Laboratory 4: Implementing Discrete and Continuous Time Population Models in R

Bio 535, Fall 2008

Introduction

This laboratory exercise will provide you experience in constructing and running a single compartment (state-variable) model with logistic feedback regulation. You will learn to encode and solve both a discrete-time and continuous-time version of this model and investigate some of the important dynamical consequences of this modeling decision. You will also further develop your scientific programming skills in R.

Please report your findings, along with any necessary tables and figures and your brief answers to the embedded questions (5 pts.). Your report is due in our class meeting next Thursday.

Discrete vs. Continuous Time Equations

According to Gurney and Nisbet (1998), "A dynamic model is a mathematical statement of the rules governing change". We can distinguish two types of mathematical statements: an update rule (discrete time) and a differential equation (continuous time).

An **update rule** describes "the relationship between the current and future state of the system" Let N_t be the current state and $N_{t+\Delta t}$ be the state after the discrete interval of time Δt. Then we can write the generic update rule as $N_{t+\Delta t} = f(N_t)$. This type of equation is referred to as a **difference equation**. Equations of this form are particularly suited for projecting the state of the system at regular intervals and are often used to model species that reproduce with non-overlapping generations and simultaneous reproduction, like many semelparous species. Mature adults of these organisms reproduce once and then die. For example, the checkerspot butterfly *Euphudrias editha* breed once per year. Adults fly for a short period of time, lay their eggs near April 1, and die (Hastings 1997).

A **differential equation** specifies the rate of change of a state variable N with respect to time t and is a continuous time equation. These equations are formally defined as

$$\frac{dN}{dt} = \lim_{\Delta t \to 0} \frac{N_{t+\Delta t)} - N_t}{\Delta t}. \qquad (1)$$

The **logistic equation** that we discussed in class

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{2}$$

where N is the population density[1], r intrinsic rate of growth, and KL is the carrying capacity of the environment. Equation (2) is an example of a differential equation. Gurney and Nisbet (1998) state "A model that uses derivatives is essentially an update rule model with very small time steps." Differential equations are a bit more complicated to implement and use, but are often worth the investment. For example, differential equations are generally better for modeling species with overlapping generations or variables that are affected continuously.

Task 4.1 Continuous Time Model

We will start with the continuous time model to develop your intuition about the logistic equation dynamics before you work with the discrete time version.

Numerical Approximation with Euler's Rule

Most differential equations cannot be solved analytically, but we there are methods for numerically *approximating* the solution. As described by Haefner in Chapter 6, these methods differ in their accuracy. Here, we will use Euler's rule to approximate the solution to the differential equation for exponential growth $\left(\frac{dN}{dt} = rN\right)$. Euler's solution, which we will discuss in class, is one of the more intuitive numerical approximation technique. However, there are several additional methods that reduce the approximation error. In the next section will use one of R's built in ordinary differential equation (ODE) solvers that utilizes a more advanced method.

Task 4.1.1 Download the example program titled bio534-euler-exp-growth.r from the course website. Examine the program to understand how it works. Then, execute the program using the default parameters. Next, change the parameters to investigate how they alter the program function. Please make any changes you find interesting and useful to learn about the program. Finally, try alternative values of the time step (dt) of 1, 0.1, 0.01, and 0.001 and compare the approximated population trajectories to the analytically exact solution for this equation, $N_t = N_0 e^{rt}$. What happens as dt increases? Why? Plot all 5 solutions on the same figure.

Task 4.1.2 Now modify the Euler script you downloaded so that it solves the differential equation for logistic growth. To start, set $K = 100$ and execute the program. Explore the effects of using different values of K and initial population sizes.

[1] X is often the symbol used to denote a generic state variable, especially in ecosystem ecology. In population ecology, however, it is common to use N as the symbol for population density. The trick is to not to memorize a particular symbol, but to learn to recognize the "role" a particular symbol has in an equation (e.g., state-variable, parameter, driving variable)

Task 4.1.3 Most computer packages like R and MATLAB have more sophisticated ODE solvers built into the language. R uses a routine called *lsoda* that is included in the "odesolve" package (see Ellner and Gukenheimer 2006 Section 13 for more instructions). Once a package is installed on the machine, you will need to load it by typing "library(package-name)". For this task you will download two R scripts from the website to learn how to numerically approximate the solutions to ODE's using lsoda in R.

Download exponential.r and exponential-run.r from the website. Again, examine how these two programs are structured and documented. *exponential.r* defines a new function[2] in R that is then used in the *exponential-run.r* script. Run the model function file and then the run file and observe their action. Then, modify the model to represent the logistic model. As in Task 4.1.2, investigate alternative parameter values to learn how the program works.

If you are interested, you might set up the models in the Euler solution and the lsoda solution to be identical and compare the solutions. Is there a significant difference in the numerical approximations when dt is 1? What about when dt is 0.01?

Task 4.2: Discrete Time Model

The Ricker model is a discrete-time analogue of the continuous time logistic model that was first formulated by Ricker (1954) to model fisheries stocks. The update rule is

$$N_{t+1} = aN_t e^{-bN_t} \tag{3}$$

where N_t is the number of mature individuals at time t in years. Gurney and Nisbit (1998) describe their application of the model to a fishery as follows:

> "We work with a time increment (Δt) of 1 year, and denote the stock of mature individuals at the census date in year t by X_t. Juveniles mature the year after their birth. Adult fish spawn once before dying and produce a maximum of [a] viable recruits to the following year's stock. Due to cannibalism on eggs by adults, the juvenile survivorship in a year when there are X_t adults is e^{-bX_t}, where b is a parameter related to the intensity of cannibalism." (p. 27)

Task 4.2.1 Your next task is to write an R script to encode the Ricker model described above using a for loop. To begin, let $N_0 = 100$, $a = 0.8$, and $b = 0.001$. Then, investigate how the model changes when you change parameter b. Reset b to 0.001 and explore how the behavior changes as you increase a to about 20. What do you observe? Describe the behavior changes you see and document your observations with plots. What do you surmise is happening in this deterministic model (hint: see reading from Otto and Day)? How does changing the initial population size influence your result?

Exploring the "sensitivity" of the model solution to changes in parameters and initial conditions as you are doing in this exercise is a simple form of sensitivity analysis, and is a powerful technique to learn about the functions or models you build or use.

[2] Functions are different from scripts in that they functions as subroutines we can call from other functions or scripts similar to any of the more familiar R commands (e.g., ls()). Ellner and Guckenheimer's lab manual (2006), which we used for the first laboratory, has a nice description of what functions are and how they work (Section 9).

References

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