In any event, once you know the coordinates $x(\Delta t)$ and $y(\Delta t)$, then you can use (4) again (with the definition from one-variable calculus of $\frac{d}{dt}x$ and $\frac{d}{dt}y$) to tell you (approximately) the values for $x(2\Delta t)$ and $y(2\Delta t)$. Indeed, for small $\Delta t$, these differ only slightly from $x_0 + f[x(\Delta t), y(\Delta t)]\Delta t + f(x_0, y_0)\,\Delta t$ and $y_0 + g[x(\Delta t), y(\Delta t)]\Delta t + g(x_0, y_0)\,\Delta t$, respectively. Then, you can iterate the preceding to find $x$ and $y$ at $t = 3\Delta t, 4\Delta t, \ldots$, etc.

## 6.4 Generalities

Imagine a movie of the $xy$-plane with the position $(x(t), y(t))$ of the solution to (4) represented by a moving point in the plane. Then (4) tells you how the $x$- and $y$-coordinates of the moving point change with time. In particular, you can develop a sort of heuristic picture by first drawing the $(x, y)$ plane and indicating the regions where $f = 0$, $f > 0$, and $f < 0$. Do likewise for the function $g$. Then, if you are in a region where, for example, $f > 0$ and also $g > 0$, you know that the path of $(x(t), y(t))$ moves up and to the right as the movie progresses because both $x(t)$ and $y(t)$ are increasing where $f > 0$ and $g > 0$. Similar analysis tells you the rough direction of motion for $(x(t), y(t))$, where $f > 0$ and $g < 0$ (down and to the right), and where $f < 0$ and where $g > 0$ or $g < 0$. This sort of analysis is called ***phase plane analysis.***

## 6.5 Summary of Phase Plane Analysis

Here is a summary of phase plane analysis for a differential equation of the form in Equation (4) where $f$ and $g$ are two given functions on the $xy$-plane.

### 6.5.1 General Strategy

- Pick a starting point in the plane; there is a unique solution $\mathbf{v}(t) = \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}$ to (4) that sits at your chosen starting point at $t = 0$.
- Think of $\mathbf{v}(t)$ as tracing out a path (trajectory) in the $xy$-plane as $t$ increases. A goal is to predict the behavior of this path.
- The phase plane analysis described next is designed to help you predict the trajectory.

Here are the six steps for the phase plane analysis:

*Step 1:* Draw the curves where $f(x, y) = 0$. These are called the $x$ null clines for the following reason: When $\mathbf{v}(t)$ lies on one of these null clines, then $\frac{dx}{dt} = 0$. Draw vertical slash marks on the $x$ null clines to remind yourself that a trajectory that crosses such a null cline can only do so if it is moving purely in the vertical direction at the instant of crossing.



*Step 2:* Likewise, draw the curves where $g(x, y) = 0$. These are called the $y$ null clines because when $\mathbf{v}(t)$ happens to sit on one, then $\frac{dy}{dt} = 0$. Draw horizontal slash marks on these null clines to remind yourself that a trajectory that crosses a $y$ null cline does so by moving purely in the horizontal direction at the instant of crossing.

*Step 3:* Label the points where the $x$ null clines intersect the $y$ null clines. If $\mathbf{v}(t)$ is ever at one of these points, then both $\frac{dx}{dt}$ and $\frac{dy}{dt}$ vanish. This means that the trajectory stays at such a point for all time. These intersection points of $x$ null clines and $y$ null clines are called ***equilibrium points.*** If the system that is described by Equation (4) is going to settle into a steady state, then $\mathbf{v}(t)$ will have to approach one of the equilibrium points as $t$ gets large.

*Step 4:* Label the regions of the $xy$-plane where $\frac{dx}{dt} < 0$ and where $\frac{dx}{dt} > 0$. (Note that these regions are always separated by $x$ null clines.) Likewise, label the regions where $\frac{dy}{dt}$ is positive and negative.

*Step 5:* Go back and put arrows on the vertical hash marks of the $x$ null clines. These arrows indicate whether motion across the null cline is up or down. The arrows are up on the parts of the $x$ null cline in the $\frac{dy}{dt} > 0$ regions, and down on those parts of the $x$ null cline in the $\frac{dy}{dt} < 0$ regions. Likewise, draw arrows on the horizontal slash marks that decorate the $y$ null clines. The arrows are right pointing on the parts of the $y$ null cline in the $\frac{dx}{dt} > 0$ regions and left pointing on the parts in the $\frac{dx}{dt} < 0$ regions.

*Step 6:* With the preceding completed, the analysis proceeds by observing that if the trajectory $\mathbf{v}(t)$ lies in a region where

(a) $\frac{dx}{dt} > 0$ and $\frac{dy}{dt} > 0$, then both $x(t)$ and $y(t)$ are increasing, so the trajectory must be moving up and to the right on the $xy$-plane.

(b) $\frac{dx}{dt} > 0$ and $\frac{dy}{dt} < 0$, then $x(t)$ is increasing but $y(t)$ is decreasing so the trajectory moves down and to the right.

(c) $\frac{dx}{dt} < 0$ and $\frac{dy}{dt} > 0$, then $x(t)$ is decreasing and $y(t)$ is increasing, so the trajectory moves up and to the left.

(d) $\frac{dx}{dt} < 0$ and also $\frac{dy}{dt} < 0$, then $x(t)$ and $y(t)$ are both decreasing, so the trajectory moves down and to the left.

*Note:* This sort of analysis is not quantitative (it is hard to get real numbers out of it), but it is a very powerful tool for analyzing the long-time evolution of a solution to an equation such as given in (4). However, there now exist good computer programs that will trace the trajectories in the $xy$-plane of solutions to differential equations like that in Equation (4).

## 6.6 Phase Plane Analysis for the Epidemic Model

As an example of phase plane analysis, consider the example in Equation (2) where $\lambda = 10^{-6}$. These equations read

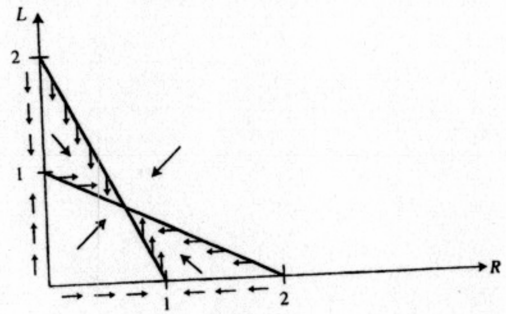


Figure 5.6

- The trajectory starts in Region (IV) and moves up and to the right initially. At some point, $L$ becomes larger than $R$, and then sometime later, the trajectory enters Region (III) moving horizontally and to the right. In Region (III), the trajectory moves down and to the right, but it can never leave Region (III) since all of the hash mark arrows are pointing to this region. Thus, the trajectory is forced to approach ever closer the equilibrium point (2/3, 2/3) as time evolves.

- The trajectory starts in Region (IV) and moves up and to the right initially. The value of $R$ stays larger than $L$, and the trajectory eventually enters Region (II) by crossing the $R$ null cline where $L = 2(1 - R)$ moving vertically. Once in Region (II), the trajectory moves up and to the left. The trajectory cannot exit Region (II) since all of the hash marks on the boundary of the region are pointing in. Thus, in this case also, the trajectory is forced to approach ever closer to the equilibrium point (2/3, 2/3) as time evolves.

- The values of $R$ and $L$ approach equality as the trajectory advances up and to the right in Region (IV). Moreover, the trajectory stays in Region (IV), but approaches ever closer to the equilibrium point (2/3, 2/3).

Thus, we see that in the case where $a = 1/2$ at least, all the preceding scenarios have the same result at large time: The initial value of $R = 0.51$ and $L = 0.5$ evolves in time toward the equilibrium point where $R$ and $L$ are equal with value 2/3. As $R$ and $L$ are definitely not equal in real life, we can see that the case $a = 1/2$ for the model in Equation (1) can be discarded.

In fact, the $a = 1/2$ behavior is characteristic of all $a < 1$ versions of the model in Equation (1). Although there are quantitative differences with respect to the precise value for $R$ and $L$ of the limiting equilibrium point, the trajectory nonetheless approaches an equilibrium point where $R = L$. Thus, the case $a < 1$ in the model in Equation (1) does not match real-world data.



On the other hand, the case $a > 1$ is very much like that for $a = 2$, and in this case, the conclusions in (11) still hold. In particular, in the $a > 1$ case, one of the possibilities comes pretty close to the real-life situation. However, before we pat ourselves on the back, we should stop to ask whether $a > 1$ is a reasonable assumption. Indeed, this case, where $a > 1$, presents a simplified model for the situation where right-curling shells are more tolerant of the presence of other right-curling shells than other left-curling shells. Is this a reasonable assumption? What do you think?

Here are some possible scenarios: Perhaps shells cannot distinguish the curling direction of their neighbors. Alternately, suppose that shells do detect the curling direction of their neighbors, but are less tolerant of like-curling neighbors rather than more tolerant. Indeed, suppose that like-curling shells breed only with each other. Furthermore, suppose that snails come in males and females. (Do they?) Then right-curling males might fight right-curling males for dominance, but tolerate right-curling females; and likewise, right-curling females might fight right-curling females and tolerate right-curling males. Meanwhile, both ignore left curlers as these do not represent competition for breeding success, only competition for food. [Here is where a model suggests directions for field research and experiments. The point is that the question of whether the constant $a$ in (1) is greater than 1 may, in principle, be verified by field research.]

## 5.3 The Lotka-Volterra Equation, a Predator-Prey Model

Austrian biophysicist Alfred Lotka and Italian mathematician Vito Volterra separately wrote down and analyzed a system of differential equations that model the interaction of predator and prey species. We give the example of the predator being foxes and the prey being hares. Let $F(t)$ denote the number of foxes at time $t$, and let $H(t)$ denote the number of hares. The model assumes that rates of change of $F(t)$ and $H(t)$ obey the equation

$$\frac{dH}{dt} = (a - bH - cF)H,$$
$$\frac{dF}{dt} = (-d + eH)F, \qquad (10)$$

where $a$, $b$, $c$, $d$, and $e$ are positive constants that we might hope to determine from field research data.

To help see the significance of these constants to the model, consider first writing the first line in (10) as

$$\frac{dH}{dt} = \alpha H, \qquad (11)$$

where $\alpha = a - bH - cF$ is the net birth-death rate for hares when $H$ is the number of hares and F is the number of foxes. Notice that when $F = 0$, so there are no foxes, then (11) is exactly the logistics equation that we studied previously. Thus, we can identify $a$ as an intrinsic growth rate of hare in an ideal environment and we can identify $a/b$ with the carrying capacity of the environment in the absence of foxes. Thus, we could, in principle, measure $a$ and $b$ by raising hares in a sufficiently large enclosure that is fenced to keep all foxes at bay. Meanwhile, if we let $F$ be nonzero, we see that the term $-cFH$ in (10) models the predatory effects of foxes on the hares. Note that this effect increases with increasing number of foxes (as we might expect) and also with increasing number of hares (which is debatable). We might try to deter- mine the constant $c$ by measuring the birth versus death rate of hares in a patch of the environment that is not fenced to preclude fox predation.

In the second line of (10) we can identify the quantity $-d + eH$ as a net birth- death rate for foxes. Here, we see that when $H = 0$, the fox equation reads $F' = -dF$, with solution $F(t) = F(0)e^{-dt}$. This decreases to zero as $t$ increases which is expected: Without hares, the foxes will starve. (Of course, this assumes that there is no alternative source of prey. Such an assumption may not be tenable in any given environment.) The term $+eHF$ in the second line of (10) models the positive effect of hares on the birth rate of foxes. That is, if hares are present, the foxes eat well and the birth rate increases, while the death rate decreases. So hares have a positive effect on the rate of change of $F$. The measurement of $d$ and $e$ can also be made (perhaps) by raising foxes in an enclosed environment where there food supply is controlled and their birth and death rates as a function of food supply are monitored.

To simplify the subsequent story, I will now choose the constants $a$, $b$, $c$, $d$, and $e$ that appear in (10) so that the equations read

$$\frac{dH}{dt} = (2 - H - F)H,$$
$$\frac{dF}{dt} = (-1 + H)F. \tag{12}$$

As in the previous examples, the analysis of these equations for $H$ and $F$ starts with the drawing of a plane with axis labled $H$ (say the horizontal axis) and $F$ (say the vertical axis). We next draw the $H$ null clines. From the right side of the first line in (12), we see that these occur where

$$H = 0 \quad \text{or} \quad F = 2 - H. \tag{13}$$

Mark these $H$ null clines with vertical slash marks to indicate that the trajectories cross these lines moving vertically.

The next step is to draw the $F$ null clines. From the right-hand side of the second line of (12), we see that these occur where $F = 0$ or $H = 1$. Mark the $F$ null clines with horizontal slash marks to indicate that the trajectories cross them moving horizontally. The resulting $(H, F)$ plane looks like Figure 5.7.

As remarked previously, the equilibrium points are the points where the $H$ null clines cross the $F$ null clines. In this example, they are $(0, 0)$, $(2, 0)$, and $(1, 1)$. Note that if a trajectory starts at an equilibrium point, it stays there forever since both the derivatives of $H$ and of $F$ vanish at such a point. (That is why they are called equi- librium points.) Note that neither $(1, 0)$ nor $(0, 2)$ are equilibrium points. Indeed, neither is the intersection of an $H$ null cline with an $F$ null cline as the former is the intersection of two $H$ null clines and the latter is the intersection of two $F$ null clines.



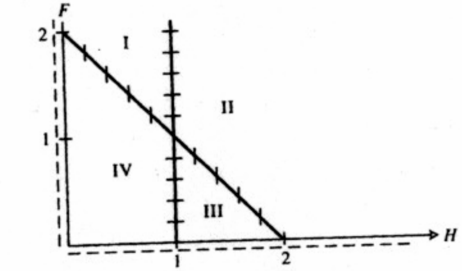


Figure 5.7

As indicated in Figure 5.7, the null clines break the plane into four regions. (The fact that all of our examples have four regions is a coincidence. There could be, in general, any number of regions.) By choosing a point in each region in turn, we can decide on the general direction of motion in that region by plugging into the right-hand side of (12) the $H$ and $F$ values for the chosen point. For example, the point $(3, 1)$ is in Region (II) and we see from the right-hand side of (12) that at this point

$$\frac{dH}{dt} = -6,$$
$$\frac{dF}{dt} = 2, \tag{14}$$

and so the motion in Region II is up and to the left. The general direction of motion in the remaining regions can be determined by a similar strategy. The resulting directions are marked on the $H$-$F$ plane as in Figure 5.8.

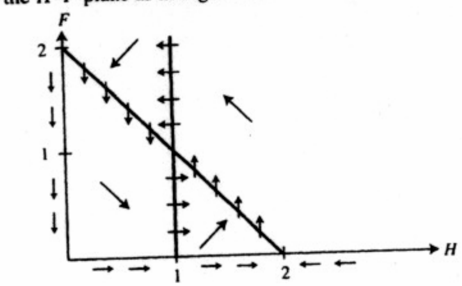


Figure 5.8

Figure 5.8 also has arrows exhibited on the null-cline slash marks to indicate the direction of motion across these null clines. These arrows can be determined as follows: We note that in Region (I) the motion is down and to the left, while in Region (II), it is up and to the left, so on the null cline between these two regions, the motion must be to the left. Likewise, the motion in Region (I) is down and to the left, while in Region (IV), it is down and to the right, so the motion on the null cline between these regions is down. On the other hand, the motion in Region (III) is up and to the right and as that in Region (IV) is down and to the right, the motion on the null cline between them must be purely to the right. The direction of motion on the null cline between Regions (II) and (III) is determined by a similar analysis.

To determine the direction of motion across the part of the boundary of Region (I) on the $F$-axis, we note that the motion in Region (I) is down and to the left and on this null cline, the direction is purely vertical, so it must be down. In Region (IV), the motion is down and to the right, so the motion on the $F$-axis part of the boundary of Region (IV) (which is vertical) must also be down, while that on the $H$-axis part of Region (IV) (which is horizontal) must be to the right. The directions of the arrows on the other parts of the $H$-axis are determined by a similar analysis.

With the $H$-$F$ plane completely marked, we are now ready to consider the qualitative properties of hare-fox evolution as predicted by our model.

In particular, suppose we start at the point (3, 1) in Region (II). The motion here is up and to the left, and so the trajectory takes off in this direction. This up and to the left motion persists until the $F$ null cline at $H = 1$ is crossed from right to left and the trajectory enters Region (I). Here, the motion is down and to the right. This motion proceeds until the trajectory hits the $H$ null cline where $F = 2 - H$. The trajectory crosses this null cline pointing down and continues into Region (IV).

At this point, the careful reader might wonder why the trajectory has no collision with the $F$-axis. The reason is quite simple: Motion on the $F$-axis is straight down, and this precludes a trajectory from hitting this axis from the side. Indeed, if a trajectory were ever to hit the $F$-axis, it would move straight down it. Then, if we imagine filming the action and running the film backward, we would see the trajectory move up the $F$-axis. As the time derivative of $H$ on the $F$-axis is exactly zero, we would never see the trajectory leave this axis and thus it couldn't have hit the $F$-axis to begin with unless it started there. There is a general principle at work here:

- A vertical $H$ null cline cannot be crossed since motion on this line is purely vertical.
- A horizontal $F$ null cline cannot be crossed since motion on this line is purely horizontal.

In any event, once in Region (IV), the trajectory moves now down and to the right until it crosses the $F$ null cline at $H = 1$. (The trajectory can't hit the $H$-axis unless it starts there since the time derivative of $F$ is zero there. This is the second point above.) The trajectory then crosses the $H = 1$ part of the $F$ null cline moving from left to right and enters Region (III) and then moves up and to the right. This motion persists until the $H$ null cline where $H = 2 - F$ is crossed, this time moving up. The trajectory then reenters Region (II) and begins to cycle around again.

Figure 5.9 contains a rough sketch of the trajectory as determined so far.



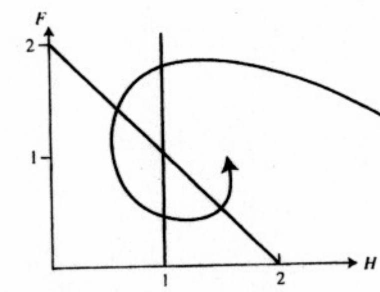


**Figure 5.9**

Thus, we see that the trajectory circles around the equilibrium point at (1, 1). However, at this point, we do not have the tools to decide between the following two possibilities:

- The trajectory approaches a closed loop trajectory that encircles the equilibrium point (1, 1). The latter would describe a cyclic oscillation of the predator and prey numbers.
- The trajectory spirals slowly into the equilibrium point (1, 1). Note that (approximately) cyclic behavior in natural predator-prey populations is not uncommon.

## 5.4 Lessons

Here are some key points from this chapter:

- Information can be obtained from a differential equation as in (1) or (10) without having to solve the equation.
- Study the phase plane analysis for the examples of (1) and (10). In particular, familiarize yourself with the drawing and marking of null clines and equilibrium points in these examples, and study how they are used to discern the general direction of movement of a solution on the phase plane.

## READINGS FOR CHAPTER 5

### READING 5.1

*Left Snails and Right Minds*

***Commentary:*** We are returning to this article from Chapter 2 (Reading 2.2; see page 23) to try to model the interaction between left-curling and right-curling snails of the same species. Let $L(t)$ and $R(t)$ denote their respective populations after time $t$. Here is a model: $\frac{dL}{dt} = L - L^2 - aRL$ and $\frac{dR}{dt} = R - R^2 - aLR$. Here, $a$ is a positive constant that measures the relative interaction between right- and left-handed snails.