<u>Computer Solution of Differential Equations</u>
Zoology 535, Ecosystem Analysis

Many ecological models are written as systems of differential equations. Any one of the equations has the generic form

$$dx_i/dt = f(\mathbf{x},\mathbf{E},\mathbf{p},t) \qquad (1)$$

where x_i is one of the state variables, t is time, f is a function that gives the instantaneous rate of change in x_i, **x** is a vector of the values of all of the state variables being modeled, **E** is the environmental forcing variables, and **p** is the parameters.

Usually we would like to know the time course of all the **x**s. For all but the simplest models, we cannot find an explicit function that tells us the values **x**, so these values need to be found numerically using a computer.

The simplest way to solve the differential equations on the computer is to rewrite them as difference equations:

$$\Delta x_i / \Delta t = f(\mathbf{x}[t],\mathbf{E}(t),\mathbf{p},t) \qquad (2)$$

Since by definition

$$\Delta x_i = x_i[t+1] - x_i[t] \qquad (3)$$

then over a time step of length h

$$x_i[t+1] = x_i[t] + f(\mathbf{x}[t],\mathbf{E}(t),\mathbf{p},t)h \qquad (4)$$

Given a starting value, x_i can be updated one step at a time: $x_i[1]$ is used to calculate $x_i[2]$, which is then used to calculate $x_i[3]$ and so forth. This method is called Euler's method. Euler's method often works, especially if f is linear in **x**. The outcome of Euler's method can be sensitive to the time step h.

Euler's method is inaccurate because it is asymmetrical. It uses the rate at the beginning of the time interval over the entire time interval. It is better to use a method that accounts for the changes in the rate during the time interval. The most common method in ecological applications is the Runge-Kutta method (Press et al. 1988, pp. 569-580). It uses trial steps across each time interval to account for the nonlinearity of f. The simplest Runge-Kutta method uses the rate at the beginning of the interval to estimate x at the middle of the interval, and then calculates a rate for the middle of the interval. In equations:

Rate at beginning of interval = k1 = f(t,x[t])h

Rate at middle of interval = k2 = f(t+0.5h,x[t]+0.5k1)h

Value of x at the end of the interval = $x[t+h] = x[t] + k2$

In the equations above, **E** and **p** are omitted to simplify the notation.

The most common Runge-Kutta method, called the fourth-order method, calculates the rates at four points in time: at the beginning of the interval, at two trial midpoints, and at a trial endpoint. The final estimate is a weighted average where the weights are designed to cancel out errors. The formulas are:

$k1 = f(t,x[t])\ h$
$k2 = f(t+0.5h,x[t] + 0.5k1)h$
$k3 = f(t+0.5h,x[t] + 0.5k2)h$
$k4 = f(t+h,x[t]+k3)$

$x[t+h] = x[t] + (k1/6) + (k2/3) + (k3/3) + (k4/6)$

To simulate a model using the Runge-Kutta method, you will need to write a main program and a function that calculates the derivatives at each time step. The flow of information is

Main program <---> Runge-Kutta function <---> Derivative Function

The Main program sets the conditions for the simulation (initial conditions and so forth), calls the Runge-Kutta function, and outputs graphs or tables of the results. The derivative function defines the parameters, sets up environmental forcing, and calculates the derivatives. Many examples are found in the computer exercises for Zoology 535.