

Set up your simulation with these initial concentrations of reactants:

$$[S] = 100 \quad [B] = 90 \quad [E] = 10$$

Let other starting concentrations = 0. For the rate constants  $k_i$ :

$$\begin{array}{llll} k_1 = 0.005 & k_2 = 0.005 & k_3 = 0.01 & k_4 = 0.001 \\ k_5 = 0.1 & k_6 = 0.1 & k_7 = 0.01 & k_8 = 0.1 \end{array}$$

Graphical output should show the concentrations of the eight reactants over at least 40 units of time. Use simple Euler methods with  $\Delta t = 0.1$ .

### Conclusion

This chapter has presented examples of systems which lend themselves to deterministic simulations involving numerical integration. Only Exercise 6-1 could have been solved analytically. The other exercises involved sets of equations that would have been very difficult, if not impossible to solve by this method. They provided good examples of the power and simplicity of numerical integration.

## CHAPTER 7 MODELS OF HOMOGENEOUS POPULATIONS OF ORGANISMS

In Chapter 6 we simulated chemical reactions among populations of molecules using deterministic models. We assumed that all the molecules of a given type were the same (homogeneous), and ignored the differences that exist among individual molecules. Our reaction rates were really average rates, and would not necessarily apply to any given molecule. Average rate is a reasonable predictor of overall reaction rate, given the large numbers of molecules involved in most chemical reactions.

When the first attempts were made to construct models of homogeneous populations of organisms, it was logical to use some of the same principles as in models of homogeneous molecules. Particularly important was the "law of mass action" which states that the rate of interaction depends directly on the product of the concentrations of the interacting types of molecules. The pioneering work of Lotka (1925) frequently made use of this law. (This law is probably impossible to prove in a formal sense; its validity is based upon a very large number of observations, made without finding an exception.)

Homogeneous populations of organisms are assumed to be composed of a single type and described by a single variable, density. Differences in age, sex, genotype, phenotype, etc., are ignored or assumed to be irrelevant for the model. The density variable for organisms is identical to the concentration variable for molecules. Density is typically expressed as number per unit area (e.g. wolves  $\text{ha}^{-1}$ ) or number per unit volume (e.g. *Paramecium*  $\text{ml}^{-1}$ ). The models for homogeneous populations assume that interactions (predation, parasitism, competition) between populations will proceed at rates directly proportional to the product of the densities of the populations.

Most populations of most organisms are not homogeneous, and the unreality of the models in this chapter is admitted at the outset. However, they are constructed from principles that make elementary biological

sense. These models are important in the scientific literature of populations, even if most current references are critical. More importantly for us, they provide simple models for simulation, and the understanding gained in working with them will prepare you for the more complex models in following chapters.

### 7.1 The Verhulst-Pearl Equation

The first model in Chapter 1 was an equation for simulating growth of biological populations in an unlimited environment, with constant growth rate:

$$\frac{dN}{dt} = kN \quad (1.3)$$

You used this equation extensively in the exercises of Chapter 5. Everyday observation suggests that this equation is not a good model of biological growth, because we are not up to our ears in bacteria or elephants. The simplest modification for limiting growth is to assume that  $k$  in Equation 1.3 is not a constant, but decreases as  $N$  increases. The simplest assumption is that  $k$  decreases linearly with  $N$ , so that

$$k = a - bN \quad (7.1)$$

If the organisms are scarce so that resources are assumed to be plentiful, growth rate will approach  $a$ . There is also a greater, limiting density of the population where growth rate is zero, and at densities greater than this, growth rate is negative. If this expression is substituted for  $k$  in Equation 1.3, the following equation results:

$$\frac{dN}{dt} = (a - bN)N = aN - bN^2 \quad (7.2)$$

This equation is one form of the Verhulst-Pearl logistic, first proposed by Verhulst in 1838 and rediscovered by Pearl and Reed in 1920 (see Hutchinson 1978). Another form was given in Chapter 1:

$$\frac{dN}{dt} = cN(L - N) \quad (1.16)$$

The equation is usually expressed with the following terminology:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) \quad (7.3)$$

All of these forms are formally identical, with  $a = r$ ,  $L = K$ , and  $b = c = r/K$ . Here,  $r$  is the term for rate of per capita growth at minimal density,

and  $K$  is the term for the population density at which the growth rate is zero.

Equation 7.3 is perhaps the most easily interpreted form of the logistic. When  $N$  is small relative to  $K$ ,  $(1 - N/K)$  is close to 1 and growth is almost exponential at rate  $r$ . When  $N = K$ , the growth rate of the population is zero. Hence, a population will grow asymptotically to the value  $K$ . If  $N$  exceeds  $K$ , the growth rate is negative and the population declines toward  $K$ .

The form of the logistic in Equation 7.2 shows clearly the relationship of the logistic to the law of mass action. The first term  $aN$  is that for unlimited growth, and represents the growth potential of the population. The second term is negative, and is a function of  $N \times N$ . It may be thought of as a loss of potential population, resulting from the negative effects of the interaction of organisms, one with another. With time, population density will approach a steady-state in which the potential for increase is exactly balanced by the potential loss. The second term provides a good example of the application of the law of mass action to population dynamics.

**Exercise 7-1:** Pearl (1927) collected these data from a culture of yeast cells:

Hours:	0	1	2	3	4	5	6	7	8	9	10	12	14	18
Yeast:	4	7	12	19	28	48	70	103	140	176	205	238	256	265

Yeast were measured as biomass ( $\text{mg } 100\text{ml}^{-1}$ ), and this may be taken as a suitable measure of population density. You should find estimates of values for  $r$  and  $K$  of yeast based on Pearl's data. This may be done by fitting constants using the techniques of Chapter 3. (Note that the form of the logistic used in Chapter 3 is like that of Equation 1.16.)

After finding values for  $r$  and  $K$ , simulate the growth of yeast using Equation 7.3 with numerical integration. Plot your simulation data ( $N$ ) as a continuous line through time. On the same graph, also plot Pearl's data as discrete points, using circles if possible. To obtain a good fit of the simulation data to the actual data, it will be necessary to use the Improved Euler method with  $\Delta t = 0.1$ , or to use a small value of  $\Delta t$  (e.g. 0.0001) with the simple Euler method. (The latter approach may consume a lot of computing time.)

**Exercise 7-2:** Write and implement a program to simulate logistic growth using Equation 7.3. Set  $K = 100$  and  $r = 0.1$ . Use a simple Euler method with  $\Delta t = 0.1$ , and begin the simulation with  $N = 2$ . Allow the simulation to run sufficiently long for  $N$  to approach  $K$  very closely. On the same graph, also show the result of a simulation for a population that begins with  $N = 120$ .

Write a short program to plot population growth rate ( $dN/dt$ ) for values of  $N$  from 0 to 120. Use the values of  $K$  and  $r$  above. (Your graph will have to show negative rate values where  $N$  exceeds  $K$ .) Also produce a plot showing per capita growth rate ( $dN/N/dt$ ) for values of  $N$  from 1 to 120. This latter plot should produce the straight line of Equation 7.1. The  $x$ -intercept for both of these plots should be  $K$ . The first graph should show a maximum population growth rate of  $rK/4$ , at a density of  $K/2$ .

## 7.2 Time Lags and Oscillations in Population Growth

Population growth following the Verhulst-Pearl logistic results in a stable population size near  $K$ , the "carrying capacity". This stability is the result of a balance between the two elements of Equation 7.2, the positive feedback of the  $aN$  term, and the negative feedback of the  $-bN^2$  term. A basic principle of control theory (see Chapter 17) is that oscillations around a stable limit may be caused by delay in the time that information about the current state is fed into the negative feedback loop.

This idea is interesting here because logistic growth to a stable upper limit is rarely displayed by organisms more complex than yeast and bacteria. Instead, their populations oscillate above and below an apparent upper limit. The classic observations of Slobodkin (1954) on *Daphnia* seem to be good examples of this. Evidently the fluctuations result from the passage of time between egg formation and egg hatching. The number of eggs a daphnid produces is not determined by resources available at the instant of hatching, but instead at the time the eggs are formed. Several days may elapse between egg formation and hatching, and the population may reach the stable limit during this interval. The result is a population that overshoots the limit, and must decline in density. There are time lags associated also with mortality and with recovery of reproductive potential. The result is an oscillating population.

Delays and lags are best simulated with age-class models like those discussed in Chapter 9. However, some approximations may be obtained by building a time lag into the logistic. For example, Equation 7.3 may be modified to be

$$\frac{dN_t}{dt} = rN_t \left( 1 - \frac{N_{t-f}}{K} \right) \quad (7.4)$$

where  $N_{t-f}$  refers to the population density at  $f$  intervals of time prior to  $t$ :

$$N_{t-f} \dots \rightarrow N_{t-2} \rightarrow N_{t-1} \rightarrow N_t$$

Writing a computer simulation of the time lag model requires that several previous population densities be retained so that  $N_{t-f}$  is available when needed.

Another type of time lag is the delay between birth and reaching reproductive age. This lag would appear in the  $rN$  term of the logistic (Equation 7.3). This lag may be simulated by using  $rN_{t-f}$  instead of  $rN_t$ . Here,  $f$  would represent the number of time intervals required to reach reproductive age. Both of these time lags are described by Wangersky and Cunningham (1957).

**Exercise 7-3:** Write a computer program to simulate populations growth in which there is a time lag in resource use, based on Equation 7.4. Set  $K = 1000$ ,  $N_0 = 2$ , and  $r = 0.5$ . Allow your simulation to proceed for about 50 time intervals, plotting  $N_t$  against time. You should produce 5 different graphical outputs, for time lags of 0 to 4 time units. Use  $\Delta t = 1$ ; otherwise, saving and updating of the previous  $N_t$  values will be cumbersome. The flowchart in Figure 7.1 and the program listing in Figure 7.2 may provide some assistance in writing your program.

## 7.3 Variable Carrying Capacity and the Logistic

The value of the carrying capacity  $K$  is constant in the above discussions of the logistic. Because organisms rarely live in environments with a constant  $K$ , it is instructive to consider simulations in which  $K$  is a variable.  $K$  might vary in an orderly fashion if the food supply of the population were tied to an annual cycle, for example. Consider an insect in the tropics, consuming vegetation whose amount is determined by wet and dry seasons. In Chapter 11 we shall work with several models for such weather variation. Here, we shall consider a very simple annual cycle based on a modified sawtooth or ramp function, as shown in Figure 7.3.

Such a line can be obtained with:

$$K_t = C + kt \quad (7.5)$$

where

$$\tau = \begin{cases} t & 0 \leq t \leq 26 \text{ weeks} \\ 52 - t & 26 < t \leq 52 \text{ weeks} \end{cases}$$

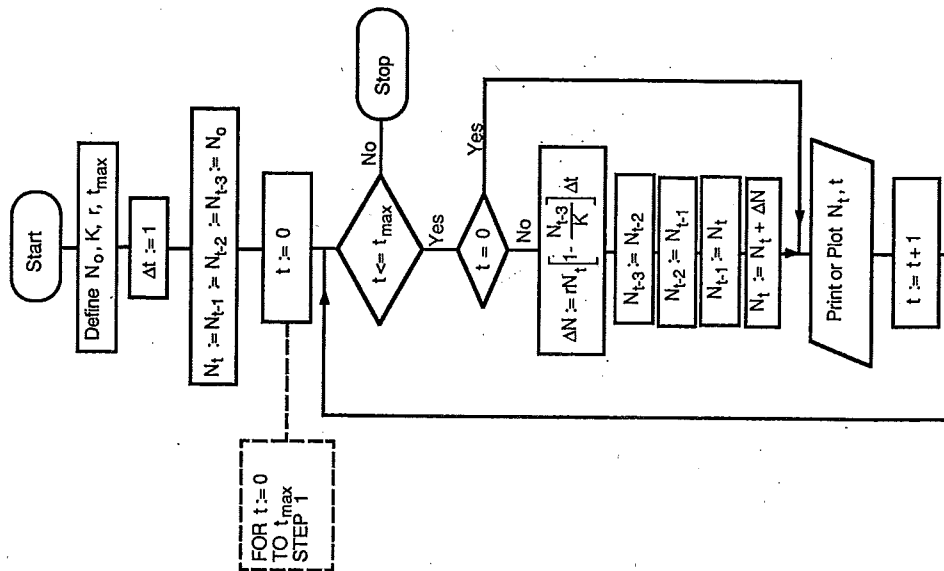


Figure 7.1. Flowchart for program to simulate population growth with the Verhulst-Pearl model with a time lag of three time units.

```

10 REM THIS PROGRAM IS BASED IN THE
20 REM GRAPH PROGRAM (APPENDIX 2)
30 REM *****
80 REM NT = POP SIZE AT TIME T
  N1 = POP SIZE AT TIME T-1
  N2 = POP SIZE AT TIME T-2
  N3 = POP SIZE AT TIME T-3
  N4 = POP SIZE AT TIME T-4
  N5 = POP SIZE AT TIME T-5
  K = CARRYING CAPACITY
  R = GROWTH RATE CONSTANT
  DN = DELTA N

90 REM

100 :
110 XM = 50 : YM = 4000
120 X$ = "TIME" : Y$ = "DENSITY"
130 GOSUB 3000 : REM DRAW GRAPH AXES
140 :
150 K = 1000 : R = .5
160 NT = 2
170 DT = 1
180 N1 = NT : N2 = NT : N3 = NT
190 N4 = NT : N5 = NT
200 XA = 1 : XD = 0 : REM LINE PLOT
210 :
220 FOR T = 0 TO 50
230 IF T = 0 GOTO 320
240 DN = R * NT * (1 - N5 / K) * DT
250 N5 = N4
260 N4 = N3
270 N3 = N2
280 N2 = N1
290 N1 = NT
300 NT = NT + DN
310 IF NT < 0 THEN NT = 0
320 Y = NT : X = T : GOSUB 4000
330 NEXT T
340 END

```

Figure 7.2. A sample BASIC program for simulating population growth based on the Verhulst-Pearl model, with a time lag of five time units.

In this equation  $C$  is the annual minimum of carrying capacity  $K$ , and  $k$  is the slope relating its increase to time expressed as a week of the year. The equation produces an increase in  $K$  for weeks 0 through 26 of a calendar year, and a decline for the remainder of the year. The upper population limit thus fluctuates on a roughly seasonal basis.

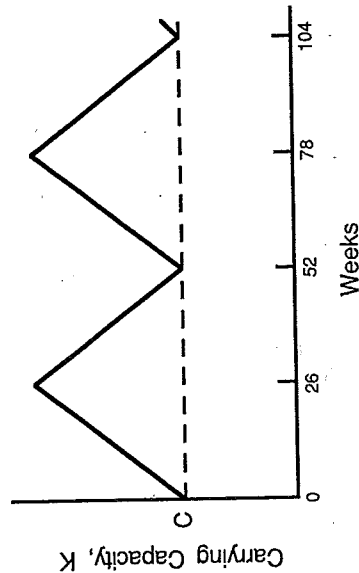


Figure 7.3. Diagram of a modified sawtooth pattern of annual variation in carrying capacity based on seasonal fluctuations with a peak in mid-year.

**Exercise 7-4:** Implement a simulation for population growth in an environment in which  $K$  varies in an annual sawtooth pattern (Equation 7.5). Set  $C = 30$  individuals,  $N_0 = 2$  individuals,  $r = 0.3 \text{ week}^{-1}$ , and  $k = 6 \text{ individuals week}^{-1}$ . Run your simulation for 2 years (104 weeks), using a time unit of 0.1 week. Plot  $N_t$  and  $K_t$  vs. time on the same graph. Simple two stage Euler integration will be adequate for this simulation with  $\Delta t = 1$ .

#### 7.4 A Simple Model for Harvesting Populations

Most biological populations are harvested or exploited by other biological populations. We can imagine a cat exploiting a mouse population in a barn. Left to itself, we assume the mouse population would follow a logistic growth pattern. However, the cat removes a constant number of mice per day, so that the logistic is modified with another term:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - C \quad (7.6)$$

where  $C$  represents the removal rate of mice by the cat. (This term is unrealistic in the case where  $N$  is zero or less, because it indicates that the cat can catch mice when none exist. We will increase the realism of this term in the next section of this chapter.) Even this simplified model of harvest demonstrates that the cat has to plan her harvesting strategy with some care. The value of  $C$  has a realistic impact on the stable upper limit of population size, and it also imposes a critical lower limit. If the cat begins to harvest a small population of mice at rate  $C$ , the population may decline, but the same harvest rate applied to a larger population may permit the mouse population to grow.

**Exercise 7-5:** Using Equation 7.6, simulate harvest of a population growing logistically. Use the approach and values of Exercise 7-2 to set up the simulation. Use three values of  $C$ : 0, 1, 2. For each value of  $C$ , produce a graph showing  $N$  vs. time starting with populations of size 2, 15 and 30. To gain some insight into your results, again follow Exercise 7-2 in producing a graph of  $dN/dt$  vs.  $N$ , using the three values of  $C$ .

#### 7.5 The Lotka-Volterra Model of Predation

Lotka in 1925 and Volterra in 1926 independently developed a model for predator-prey interaction (Hutchinson 1978). Although this model is as primitive as the logistic and the harvesting models above, it has served as a basis for many predation models and it is a useful starting point for an investigation of predation.

The model consists of two equations. The first describes the changes in prey population density:

$$\frac{dN}{dt} = rN - gNP \quad (7.7)$$

In this equation,  $N$  is the density of prey and  $r$  is rate of prey population growth as in Equation 7.3.  $P$  is density of predators and  $g$  is a rate constant representing the efficiency of predation. Note that the prey population may grow without limits, except for whatever loss occurs by predation. If predators are absent ( $P = 0$ ), then Equation 7.7 becomes the equation for exponential growth (Equation 1.3).

The equation for change in predator population density is

$$\frac{dP}{dt} = hNP - mP \quad (7.8)$$

In this equation the growth of the predator population is seen to depend solely on the existence of prey ( $hNP$ ), so that when  $N$  is zero, the predator population declines exponentially with rate  $m$ , the predator's death-rate constant. The constant  $h$  includes the capture rate ( $g$  in Equation 7.7) multiplied by a factor for the efficiency of the conversion of captured prey into predators. Both equations include the cross-product term, ( $NP$ ), that is typical of models based in the law of mass action.

To help in visualizing the behavior of models for two interacting species, it is useful to show the population densities graphed against each other, making a phase plot. The time dimension does not appear directly on these plots. It is also valuable for phase plots to include lines, called isoclines, that indicate equilibrium values for each species. An isocline effectively divides the phase plot into two regions, one in which the population will increase, and another in which it will decrease. With predator-prey models, prey density is conventionally given on the  $x$ -axis, and predator density on the  $y$ -axis. The prey isocline is a line comprising all the points for which  $dN/dt = 0$ . The equation for the line is found by setting Equation 7.7 to zero and solving to find

$$P = \frac{r}{g} \quad (7.9)$$

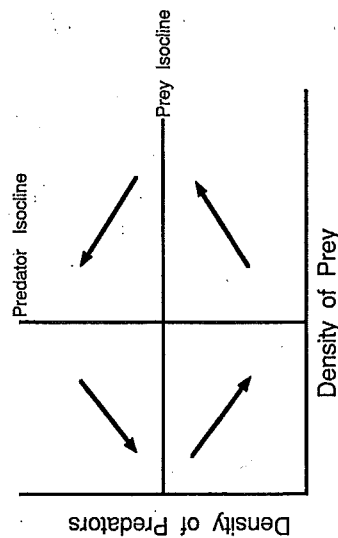


Figure 7.4. A phase plot of predator-prey population interactions, based on the simple Lotka-Volterra model. Construction of isoclines is described in the text.

This describes a line running parallel to the prey axis. Hence, for combinations of predator and prey densities above the line, the prey population will decrease; below it they will increase. An isocline for predator numbers may be constructed similarly by setting Equation 7.8 equal to zero and solving:

$$N = \frac{m}{h} \quad (7.10)$$

The predator isocline is a vertical line, to the right of which predators will increase, and to the left, decrease. A phase plot for predator-prey interactions following the Lotka-Volterra model is shown in Figure 7.4.

**Exercise 7-6:** Write and implement a computer simulation using numerical integration of the Lotka-Volterra predation model (Equations 7.7 and 7.8). Be sure to use the two-stage approach that was described in Chapter 6. Set the following values for the constants of the model:

$$r = 0.1 \quad g = 0.002 \quad m = 0.2 \quad h = 0.0002$$

Start your simulation with  $N = 1500$  and  $P = 50$ . Your output should consist of two graphs. The first should show density of prey and density of predators vs. time. (It may be necessary to divide or multiply predator or prey density by some constant to show meaningful fluctuations on the graph.) The second graph should be a phase plot of predator density vs. prey density. For clarity, your program should draw the predator and prey isoclines (use Equations 7.9 and 7.10), and plot the densities as a continuous line. For both graphs, allow the simulation to proceed for at least two complete predator-prey cycles.

The Lotka-Volterra model is very sensitive to small error in the numerical integration process. This simulation requires the accuracy of the Improved Euler method with a  $\Delta t = 0.1$  or less. The simple Euler may be used with  $\Delta t = 0.001$  or less, but this will result in a relatively slow output of results.

**Exercise 7-7:** Your simulation in Exercise 7-6 should display the stable oscillations characteristic of the Lotka-Volterra model. Ginzburg and Golenberg (1985) used the model to show that use of pesticides can be complex, even with this simple model. Assume the prey to be an agricultural "pest" insect that harms a crop. It is preyed upon by another insect which is therefore "beneficial". The population cycles of predator and prey follow the Lotka-Volterra model. Set up your program from Exercise 7-6 so that it will run for at least 4 complete cycles. Then modify the program to simulate the

one-time application of a pesticide near the peak of the prey (pest) density of cycle number 2, so that the density of prey is suddenly lowered to 55 percent of its pre-pesticide density. After you have obtained the simulation results for this pesticide application, make another simulation run, but with the program modified so that the pesticide is applied at a time near the minimal prey density, instead of the maximum. The simple change in timing of pesticide application can have great impacts on dynamics of predator-prey systems.

## 7.6 Modifications of the Lotka-Volterra Predation Model

The Lotka-Volterra model is attractive because it can produce the oscillations that sometimes have been observed in some predator-prey interactions. As a result, the model has been studied, criticized and improved by dozens of modelers, who have published enough modifications of the basic model to fill a small book (Wangersky 1978). We will discuss briefly two of these modifications, chosen because they produce interesting simulations that mimic the fascinating graphical analyses of Rosenzweig (see Rosenzweig and MacArthur 1963, Rosenzweig 1969, Ricklefs 1979).

A rather obvious criticism of the basic model (Equations 7.7 and 7.8) is that the cross-product expression is unrealistic. The model follows the law of mass action, and is based on the assumption that predation losses always are proportional to prey density. Thus, doubling the prey population will result in a doubling of predation rate, regardless of the predator population. This provokes some mental images of slow-growing predators becoming exhausted with capturing and consuming rapidly-growing prey. Several models have incorporated a term to model saturation of predators, thus limiting predation rate. One of the simpler models uses the hyperbolic approach to an upper limit:

$$\frac{dN}{dt} = rN - \frac{uNP}{k + N} \quad (7.11)$$

In this equation,  $u$  is a constant representing the maximum predation rate under satiating conditions, and  $k$  describes how rapidly the asymptote is approached. Asymptotic terms of this form have been used by Holling (1959) and Tanner (1975). One method of deriving this equation was shown in Section 2.4.

Another obvious problem with the Lotka-Volterra models is that there are no limits to the growth of either predator or prey population other than that imposed by each other. Leslie and Gower (1960) added some

logistic-like terms to the predation model:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} - gP \right) \quad (7.12)$$

$$\frac{dP}{dt} = sP \left( 1 - \frac{P}{jN} \right) \quad (7.13)$$

In Equation 7.12, growth of the prey population is limited both by the carrying capacity  $K$ , and by predation. The growth of predators (Equation 7.13) is a function of a growth rate constant  $s$ , and a constant  $j$  that relates maximum predator density to prey density. When predators are scarce and prey are abundant, predator growth rate is high and approaches  $sP$  as an upper limit. As prey becomes rare or predators more abundant, the parenthetical term for predator growth becomes small or negative, thus controlling predator growth rate.

**Exercise 7-8:** The following equation incorporates both the Holling-Tanner and the Leslie-Gower modifications to the Lotka-Volterra model for prey growth:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} - \frac{uP}{k + N} \right) \quad (7.14)$$

Implement a simulation of predator-prey dynamics with this equation and Equation 7.13, using the two-stage procedures of Euler numerical integration. The following are suggested values for the constants of the equations:

$$r = 0.4 \quad K = 900 \quad u = 2.5 \quad k = 200 \quad s = 0.1 \quad j = 0.5$$

Simple Euler integration is adequate with  $\Delta t = 0.01$ , or use the Improved Euler method with  $\Delta t = 0.1$ . Begin your simulation with initial values of  $N = 25$  and  $P = 5$ . Plot the densities of predators and prey vs. time on a single graph. Allow sufficient time for the simulation to proceed to a steady-state.

**Exercise 7-9:** Solve Equations 7.13 and 7.14 for the values of the predator and prey isoclines. Modify the program from Exercise 7-8 so that it will draw these isoclines on a phase plot of prey density ( $x$ -axis) vs. predator density ( $y$ -axis). Run the simulation using the parameters and starting values of Exercise 7-8. Then repeat the simulation with these constants:

$$r = 0.3 \quad K = 1000 \quad u = 1 \quad k = 200 \quad s = 0.03 \quad j = 0.45$$

Begin the simulation with  $N = 60$  and  $P = 10$ .

## 7.7 Volterra's Model for Two-Species Competition

Models for competing species are attempts to describe dynamics of populations of species that inhabit the same environment and use the same resources. These models are generally based on a pair of modified logistic equations that were first proposed by Volterra (Hutchinson 1978). The equations were developed subsequently in the classical publications of Gause and Witt (1935) and Gause (1934). The assumptions for this competition model are expanded slightly from those of the logistic growth model. The two populations involved are assumed to follow a pattern of logistic growth, and to be in an environment where both use and compete for some resource that limits their population densities. Thus the growth of each species will be controlled not only by its own density, but also by the density of the competitor.

The differential equations involved are

$$\frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1 + \alpha N_2}{K_1} \right) \quad (7.15)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2 + \beta N_1}{K_2} \right) \quad (7.16)$$

In these equations,  $N_1$  and  $N_2$  are the densities of species 1 and 2,  $r_1$  and  $r_2$  are the growth rate constants for the two species,  $K_1$  and  $K_2$  are the carrying capacities for each species when growing alone, and  $\alpha$  and  $\beta$  are competition coefficients. These equations are like the logistic (Equation 7.3) with the addition of another term describing the effect of the other species on population growth. This extra term is a function of the product  $N_1 N_2$  that represents another application of the law of mass action.

The coefficient  $\alpha$  is a factor that "converts" individuals of species 2 into individuals of species 1;  $\alpha$  has units of  $N_1/N_2$ . For example, if  $\alpha$  is 1.5, then from the view of species 1, an individual of species 2 uses as much of the limiting resource as 1.5 individuals of species 1. Likewise, the coefficient  $\beta$  converts individuals of species 1 into individuals of species 2, from the viewpoint of species 2;  $\beta$  has units of  $N_2/N_1$ . Rarely will  $\alpha = 1/\beta$  because species generally do not have identical competitive abilities.

Like the Lotka-Volterra predation equations discussed above, it is helpful to plot data from simulations of competition as phase plots, graphing densities of  $N_1$  vs.  $N_2$ . As in the case of predation, drawing isoclines divides the phase plots into regions where the populations increase and decrease. These lines are similarly solved by setting Equations 7.15 and

7.16 to zero. The isoclines for species 1 and 2 are, respectively,

$$N_1 = K_1 - \alpha N_2 \quad (7.17)$$

$$N_2 = K_2 - \beta N_1 \quad (7.18)$$

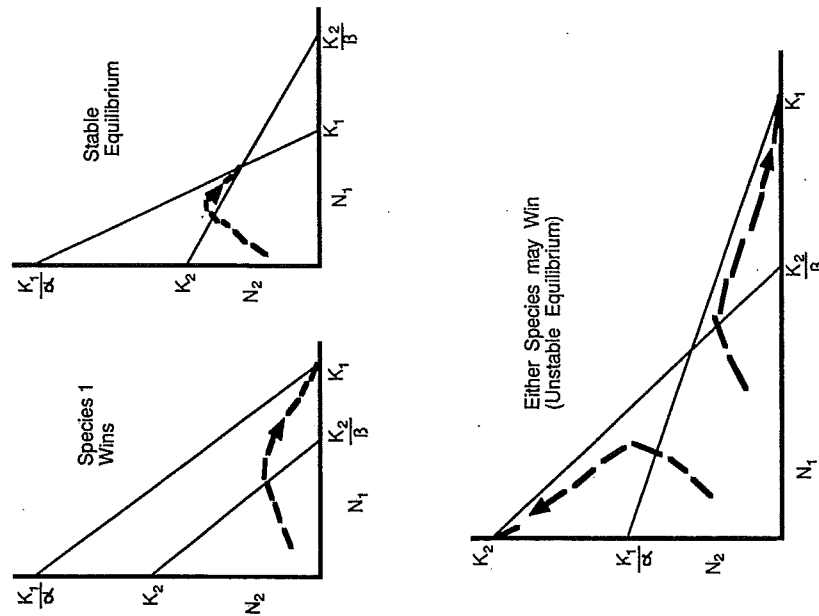


Figure 7.5. Sample phase plots for competitive interactions between two populations, based on the model of Volterra.



When drawn on a phase plot, Equation 7.17 has an intercept of  $K_1$  on the  $N_1$ -axis and  $K_1/\alpha$  on the  $N_2$ -axis. Similarly, Equation 7.18 has

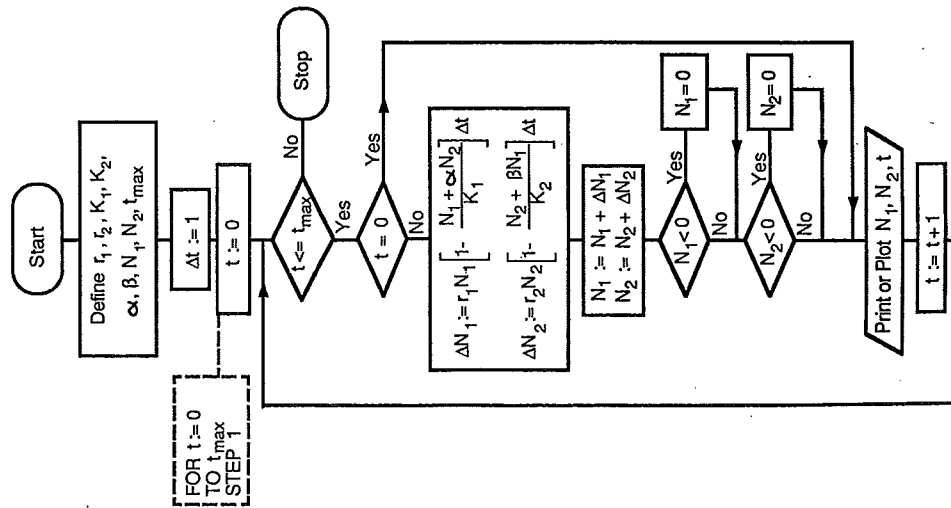


Figure 7.6. Flowchart for program to simulate population growth for two competing populations following the Volterra model.

an intercept of  $K_2$  on the  $N_2$ -axis and  $K_2/\beta$  on the  $N_1$ -axis. Because Equations 7.17 and 7.18 describe straight lines on a phase plot, the isoclines are easily drawn, defining the regions of the graph where the species grow and decline. The result of some competitive interactions may be predicted easily from phase plots with isoclines. Figure 7.5 illustrates some examples. In general there are four possible graphical arrangements of the isoclines, representing the different possible combinations of  $K_1$ ,  $K_2$ ,  $\alpha$ , and  $\beta$  in Equations 7.17 and 7.18.

**Exercise 7-10:** Write and implement a computer simulation for the competition model of Volterra. The flowchart of Figure 7.6 may be of assistance. Your output should be in the form of a phase plot diagram, as illustrated in Figure 7.5. If you are using the GRAPH program to produce your output, write your program so that it first draws the isoclines for the two species, and then plots the points for  $N_1$  vs.  $N_2$  through time as circles. Test your simulation first with these values for the constants of Equations 7.17 and 7.18:

$$r_1 = 0.8 \quad r_2 = 1.0 \quad K_1 = 300 \quad K_2 = 300 \quad \alpha = 0.5 \quad \beta = 0.6$$

Begin your simulation with  $N_1 = N_2 = 10$ . Use two-stage simple Euler integration, with  $\Delta t = 1$ . Allow the simulation to run for enough time to reach an equilibrium, about 25 to 30 time units. Decide which of the possible four types of interaction this simulation demonstrates: stable equilibrium, unstable equilibrium, species 1 always wins, or species 2 always wins. Then, modify the constant values and rerun the simulation to produce three other graphical results that demonstrate the other three competitive interactions.

## Conclusion

This chapter has been concerned with the classical techniques for modeling the dynamics of homogeneous populations. The models we have considered are based in the law of mass action. The simple cross-product approach lacks realism for most population interactions. The unrealistic assumptions of some of these models have prompted some biologists to question the validity of modeling and simulation generally. These models, however, have provided a starting point for descriptions of more complex systems, and were never really intended to be much more than this.