CHAPTER 4

The Projects

With the following projects, we have reached the heart of the text. The models follow a rough arrangement by discipline, and I have tried to put similar models together, with complexity gradually increasing. For instance, I regard the model for the spruce budworm versus the balsam fir (project 4.16) as being the most beautiful in the entire sequence. It will take some effort to put together its various components, and thus it will be best first to work through the simpler models involving competition between different species. It works well when a group of students cooperate over a set of projects in the same area. The mathematics is all within your grasp, but in some cases it requires careful handling, an example being Zeeman's model for the heartbeat (project 4.26). Here, you are assumed to have some experience with equilibria and limit cycles—experience that you can acquire from the predator–prey projects, for instance. In some cases some of the fussier mathematical details of a derivation have been omitted, but I hope that you can fill these in if need be. In the problems related to physics some background in mechanics is assumed, but no more than that required in most introductory courses on differential equations. Some projects require more *programming* than others. For instance, the model for the interaction of two galaxies (project 4.39) is a rewarding one, but requires larger and faster computing facilities than the others, and also some careful programming. Many of the other projects can be set up in a matter of minutes.

The projects are all presented (as any practical, true-to-life situation must be) in *words*. If you have a prejudice against "word problems," then you do yourself a favor if you abandon it *now*. Be prepared to read through the description of a model several times, gradually assimilating it, until you have made it your own. In many cases a reference is given. Follow it up if you can; you will probably find more detail and further references. I can almost guarantee that you will be enchanted by the original paper for the model of the spruce budworm versus the balsam fir. More generally, a text such as that by M. Braun [5] provides more discussion on setting up models and includes several of those considered here. Remember that a "model" is just that; it will have limitations and imperfections. Think of it as opening a door to a new world. If you become uncomfortable with some of the limitations, see if you can remove them for yourself.

In any model you must identify the independent and dependent variables and the parameters, and interpret them physically. You must decide what sort of output will be interesting; this might be printed or plotted. Remember that with printed output, the more the better, especially in the debugging period. (But don't go too far. In his text [37], R. M. May comments unkindly that some computing operations would benefit from the inclusion of an on-line incinerator.

Was he thinking of you?) Different projects have totally different demands so far as output is concerned. For example, for the descent of Skylab (project 4.34), it is interesting to follow the changes in altitude in the last few revolutions. For the trip to the Moon (project 4.32), the question is "did we hit it?" In other projects there are more subtle questions having to do with stability. Formulate your questions before you start to compute. Don't generate aimless output. You will make several runs using different values of initial conditions or parameters. Plan your tactics in advance and interpret these changes physically. But be ready to listen to suggestions that the output may make. Establish a dialog with your model.

In setting up a program, first look for changes in notation that will help simplify the problem. We have discussed such changes already and suggest them in many projects. Then very carefully change the notation from that of the project to that of the program. Again, we shall offer many suggestions especially in the earlier projects. You will need to set NEQ and write a subroutine for FUN. You will also need to arrange for the input of initial conditions and values of parameters, and for whatever output you want. And don't forget to include instructions for stopping the program. For a start, I suggest that you do not require high accuracy (the accuracy can always be improved later), so that your value of TOL can be moderate, say 10^{-5} for most cases, where the values of the variables do not differ greatly from one.

How do you try to debug your program? With certain parameters set equal to zero, there may be an exact known solution; verify this numerically. Otherwise, approach your project with some insight about the kinds of answers you *should* be getting. Make sure that your insight and the program agree. Doing so takes experience, but experience that you will soon gain.

The first two projects are introductory, being concerned with background, orientation, and the kind of questions that you should ask of the later projects. Read them carefully, and if possible do calculations to confirm some details. Some of the later projects are specific about what needs to be found, others will seem vague. I have tried to keep whatever vagueness there is within bounds and, especially at the start, suggest enough details to start you off. But remember that you need to develop initiative and imagination. Ask your own questions; don't expect the scope of a project to be clear at the first reading.

The projects are to be enjoyed. Play with them, alter them, and generalize them. Look for more, and when you find them, I will be interested in hearing from you.

Happy computing!

4.1 A MODEL FOR DISCUSSION: RICHARDSON'S "ARMS RACE"

For illustrative purposes, I have chosen for discussion a simple model for which analytical solutions can be found. None of these solutions will be used, however, since we need to prepare for situations where they are not available. Rather, the aim is to see how qualitative properties can be derived from a preliminary survey of a problem. The numerical work can then follow along lines suggested by these properties. Asking the computer questions helps to avoid aimless output.

The model presented is due to L. F. Richardson [50]. Discussions appear in several texts, in particular those by Rapoport [48] and Braun [5]. Remember always that what we will be looking at is "just" a model. That is, any conclusions drawn depend on the assumptions made, and the assumptions are bound to be oversimplified. Even so, you may find some conclusions interesting, suggestive, and even worrisome. They can lead to further questions to ask, and often to generalizations of the model.

Richardson writes:

> Why are so many nations reluctantly but steadily increasing their armaments as if they were mechanically compelled to do so? Because, I say, they follow their traditions which are fixtures and their instincts which are mechanical; and because they have not yet made a sufficiently strenuous intellectual and moral effort to control the situation. The process described by the ensuing equations is not thought of as inevitable. It is what would occur if instinct and tradition are allowed to act uncontrolled.

Two countries are involved, called Jedesland and Andersland. Richardson quotes from a speech made by the defense minister of Jedesland:

> The intentions of our country are entirely pacific. We have given ample evidence of this in the treaties which we have recently concluded with our neighbors. Yet when we consider the state of unrest in the world at large and the menaces by which we are surrounded, we should be failing in our duty as a government if we did not take adequate steps to increase the defenses of our beloved land.

Hence an arms race.

To set up the model we need variables; dependent and independent. The independent variable is the time t, and we shall take the unit of time to be the year. The dependent variables, which are not so easy to quantify, will represent the expenditures $x(t)$ and $y(t)$ on armaments of Jedesland and Andersland, respectively; these could also be interpreted in terms of actual armaments or as some kind of "war potential." Now consider the factors that would cause x to change. Three will contribute to the model: (1) the state of preparedness for war of the other country, Andersland, will tend to increase x; (2) the cost of armaments will tend to decrease the rate of change of x; and (3) a sense of grievance against Andersland will tend to increase x. In the model, these factors are assumed to lead to the equation

$$\frac{dx}{dt} = ay - mx + g, \tag{4.1.1}$$

where a, m, and g are constants. In the same way, we have for Andersland,

$$\frac{dy}{dt} = bx - ny + h. \tag{4.1.2}$$

These are the equations for the model.

Note that there are alternative interpretations of the terms of the equations. For example, the incentive to arm could depend on the imbalance of armaments, so that $ay - mx = a(y - \frac{m}{a}x)$ would have a representing a rate of arming, with m/a a parameter describing the desired balance. ($m/a = 1$ would stand for parity.) Or, the "grievance" terms might include covert activity, or even ceremonial expenses such as presidential guards or military bands. Or they could be negative, indicating good will, rather than grievance. Further, the coefficients might change with time; an election or a change of administration or some international incident could change g or h abruptly. All these possibilities, and perhaps more, should be remembered when making interpretations.

The two equations can be solved completely, but we shall not do this here. But note that the solutions will involve exponential terms (although not, in this instance, trigonometric terms; do you see why?). A term e^{pt} with positive p will increase without bound, and could mean war! It would be satisfactory if p could be negative, for things might then settle down.

The first and a very important question to ask (and one that will recur many times in these projects), is "is there an equilibrium?" By "equilibrium" we mean a state of affairs in which everything remains constant. If so, the time rates of change will be zero. Assuming that we have equilibria, the next question is, "are they stable or unstable?" That is, if we start close to an equilbrium, will we forever remain close (stability), or will we move further away? Discussion of stability is often not at all easy, and advanced theoretical mathematics can be involved; but the use of the computer can be very helpful. Putting the time derivatives equal to zero in (4.1.1) and (4.1.2), we have the conditions for equilibrium:

$$\left.\begin{aligned} L_1: \quad 0 &= ay - mx + g, \\ L_2: \quad 0 &= bx - ny + h. \end{aligned}\right] \qquad (4.1.3)$$

Provided that $D \equiv nm - ab \neq 0$, these two equations have the unique solution

$$x_e = (ah + ng)/D, \quad y_e = (bg + mh)/D. \qquad (4.1.4)$$

If both x_e and y_e are positive, we have an equilibrium.

In discussing the progress of the arms race, you might assume that it would be best to show tables or diagrams of x and y as functions of the time. This might be so, but often it is better to look at a "phase-plane" diagram in which one dependent variable is plotted against the other. Here, this is the x-y plane. L_1 and L_2 in (4.1.3) are equations of straight lines in this plane, and the equilibrium is at the intersection of these lines. Further, each of these lines divides the plane into regions where a derivative is positive or negative, as shown in Figure 4.1.

Figures 4.2(a) and (b) show situations for which g and h are both positive; in (a) there is an equilibrium, in (b) there is not. From the properties shown in

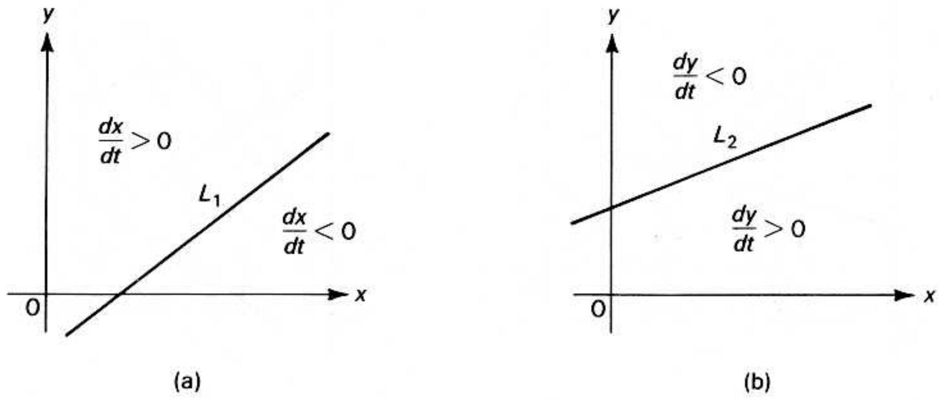

Figure 4.1 (a) (b)

Figure 4.1, a few arrows have been sketched, showing the directions of the "flow" of the solutions. These suggest a stable equilibrium in Figure 4.2(a) and war in 4.2(b).

Next, consider cases where g and h are both negative, so that there is a background of "good will." The two principal possibilities are shown in Figures 4.2(c) and (d), where, again, some arrows have been sketched in to show the flow of solutions. In (d), where there is no equilibrium, we have total disarmament. The equilibrium of (c) is unstable: if we start close to it, we can end either with war or disarmament.

These discussions can be carried out in more detail, and further special cases can be investigated. Now suppose that you want to look at some of the actual solutions for given values of the constants. For this particular project you could solve the equations, substitute various values of t into the solutions, and construct tables or figures. Alternatively, you could solve the differential equations numerically. There would be no need to apologize for doing so; in fact you would be saving time, since there would be no need to call the exponential function repeatedly. The differential equations themselves implicitly generate these special functions more economically than the explicit routines. Some examples, corresponding to the cases of Figure 4.2, are shown in Figure 4.3. The lines L_1 and L_2 have been included in the figure. The qualitative conclusions from Figure 4.2 are confirmed, but it is also nice to see some actual solutions, or "orbits," as we shall often call them.

The following "assignments" are suggestions that are intended to show some ways in which a project can be discussed and expanded. See if you can think of some more.

1. Draw figures and discuss the cases where g and h have different signs.
2. Discuss the cases where g and h are both zero.

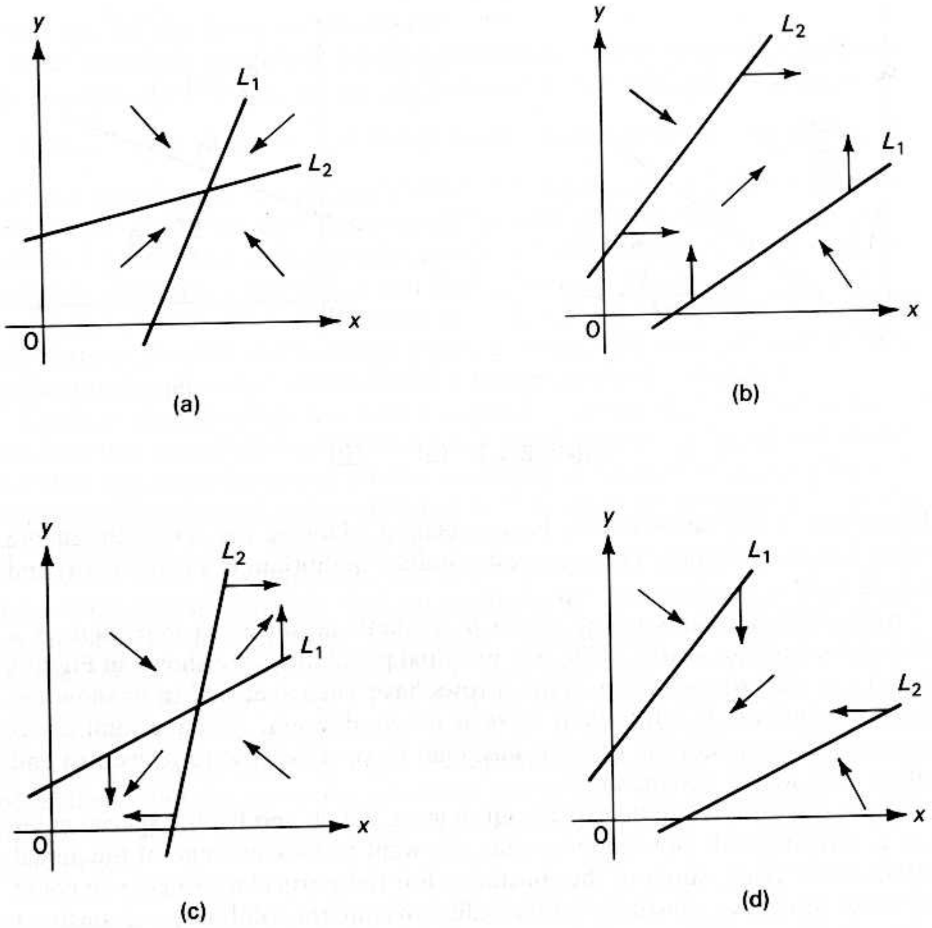

Figure 4.2 (a) (b) (c) (d)

3. Discuss the cases where the lines L_1 and L_2 are parallel.
4. Calculate some actual orbits for the cases in assignments 1 to 3.
5. Make a summary of *all* possible cases in terms of the properties of the parameters. See if you can then interpret these cases using a physical interpretation for the parameters.
6. Solve the two differential equations analytically and confirm the details found in the preceding assignment.
7. Divide the equations of the model by each other to eliminate t, and find an equation of the form $dy/dx, = f(x,y)$. Can you solve it? Construct some direction field diagrams for this equation, comparing the direction lines with the arrows in Figure 4.2. (If you are ingenious, you will incorporate arrows into your direction field diagram!)

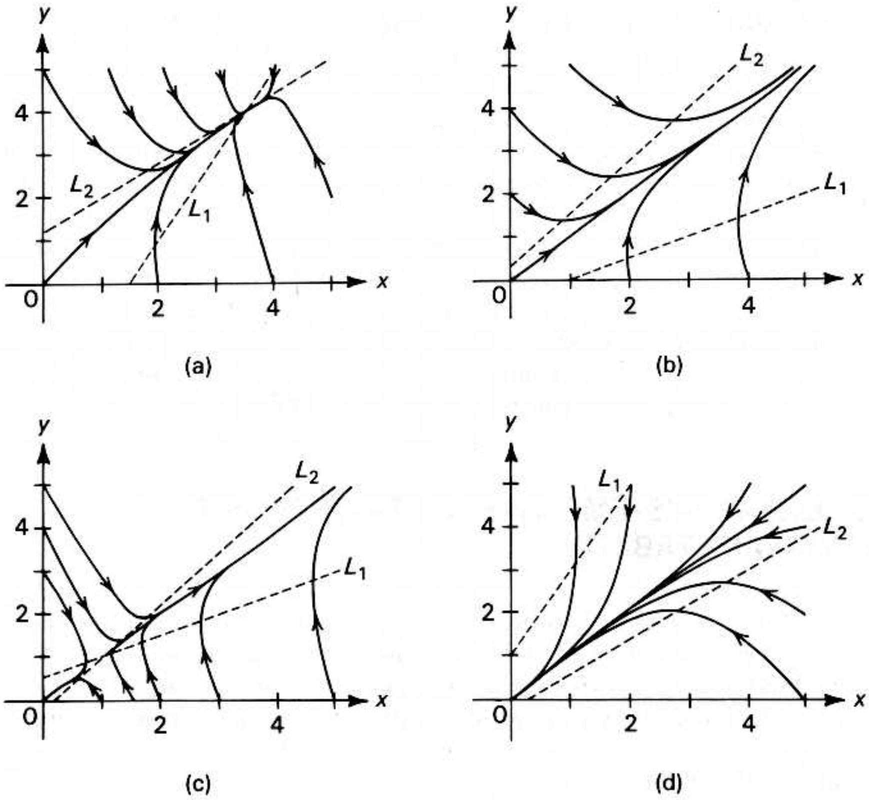

Figure 4.3 (a) $x' = y - 2x + 3,\ y' = 4x - 5y + 6.$
(b) $x' = 2y - x + 1,\ y' = 5x - 4y + 1.$
(c) $x' = 2y - x - 1,\ y' = 5x - 4y - 1.$
(d) $x' = y - 2x - 1,\ y' = 4x - 5y - 1.$

8. Look up the discussions in the texts by Rapoport [48] and Braun [5], and see how the model has been applied to real cases.
9. Formulate the model for three countries, and discuss some special cases. Can you relate your model to actual nations today?
10. Suppose that x and y are divided into $x = x_1 + x_2$, and $y = y_1 + y_2$, where x_1 and y_1 stand for conventional weaponry and x_2 and y_2 for nuclear weaponry. Set up a model for this situation.
11. Instead of war, reformulate the model to describe the behavior of neighbors who compete against each other for "status," buying cars, stereos, expensive vacations—and even computers.
12. Suppose that the disincentive terms $-mx$ and $-ny$ become $-nx^2$ and $-ny^2$. The model is now nonlinear and much more complicated. But you

can still discuss it in a qualitative way exactly as we did the simple case. Look for possible equilibria and investigate their stability. When you think that you have a good feel for the system, perform some numerical integrations and fill in some details.

13. Consider parameters $m = n = h = a = b = 1$, but suppose that a is varying subject to periodic political pressure in such as way that $a(t) = 1 + \sin(\pi t/2)$. Notice that if a were suddenly to become constant, the consequence could be disarmament or war, depending on when the change happened. Find out what can happen with this varying $a(t)$.
14. Suppose that as arms expenditures mount, negotiations take place whose intensity is proportional to the product xy, so that the term pxy is subtracted from the right-hand sides of (4.1.1) and (4.1.2). Discuss this case. Could it avert a war which might otherwise take place?

4.2 LINEAR SYSTEMS, LINEAR STABILITY, AND NONLINEAR STABILITY

This project is intended to provide some essential background for the discussion and interpretation of *stability* in the projects to come. In many cases (although not all), orbits close to a position of equilibrium resemble the orbits that occur in a linear system, so we start with a discussion of linear systems with two variables.

Consider the system

$$\frac{dx}{dt} = ax + by, \quad \frac{dy}{dt} = cx + dy. \tag{4.2.1}$$

If we differentiate the first equation and then eliminate y and y', we find that

$$x'' - (a + d)x' + (ad - bc)x = 0. \tag{4.2.2}$$

Now if we let $x = e^{rt}$ for constant r, we find that r must be a root of the characteristic equation

$$r^2 - (a + d)r + (ad - bc) = 0. \tag{4.2.3}$$

Thus, the origin is the equilibrium of the system (4.2.1), and the character of the motion near to the origin depends on the nature of the roots (4.2.3). The possibilities are illustrated by actual computations, plotted in Figure 4.4.

In Figure 4.4(a) the equations are

$$x' = 2x + y, \quad y' = x + 2y,$$

with

$$r = 1, 3.$$

Each orbit in the figure has a different initial condition. Both roots are real and positive, so that all motion is away from the equilibrium. We have an *unstable node*.

In Figure 4.4(b) the equations are

$$x' = -4x + y, \quad y' = x - 2y,$$

with

$$r = -3 \pm \sqrt{2}.$$

Both roots are real and negative, and all motion is toward the equilibrium. We have a *stable node*.

In Figure 4.4(c) the equations are

$$x' = x + 4y, \quad y' = 2x - y,$$

with

$$r = 3, -3.$$

Both roots are real, but one is positive and one negative. We then have a *saddle point*, which is *unstable*.

In Figure 4.4(d) the equations are

$$x' = x + 4y, \quad y' = -2x + y,$$

with

$$r = 1 \pm i\sqrt{8}.$$

The roots are complex with positive real part, and we have *unstable spirals*.

In Figure 4.4(e) the equations are

$$x' = -x + 4y, \quad y' = -2x - y,$$

with

$$r = -1 \pm i\sqrt{8}.$$

The roots are complex with negative real part, and we have *stable spirals*.

In Figure 4.4(f) the equations are

$$x' = x + 4y, \quad y' = -2x - y,$$

with

$$r = \pm i\sqrt{7}.$$

The roots are purely imaginary, and all the solutions are ellipses with center at the equilibrium. In this case the equilibrium is called a *center* and is *stable*.

In cases (b) and (e) the stability is called *asymptotic*.

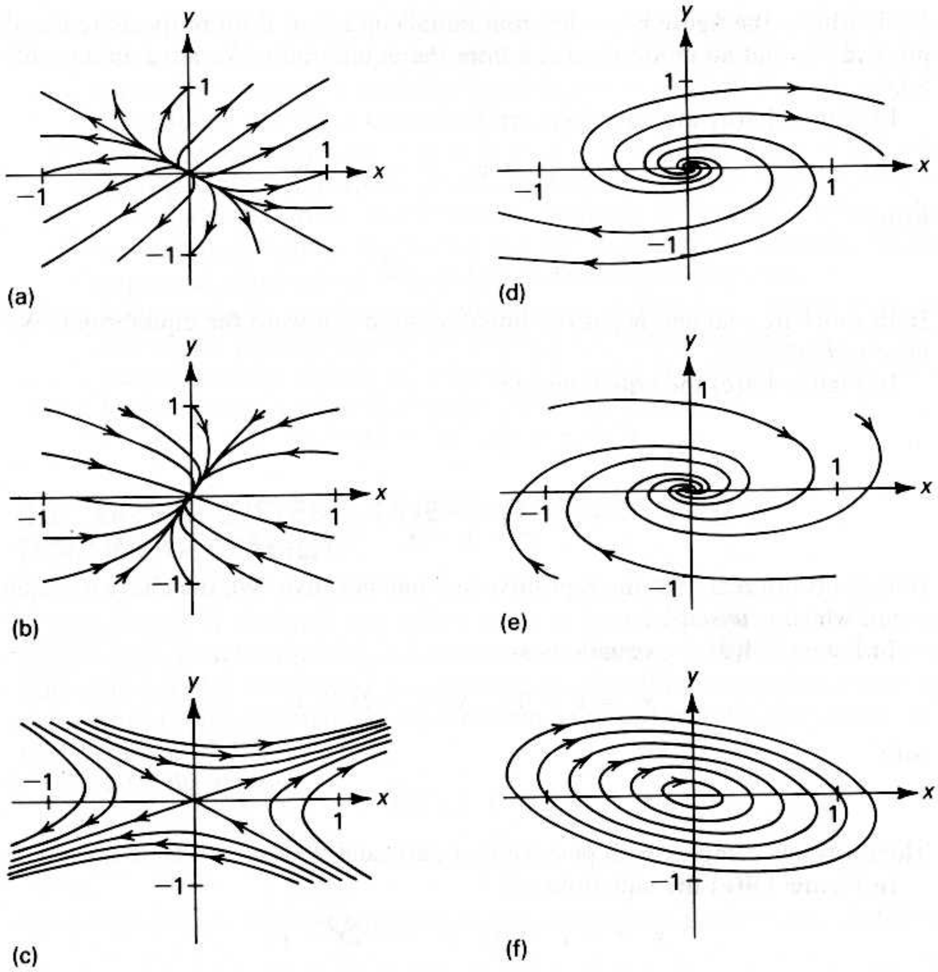

Figure 4.4 (a) (b) (c) (d) (e) (f)

Next, consider two nonlinear equations

$$\frac{dX}{dt} = F(X,Y), \quad \frac{dY}{dt} = G(X,Y). \tag{4.2.4}$$

Suppose that there is an equilibrium at the point $X = A$, $Y = B$; then we must have

$$F(A,B) = G(A,B) = 0. \tag{4.2.5}$$

To investigate what happens *close* to the equilibrium, let

$$X = A + x, \quad Y = B + y, \tag{4.2.6}$$

where x and y are considered to be small enough, during the investigation, for their squares and products to be ignored. Next, substitute (4.2.6) into (4.2.4), and expand each right-hand side in a Taylor series in powers of x and y. The leading terms are then zero by (4.2.5), and all nonlinear terms are ignored. What remains are the linear equations (4.2.1), where

$$a = F_X(A,B), \quad b = F_Y(A,B), \quad c = G_X(A,B), \quad d = G_Y(A,B). \qquad (4.2.7)$$

It turns out that the stability characteristics of the nonlinear system and the linearized system are the same, with the possible exception of case (f), where the linear system has a center. You will see these characteristics repeatedly when following orbits that pass close to equilibria.

Equilibria of systems having more than two equations can be investigated in the same way, although clearly the geometrical classification is no longer so simple.

Here are some assignments to help you gain experience with these ideas

1. Choosing your own numerical values, confirm the qualitative details of the six cases presented in Figure 4.4.
2. If $ad - bc = 0$, then there is a *line of equilibria* through the origin. Verify this and consider possible orbits.
3. Here is an example where there is linear stability but nonlinear instability. For the system of equations

$$X' = Y + aX(X^2 + Y^2)^{1/2},$$
$$Y' = -X + aY(X^2 + Y^2)^{1/2}, \quad a > 0,$$

the origin is an equilibrium, and close to it the linearized equations are

$$x' = y, \quad y' = -x,$$

which describe a center which is stable. To see that the origin is actually an unstable equilibrium of the nonlinear system, let

$$R^2 = X^2 + Y^2,$$

so that

$$RR' = XX' + YY' = aR^3.$$

Then

$$R' = aR^2,$$

so that for a positive, every orbit recedes away from the origin, regardless of how close to the origin it may start. Have a look at some actual orbits.

Note that for a negative, the origin is asymptotically stable.

4. You are invited to investigate the linear and nonlinear stability of the origin (in 4-space) for the system:

$$x_1' = -y_1 + x_2y_1 + x_1y_2, \quad x_2' = 2y_2 + x_1y_1,$$

$$y_1' = x_1 + x_1x_2 - y_1y_2, \quad y_2' = -2x_2 + \frac{1}{2}(x_1^2 + y_1^2).$$

4.3 THE PREDATOR–PREY MODEL OF VOLTERRA

In the predator–prey model of Volterra, we are concerned with just two species: the predators can survive only if they can consume their prey, whereas the prey population is limited only by the predation. With t standing for time, let $x(t)$ represent the prey population and $y(t)$ the predator population. (Remember that these variables can be scaled: one unit of x, for instance, might represent a thousand or a million actual individuals.)

In the absence of predators, x is assumed to increase according to the Malthusian law $dx/dt = ax$, with constant a. Loss due to predation is assumed to be proportional to the number of encounters between the two species, i.e., to the product xy. Altogether, then,

$$\frac{dx}{dt} = ax - bxy. \tag{4.3.1}$$

Without their food, the predators would die away according to $dy/dt = -cy$; with it, we have

$$\frac{dy}{dt} = -cy + dxy. \tag{4.3.2}$$

Equations (4.3.1) and (4.3.2) constitute Volterra's justly famous model.

If one equation is divided into the other, then the time t disappears, and we have a separable equation in x and y that can be solved. For solutions in terms of the time, numerical integration is needed. In the x-y phase plane, the solutions, or orbits, are closed curves around the equilibrium point $(c/d, a/b)$, which is therefore stable. A feature of this model (which you are invited to confirm!) is that provided the initial populations are not zero, neither species can die out.

Choose some values for the parameters (if you are desperate with indecision, set them all equal to one), and confirm numerically the results just stated. Then look at orbits close to the equilibrium and move further away, noting the much greater swings in the population numbers.

Consider varying some of the parameters. For instance, suppose that the two populations are in equilibrium; all of a sudden the predators become fiercer. What will happen?

Another application of this model is to the pest control model of the preceding project. Suppose that in the orchard there already exists a balance of prey (pests) and predators (good guys). The owner of the orchard wants to reduce the pest population, so he sprays the orchard with an insectide. The insectide unfortunately kills both predator and prey. What happens to the pest population?

4.5 THE PREDATOR–PREY MODEL WITH INTERNAL COMPETITION

Because of limited resources, the Malthusian model of population growth is often replaced by the logistic equation

$$\frac{dx}{dt} = ax - ex^2. \tag{4.5.1}$$

If a population is *growing* according to this equation, it will approach the value $x_a = a/e$ asymptotically from below. This value would represent the greatest population that the environment can support. So if the two species of project 4.3 are competing internally for resources, space, etc., the equations become

$$\left.\begin{aligned} \frac{dx}{dt} &= ax - bxy - ex^2, \\ \frac{dy}{dt} &= -cy + dxy - fy^2. \end{aligned}\right] \tag{4.5.2}$$

These equations should be investigated in the first place using the methods of project 4.1. For equilibria, we have the origin, the point $(a/e,0)$, and possibly the point of intersection of the two lines

$$\left.\begin{aligned} L_1&: \quad a - by - ex = 0, \\ \text{and} \\ L_2&: \quad -c + dx - fy = 0. \end{aligned}\right] \tag{4.5.3}$$

Do what you can to investigate possible situations, and include a discussion of stability.

For the numerical work, start with previous results in which e and f are zero; you might take initial conditions corresponding to the equilibrium in that case. Then introduce small numbers for e and f, and see what happens. Then, with f zero, gradually increase e.

It can be shown that if $ce - ad$ is positive, then the predators will die out. Can you justify this mathematically? Try. But make a numerical confirmation. You might take $a = c = d = 1$ and then consider values of e less than, equal to, and greater than one.

4.6 THE PREDATOR–PREY MODEL WITH CHILD CARE

Suppose that the prey population x is divided into x_1 children and x_2 adults, so that $x = x_1 + x_2$. The children are protected from the predators, and x_1 is increased by birth and decreased by natural death (or maybe by being eaten by the adults) and by growing up into adulthood. We assume that the birth rate is proportional to the adult population x_2 and that the rates of attrition are a_1x_1 for growing up and a_2x_1 for death. Then

$$x_1' = ax_2 - a_1x_1 - a_2x_1. \tag{4.6.1}$$

The adults' numbers are increased by the kids growing up and are decreased by death, with rate proportional to x_2, and predation, when they venture out hunting for food for the family. Using the same model for predation as before,

$$x_2' = a_1x_1 - a_3x_2 - bx_2y. \tag{4.6.2}$$

Finally, for the predators,

$$y' = -cy + dx_2y. \tag{4.6.3}$$

This system is much more complicated than any of the previous ones. It should be explored gradually. If $y = 0$, we can follow the population of the prey species when left to itself. This follows a linear system with equilibrium for $x_1 = x_2 = 0$; if this were stable, then the population would die out even without predation. Look for parameters such that the population will always increase for $y = 0$. Now introduce predation. For $y \neq 0$, there is a nontrivial equilibrium. Find it.

Next, take values for the parameters $a = 2$, $a_1 = a_2 = a_3 = 0.5$, and $b = c = d = 1$. (Or, better, make up your own values.) Confirm that without predation, the prey population will increase without limit. Find the equilibrium with predation included, and investigate its stability by calculating orbits starting close to this equilibrium. Try plotting $x = x_1 + x_2$ as a function of y. Investigate other cases, putting a physical interpretation onto any changes you make with the parameters.

4.7 PREDATOR–PREY MODELS WITH MORE THAN TWO SPECIES

A third species having population given by z can be introduced into Volterra's model in many ways. For instance, it might prey on both of the others, but be preyed upon by neither. We could then have the system of equations:

$$\left.\begin{aligned} x' &= ax - bxy - exz, \\ y' &= -cy + dxy - fyz, \\ z' &= -gz + hxz + iyz. \end{aligned}\right] \qquad (4.7.1)$$

We could start this model with no z and a state of equilibrium between x and y; now introduce small values of e and f and see what happens. See if you can find values for the parameters such that there is a nontrivial equilibrium (i.e., one for which the populations are not all zero), and then investigate its stability numerically.

Another example, mentioned in Braun [5], concerns three species on the island of Komodo in Malaysia: we have giant carnivorous reptiles, vegetarian mammals, and plants. Let the populations of these be given respectively by x, y, and z. The reptiles eat the mammals, the mammals eat the plants, and the plants compete among themselves. The resulting system is

$$\left.\begin{aligned} x' &= -ax + bxy, \\ y' &= -cy - dxy + eyz, \\ z' &= fz - gz^2 - hyz. \end{aligned}\right] \qquad (4.7.2)$$

As usual, choose simple values for the parameters, and look for and investigate the stability of equilibria. If one species dies out, can the others survive? If the two animal species were to fertilize the plants with their droppings and corpses, then the terms $+\ ix\ +\ jy$ should be added to the right of the equation for z'. What would be the effect of this?

Think up and experiment with other, similar models.

4.8 COOPERATION BETWEEN SPECIES

Different species do not have to eat one another; the reverse process is "cooperation", producing food, for instance, that enhances the growth of both. For the case of two cooperative species, the equations (4.5.2) might be modified to give

$$\left.\begin{aligned} x' &= ax + dxy - ex^2, \\ y' &= cy + dxy - fy^2. \end{aligned}\right] \qquad (4.8.1)$$

Find conditions for these equations to have a nontrivial equilibrium, and investigate its stability in the usual qualitative ways. Then investigate the system numerically.

A model involving three species and some cooperation was proposed by D. C. Culver and A. J. Beattie in 1980.* An account can be found in an article by W. M. Post, et al. [45]. The species for this model are violets, ants, and rodents. Violets produce seeds with density x. Some of the seeds are taken by ants, having density y. The ants use the seed covering for food, but leave the remainder, which is still an intact seed, in their refuse piles, which are good sites for germination. The seeds are also destroyed by rodents, which have density z. The model has the following equations:

$$\left.\begin{aligned} x' &= ax - ex^2 + bxy - gxz, \\ y' &= cy - fy^2 + dxy, \\ z' &= -hz + ixz. \end{aligned}\right] \qquad (4.8.2)$$

Without the rodents, we have the system (4.8.1), so for a start the rodents can be introduced with small g. Again, find nontrivial equilibria and investigate their stability numerically. See if you can vary a parameter to switch from stability to instability or the reverse.

Incidentally, *mutualism* is another word you will see for cooperation that results in a mutual benefit.

4.9 A MODEL FOR CANNIBALISM

I am indebted to my colleague Dr. John Bishir for this model and for the details to be described.** Cannibalism is common in many species. It may be explicit, as a source of food or as a means of population control. Or it may be implicit: members of the same species compete for limited resources and the young have to accept what is left over when the adults have satisfied themselves; or in a forest young trees suffer from a shortage of resources and light because of the presence of older trees.

For this model, a species is divided into four stages: eggs, larvae, pupae, and adults. An individual may eat members of the same or a lower stage; so, for instance, a larva may eat other larvae or eggs, but not pupae or adults. Eggs are laid only by adults. In the first three stages depletion may be caused by natural death, by being eaten by members of the same or a higher stage, or by growing into the next stage. Let the members of the stages have populations v_1,

* From Heithaus, Culver, and Beattie, "Models of Some Ant–Plant Mutualisms," *American Naturalist* 116 (1980) pp. 347–361. Copyright © The University of Chicago Press.

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