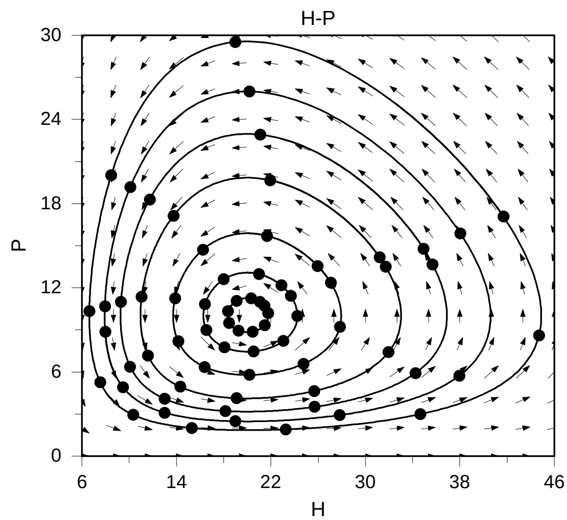
CHAPTER

9 Population Models



Predator-prey cycles with a direction field. Markers are equally spaced in time.

Overview Population biology is the study of how communities of organisms change. The structure of a population can be quite intricate, such as species interactions in a tropical rain forest. Other communities may involve only a few species and are simpler to describe. There are many aspects of population biology, including ecology, demography, population genetics, and epidemiology. In each of these areas, mathematics plays an important role in modeling how populations change in time and how the interaction between the environment and the community affects that change. We'll explore mathematical models in ecology and epidemiology.

Key words Logistic model; growth rate; carrying capacity; equilibrium; steady state; competetion; coexistence; exclusion; predator-prey; epidemiology

See also Chapter 1 for more on the logistic equation, Chapter 7 for predator-prey models, and Chapter 8 for chemical mass action.

◆ Modeling Population Growth

The increasing awareness of environmental issues is an important development in modern society. This awareness ranges from concern about conserving important natural resources to concern about habitat destruction and the endangerment of species. Human population pressures are ever-increasing, and this growth has led to intense exploitation of the environment. To reduce the negative effects of this exploitation, scientists are seeking to understand the ecology and biology of natural populations. This understanding can be used to design management strategies and environmental policies.

The simplest ecological models describe the growth of a single species living in an *environment* or *habitat*. Characteristics of the habitat—temperature, moisture, availability of food—will affect how well the species survives and reproduces. Intrinsic biological characteristics of the species, such as the basic reproductive rate, also affect the growth of the species. However, a mathematical model that incorporates *all* possible effects on the growth of the population would be complicated and difficult to interpret.

✓ "Check" your understanding by answering this question: What are some other characteristics of a species and its environment that can affect the productivity of the species?

The most common procedure for modeling population growth is first to build elementary models with only a few biological or environmental features. Once the simple models are understood, more complicated models can be developed. In the next section we'll start with the *logistic model* for the growth of a single species—a model that is both simple and fundamental.

◆ The Logistic Model

The ecological situation that we want to model is that of a single species growing in an environment with limited resources. Examples of this situation abound in nature: the fish population of a mountain lake (the limited resource is food), a population of ferns on a forest floor (the limited resource is light), or the lichen population on a field of arctic rocks (the limited resource is space). We won't attempt to describe the biology or ecology of our population in detail: we want to keep the mathematical model simple. Instead, we'll summarize a number of such effects using two *parameters*. The first parameter is called the *intrinsic growth rate* of the population. It is often symbolized using the letter r, and it represents the average number of offspring, per unit time, that each individual contributes to the growth of the population. The second parameter is called the *carrying capacity of the environment*. Symbolized by K, the carrying capacity is the largest number of individuals that the environment can support in a steady state. If there are more individuals in the population than the carrying capacity, the population declines because there are too few resources to support them. When there are fewer individuals than K, the environment has not been overexploited and the population grows.

Our mathematical model must capture these essential characteristics of the population's growth pattern. To begin, we define a variable that represents the size of the population as a function of time; call this size $N(t)$ at time t. Next, we specify how the size $N(t)$ changes in time. Creating a specific rule for the rate of change of population size is the first step in *building a mathematical model*. In general, a model for changing population size has the form

$$\frac{dN}{dt} = f(t, N), \quad N(0) = N_0$$

for some function f and initial population N_0. Once the details of f are given, based on the biological and ecological assumptions, we have a concrete mathematical model for the growth of the population.

To complete our description of the logistic model, we need to find a reasonable function f that captures the essential properties described above. We are looking for a simple function that gives rise to

- population growth when the population is below the carrying capacity (that is, $N'(t) > 0$ if $N(t) < K$);
- population decline if the population exceeds the carrying capacity (that is, $N'(t) < 0$ if $N(t) > K$).

One such function is $f(t, N) = rN(1 - N/K)$. The *logistic model* is the IVP

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \quad N(0) = N_0$$

where r, K and N_0 are positive constants. Figure 9.1 shows some typical solution curves.

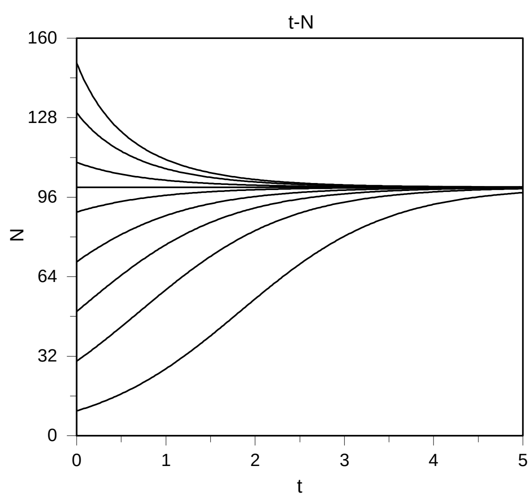


Figure 9.1: Some solution curves for the logistic equation.

Let's observe a few important features of our model. First, the algebraic sign of $N'(t)$ follows the desired relationship to the population size N. Second, if either $N = 0$ or $N = K$, there is no change in the population size: $N'(t) = 0$. Thus, $N = 0$ and $N = K$ are *equilibria* or *steady states*. The first steady state corresponds to the extinction of the species in its environment, and the second corresponds to a population in perfect balance, living at the carrying capacity of the habitat.

Notice the effect of the parameters r and K. As the carrying capacity K increases, the environment supports more individuals at equilibrium. As the growth rate r increases, the population attains its steady state in a faster time. An important part of understanding a mathematical model is to discover how changing the parameters affects the behavior of the system that is being modeled. This knowledge can lead to predictions about the system, and to a much deeper understanding of population processes. In Exploration 9.1 you will study the logistic model and variations of it. See also Chapter 1.

✓ Do you think the intrinsic annual growth rate r of the earth's human population is closer to 0.01, 0.03, or 0.05? It's anyone's guess as to the carrying capacity. What is your estimate, given that the current population is about 6 billion?

◆ Two-Species Population Models

The logistic model applies to a single species. Most habitats support a variety of species; interactions can be both *intraspecific* (between individuals of the same species) or *interspecific* (between individuals of different species). These interactions can take many forms. For example, competition between individuals of the same species for food resources, nesting sites, mates, and so on, are intraspecific interactions that lead to regulated population growth. Important interspecific interactions include predation, competition for food or other resources, and symbiotic relationships that are mutually beneficial. Such interactions can be very complex and can involve a large number of species. Again, the first step in modeling complicated ecologies is to build and analyze simple models. We'll present two such models here (involving only two species) and consider others in the last three explorations.

✓ Can you think of a mutually beneficial interaction between humans and another species?

◆ Predator and Prey

As we noted, an important interaction between species is that of predator and prey. Such interactions are very common: animals must eat to thrive, and for every eater there is the eaten! Spiders prey on flies, cows prey on grass, mosquitoes prey on humans, and humans prey on shiitake mushrooms, truffles, salmon, redwood trees, and just about everything else. We'll now build a simple model to describe such interactions.

Consider two species, the prey species (H, because they're "harvested" or "hunted") and the predator species (P), but for the moment, imagine that they don't interact. In the absence of the predator, we assume that the prey grows according to the logistic law, with carrying capacity K and intrinsic growth rate $a > 0$. The model for the prey under these conditions is

$$H' = aH(1 - H/K)$$

Now suppose that in the absence of its food source (the prey), the predator dies out; the model for the predator is

$$P' = -bP$$

where $b > 0$. If this situation persists, the prey will grow to fill the habitat and the predator will become extinct.

Now suppose that the predator does feed upon the prey, and that each predator consumes, on the average, a fraction c of the prey population, per unit time. The growth rate of the prey will then be decreased (since they're being eaten) by the amount cHP. The predators benefit from having consumed the prey, so their growth rate will increase. But because a given predator may have to consume a lot of prey to survive, not all prey produce new predators in a one-for-one way. Therefore the increase in the growth rate of the predators in this case is dHP, where d is a constant which may be different than c. Putting this all together, we obtain our model for the predator-prey system:

☞ When two species interact at a rate proportional to the product of the two populations, it's called *population mass action*.

$$\begin{aligned} \frac{dH}{dt} &= aH\left(1 - \frac{H}{K}\right) - cHP \\ \frac{dP}{dt} &= -bP + dHP \end{aligned} \tag{1}$$

Analyzing this model gives insight into a number of important ecological issues, such as the nature of coexistence of predator and prey, and the understanding of population cycles. Figure 9.2 on the next page shows a phase plot for the predator-prey system described by ODE (1). Exploration 9.3 examines this predator-prey model.

✓ What is the long-term future of the prey species in Figure 9.2? The predator species?

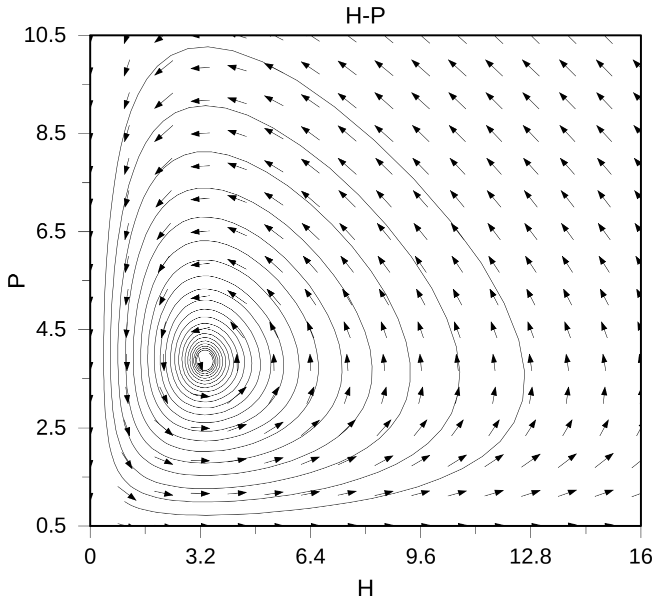


Figure 9.2: An orbit of a predator-prey model with logistic prey growth.

◆ Species Competition

Another common interaction between species is *competition*. Species can compete for space, food, light, or for other resources. In the absence of its competitor, each species grows logistically to its carrying capacity. However, the presence of the competitor changes the situation, and the growth rate of each species is diminished by the presence of the other. Let N_1 and N_2 represent the numbers of the two species. We model the competition between these species with the following equations:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} - \alpha_{12} N_2\right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} - \alpha_{21} N_1\right) \end{aligned} \tag{2}$$

The parameter α_{12} measures the effect of Species 2 on Species 1, and α_{21} measures the effect of Species 1 on Species 2. If $\alpha_{12} > \alpha_{21}$, then Species 2 dominates Species 1, because Species 2 reduces the growth rate of Species 1 more *per capita* than the reverse. The analysis of this model gives insight into how species maintain their diversity in the ecology (*coexistence*) or how such diversity might be lost (*competitive exclusion*). A phase plot for the competitive system is shown in Figure 9.3. Exploration 9.4 examines a related model for so-called mutualistic interactions.

☞ Could the competition be so fierce that both species become extinct?

✓ Does Figure 9.3 show coexistence or competitive exclusion?

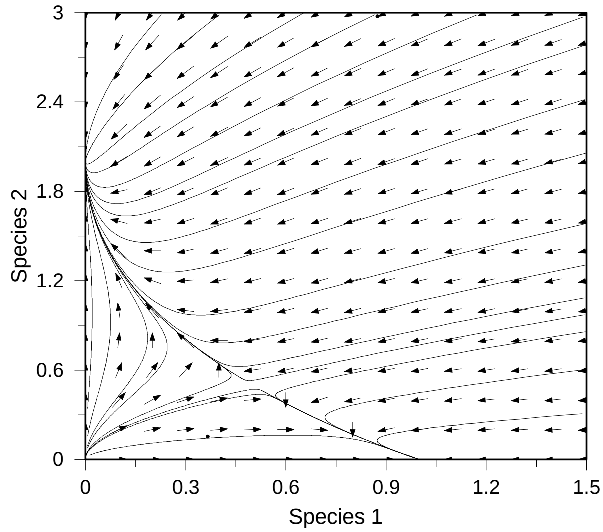


Figure 9.3: Orbits for a model of two competing species.

◆ Mathematical Epidemiology

An important use of mathematical models is to describe how infectious diseases spread through populations. This field is called epidemiology. Quantitative models can predict the time course of a disease or the effectiveness of control strategies, such as immunization. Again, the development proceeds from the simplest model to more complex ones.

The most elementary model for an epidemic is the so-called SIR model (presented in Module 9): Consider a population of individuals divided into three groups—those susceptible (S) to a certain disease, those infected (I) with the disease , and those who have recovered (R) and are immune to reinfection, or who otherwise leave the population. The SIR model describes how the proportions of these groups change in time.

The susceptible population changes size as individuals become infected. Let's think of this process as "converting" susceptibles to infecteds. If we assume that each infected individual can infect a proportion a of the susceptible population per unit time, we obtain the rate equation

☞ Another instance of population mass action.

$$\frac{dS}{dt} = -aSI \tag{3}$$

The infected population is increased by conversion of susceptibles and is decreased when infected individuals recover. If b represents the proportion of infecteds that recover per unit time, then the rate of change of the infected population satisfies

$$\frac{dI}{dt} = aSI - bI \tag{4}$$

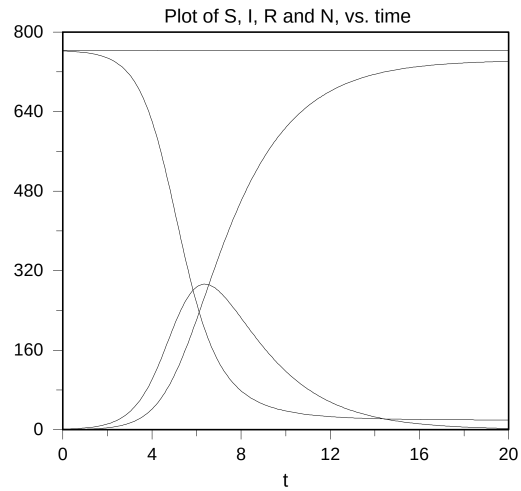


Figure 9.4: A plot of suceptibles (falling curve), infecteds (the “bump”), recovereds (rising curve), and their sum (top line).

Lastly, as infecteds recover they augment the recovered population, so that

$$\frac{dR}{dt} = bI \tag{5}$$

The ODEs (3)–(5) together with the initial values $S(0)$, $I(0)$, and $R(0)$ define the SIR model. A component plot of S, I, R, and $N = S + I + R$ appears in Figure 9.4.

✓ Can you explain why $N(t)$ stays constant as time changes?

We can learn many important things from this model about the spread of diseases. For example, analysis of the model can reveal how the rate of spread of the disease through the population is related to the infectiousness of the disease. Our common experience suggests that not all diseases become epidemic: sometimes a few people are afflicted and the disease dies out. Analysis of the SIR model can also give insight into the conditions under which a disease will become epidemic. This is an important phenomenon! These and other matters will be examined in Exploration 9.5.

✓ What factors can you think of that might influence the spread of a disease in a human population?

References

Bailey, N.T.J., *The Mathematical Theory of Infectious Diseases and its Applications*, 2nd ed., (1975: Hafner Press)

Edelstein-Keshet, L., *Mathematical Models in Biology*, (1988: McGraw-Hill)

Answer questions in the space provided, or on attached sheets with carefully labeled graphs. A notepad report using the Architect is OK, too.

Name/Date ______________________________

Course/Section ______________________________

Exploration 9.1. The Logistic Model

In this exploration you will consider a population that grows according to the logistic law: $N' = rN(1 - N/K)$, where r is the intrinsic growth rate and K is the carrying capacity of the environment.

☞ Using the ODE Architect Library.

1. Open the ODE Architect Library. In the folder "Population Models," open the file "Logistic Model of Population Growth." The logistic equation will be automatically entered into the Architect. The graphs show several solution curves. Set the initial condition for the population size to $N_0 = 25$ and set $K = 100$. Plot eight solutions by sweeping the growth rate constant from $r = -0.5$ to $r = 2$; print your graph. Describe the effect of r on the solutions of the logistic equation. Your description should address the following questions: How does the growth rate constant affect the long-term behavior of the population? How does the rate constant affect the dynamics of the system?

2. Set the IC to $N_0 = 25$ and $r = 1.2$. Plot eight solution curves by sweeping the carrying capacity K from 70 to 150; print your graph. Describe the effect of the parameter K on the solutions of the logistic equation. Your description should address the following questions: How does the carrying capacity affect the long-term behavior of the population? How does the carrying capacity affect the dynamics of the system?

3. Study the graphs that you produced for Problems 1 and 2. Notice that sometimes the rate of change of population size is increasing (i.e., $N'(t)$ is increasing and the graph of $N(t)$ is concave up) and sometimes it is decreasing ($N'(t)$ is decreasing and the graph of $N(t)$ is concave down). By analyzing your graphs, try to predict a relationship between r, K, and N that distinguishes between these two situations. Use ODE Architect to test your prediction by graphing more solution curves. Lastly, try to confirm your prediction by exact analysis of N'' using the logistic ODE.

Answer questions in the space provided, or on attached sheets with carefully labeled graphs. A notepad report using the Architect is OK, too.

Name/Date ____________________

Course/Section ____________________

Exploration 9.2. Harvesting a Natural Resource

Human societies use resources from their environments. We harvest animals and plants for food, construction, fuel, and many other uses. The harvesting of a biological resource must be done carefully, because overexploitation of the population can cause severe harm, or even extinction, to the resource. As a society we have become much more sensitive about the need to balance the benefits of resource consumption against the impact of that consumption on the exploited populations and their environment.

Resource management is an important tool for minimizing the negative effects of harvesting. Mathematical models are tools for understanding the impact of harvesting on a population, so that we can then design management policies, such as quotas on the annual harvest.

In this exploration, you will analyze a simple model for harvesting a single species. To be specific, suppose that the habitat is a forest and the resource is a species of pine tree. The number of trees grows logistically with an intrinsic growth rate r, and the forest will support at most K trees (measured in millions of board feet). You are a consulting ecologist, asked to model the effect of a lumber company's harvesting strategy on the pine forest. The company harvests the trees *proportionally*: in a unit of time (a year, for example), the company removes a fixed fraction h of the trees. Harvesting reduces the net rate of growth of the forest; this leads you to propose the following model for the effect of harvesting:

$$N' = rN\left(1 - \frac{N}{K}\right) - hN, \quad N(0) = N_0 \tag{6}$$

The last term, $-hN$, is the *harvesting term*. Notice that when $h = 0$ (i.e., no trees are harvested), the model reduces to the logistic equation.

1. Open ODE Architect and enter the ODE for the harvesting model given by equation (6). Set the growth rate to $r = 0.1$ year^{-1}, the carrying capacity to $K = 1000$ million board feet, and the population size IC to $N_0 = 100$ at $t = 0$. Describe the growth of the forest when there is no harvesting ($h = 0$). You'll have to choose a good time interval to best display your results.

2. Keep r and K fixed and plot solution curves for various (positive) values of the harvesting rate h. You can do this exploration most efficiently by sweeping the parameter h. After you have studied a variety of harvest rates, explain how harvesting affects the pine population. Your explanation should address the following questions: How does the growth of the pine population with harvesting compare to its growth without harvesting? What is the long-term effect of harvesting? How are the time dynamics of the forest growth affected by harvesting?

3. The annual yield Y of the harvest is the amount of lumber removed per year. This is just $Y = hN$ when there are N units of lumber in the forest. The yield will vary through time as the amount of lumber (trees) in the forest varies in time. If the harvest rate is too high, the long-term yield will tend to zero ($Y \to 0$) and the forest will become overexploited. If the harvest rate is very low, the yield will also be very low. As the consultant to the company, you are asked: What should the harvest rate be to give the largest *sustainable yield* of lumber? That is to say, what optimal harvest rate will maximize $\lim_{t\to\infty} Y(t)$? Attack the problem graphically using ODE Architect to plot graphs of the yield function for various values of h. Assume that $r = 0.1$, $K = 1000$, and $N_0 = 100$. If you can, provide an analytic solution to the question, and check your results using the Architect. Suppose that the company follows your recommendation and harvests pine at the optimal rate. When the size of the forest reaches equilibrium, how much lumber (trees) will there be, and how does this amount compare to the size of the forest without harvesting?

Answer questions in the space provided, or on attached sheets with carefully labeled graphs. A notepad report using the Architect is OK, too.

Name/Date ____________________

Course/Section ____________________

Exploration 9.3. Predator and Prey

Predator-prey interactions are very common in natural populations. These interactions can be modeled by a system of nonlinear equations:

$$H' = aH\left(1 - \frac{H}{K}\right) - cHP, \quad P' = -bP + dHP$$

where H and P are the prey and predator population sizes, respectively.

1. Give a biological interpretation of the parameters a, b, c, d, K of the predator-prey model.

2. Open ODE Architect and enter the modeling equations for the predator-prey system above. Assign the following values to the parameters: $a = 1.0$, $b = 0.25$, $c = 1.0$, $d = 0.15$, $K = 100$. After you have entered the equations and parameters, set the solve interval to 60, and the number of points plotted to 500. Solve the system forward in time using the initial conditions $H(0) = 1$, $P(0) = 1$. Plot graphs of the orbits in the HP-phase plane, and plot the individual component graphs for predator and prey. Experiment with other initial conditions. Describe the nature of the solutions and locate all equilibrium solutions.

3. Fix $a = 1.0$, $b = 0.25$, $c = 1.0$, and $d = 0.15$ as in Problem 2. Plot several solutions from the fixed initial conditions $H(0) = 1$, $P(0) = 1$, for varying values of K. For example, let K range over several values between 100 to 10,000. How does changing the carrying capacity of the prey affect the behavior of the system? Make a conjecture about the limiting behavior of the system as $K \to \infty$.

4. Test the conjecture that you made in Problem 3 in two steps:

(a) Take the limit as $K \to \infty$ in the predator-prey equations and obtain a new system of equations that describes a predator-prey system where there is no resource limitation for the prey.

(b) Explore this system using ODE Architect; this new system is often called the *Lotka–Volterra* model. Plot several orbits using markers that are equally spaced in time. Do the cycles have a common period? How do the time markers help you answer that question? Compare your graphs with the chapter cover figure. Also plot graphs of H against t and P against t for various values of $H(0)$ and $P(0)$. What do these graphs tell you about the periods?

☞ Finally, you get a chance to figure out what is going on in the chapter cover figure.

How does the behavior of the Lotka–Volterra model differ from the model you explored in Problems 1–3?

Answer questions in the space provided, or on attached sheets with carefully labeled graphs. A notepad report using the Architect is OK, too.

Name/Date ____________________

Course/Section ____________________

Exploration 9.4. Mutualism: Symbiotic Species Interactions

For both predator-prey and species competition, the growth rate of at least one of the species is reduced by the interaction. Though eating the prey helps the predator, it certainly harms the prey; for competitors the reduction in growth rate is reciprocal. Not all species interactions must be negative: there are many examples where the species cooperate or otherwise *mutually enhance* their respective growth rates. A famous example is the yucca plant–yucca moth system: the yucca plant can be pollinated only by the yucca moth, and the yucca moth is adapted to eat nectar only from the yucca plant. Each species benefits the other, and their interaction is positive for both. Such interactions are called *mutualistic* or *symbiotic* by ecologists. In this exploration we will present and analyze a simple model for mutualism.

Our model will be very similar to the competition model studied in Module 9. To obtain a model for mutualism, we just change the signs of the interaction terms so that they are always positive: each species enhances the growth rate of the other. We then obtain the following equations:

$$\frac{dN_1}{dt} = N_1\left(r_1 - e_1 N_1 + \alpha_{12} N_2\right), \quad \frac{dN_2}{dt} = N_2\left(r_2 - e_2 N_2 + \alpha_{21} N_1\right) \tag{7}$$

The parameters r_1, r_2, α_{12} and α_{21} retain their meanings from ODE (2) in the competition model. However, the interaction terms $\alpha_{12}N_1N_2$ and $\alpha_{21}N_1N_2$ have *positive* sign and thus enhance the respective growth rates.

Notice that in the absence of interaction, the carrying capacities of the two species are $K_1 = r_1/e_1$ and $K_2 = r_2/e_2$ in this version of the model.

☞ You may want to use the Dual (Matrix) sweep feature here.

1. Open the ODE Architect Library, go to the "Population Models" folder; now open the file "Mutualism: Symbiotic Interactions." This file loads the equations that model a mutualistic interaction. Fix $r_1 = 1$, $r_2 = 0.5$, $e_1 = 1$, $e_2 = 0.75$. Vary the values of each of the interaction coefficients from 0 to 2. For each combination of values for α_{12} and α_{21} that you try, draw a phase portrait of the system (7) in the first quadrant. Describe every possible kind of behavior of the system; try enough combinations of the parameters to feel confident that you have covered all the possibilities. Answer the following questions: Is species coexistence possible? Can competitive exclusion occur? Will the populations of both species remain bounded as time increases?

2. Using pencil and paper, deduce the conditions under which a two-species equilibrium will be present. Check your conditions using the Architect to solve the model. When a two-species equilibrium is present, does it necessarily have to be stable? Compare two-species equilibria to single-species equilibria (the carrying capacities): does mutualism increase or decrease the abundance of the species at equilibrium?

3. Do you think that a mutualistic interaction is always beneficial to an ecosystem? Under what conditions might it be deleterious? Compare the behavior of mutually interacting species to that of competing species. How are the two behaviors similar? How are they different?

Answer questions in the space provided, or on attached sheets with carefully labeled graphs. A notepad report using the Architect is OK, too.

Name/Date ______________________________

Course/Section ______________________________

Exploration 9.5. Analyzing the SIR model for an Epidemic

We will now explore the SIR model for the spread of an epidemic. Recall the ODEs for this model: $S' = -aSI$, $I' = aSI - bI$, $R' = bI$. The parameter $a > 0$ is the infection rate constant and $b > 0$ is the removal (recovery) rate constant of infecteds. Notice that $S' + I' + R' = 0$, i.e., the total number of individuals N is constant and equals $S(0) + I(0) + R(0)$. The ODE Architect Library has an equation file for the SIR model in the "Population Models" folder. In this file you will find values of a, b, and N that correspond to an actual epidemic.

1. Set the IC to $I(0) = 20$ and $R(0) = 0$. Set the solve interval to 24 time units, and make ten plots by sweeping the initial number of susceptibles from $S(0) = 100$ to $S(0) = 500$. Now examine the graph panel for I vs. t. Which of the curves corresponds to $S(0) = 100$ and which to $S(0) = 500$? By definition, an epidemic occurs if $I(t)$ increases from its initial value $I(0)$. For which of the curves that you plotted did an epidemic occur?

2. The behavior that you studied in Problem 1 is called a *threshold effect*. If the initial number of susceptible individuals is below a threshold value, there will be no epidemic. If the number of susceptibles exceeds this value, there will be an epidemic. Use ODE Architect to empirically determine the threshold value for $S(0)$; use the values of a and b in the Library file. Now analyze the equation for dI/dt and determine a sufficient condition for $I(t)$ to initially increase. Interpret your answer as a threshold effect. Use the values of the infection and removal rates that appear in the Library file to compare your analytic calculation of the threshold with that obtained from your empirical study.

3. Clear your previous results from the Architect but keep the same values for a and b. Set the initial conditions for I, R, and S to 10, 0, and 200, respectively. Solve the equations for a time interval of 24 units. Notice from the plot of $I(t)$ that the number of infecteds steadily diminishes from 10 to nearly zero. Also notice that over this same period of time, the number of susceptibles declines by almost 50, and the number of recovered individuals increases from zero to nearly 50. Explain this seemingly contradictory observation.

4. A disease is said to be *endemic* in a population if at equilibrium the number of infecteds is positive. Is it possible in the SIR model for the disease to be endemic at equilibrium? In other words, can $\lim_{t\to\infty} I(t) > 0$? Explain your answer.