change through time.

I acknowledge also the exceptional support provided by Rachael Ballard, Assistant Editor at John Wiley & Sons Ltd, who believed in this project from the beginning and provided encouragement and assistance throughout the reviewing and revision process.

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Ruth Bernstein

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EXERCISE 1

Exponential Population Growth

A small population in a favorable environment can grow at a rapid rate. There will be few deaths, except from old age, and the rate of reproduction will far exceed that needed to replace these deaths. This type of growth, known as exponential growth, can be modeled either in continuous time (by differential equations) or in discrete time (by difference equations).

Populations with Continuous Growth

A population that has no defined reproductive season exhibits continuous growth, because births occur at all times of the year. Human population growth is an example of continuous growth. The increase in numbers of individuals through time is described by the differential equation

$$\frac{dN}{dt} = rN \quad (1.1)$$

where dN is the symbol for change in numbers and dt is the symbol for change in time. Thus, dN over dt means the change in numbers that occurs over a particular period of time. The symbol r is the population growth rate per individual (i.e., the rate at which the

population increases in numbers divided by the total number of individuals in the population at that time); it is a constant in the equation. The symbol N is the number of individuals in the population at each point in time. This differential equation, which describes the instantaneous rate of increase, can be used to find an equation that predicts the number of individuals in the population at some future time t , an equation in which the slope at each point in time is equal to r times the number of individuals in the population at that point in time. To have MATLAB find this predictive equation for you, follow the instructions below.

Open Microsoft Word and press *enter* a few times so that your first graph will not be at the very top of the page. Open MATLAB on top of Word. In the MATLAB command window (which has the prompt `>>`), type the following:

```
>> nt=dsolve('Dn=r*n', 'n(0)=no', 't')
```

The command `dsolve('Dn=r*n')` tells the program to solve the differential equation defined by r multiplied by n (MATLAB uses a small n for N). An asterisk means multiply. (Each equation is always identified by enclosure within single quotation marks.) The command `'n(0)=no'` tells the computer that the initial number of individuals $n(0)$ is defined by `no`. The time period during which the population grows is identified by `t`. MATLAB answers with

```
nt=no*exp(r*t)
```

which is the equation for predicting the population size at any time. It is computer language for

$$N_t = N_0 e^{rt} \quad (1.2)$$

Now use MATLAB to predict the growth of the US population over the next 100 years. The present population (i.e., `no`) consists of about 300 million and the growth rate (r) is 0.017 per individual per year. When a computer program is used in calculus, continuous time is approximated by having time change in tiny steps from time 0 to time t . Here, time increments of 1 year give an almost smooth curve. To tell the computer to plot population size over a time period of 100 years, in increments of 1, the command is `t=0:1:100:`

```
>> no=300;
>> r=0.017;
>> t=0:1:100;
```

(A semicolon placed at the end of a command stops the computer from displaying its response to your entry.) To place your results on a figure, simply type

```
>> figure
>> hold on
>> plot(t,eval(vectorize(nt)),'r')
```

The `figure` command tells the computer to set up a graph. The `hold on` command says that you will be placing more than one curve on the graph, so the computer should keep this figure window open until you have added all these curves. The `plot(t, eval(vectorize(nt)))` command tells the program to plot t on the X axis and the solution to the equation that predicts nt (see above) on the Y axis. The term `vectorize` produces a version of the equation that can be plotted on a graph. The 'r' part of the command produces a red curve on the graph. (The symbols for other colors and line styles are provided on page 159. If you do not have a color printer, you may wish to use line styles rather than colors to distinguish between the different curves on a graph.)

Population growth is determined by rates of immigration and emigration as well as by births and deaths. In the United States, for example, the actual rate of increase r is 0.017, but without immigration (and the children of immigrants), the population growth rate would be approximately 0.007. To simulate population growth under these conditions, type

```
>> r=0.007;
>> plot(t,eval(vectorize(nt)),'b')
```

Thus, the population would grow even without immigration. The cause of this growth is not a high birth rate but rather a steady increase in lifespan, brought about by medicine and other survivorship-enhancing aspects of the society. When the length of life stabilizes (near the maximum lifespan set by the genes of each individual), the population will decline because the number of children born per couple is less than two: on average, each woman in the United States leaves 1.8 children in her lifetime. If all children survive to reproductive age, then the population growth rate (with neither immigration nor a continuing increase in lifespan) would be: $r = -0.00513$. Simulate this rate of growth by typing

```
>> r=-0.00513;
>> plot(t,eval(vectorize(nt)),'g')
```

In the figure window, label the graph by scrolling down “insert.” Then click each label that you want to apply. Give the graph a title and label the axes: the X axis is years and the Y axis is number of individuals (times 1 million). Label each curve by clicking “A” and

then clicking a spot near the curve where you type the label. The red curve is with immigration; the blue curve is without immigration; the green curve is with neither immigration nor increasing lifespan.

Move this graph to a Word document by scrolling down the “edit” icon at the top of the graph window and clicking “copy figure.” Then open the Word document (by clicking on the window beneath MATLAB or by clicking on the Word icon at the bottom of the screen) and click “paste.” Write a legend for the figure. Move the cursor below the figure to position the document for your next graph. Return to MATLAB by clicking on its window. In the command window, scroll down “edit” and click “clear command window.”

Populations with Discrete Growth

Now consider ground squirrels, which breed only in the spring. Population growth occurs in discrete time periods rather than in continuous time throughout the year. The population size at time $t + 1$ is given by the difference equation

$$N_{t+1} = RN_t \tag{1.3}$$

where N_{t+1} is the number in the population one year from now, N_t is the number now, and $R = 1 + (B - D)$, in which B is the number of births per individual per year and D is the number of deaths per individual per year. The equation begins with a 1 so that when multiplied by N_t you get N_t , which is the number of individuals in the population before the reproductive season. This R is called the geometric growth factor.

We now want to modify the equation to be able to predict the population size for more than one year in the future. When R is constant, the equation for predicting the number of individuals one year from now can be written

$$N_1 = RN_0$$

and the equation for predicting the number of individuals two years from now is then

$$N_2 = RN_1$$

or

$$N_2 = R(RN_0) \text{ or } N_2 = R^2N_0$$

the equation for predicting the number of individuals three years from now is

$$N_3 = R(N_2) \text{ or } R(R^2N_0) \text{ which is } R^3N_0$$

and so on for any time period t . Thus, the general equation is

$$N_t = (R)^t N_0 \tag{1.4}$$

which is written in MATLAB language as `nt=(r^t)*no`, where nt stands for N_t and no stands for N_0 , r stands for R , and t stands for time. The asterisk indicates multiplication. The symbol \wedge indicates an exponent; the symbols r^t are enclosed within parentheses to indicate that this mathematical procedure (r^t) is to be carried out first – before multiplying by no . Enter this equation as

```
>>nt=(r^t)*no;
```

Now assign some values to the parameters. Assume an initial population of 100 ground squirrels. Assume that R (the rate of growth per year) is equal to 1.05 (i.e., each year, the number of individuals in the population is 1.05 times the number of individuals in the population the previous year). Show on a graph how this looks over a time period of 30 years.

```
>>no=100;
>>r=1.05;
>>t=0:1:30;
>>figure
>>plot(t,eval(vectorize(nt)),'b')
```

Label the graph. Move it to a Word document (i.e., in the graph window, scroll down “edit”, click “copy figure,” and then, in the Word document, click “paste”). Write a figure legend.

