6 Systems of Differential Equations

Homer: Hey Flanders, it's no use praying. I already did the same thing, and we can't both win.

From: *The Simpsons*

6.1 Introduction

In the real world, living things interact. Our mathematics must reflect these interactions if it is to produce more than a caricature of reality. In this chapter we will consider systems of two differential equations involving a pair of unknown functions that represent some interacting quantities. More elaborate models use systems with more variables, whose mathematical treatment is beyond the scope of these notes. So as not to interrupt the narrative, we discuss a few algebraic preliminaries in this introduction. First, we review the technique for solving a pair of simultaneous algebraic equations.

Example 6.1: Find all solutions to the system of equations

$$\begin{aligned} x+y&=100 \\ 2x-3y&=25 \end{aligned} \tag{6.1}$$

Solution:

This system is linear, meaning that the unknowns both appear to at most the first degree. It is always possible to solve such equations by following a systematic procedure, known as elimination. Specifically, we first solve one of the equations for one of the variables in terms of the other. For example,

$$x+y=100 \quad \overbrace{\Rightarrow}^{\text{(implies)}} \quad y=100-x\,.$$

Then the latter equation is substituted for y in the second equation of the system, thereby eliminating y from that equation. Here we obtain

$$2x-3y=25 \quad \overbrace{\Rightarrow}^{y=100-x} \quad 2x-3(100-x)=25$$

or

$$5x-300=25\,.$$

This last equation is solved for x, giving $x=65$. The relationship $y=100-x$ then gives $y=35$ and so our system has the unique solution $x=65,\ y=35$, as can be verified by direct substitution of these values in the system (6.1).■

We will need to solve slightly more complicated systems than linear ones. In our work we will encounter systems in which each equation factors into a product of first-degree expressions. The solution(s) of the system can be obtained by using elimination and splitting the analysis into several cases, as we illustrate in Example 6.2.

Example 6.2: Find all solutions of the system of equations

$$\begin{aligned} x(100 - x - y) &= 0 \\ y(210 - 2x + 3y) &= 0 \end{aligned} \tag{6.2}$$

Solution:

This is a non-linear system because if we were to expand the equations we would obtain expressions involving products of variables with each other. We can apply the method of elimination, taking into account that in the first step there may be more than one possibility for expressing one variable in terms of the other. Consider the first equation $x(100 - x - y) = 0$. This equation is satisfied if either $x = 0$ **or** $100 - x - y = 0$. We need to examine both possibilities.

Case i) $x = 0$. If we substitute this in the second equation of the system we get $y(210 + 3y) = 0$. Therefore, either $y = 0$ or $y = -70$. Thus we have the solution pairs $x = 0,\ y = 0$ and $x = 0,\ y = -70$.

N.B. It is not correct to substitute the condition $x = 0$ in the equation $100 - x - y = 0$ arising from the other factor of $x(100 - x - y) = 0$. ***In doing so you are finding values of*** x ***and*** y ***that satisfy*** $x = 0$ ***and*** $100 - x - y = 0$***, a more severe requirement than what we are looking for***. The resulting values (here $x = 0$ and $y = 100$) will almost never satisfy the second equation of our system.

Case ii) $100 - x - y = 0$. We solve this equation for y in terms of x, as we did in Example 6.1, obtaining $y = 100 - x$. This value is then substituted for y in the second equation, which becomes

$$(100 - x)(210 - 2x + 3(100 - x)) = 0.$$

Leaving the equation factored, we simplify the second factor yielding

$$(100 - x)(510 - 5x) = 0.$$

This gives the solutions $x = 100$ and $x = 102$. Since $y = 100 - x$ we get the solution pairs $x = 100,\ y = 0$ and $x = 102,\ y = -2$. Altogether there are four solutions to the system, which we list as ordered pairs $(0,0),\ (0,-70),\ (100,0),\ (102,-2)$. ■

The solutions of a single equation of the type $ax + by + c = 0$ form a line in the plane. This line divides the plane into two regions. In one of these regions the expression $ax + by + c$ will have a positive sign and in the other this expression will have a negative sign. We will need to determine the correct sign for each region. Let's consider how to do this conveniently.

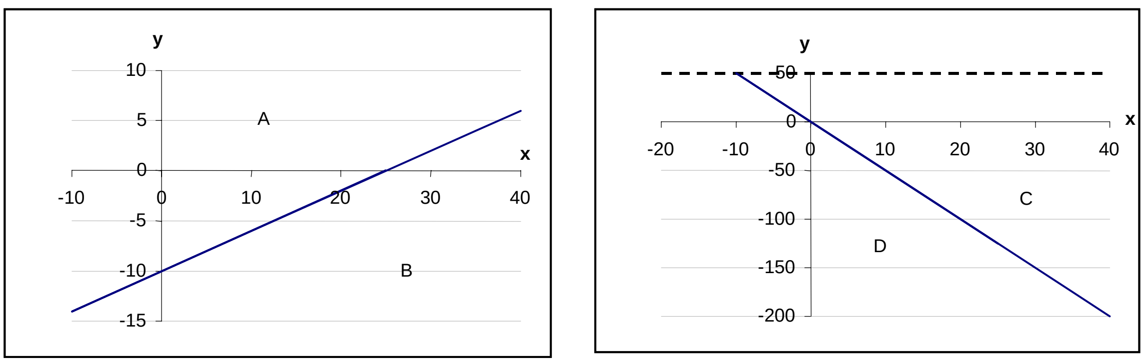
Example 6.3:

a) Find the sign of the expression $50-2x+5y$ in each of the two regions on either side of the line $50-2x+5y=0$.

b) Find the sign of the expression $y+5x$ in each of the two regions on either side of the line $y+5x=0$.

Solution:

a) We first plot the line, using the intercepts as our two points for drawing the line. These are $(25,0)$ and $(0,-10)$. The line is shown in the left panel of Figure 6.1 below.



(a) (b)

Figure 6.1

The expression $50-2x+5y$ is not zero at any point in A. Therefore, it must have the same sign at any point in that region. To evaluate this sign, choose any convenient point in A and substitute its coordinates in the expression. In this case we can select the origin. The expression $50-2x+5y$ evaluated at $(0,0)$ has value 50, which is positive. Hence, the expression is positive in region A and therefore negative in region B.

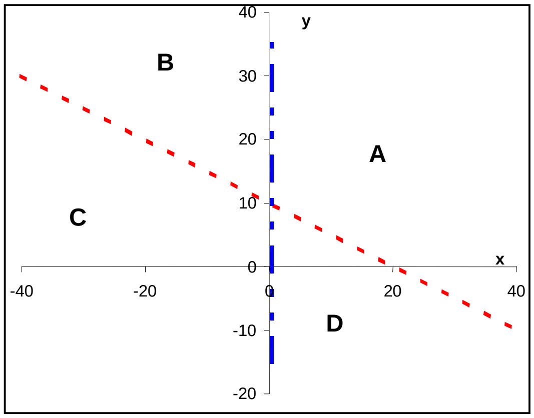
b) The line defined by the equation $y+5x=0$ passes through the origin (see Figure 6.1(b)). Therefore, we cannot use the origin to make the sign determination in the regions labeled C and D. However, we can use any other point on the positive x axis to determine the sign in region C. For $x=10$, $y=0$ the expression $y+5x$ is positive so that this expression is positive in C and negative in D.■

We can extend the technique in Example 6.3 to solve a more general problem.

Example 6.4: Plot the solution of the equation $x(20-x-2y)=0$ and determine the sign of the expression $x(20-x-2y)$ at any point in the plane that is not a solution of the equation.

Solution:

If (x, y) satisfies $x(20-x-2y)=0$ then we must have $x=0$ or $20-x-2y=0$. These give two lines, dividing the plane into four regions labeled A, B, C, and D in the figure.



In each of these regions the expression $x(20-x-2y)$ is not zero and therefore has a fixed sign. The sign of the product can be determined by examining the sign of each factor. Consider region A. The factor x is clearly positive. The sign of $20-x-2y$ can be determined using the method of Example 6.3. At the origin this expression is positive and hence is negative at any point of A, which lies in the opposite region as the origin with respect to the line $20-x-2y=0$. Therefore, in region A the expression $x(20-x-2y)$ has sign $(+)\times(-)=(-)$.

The signs in the other regions can be determined from knowledge of the sign in region A. When we pass from one region to another across a boundary line there is a change of sign in exactly one of the factors in the product $x(20-x-2y)$. Thus in region B, the factor x becomes negative, the second factor remaining negative. Therefore, the expression $x(20-x-2y)$ is positive in region B. By similar reasoning, in region C the expression has a negative sign and a positive sign in region D. ■

6.2 Competition Models

Up to now we have studied population models which only indirectly took account of the existence of other species. Namely, the existence and size of other populations may affect the environment's carrying capacity K for a particular species. We want to model this effect more explicitly.

We assume that there are two species with population sizes N_1 and N_2, respectively. If each species were isolated we assume that a logistic law would govern the growth of the population. Thus, for example we would have

$$\frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1}{K_1}\right) \text{ and } \frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2}{K_2}\right).$$

To account for an interaction between the species we assume that the presence of each depresses the growth rate of the other, in a manner similar to the way each individual species suppresses its own growth rate. Thus, we take as our simplest model of competition the following pair of linked differential equations:

$$\frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1}{K_1} - a_{21} N_2\right) \tag{6.3}$$

$$\frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2}{K_2} - a_{12} N_1\right) \tag{6.4}$$

The parameters $r_1, r_2, K_1, K_2, a_{21}, a_{12}$ are all assumed to be positive. The number a_{21} measures the effect of a member of species 2 on species 1 (hence the subscript a_{21}). The larger the value of a_{21} the greater effect an increase in N_2 will have on decreasing the growth rate of N_1. A similar interpretation applies to a_{12}. On the other hand, the coefficients $1/K_1$ and $1/K_2$ can be viewed as measuring the strength of the competition among members of the same species. From a biological viewpoint, if a_{21} is smaller than $1/K_2$, so that the interspecies effect of species 2 on species 1 is smaller than the intraspecies effect that members of species 2 have on each other, and if similarly a_{12} is smaller than $1/K_1$, we consider the species to be non-competitive. In this case, we would expect, and the model confirms, that both species could coexist in the same environment. In any of the other cases there is a significant competitive pressure on one of the species which will drive it to extinction, a result known in population ecology as the *principle of competitive exclusion:* Species competing in the same ecological niche cannot coexist.

Since we have never considered pairs of differential equations we describe the methodology through the analysis of a concrete example. Namely, we will examine the system

$$\frac{dN_1}{dt} = .15 N_1\left(1 - \frac{N_1}{75} - \frac{N_2}{75}\right) \tag{6.5}$$

$$\frac{dN_2}{dt} = .05 N_2\left(1 - \frac{N_2}{50} - \frac{N_1}{25}\right) \tag{6.6}$$

Here we have $K_1 = 75$, $K_2 = 50$, $a_{21} = 1/75$ and $a_{12} = 1/25$. Notice that if either $N_1 = 0$ or $N_2 = 0$, so that one of the species is absent, the equation for the growth of the other species is of the logistic type. For example, if $N_2 = 0$ then the differential equation (6.5) becomes

$$\frac{dN_1}{dt} = .15N_1\left(1 - \frac{N_1}{75}\right),$$

which is a logistic equation with a carrying capacity of 75 for species 1. Similarly, if $N_1 = 0$, the equation for species 2 would be logistic with a carrying capacity of 50. In the general situation, as for single differential equations, it is necessary to specify the initial size of each population.

Example 6.5: Examine the long-term behavior of the solutions to (6.5) and (6.6) if the initial conditions are

a) $N_1(0) = 15$ and $N_2(0) = 10$

b) $N_1(0) = 10$ and $N_2(0) = 15$.

Solution:

What might we expect for the long-term population trends? We can set up a table containing the measures of inter and intraspecies competition described above.

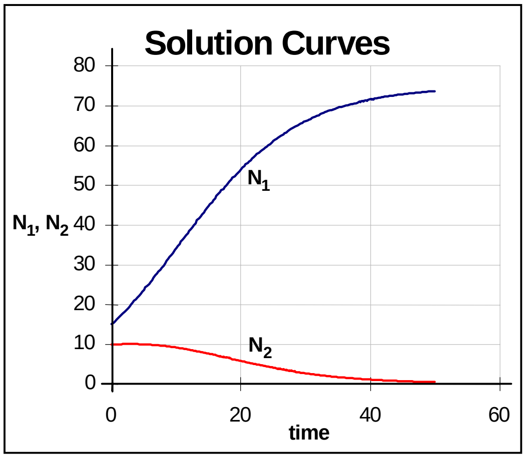
species	1	2
1	$1/K_1 = 1/75 \approx .013$	$a_{12} = 1/25 = .04$
2	$a_{21} = 1/75 \approx .013$	$1/K_2 = 1/50 = .02$

Table 6.1

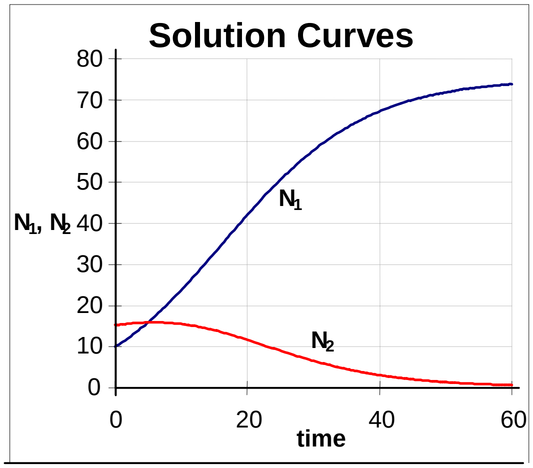
Species 1 exerts a greater effect on species 2 than it does on itself (.04 > .013), while species 2 exerts a greater pressure on itself than it does on species 1 (.02 > .013). As long as both species are present to begin with, species 1 should out-compete species 2. The net effect should be the demise of species 2. Does the model actually exhibit this behavior?

Knowing the initial values and the differential equations (6.5) and (6.6), we can use numerical methods to solve the system, at least approximately. In principle we could use Euler's method. Knowing the initial values enables us to evaluate the right side of each of the differential equations, which tells us the initial slopes of our unknown functions. We then use a pair of updating equations of the form $N_{i,new} = N_{i,old} + (\Delta t)N'_{i,old}$ for $i = 1,2$, with a small time increment Δt, to get estimates for the values of N_1 and N_2 at a later time. This process is repeated, as we did for Euler's method in dealing with a single equation. In practice, most computer implementations use more accurate methods than the simple Euler technique.

The figure below gives the solutions obtained using the Modified Euler method applied to systems for each of the initial values a) and b).



(a)



(b)

Figure 6.2

The value of N_1 increases, possibly towards the environmental carrying capacity of 75; the value of N_2 decreases (after increasing for a short time), apparently approaching zero. This behavior is in line with our prediction.■

6.3 Steady States and Phase Plots

In the competition example the biological interpretation of the coefficients aided our predictions of the mathematics. We would like to place this analysis on a firmer mathematical foundation. Our experience with single equations suggests that equilibrium values or steady state solutions play an important role in understanding the behavior of arbitrary solutions. The steady state solutions for a system are constant values of N_1 and N_2 that solve the equations. As in the one variable case, the steady states are obtained by setting each derivative equal to zero and solving for N_1 and N_2.

Example 6.6: Find the steady state solutions of the system of differential equations (6.5) and (6.6).

Solution:

From (6.5) and (6.6) we obtain the two algebraic equations

$$.15N_1\left(1-\frac{N_1}{75}-\frac{N_2}{75}\right)=0 \tag{6.7}$$

and

$$.05N_2\left(1-\frac{N_2}{50}-\frac{N_1}{25}\right)=0. \qquad (6.8)$$

These equations are similar to those in Example 6.2. We can apply the same techniques, noting for instance that an equation such as $1-\frac{N_2}{50}-\frac{N_1}{25}=0$ is usually best handled by first multiplying both sides by the least common denominator, 50, obtaining $50-N_2-2N_1=0$. We find four solutions to the system (6.7) and (6.8): These are:

- $N_1=0$ and $N_2=0$ (both populations are non-existent)
- $N_1=0$ and $N_2=50$ (Species 1 is not present; species 2 fills the environment to its carrying capacity of 50.)
- $N_1=75$ and $N_2=0$ (Species 2 is not present; species 1 fills the environment to its carrying capacity. The solutions in Figure 6.2 appear to be approaching this state.)
- $N_2=100$ and $N_1=-25$. Since the latter value is negative, it is not relevant to a discussion of population and we ignore it. For the purposes of population modeling we only need to consider steady state solutions in which both functions have non-negative values.■

Having found the steady state solutions, we would like to understand the stability properties of each. The solutions of the initial value problems listed in Example 6.5 appear to approach the steady state $N_1=75$ and $N_2=0$. Is it possible to predict this from the equations? In general, making such predictions is more complicated for systems than it is for single equations and we will not attempt to give a thorough analysis. Rather, we introduce some tools that are useful in understanding the results as obtained, for example, using a numerical routine on a computer.

First, we need an important geometrical representation of the solutions. In Figure 6.2 we drew the graphs of both solutions as functions of time. An alternative way to compare solutions is to plot for each value of t the point $(N_1(t),N_2(t))$, in other words a plot of N_2 vs. N_1. This plot is known as a *phase plot* and the N_1, N_2 plane is called the *phase plane* of the system.

Example 6.7: Find the phase plot for the solution to the initial value problem described in Example 6.5a).

Solution:

For the solutions to Example 6.5a), the phase plot is shown in Figure 6.3. The phase plot has been generated from the values of the solutions $N_1(t)$ and $N_2(t)$ by plotting the pair (N_1, N_2) for each value of t appearing in the modified Euler approximation scheme.

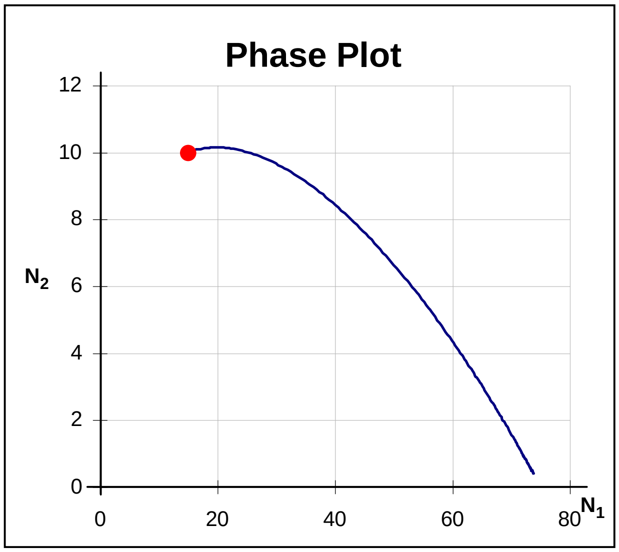


Figure 6.3

The dot marks the initial value for the two variables. The picture shows that initially both N_1 and N_2 increase, but that eventually N_2 decreases towards zero while N_1 increases, perhaps towards some limiting value. The reader should compare this behavior with the graphs of the solutions shown in Figure 6.2(a). Notice, however, that the phase plot provides no clue as to how much time is required for the solutions N_1 and N_2 to evolve towards this steady state. The phase plot merely shows the relationship between the variables N_1 and N_2, sometimes in a striking way that is not apparent from the individual graphs.■

6.4 Stability Analysis and Null-clines

As noted above, the phase plot has less information than the plots of the individual solutions $N_1(t)$ and $N_2(t)$ from which it is derived. Surprisingly though, we can often make predictions about the shape of the phase plot and such predictions are quite useful in understanding the behavior of the solution functions $N_1(t)$ and $N_2(t)$. In the case of a single differential equation, stability analysis required us to determine the sign of $\frac{dN}{dt}$. For a theoretical understanding of the behavior of the systems we need to consider the signs of both $\frac{dN_1}{dt}$ and $\frac{dN_2}{dt}$. These signs tell us when N_1 and N_2 are increasing or decreasing and enable us to follow, at least roughly, the path taken by the phase plot in the phase plane. The determination of the signs of the derivatives adds another ingredient to the phase plot, the so-called null-clines. A *null-cline* is a curve in the phase plane along which $N_1{}' = 0$ or $N_2{}' = 0$. These curves separate the phase plane into regions in which the signs of $\frac{dN_1}{dt}$ and $\frac{dN_2}{dt}$ do not change.

Example 6.8: Find the null-clines for the system of equations (6.5) and (6.6).

Solution:

The null-clines for N_1 (called N_1 null-clines) are found by setting $\frac{dN_1}{dt} = 0$. This leads to either $N_1 = 0$ or $1 - \frac{N_1}{75} - \frac{N_2}{75} = 0$. The first of these is the vertical axis in the phase plane. The second can be written as $75 = N_1 + N_2$ and is a straight line with intercepts equal to 75. These are the dotted lines in Figure 6.4 below. These lines are also labeled with a circled ① to identify the null-cline with which it is associated. Similarly the null-clines associated with $N_2{}' = 0$, ($N_2 = 0$ and $50 = 2N_1 + N_2$) are the solid bold lines (also labeled ②) in the same figure. ***Notice that the point of intersection of an N_1 null-cline and an N_2 null-cline is a steady state solution, since by definition both derivatives vanish at such a point***. Figure 6.4 shows three such intersections (represented using diamonds). The fourth steady state solution is located in the second quadrant and is not visible.

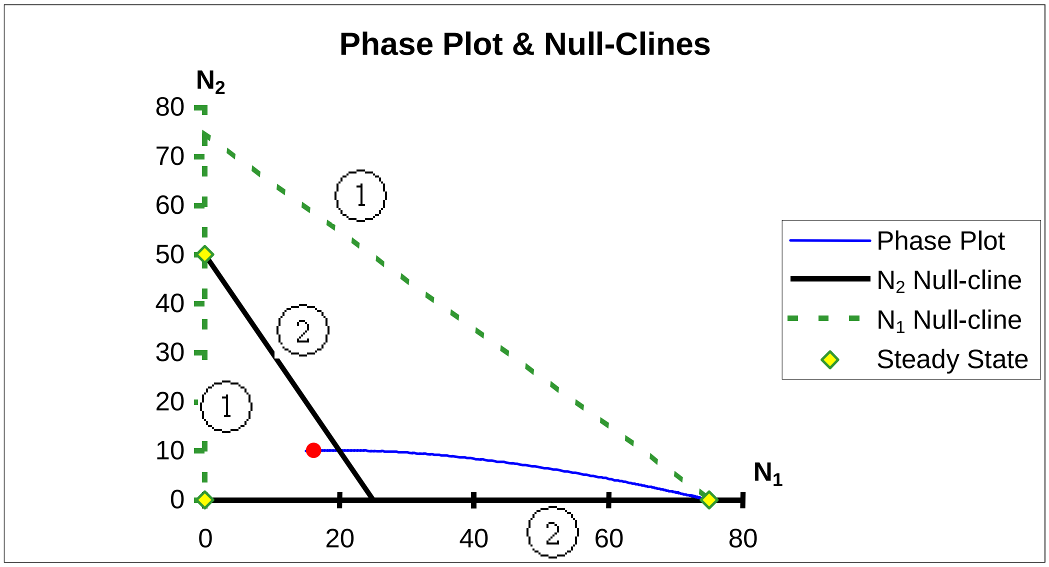


Figure 6.4

■

In any of the regions between two null-clines neither derivative can vanish, and therefore must have a fixed sign. This sign tells us whether the corresponding function N_1 or N_2 is increasing or decreasing. We encode this information into the null-cline plot using arrows, similar to the stability diagrams that we considered in chapter 4. The resulting figure is called an *arrow diagram* and can be used to make predictions about the shape of phase plots.

Example 6.9: Draw an arrow diagram for the system in Example 6.5.

Solution:

Consider the region above the slanted N_1 null-cline in Figure 6.4. We need to determine the sign of the product $.15N_1\left(1-\frac{N_1}{75}-\frac{N_2}{75}\right)$ in that region. Multiplying the expression by 75 does not change its sign and thus we consider the simpler $.15N_1(75-N_1-N_2)$. The sign analysis for the latter expression can be carried out using the technique in Example 6.4. Recall that this involves examining the signs of the two factors. The factor N_1 is certainly positive in the region above the slanted null-cline. The sign of $(75-N_1-N_2)$ can be determined using the technique of Example 6.3. When $N_1=0$ and $N_2=0$ (in the region below the slanted N_1 null-cline) the expression $(75-N_1-N_2)$ is positive. Therefore, in the region above the slanted line the latter expression is negative. Hence

$$\frac{dN_1}{dt}=.15N_1\left(1-\frac{N_1}{75}-\frac{N_2}{75}\right)<0\,.$$

Thus N_1 will decrease, which we indicate (Figure 6.5 below) using a horizontal arrow pointing towards the left. By a similar argument we deduce that in the same region $50-N_2-2N_1<0$ so that

$$\frac{dN_2}{dt}=.05N_2\left(1-\frac{N_2}{50}-\frac{N_1}{25}\right)<0\,.$$

This implies that N_2 decreases, which we indicate by drawing a short downward pointing arrow. Since a phase curve has an N_1 and an N_2 component, the net effect will be that a phase curve in this region will tend in the direction of the diagonal arrow.

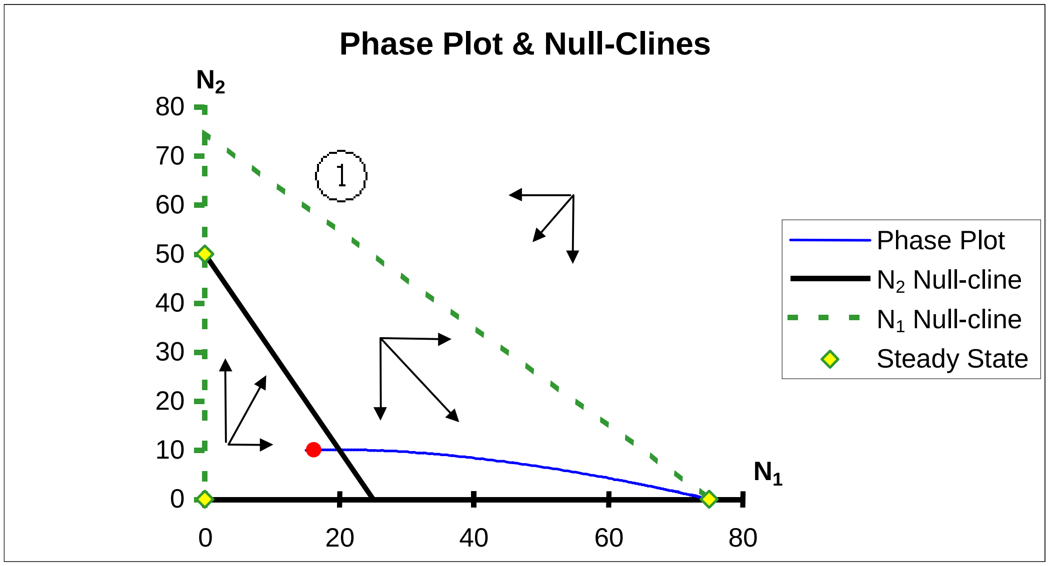


Figure 6.5

Once we are certain of the arrow directions in one region, it is a simple matter to determine the correct directions in each of the remaining regions. For example, in Figure 6.5, when we cross the slanted N_1 null-cline the sign of N_1' changes from negative to positive. Hence, in the new region N_1 is an increasing function, indicated by the rightward pointing horizontal arrow. The sign of N_2' does not change when crossing an N_1 null-cline, so N_2 remains a decreasing function. In this way we establish the pattern of arrows in Figure 6.5. The resulting diagram (without the phase plot) is the arrow diagram for the system.■

Having the null-clines and the associated direction arrows allows us to better understand the phase plot. Figure 6.5 shows the phase plot associated with the initial value problem described in Example 6.5a). The initial point is in a region where the solution moves up and to the right, which our solution does. It then crosses into the middle region where N_1 increases and N_2 decreases. Once in this region N_2 continues to decrease approaching zero at a slower and slower rate since the horizontal axis is an N_2 null-cline. N_1 must keep increasing, but its rate of increase must slow down as it approaches the null-cline $N_1' = 0$. Consequently, the phase plot approaches the point (75, 0).

In the figure below, we have added some additional phase plots with different initial values. The collection of phase plots is called a *phase portrait*, since it gives us an overall picture of the behavior of the system for a variety of initial conditions. You should go through the reasoning in the above paragraph to make sure you understand why each curve follows the trajectory shown. In particular, note that a phase plot makes a vertical crossing of an N_1 null-cline, since on that null-cline the value of N_1 does not change. Similarly a phase plot makes a horizontal crossing of an N_2 null-cline. These observations are useful in making preliminary sketches of the phase plots.

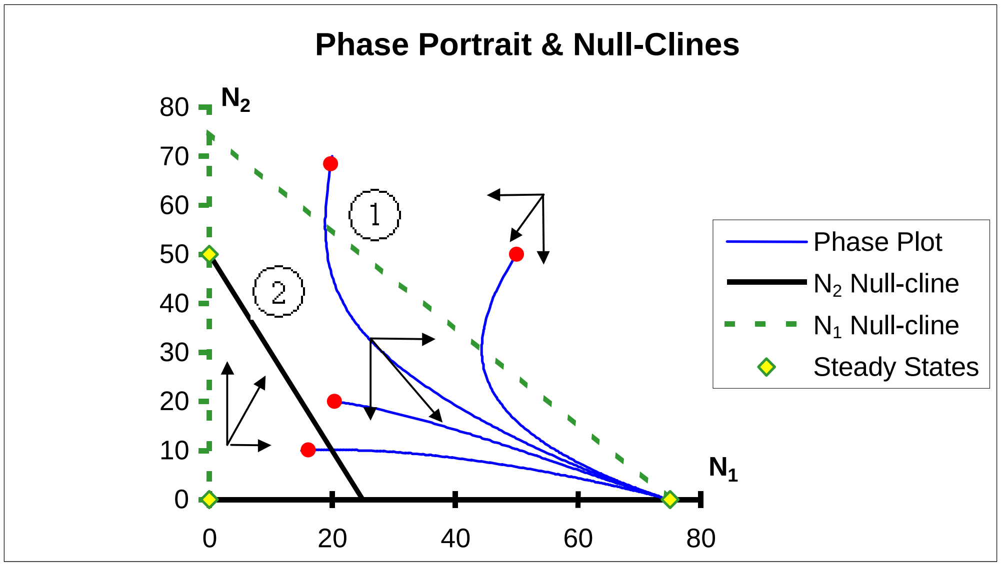


Figure 6.6

Having generated a phase portrait, we can use it to characterize the stability of the steady state solutions. It would appear from Figure 6.6 that the steady state (75, 0) is stable and the other steady states are unstable. The stability classification in this example was rather clear-cut once the phase portrait has been generated. For other systems of differential equations stability may appear in subtler form. It is possible that a solution may begin near a steady state and simply remain near it without approaching it. The models in the next section display this behavior. A more striking example of the phenomenon is provided in the predator-prey system in exercise 12.

We summarize the steps for analyzing a system that are discussed in this and the previous section. In the next section we will use this procedure to analyze another model of biological interest.

Given a system of differential equations: $\dfrac{dN_1}{dt} = f(N_1, N_2)$ and $\dfrac{dN_2}{dt} = g(N_1, N_2)$, together with initial conditions $N_1(0) = N_1^*$ and $N_2(0) = N_2^*$:

- Use a computer to solve the system numerically over a time interval sufficiently long to give you a good idea how the solutions are behaving. It is good practice to check the calculation by performing the same computation with half the step size (hence double the number of intervals). An accurately computed solution should not change much.

- To understand the behavior of the solution (or to make generalizations regarding other solutions), find

  a) the steady state solutions,

  b) the null-clines,

c) an arrow diagram based on the sign of the derivatives in the regions between the null-clines.

- Use the arrow diagram to confirm the computed phase plot and make some predictions as to the phase plot of some other solutions with different initial values. Check these with a computer.

- If your equation involves some parameters, (such as K, r and the a_{12}, etc) try to make some general statements relating the parameters to the behavior of the solutions. This step may be very difficult to carry out.

6.5 The Spread of Disease

We can apply our methodology to create a simple model for the spread of disease. We make certain biological assumptions to derive the rather simple differential equations for this model. We categorize each member of the population into one of three states: S denotes the susceptible members, those who are not infected but can become so. I denotes the infected members of the population and R denotes those who have recovered from infection or died from it (the removed category). We make the following assumptions:

i) Re-infection is impossible, so once an infected person enters the R category he or she is immune to the disease (or is dead).

ii) Only infectives can transmit the disease. Persons of type R or S cannot be transmitters.

iii) Infection occurs through contact of an infective with a susceptible person, although only a fraction of such contacts may result in infection. Infectives and susceptibles are assumed to mix freely with each other.

iv) Population changes due to births, deaths from other causes, immigration or emigration are insignificant during the time frame of interest.

We can use these assumptions to construct a system of differential equations for the quantities S, I and R. The reader will no doubt judge these assumptions as unrealistic for many common diseases. For example, measles and chicken pox have a latency period in which a person who is not symptomatic and is therefore not recognizable as infected can transmit the disease. In such cases one has to add an additional category (usually called, the exposed) to the three we have considered. Many sexually transmitted diseases would not fulfill condition i), since recovery does not provide immunity from re-infection. If the time period under consideration is long then condition iv) is also unlikely to be valid. Nonetheless, the ideas behind this model are the basis of more elaborate models that are actually used by public health officials. W. Kermack and A. McKendrick, published this model in 1927 and showed that it accounted fairly well for the data pertaining to an outbreak of plague in Bombay in the years 1905-06.

The key step in deriving the appropriate differential equations is to correctly interpret assumption iii) and how it relates to the rate at which new infections arise. If, for example, there are 10 infected individuals and 20 susceptibles then if each of the 10 infectives can meet any of the 20 susceptibles we will have $10 \times 20 = 200$ possible meetings between infected and a susceptible persons. (This is an instance of an important counting principle that we will discuss again in Chapter 10.) Some fraction or multiple of these may actually occur and a portion of the latter may lead to new infections. Thus, the rate of new infections should be proportional to the number of possible contacts between infectives and susceptibles and hence should have the form $a \times I \times S$, where a is some positive constant. However, recovery or death removes infectives and it is reasonable to assume that this happens at a constant per capita rate. Combining these two effects gives

$$\frac{dI}{dt} = aIS - bI \tag{6.9}$$

where a and b are positive constants characteristic of the disease.

From equation (6.9) we can find the equation for the change in S. Since we are ignoring births and non-disease related deaths (as well as immigration), changes in S could only come from susceptible people moving into the infected category. The term aIS in (6.9) accounting for the increase in I therefore also accounts for the decrease in S. Thus

$$\frac{dS}{dt} = -aIS \tag{6.10}$$

The removed category arises from cured infectives and so $\frac{dR}{dt} = bI$. Note that equations (6.9) and (6.10) form a system involving just I and S, so we can restrict our attention to these two equations. We refer to this pair of equations as an S-I model.

Example 6.10: Consider the S-I model with $a = .01$ and $b = .2$, and having initial conditions $S_0 = 50$ and $I_0 = 5$. Find the phase plot of the corresponding solution and determine its relationship to the steady state solutions and the null-clines.

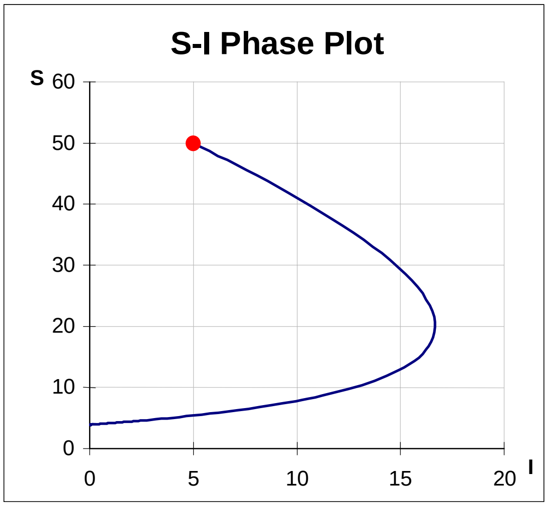
Solution:

We will follow the steps indicated above to analyze the behavior of the system

$$\begin{aligned} \frac{dI}{dt} &= .01SI - .2I \\ \frac{dS}{dt} &= -.01SI \end{aligned} \tag{6.11}$$

with initial conditions $I(0) = I_0 = 5$ and $S(0) = S_0 = 50$.

First we examine the computer generated phase plot and solution curves for S and I.



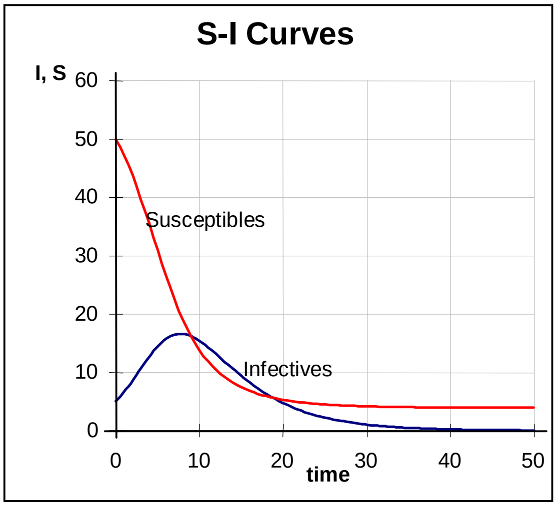


Figure 6.7

If we assume that the total $S_0 + I_0 = 55$ accounts for the entire population, then the infection rate is initially approximately 10%. The number of infectives increases until approximately 30% (17 out of 55) of the population is simultaneously infected. With fewer susceptibles the number of infectives declines. Eventually, the infection disappears, although susceptibles remain.

What are the steady state solutions for this problem? To answer this question we need to solve the simultaneous equations

$$\begin{aligned} .01SI - .2I &= 0 \\ -.01SI &= 0 \end{aligned}.$$

This system is similar to the one studied in Example 6.2. The second equation implies that $S = 0$ or $I = 0$. If $S = 0$ then the first equation yields that $I = 0$ as well, and if $I = 0$ the first equation is automatically satisfied. Thus any point on the vertical line $I = 0$ provides a steady state solution and these are the only steady states. (Clearly if there are no infected individuals then the disease cannot be transmitted, no matter what the number of susceptible persons.) The solution we are studying approaches one of these steady states.

The null-clines are also easy to find. The S null-clines are found from the second equation $-.01SI = 0$, which has as solutions the two coordinate axes, $S = 0$ and $I = 0$. The I null-clines are the solutions of $.01SI - .2I = 0$. Factoring gives the vertical line $I = 0$ (which is thus both an I null-cline and an S null-cline) and the horizontal line $S = 20$. These are shown below on the phase plot with an appropriate arrow diagram, which the reader should derive after factoring the right side of the equation for dI/dt. (Note that because the vertical S axis is both an I and an S

null -cline, the rule that was stated earlier regarding the direction of crossing of the phase plot need not apply on this axis.)

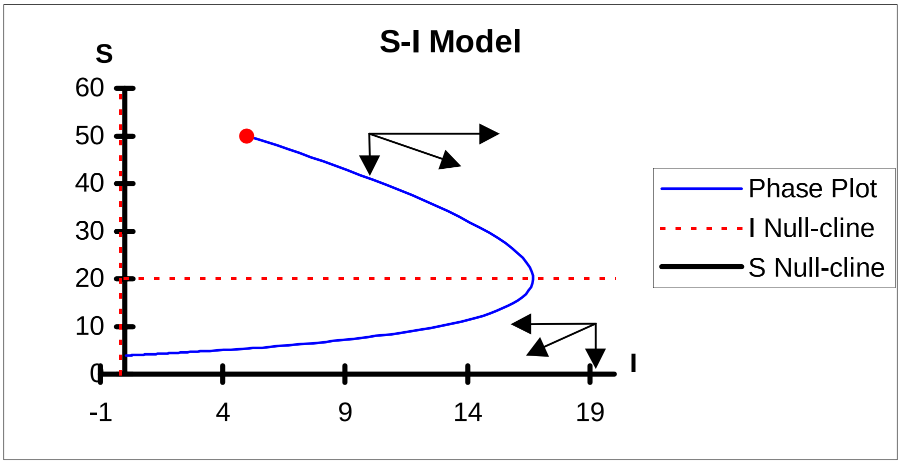


Figure 6.8

In this example, the arrow diagram shows that if the initial number of susceptible individuals were below 20 the infection would have died out without the number of infectives ever exceeding the initial number. Intuitively, with S below 20 there are not enough contacts between infectives and susceptibles to replenish the supply of infectives. Of course this does not mean that there are no new infections. It means that the number of new infections is below the removal rate, so the current number of infectives steadily decreases.

For initial values of S above 20 the phase plot will resemble the one shown, provided $I_0 > 0$. The number of infectives increases and we speak of an epidemic. Eventually the epidemic subsides as the phase plot approaches one of the stable steady states with $I = 0$ and $S \leq 20$. The initial value of S_0 that is needed to initiate an epidemic (here $S_0 > 20$) is called the *epidemic threshold* for the disease.■

6.6 Tech Notes

The *Excel* file *ode_sys.xls* provides a simple interface for studying systems of two differential equations. The spreadsheet uses the modified Euler method to generate numerical approximations to the solution of the system. The dependent variables are referred to as x and y, with t representing the independent variable. These cannot be changed, although the labeling on the graphs can be modified to conform to a desired notation.

Example 6.11: Use the file *ode_sys.xls* to produce numerical approximations to the solution of the following system:

$$\frac{dx}{dt} = -x + .1xy$$
$$\frac{dy}{dt} = y - .2xy$$

with initial condition $x(0) = 2, y(0) = 4$.

Solution:

You open the file *ode_sys.xls* and click the button to enter data. The ODE System Editor opens (Figure 6.9). The right sides of the differential equation are entered in the first two lines, taking care not to omit multiplication signs. The entries for the initial time and the initial value of x and y are entered from the data provided in the problem. (The initial time does not have to be zero, although that is usually the case.)

The user determines the final time and the number of subintervals. The choice of the final time depends on what you are trying to observe and whether you have provided enough time for that observation to emerge. Experimentation may be necessary. Similar advice applies to the number of subintervals. A good rule of thumb is to start with a small number of subintervals, say 100. If doubling the number of subintervals produces no visible change in the graphs, the original choice is probably adequate. Note, though, that a longer time interval may require you to increase the number of subintervals in order to maintain accuracy.

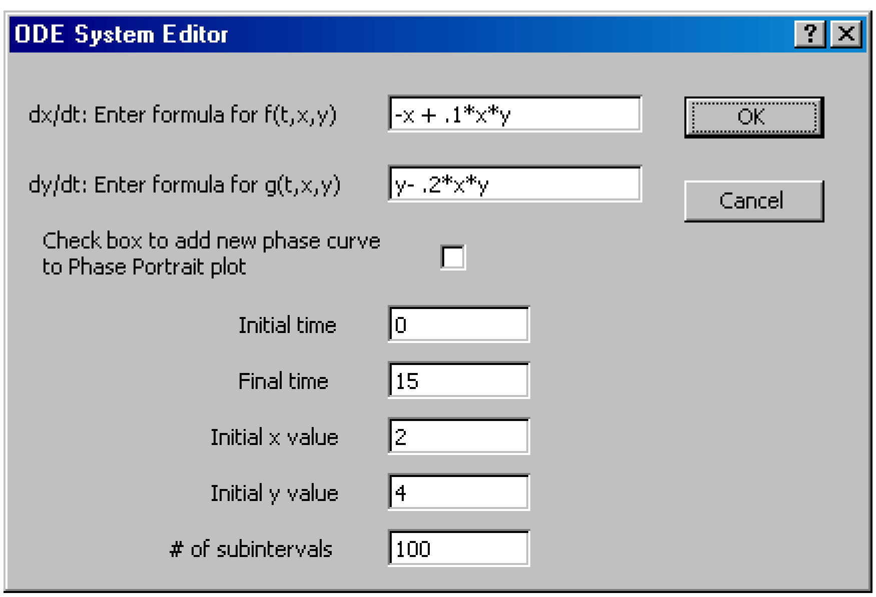


Figure 6.9

The check box (which is blank above) is useful for building a phase portrait of the system, i.e. a graph that shows a collection of phase plots (for the same system) with different initial values. If you want to remove an unwanted phase plot from the graph, just select it with the mouse and press the delete key.

The current phase plot and the associated solution graphs (as for example in Figure 6.7) can be viewed by scrolling down on the top sheet. The reader should study these graphs together as they help in understanding the relationship between these two representations of the solution. An animation of the current phase plot shows the location of the solution pair (x, y) at equally spaced time intervals. This is useful for getting some sense of the time evolution of the solutions, which is otherwise not evident from the phase plot. The Calculation sheet contains numerical values for the solutions in columns B and C, as well as a brief explanation of the computational algorithm.■

6.7 Summary

Systems of differential equations are used to model the changes over time in a system of components that continuously interact. These components can be, for example, different species in an ecosystem or, for epidemic modeling, the infected and susceptible members of a population. When only two components are involved, the differential equations express the growth rates for each component, N_1' and N_2', in terms of the current values of N_1 and N_2. Using numerical methods, we can generate graphs of the solution curves $N_1(t)$ and $N_2(t)$, as well as the ***phase plot***, in which we directly graph N_2 vs. N_1. An approximate description of the latter graph can be obtained using qualitative methods. These methods use a diagram that exhibits the ***steady states*** for the system, the ***null-clines***, and a visual encoding showing where the solutions N_1 and N_2 are increasing or decreasing.

6.8 Exercises

1. Find all solutions of each of the following systems of equations. These results are used in the later problems as indicated.

   a) $x - 3y = 0$, $x + y = 2$ (See exercise 8)

   b) $x + y = 100$, $2x - y = -25$ (See exercise 9)

   c) $-x + 0.1xy = 0$, $y - 0.2xy = 0$ (See exercise 12)

   d) $.25x\left(1 - \frac{x}{200} - \frac{y}{50}\right) = 0$, $.10y\left(1 - \frac{y}{100} - \frac{x}{100}\right) = 0$ (See exercise 10)

2. Sketch each of the following lines and determine the sign of the left side of each equation in the two regions on either side of the line.

   a) $x + y - 2 = 0$

b) $2x - y + 25 = 0$

c) $x - 3y = 0$

3. The solutions of the equation $x(x+2y-4)=0$ form a pair of lines. Sketch the lines and determine the sign of the expression $x(x+2y-4)$ in each of the four regions of the plane bounded by these lines.

4. Repeat the directions in exercise 3 for the equation $y(x-y+1)=0$.

5. The table of values below was produced using the file *ode_sys.xls* to solve the system of differential equations

$$\begin{aligned} \frac{dx}{dt} &= -x + .05y^2 \\ \frac{dy}{dt} &= y - .2xy \end{aligned} \tag{6.12}$$

with initial conditions $x(0)=2$ and $y(0)=4$, over the time interval $t=0$ to $t=5$.

a) Using the table, plot approximate graphs of the solutions $x(t)$ and $y(t)$ over the time interval [0,5] and a corresponding phase plot.

t	x	y	t	x	y
0	2.00	4.00	3	6.00	10.78
.5	1.68	5.52	3.5	5.65	9.81
1	1.89	7.68	4	5.18	9.39
1.5	2.78	10.20	4.5	4.85	9.40
2	4.30	12.03	5	4.72	9.65
2.5	5.66	11.99			

Table 6.2

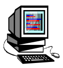
b) Find the steady state solutions for the system (6.12). Does the solution sketched in a) appear to be approaching one of these steady states?

6. Consider the competition model given by the system

$$\begin{aligned} \frac{dN_1}{dt} &= .25N_1\left(1 - \frac{N_1}{100} - \frac{N_2}{50}\right) \\ \frac{dN_2}{dt} &= .1N_2\left(1 - \frac{N_2}{100} - \frac{3N_1}{100}\right) \end{aligned} \tag{6.13}$$

a) Construct an inter-intra species competition table similar to Table 6.1. On the basis of this table how would you describe the competitive relationship between these species?

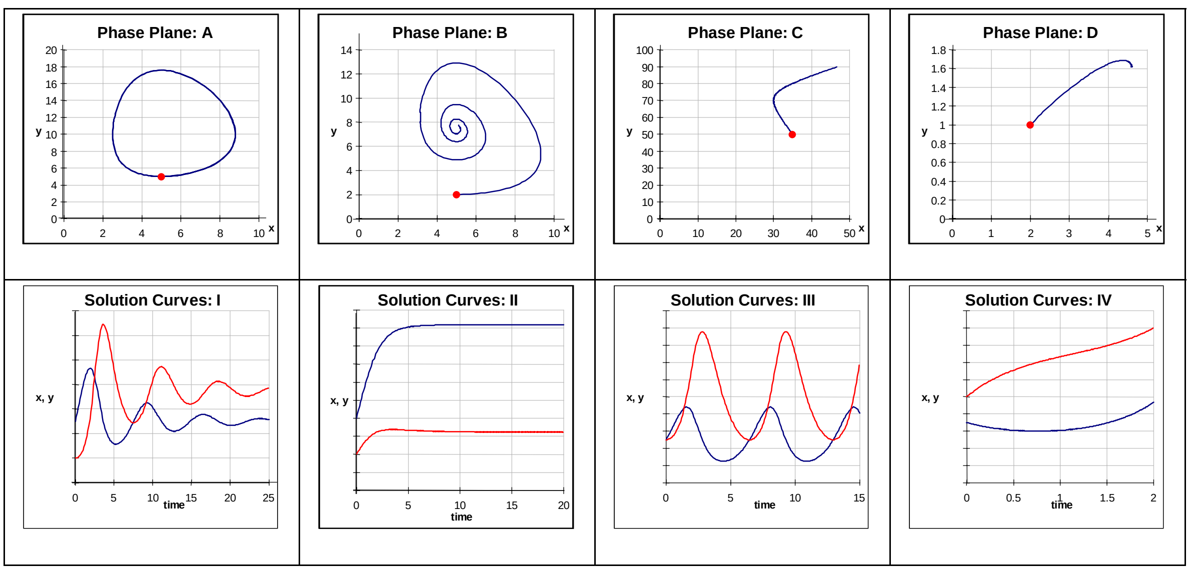
b) Find all steady state solutions for the system (6.13).



c) Construct a phase portrait (see section 6.6) for the system (6.13) using the initial values listed in the table below. In each case, determine in the longterm which species emerges as dominant. Based on the phase portrait, characterize the stability of each steady state solution you found in b).

initial x	initial y	initial x	initial y
2	4	5	21
2	10	30	52
2	20	30	60
5	20	40	50

7. The top row of the following array contains phase plots labeled A through D. Match each of the phase plots in the top row with the corresponding solution plot (numbered I through IV) in the bottom row: Identify which curve in the solution plot represents x and which represents y. Give reasons for your selection.



8. a) Consider the system $\dfrac{dx}{dt} = x - 3y$ and $\dfrac{dy}{dt} = x + y - 2$. Find all the steady state solutions of this system. (See 1a).)

b) Figure 6.10 below shows a phase plot for the solution of 8a) with initial values $x = 2$, $y = 1$ for $t = 0$ to $t = 1$. Draw the null-clines on the graph along with any steady state solutions you found in 8a).

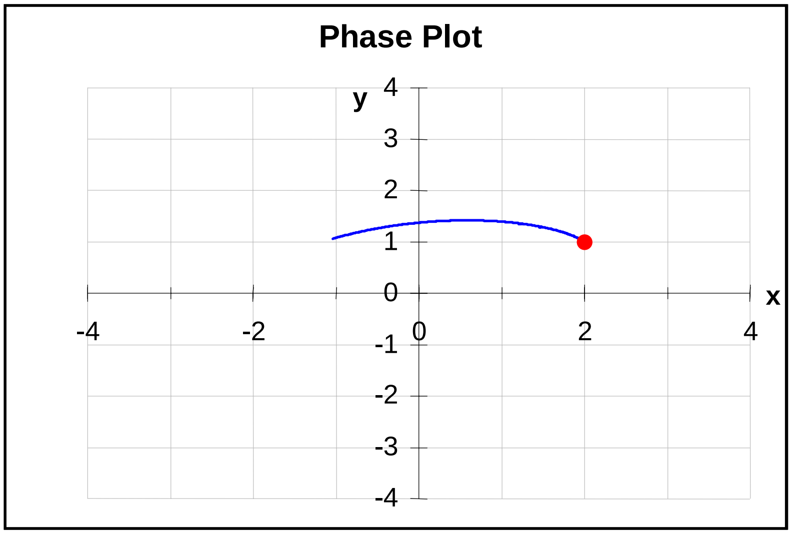


Figure 6.10

c) Using an arrow diagram, make a conjecture as to how the phase plot in Figure 6.10 continues as the time interval is extended beyond $t = 1$. If you have access to a computer, check your work by computing the phase plot numerically. Based on the results, how would you characterize the stability of the steady state solution(s).

9. Consider the following system of differential equations:

$$\frac{dN_1}{dt} = N_1 + N_2 - 100$$
$$\frac{dN_2}{dt} = 2N_1 - N_2 + 25$$

a) Determine the steady state solution of this system. (See 1b).)

b) The phase portrait in Figure 6.11 below shows the phase plots for a number of solutions of this system. Draw and label the null-clines of the system on this plot. Also mark the steady state solution you found in 9a).

c) Using an arrow diagram determine as best as you can a possible phase plane trajectory for the solution with initial conditions $N_1 = 40$ and $N_2 = 30$.

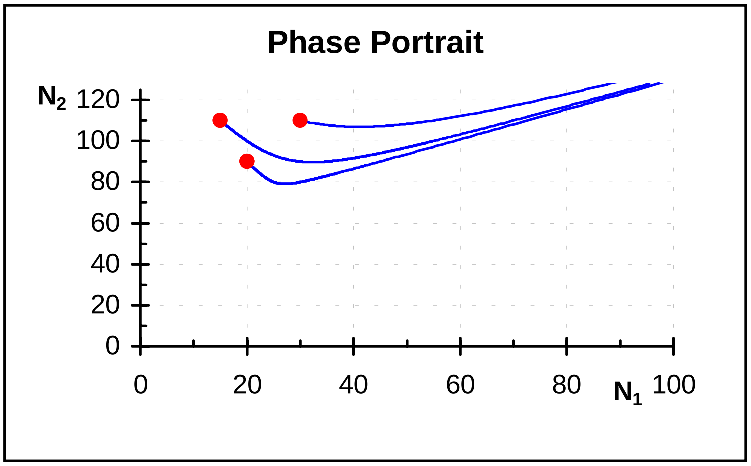


Figure 6.11

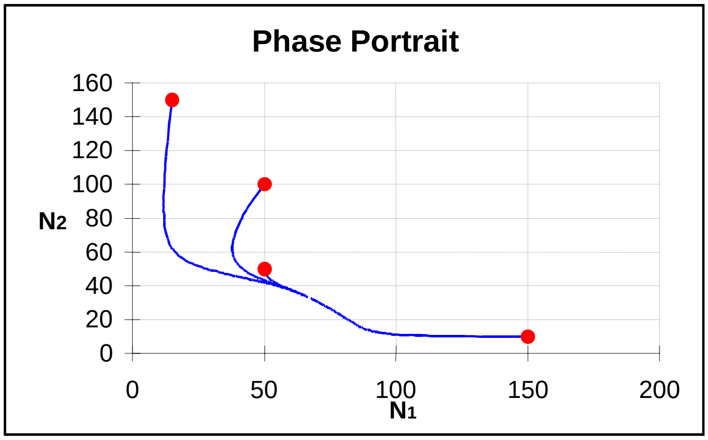
10. Consider the competition model described by the following system:

$$\frac{dN_1}{dt} = .25N_1\left(1 - \frac{N_1}{100} - \frac{N_2}{100}\right)$$

$$\frac{dN_2}{dt} = .10N_2\left(1 - \frac{N_2}{50} - \frac{N_1}{200}\right)$$

a) Find all steady state solutions for this system. (see 1d))

b) Below is a phase portrait showing four phase curves with different initial values. What if anything does the phase portrait indicate about the stability of the steady state solutions you found in a)?



c) Would the pair of species modeled by this system likely to be dependent on the same resources or not? Explain using the phase portrait and with reference to a table similar to Table 6.1.

11. For the differential equations in exercise 5, use the simple Euler method with $\Delta t = 0.5$ (as described on page 88) to estimate $x(0.5)$ and $y(0.5)$. Compare with the numerical values given in Table 6.2.

12. a) The following system is a model of predator-prey interaction, known as the Lotka-Volterra model. N_1 denotes the number of predators, N_2 the number of prey. In the absence of predators, i.e. when $N_1 = 0$, the prey are assumed to increase exponentially, while if the prey disappear the predator population follows an exponential decline. The prey are removed at a rate proportional to the product $N_1 N_2$, which measures interaction between the populations (as in the S - I model). Similarly, predators increase at a rate proportional to the same term. This gives as an example

$$\frac{dN_1}{dt} = -N_1 + 0.1 N_1 N_2$$
$$\frac{dN_2}{dt} = N_2 - 0.2 N_1 N_2$$

Find the steady state solution(s) in which both N_1 and N_2 are positive. (See exercise 1c).)

b) Figure 6.12 below shows a phase plot for the solution of 12a) with initial values $N_1 = 8$, $N_2 = 15$ for $t = 0$ to $t = 3.5$. Draw the null-clines on the graph along with any steady state solutions you found in 12a).

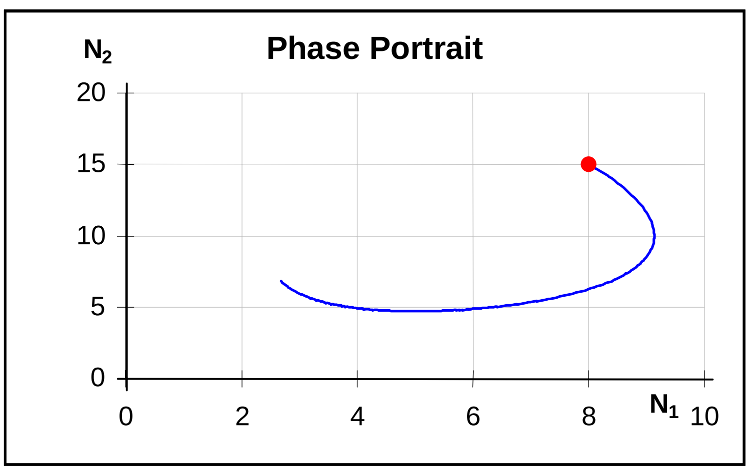


Figure 6.12

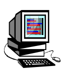
c) Using an arrow diagram, extend the phase plot in Figure 6.12 as the time interval is extended beyond $t = 3.5$. If you have access to a computer, check your work by computing the phase plot numerically. How would you explain the results in terms of predator-prey interaction? Based on the results, how would you characterize the stability of the steady state solution(s) you found in 12a).

13. The predator-prey model described in exercise 12 is sometimes criticized because of the assumption that in the absence of predators, the prey population grows exponentially. The model can be modified so that the prey population grows logistically when the predators are removed. Consider the model below:

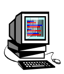
$$\begin{aligned} \frac{dN_1}{dt} &= -N_1 + 0.1 N_1 N_2 \\ \frac{dN_2}{dt} &= N_2\left(1 - \frac{N_2}{20}\right) - 0.2 N_1 N_2 \end{aligned} \qquad (6.14)$$

a) If the predators are removed from the system (6.14), what is the carrying capacity for the prey?

b) Find the steady state solutions and the null-clines of the system (6.14). Construct an arrow diagram and use it to sketch a possible phase portrait for the solution with initial condition $N_1 = 8$ and $N_2 = 15$.



c) Use the program *ode_sys.xls* to determine the phase portrait for the solution of (6.14) with initial condition $N_1 = 8$ and $N_2 = 15$. Compare with your analysis in b). What is the effect of the predation on the carrying capacity for the prey?



14. Consider the competition model described by the following system:

$$\begin{aligned} \frac{dN_1}{dt} &= .25 N_1\left(1 - \frac{N_1}{200} - \frac{N_2}{50}\right) \\ \frac{dN_2}{dt} &= .10 N_2\left(1 - \frac{N_2}{100} - \frac{N_1}{100}\right) \end{aligned}$$

Using the program *ode_sys.xls* construct a phase portrait showing on one graph the phase plots for the following initial values of the system. (Be sure to check the box labeled “add new phase curve…” in order to plot several phase plots on the same graph.) The time interval should be long enough so that you observe the long-term behavior of the system. Check the graphs of the solutions $N_1(t), N_2(t)$ to verify you have observed the system long enough to be certain of the long-term behavior.

i) $N_1 = 150, \quad N_2 = 10$ ii) $N_1 = 15, \quad N_2 = 150$ iii) $N_1 = 50, \quad N_2 = 100$

iv) $N_1 = 50, \quad N_2 = 50$ v) $N_1 = 100, \quad N_2 = 50$ vi) $N_1 = 100, \quad N_2 = 25$

Print **only** the combination phase portrait. To do this, click on the plot and then select print. The plot will print by itself on a single page. Save the worksheet, in case you need to print it again.

15. Find the steady state solutions for the system of equations in exercise 14. (See exercise 1d))

16. a) Find the equations for the first quadrant null-clines of the system in exercise 14.

b) Draw these null-clines on the graph you printed in exercise 14.

c) Indicate using arrow diagrams the direction of flow for the phase plot in each region of the first quadrant determined by the null-clines.

d) Are the solutions approaching a definite equilibrium value? If so what is it?

e) Are the species modeled by this system competing with each other? Explain using an inter-intra species competition table similar to Table 6.1.

17. Suppose we have a competition model of the form

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - a_{21} N_2\right)$$

and

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - a_{12} N_1\right)$$

with null-clines as labeled in the picture below:

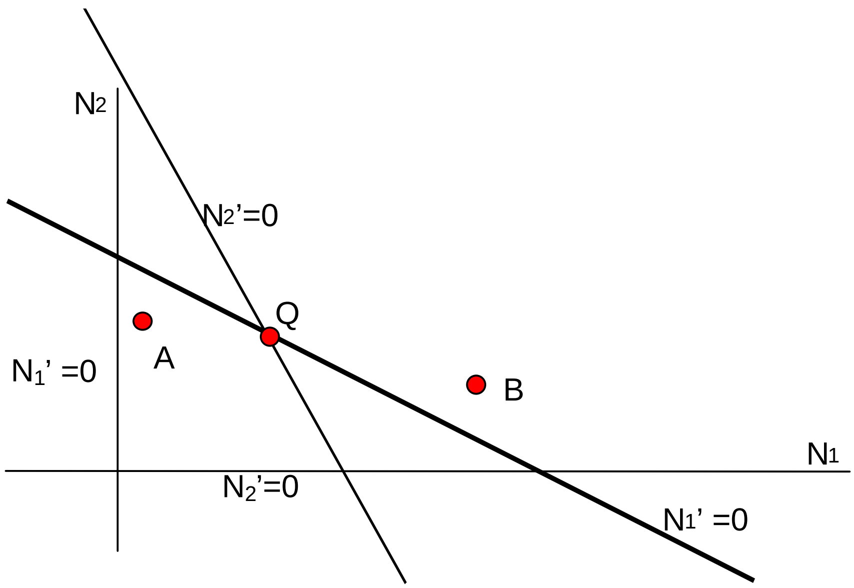


Figure 6.13

a) Draw an arrow diagram for this system and, using this, sketch the phase curves whose initial values are indicated by the points A and B.

b) What relation between the coefficients K_1, a_{21}, a_{12} and K_2 does the null-cline diagram above imply? What biological interpretation does this have and how is this related to the phase curves you sketched in a)?

18. Consider the S - I model discussed in the text:

$$\frac{dI}{dt} = .01SI - .2I$$
$$\frac{dS}{dt} = -.01SI$$

with $I_0 = 5$ and $S_0 = 50$. Interpret the units here as thousands, so for example a value of $I = .01$ actually represents 10 individuals. We want to analyze the course of epidemics with the same model equations, but with a variety of initial conditions. In each case below we have given a pair of initial values I_0 and S_0. Assume that the total population size is $I_0 + S_0$ (row 3). Construct a single phase portrait showing phase plots for each of these initial conditions. Fill in the information requested in rows 4 through 8:

- ✓ **Row 4**: The time required so that each phase plot terminates with $I \approx .02$. (These times may be different for different initial conditions.) Note: Numerical coordinates for points on the graph can be obtained from the Calculation sheet or less precisely by touching a particular point of the graph with the mouse pointer. You may also consult the graphs of I and S vs. t.
- ✓ **Row 5**: Find the maximum value for the number of infectives at any one time.
- ✓ **Row 6**: Compute the maximum percent of the population that is infected at any one time.
- ✓ **Row 7**: Find the total number of individuals infected during the course of the epidemic.
- ✓ **Row 8**: Compute the percent of the population that is infected during the course of the epidemic.

I_0	5	.01	5	.01	5	.01
S_0	30	30	50	50	75	75
Total Pop.	35	30.01	55	50.01	80	75.01
Term. time						
Max. I						
Max. % infected						
Tot. # infected						
% pop. infected						

Write a discussion based on the results. Comment on such issues as

a) Duration of epidemic as it relates to the initial numbers of susceptibles and infectives.

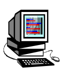
b) Severity of the epidemic as measured by the maximum % of the population infected at any one time and the total percent of the population infected.

19. Suppose that in the course of an epidemic described by the system in exercise 18, public health officials decide to undertake an immunization effort to reduce the numbers of susceptibles. Let's assume that the immunization works quickly and the effort to get people immunized is spurred on by the prevalence of the infection. Why are these assumptions captured by the following modification to the basic $S-I$ system (6.11)?

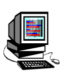
$$\begin{aligned} \frac{dI}{dt} &= .01SI - .2I \\ \frac{dS}{dt} &= -.01SI - .15I \end{aligned} \tag{6.15}$$

a) What are the steady state solutions of this system?

b) Find the null-clines and construct an arrow diagram. Using the arrow diagram, determine the epidemic threshold for the disease. Has the immunization program affected this number?



c) Determine a phase plot for the solution of (6.15) with initial conditions $I_0 = 5$ and $S_0 = 50$. Show that in this case the epidemic terminates because there are no longer any susceptible persons. How long does it take for this to happen? Compare to the duaration of the epidemic without the immunization program.



d) Using the data computed in c), how would you compute the number of people who were immunized during the course of the epidemic? Try to carry out the computation using *Excel*. Once you have an estimate of this number determine approximately the total number of people infected during the epidemic. Compare this to the situation without immunization. (Hint: From the problem description, you should be able to find numerical values for the rate of change of the number of immunized persons. The mathematical problem becomes then, if you know numerical values for the derivative of a function, how do find numerical values for the function itself?)

20. a) Consider the general S - I model described by the system

$$\begin{aligned} \frac{dI}{dt} &= a\,SI - bI \\ \frac{dS}{dt} &= -a\,SI \end{aligned},$$

where a and b are positive constants. Show using an arrow diagram that the threshold value for this disease is the ratio b/a.

b) Based on the result in a) the S - I model predicts that a small population is less vulnerable to an epidemic than a large one. Under what circumstance do you think that conclusion is valid? Can you think of situations where this statement is not true? What characteristics of the disease or environment might so the threshold value of the disease would be low enough to predict an epidemic?

21. For the S - I model described in Example 6.10 we remarked that the steady state solutions with $I = 0$ and $S \leq 20$ are stable. Using the arrow diagram explain why this would appear to be correct and why steady states with $I = 0$ and $S > 20$ are unstable. (Note: Here we use stability to mean that a solution starting near a steady state does not evolve too far away from it.)