

Equilibrium Behavior

3.1 When X' Is Zero

A major clue to the behavior of dynamical systems is given by the existence and location of *equilibrium points*. These are points in state space at which the system does not change. More formally, an equilibrium point of a differential equation $X' = f(X)$ is a point X_0 at which $f(X_0) = 0$. Since a differential equation specifies a vector field, we can also say that such a point is an equilibrium point of the vector field $X' = f(X)$.

So far, we have studied differential equation models almost entirely by simulating them. Simulation is a powerful tool. Indeed, it is sometimes the only available one. But it can also lead us astray.

To see one example of how, consider the following modification of the logistic equation:

$$X' = rX\left(1 - \frac{X}{k}\right)\left(\frac{X}{a} - 1\right) \quad (3.1)$$

We will delay discussion of the biological meaning of this equation until page 123.

One way to study this equation is to pick some values for r , a , and k and an initial condition $X(0)$ and numerically integrate the resulting equation. Figure 3.1 does this for three values of $X(0)$.

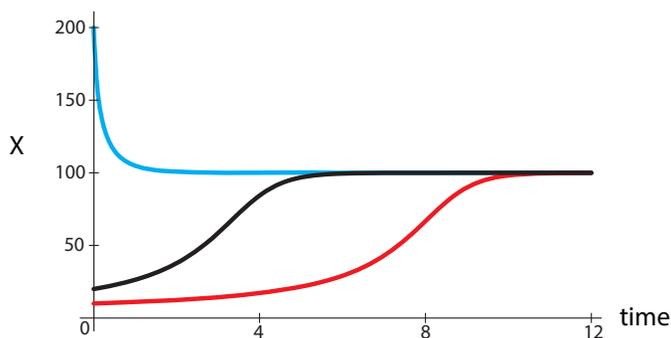


Figure 3.1: Simulations of equation (3.1) with $r = 0.1$, $k = 100$, $a = 5$ and initial conditions $X(0) = 10$ (red), $X(0) = 20$ (black), $X(0) = 200$ (blue).

Looking at Figure 3.1, we might think we understand how the model behaves. If the population starts below k , it grows slowly, speeds up, and then gradually reaches k . If it starts above k , it gradually declines to that level. The new equation appears to behave just like the logistic.

But what happens if we try one more value for $X(0)$? Suppose we start with an initial condition $X(0) = 4$ and all parameters as before. Now the population declines instead of growing (Figure 3.2).

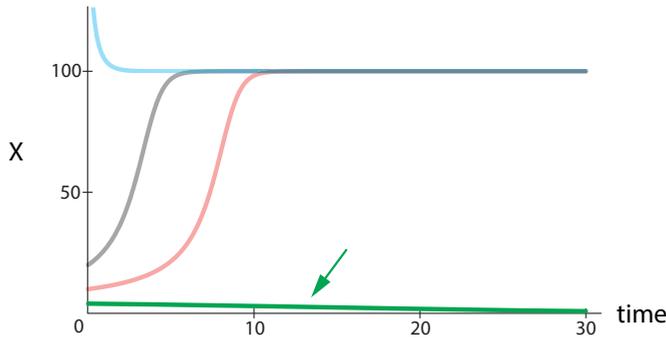


Figure 3.2: An additional simulation of equation (3.1) with initial condition $X(0) = 4$ (green, arrow). Note that the population declines.

The trick here, of course, is that the value we chose for a was 5. All initial values in Figure 3.1 were above a , while the one in Figure 3.2 is below a . Equation (3.1) models a situation in which populations fail to grow below a certain threshold size, namely a . We will return to this model later in this section.

It would be very useful to be able to figure out that that other behavior was possible, since we can't run simulations from every initial condition. There is such a method. In one dimension, it tells us the whole behavior of the system, and even in higher dimensions, it gives us very important landmarks that determine system behavior.

The first thing we need to do is to find the points where the system is not changing, that is, the *equilibrium points*.

3.2 Equilibrium Points in One Dimension

As we learned in calculus, the derivative of a constant is zero. This is true because a derivative is a rate of change, and the value of a constant function doesn't change. Looking at the same issue geometrically, we note that the graph of a constant function is a horizontal line, and the slope of a horizontal line is zero.

The converse is also true. If the derivative of a function at some point is zero, the value of the function is not changing at that point. In the context of differential equations, such points are called *equilibrium points* (or *fixed points* or *constant steady states*).

Equilibria are very important to the dynamics of all models, and they are especially important in single-variable models. The dynamics of such models are very limited—the state value can either grow without limit or go to an equilibrium point.

There are also special cases, in which the state variable is something like the position of a runner on a closed track, or the position of the hand on a clock, where moving in the same direction can bring you back to your starting point. In those cases, oscillations are possible. (See, for example, the angular variable for the pendulum in Chapter 6.)

Finding Equilibria

How do we find the equilibria of a differential equation? We know that at an equilibrium point, the derivative is zero. Since what a differential equation gives us *is* the derivative, all we have to do is set the equation equal to zero and solve for the state variable.

For example, the logistic equation,

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{k}\right)$$

is a common model for population growth that we've already encountered. To find its equilibria, we need to find the values of X for which

$$0 = rX\left(1 - \frac{X}{k}\right)$$

These can be found either by multiplying the expression out and then solving the resulting algebraic equation, or by looking thoughtfully at the right-hand side and seeing that it is the product of two terms. The only way the product of several quantities can be zero is for at least one of those quantities itself to be zero. Looking at the logistic equation shows that it is equal to zero if

$$X = 0$$

so $X = 0$ is one equilibrium point.

If X isn't zero, the population could still be at equilibrium if

$$1 - \frac{X}{k} = 0$$

This occurs when $\frac{X}{k} = 1$, implying that $X = k$ is another equilibrium point.

Have we found all the equilibria of the logistic equation? Multiplying it out would give a term with X^2 , and since a quadratic equation has at most two distinct solutions, we are done.

To find the equilibrium points of a differential equation $X' = f(X)$, set $X' = 0$ and solve the resulting equation to find the values of X that make $X' = 0$.

Exercise 3.2.1 Consider a population of organisms that reproduce by cloning and have genotypes A and a with per capita growth rates r_A and r_a . If we denote the fraction of the population having genotype a by Y , the equation describing how the prevalence of genotype a changes is

$$\frac{dY}{dt} = (r_a - r_A)Y(1 - Y)$$

- a) What does the quantity $1 - Y$ represent?
- b) Using reasoning similar to what we used for the logistic equation, find the equation's equilibria. Explain how you know you have found all of them.

Stability of Equilibrium Points

Having found a model's equilibrium points, we next want to know whether the system will stay at these equilibria if perturbed. We might also be interested in knowing whether the system can spontaneously reach a particular equilibrium if it did not start there. These are questions about the *stability* of equilibria. A simple way of thinking about stability is illustrated in Figure 3.3.

The picture on the left illustrates a stable equilibrium—if the ball in the cup is given a slight push, it will return to the bottom of the cup. In the picture on the right, the ball is on a hilltop and will roll away, never to return, with even a tiny push.

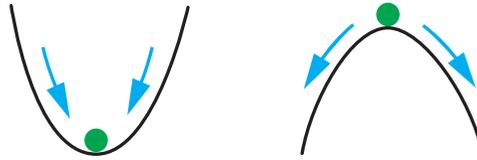


Figure 3.3: Stable (left) and unstable (right) equilibria.

Returning to the language of dynamical systems, if an equilibrium is *stable*, the system returns to it after a small perturbation. If it is *unstable*, even a tiny perturbation will send the system to a different equilibrium or a trajectory of infinite growth.

Stability Analysis 1: Sketching the Vector Field

In one dimension, a model's vector field can be used to completely figure out whether equilibria are stable. We start by drawing a line to represent the system's state space.

Then we need to find the equilibrium points and mark them on this line. Let's use the logistic equation as an example:

$$X' = rX\left(1 - \frac{X}{k}\right)$$

As we saw above, the equilibrium points of this equation are $X = 0$ and $X = k$ (Figure 3.4).

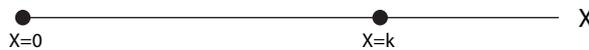


Figure 3.4: Equilibrium points of the logistic equation.

Note that the points divide the line into intervals.

The next task is to determine whether the equilibrium points are stable or unstable. In other words, we need to find out how the state point would move if nudged off an equilibrium point: toward it or away from it. In one dimension this is easy; all we have to do is figure out whether the point moves to the left or to the right, which means that we need to find out whether the sign of the vector field is positive or negative. Since the point moves to the left when the state variable is decreasing, leftward movement corresponds to a negative value of X' ; similarly, rightward movement corresponds to a positive value of X' . Thus, we need to figure out whether X' is positive or negative on each interval and draw change vectors accordingly, as in Figure 3.5. In this case, only the direction of the vectors matters; we don't have to worry about their length.

A drawing of a model's state space showing equilibrium points, a few representative change vectors, and key trajectories is called a *phase portrait* of the model. Figure 3.5 is a phase portrait of the logistic equation. (Often, in one dimension, we omit drawing the trajectories and show only the change vectors. The trajectories are obvious.)



Figure 3.5: A phase portrait of the logistic equation showing unstable (left) and stable (right) equilibria.

To create Figure 3.5, it was necessary to find the sign of the logistic equation on various intervals of the state space. Luckily, this can be done without any algebraic calculations. Instead, we take advantage of the following observations:

- 1) The parameter r , the population's per capita growth rate in the absence of intraspecific competition, is positive.
- 2) X is a population size, so it must be nonnegative (positive or zero).
- 3) The carrying capacity k is also a population size and must be positive.

$$X' = \underbrace{rX}_{\text{non negative}} \left(1 - \frac{X}{k}\right)$$

To find the sign of X' , we first note that rX is always nonnegative, so the sign of $1 - \frac{X}{k}$ determines the sign of X' . When $X < k$, $1 - \frac{X}{k}$ is positive, and when $X > k$, $1 - \frac{X}{k}$ is negative. Therefore, X' is positive on the interval $0 < X < k$ and negative on the interval $X > k$. This gives the phase portrait in Figure 3.5.

Once the phase portrait is drawn, stability becomes obvious. An equilibrium point is stable if the vector field would move the system back to the equilibrium if it was nudged off; if the vector field would carry the system away from the equilibrium point, that equilibrium point is unstable. If vectors on one side of the equilibrium point toward it and those on the other side point away from it, we say the equilibrium is *semistable*. Semistability is an unusual situation that we will not devote much attention to.

Exercise 3.2.2 Draw phase portraits to confirm each of the above statements.

Stability Analysis 1 (Continued): The Method of Test Points

In the logistic equation example, it was easy to sketch a phase portrait of the system simply by looking at the sign of each term in the equation and multiplying the signs. However, there are many models for which this won't work, or at least won't be as simple. For example, consider a population that undergoes logistic growth but also has 10% of individuals removed every year, say by fishing. If $r = 0.2$ and $k = 1000$, the change equation for this system is

$$X' = 0.2X\left(1 - \frac{X}{1000}\right) - 0.1X$$

This system's equilibria are $X = 0$ and $X = 500$.

Exercise 3.2.3 Confirm that the equilibria given above are correct.

As before, we can draw the state space and mark the equilibria at $X = 0$ and $X = 500$, dividing the line into intervals. However, it's no longer obvious how to find the sign of X' in each interval. For reasons that we will soon explain, it is enough to pick one point in each interval and find the sign of X' at that point. In the region between 0 and 500, we might choose $X = 100$. Then $X' = 0.2 \times 100 \times (1 - 100/1000) - 0.1 \times 100 = 8$, so the change vectors point to the right. Above 500, we can use $X = 1000$. Then, $X' = 0.2 \times 1000 \times (1 - 1000/1000) - 0.1 \times 1000 = -100$, so the change vectors point to the left. This means that the equilibrium at $X = 0$ is unstable and the one at $X = 500$ is stable (Figure 3.6).



Figure 3.6: Phase portrait for the logistic growth with harvesting example.

Exercise 3.2.4 Find the equilibria of $X' = 0.1X(1 - \frac{X}{800}) - 0.05X$ and use test points to determine their stability.

You may wonder what allows us to use only one point in each interval. How do we know that the sign of X' won't change between adjacent equilibrium points?

The differential equations that we deal with are nearly always *continuous* functions. Informally, saying that a function is continuous just means that you can draw its graph without lifting your pen from the paper. If a function is continuous, it can't jump from one value to another—it has to pass through all the values in between. (This is called the *intermediate value theorem*.)

This matters for our purposes, because when a continuous function goes from positive to negative or vice versa, it has to pass through zero. Since the function in question is X' , every value at which it is zero is an equilibrium point. But we've already found and plotted all the equilibria! Thus, X' can't change sign between equilibria, and we can use test points to perform graphical stability analysis.

Exercise 3.2.5 Draw several functions (by hand or using SageMath) to convince yourself that a continuous function can't change sign without passing through zero.

Stability Analysis 2: Linear Stability Analysis

Drawing vector fields to determine stability works wonderfully in 1D, somewhat in 2D, badly in 3D, and not at all in higher dimensions. The more general way to find the stability of an equilibrium point is to use linear approximation. Here we will illustrate this method for a one-dimensional vector field, but in Chapter 6, we will see it in its full glory in n dimensions.

We begin by making a new kind of plot. Since X' is a function of X , we can *plot* this function in a graph. We will put on the X axis the state space X , and on the Y axis we put the vector field X' , which is $f(X)$.

Note the places where the graph of X' intersects the X axis, that is, the line $X' = 0$. The intersection points are equilibrium points.

Exercise 3.2.6 Why is this true?

If we make this plot for the logistic vector field,

$$X' = X(1 - \frac{X}{k})$$

we get Figure 3.7.

As we already know, there are two equilibria, at $X = 0$ and $X = k$. The one at $X = 0$ is unstable, while the one at $X = k$ is stable.

Now we can connect the vector field $X' = f(X)$ to the graph of $f(X)$. When the graph is above the X axis, X' is positive, which means that X is increasing, and when the graph is below the X axis, X' is negative, which means that X is decreasing.

Look at Figure 3.7. The equilibrium point at $X = 0$ occurs when $f(X)$ goes from negative to positive. If $f(X)$ goes from negative to positive, it is increasing. This means that the tangent to $f(X)$ at $X = 0$ has a positive slope, as shown in Figure 3.8.

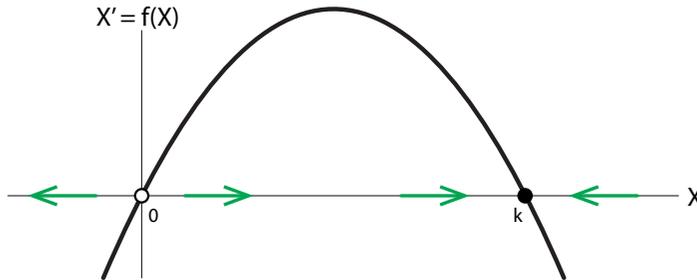


Figure 3.7: Vector field plot for logistic vector field. The black curve shows X' at each point X in state space. The points in X at which the curve intersects the horizontal axis ($X' = 0$) are equilibrium points of the vector field. Here they are at $X = 0$ and $X = k$.

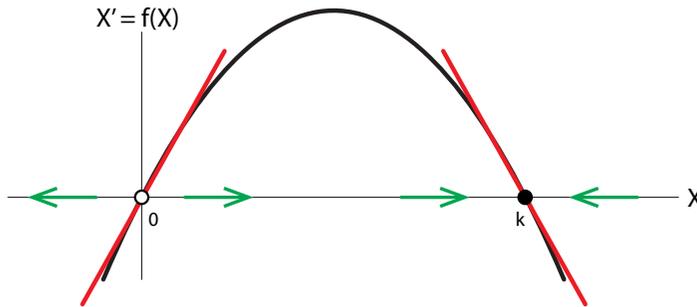


Figure 3.8: Graphical linear stability analysis. The slope of the tangent lines at the equilibrium points determines the stability of the equilibrium point: positive slopes imply unstable equilibrium points, and negative slopes imply stable equilibrium points.

Let's put this another way. This is the most important way, and it generalizes to n dimensions. Since $f(X)$ is a function of X , we can differentiate it like any other function of X . This gives us the derivative of $f(X)$ with respect to X ,

$$\frac{df(X)}{dX} = \frac{dX'}{dX} = \frac{d\left(\frac{dX}{dt}\right)}{dX}$$

We know that the derivative of a function at a point gives us the slope of the tangent to the graph of the function at that point. Clearly, if the slope of the tangent is positive, then the function is going from negative to positive. Consider the equilibrium point at $X = 0$. The slope of the tangent to $f(X)$ at $X = 0$ (the red line passing through $X = 0$) is positive, so X' is going from negative to positive. But that means that the change vectors to the left of the equilibrium point to the left, and the change vectors to the right of the equilibrium point to the right. In other words, $X = 0$ must be an unstable equilibrium point!

Now let's look at the equilibrium point $X = k$. Here the slope of the tangent (the red line passing through $X = k$) is negative, which means that X' is going from positive to negative. Therefore, the change vectors to the left of the equilibrium point to the right, while the change vectors to the right of the equilibrium point to the left. In other words, $X = k$ must be a stable equilibrium point.¹

We have discovered a deep truth: the stability of an equilibrium point of a vector field is determined by the linear approximation to the vector field at the equilibrium point. This principle, called the *Hartman–Grobman theorem*, enables us to use linearization to determine the stability of equilibria.

The 1D version of the *Hartman–Grobman theorem*, also called the *principle of linearization*, says that if the slope of the linear approximation to a vector field at an equilibrium point is positive, then the equilibrium point is unstable, and if the slope is negative, the equilibrium point is stable.

Exercise 3.2.7 Sketch graphs of two functions, as in Figure 3.7. (No equations are needed.) For each function, which we'll refer to as $f(X)$, sketch the vector field of $X' = f(X)$. Mark the equilibrium points and indicate their stability.

Calculating the Linear Approximation

Since the derivative of a function is the slope of the linear approximation to the function, this method of using derivatives to learn about stability is called *linear stability analysis*. It works whenever $\frac{df(X)}{dX}$ is not equal to zero. If $\frac{df(X)}{dX} = 0$, graphical methods are required.

We can actually calculate these linear approximations by calculating the derivative.

In the example above (with $r = 1$ for simplicity),

$$f(X) = X\left(1 - \frac{X}{k}\right)$$

we can calculate the derivative of $f(X)$ at the point X as

$$\frac{df(X)}{dX} = 1 - \frac{2X}{k}$$

At $X = 0$, that yields

$$\left. \frac{df(X)}{dX} \right|_{X=0} = +1$$

and at $X = k$,

$$\left. \frac{df(X)}{dX} \right|_{X=k} = -1$$

So the equilibrium point at $X = 0$ is unstable, and the equilibrium point at $X = k$ is stable.

¹A *semistable equilibrium* can also occur when the function touches zero without changing sign, but this is rare.

At an equilibrium point X^* (pronounced “X-star,” a common notation for equilibria):

- (1) If $\left. \frac{df(X)}{dX} \right|_{X=X^*}$ is positive, then X^* is an **unstable** equilibrium.
- (2) If $\left. \frac{df(X)}{dX} \right|_{X=X^*}$ is negative, then X^* is a **stable** equilibrium.

Exercise 3.2.8 Find the equilibria of the differential equation

$$N' = 0.1N\left(1 - \frac{N}{1000}\right)\left(\frac{N}{50} - 1\right)$$

and use linear stability analysis to find their stability. Then, use the graphical method to check your results.

Exercise 3.2.9 Do the same thing for the model $Y' = (1 - \frac{3}{2}Y)Y(1 - Y)$.

Exercise 3.2.10 Suppose we try to evaluate the stability of the $X = 0$ equilibrium point of the vector field

$$X' = 2X^2 - X$$

- a) Perform a linear stability analysis at the point $X = 0$. What is the character of this equilibrium point according to this analysis?
- b) Suppose we did a test point analysis for confirmation and chose two test points, $X = -1$ and $X = +1$. When we calculate the change vectors X' at these two points, we see that the change vector at $X = -1$ is positive,

$$X' \Big|_{X=-1} = 2(-1)^2 - (-1) = 3$$

and the change vector at $X = +1$ is also positive,

$$X' \Big|_{X=+1} = 2(+1)^2 - (+1) = 1$$

Explain why this test point method conflicts with the linear stability analysis. What have we done wrong? (*Hint: Plot the X' function.*)

Example: The Allee Effect

In some species, a minimal number of animals is necessary to ensure the survival of the group. For example, some animals, such as African hunting dogs, require the help of others to bring up their young. As a result, their reproductive success declines at low population levels, and a population that's too small may go extinct. This decline in per capita population growth rates at low population sizes is called the *Allee effect*.

As an example of the Allee effect, consider the strategy employed by Elon Musk, the developer of the Tesla electric car. Musk announced that he would give away, free of charge, all the patents that his company held on electric cars. These patents are valuable. Why would he give them away? Because he realized that for electric cars to succeed, they require substantial infrastructure: tax benefits, dedicated highway lanes, and public recharging networks. None of these would happen if there was only one electric car company. In other words, if there were only one electric car company, there would soon be no electric car companies. A critical mass is necessary.

We can model the Allee effect by adding another term to the logistic equation. The modified equation becomes

$$X' = rX\left(1 - \frac{X}{k}\right)\left(\frac{X}{a} - 1\right)$$

We already saw this model in equation (3.1). Let's carry out the full analysis of this equation.

Equilibrium Points

We start by finding the equilibrium points. Setting $X' = 0$, we solve

$$0 = rX\left(1 - \frac{X}{k}\right)\left(\frac{X}{a} - 1\right)$$

by realizing that the product of three terms can be 0 only when at least one of them is 0. So we have three choices: $X = 0$, $X = k$, and $X = a$ (Figure 3.9).



Figure 3.9: State space for the Allee effect model, with its three equilibrium points (black dots).

Stability 1: Method of Test Points

We can determine the stability of each of the three by choosing appropriate test points. If we choose values of X in the three intervals $0 < X < a$, $a < X < k$, and $k < X$, and calculate the change vectors X' , we see the direction of flow (Figure 3.10).



Figure 3.10: By drawing representative change vectors on state space, we can easily see the stability of the system's equilibrium points.

Clearly, $X = 0$ and $X = k$ are stable equilibrium points and $X = a$ is unstable. (To see the time series of these flow simulations, see Figure 3.2 on page 116).

Exercise 3.2.11 Judging by the phase portrait, what is the biological meaning of a ?

Exercise 3.2.12 Choose values for r , a , and k . Find the model's equilibria and use test points to determine their stability.

Stability 2: Linear Stability Analysis

Finally, let's confirm this with linear stability analysis. First, we graph X' as a function of X (the black curve in Figure 3.11). We see that the linear approximation to X' at the equilibrium point $X = 0$ has a negative slope, the linear approximation at $X = a$ has a positive slope, and the linear approximation at $X = k$ has a negative slope. Therefore, by the *principle of linearization*,

the equilibrium point at $X = 0$ is stable, the equilibrium point at $X = a$ is unstable, and the equilibrium point at point $X = k$ is stable.

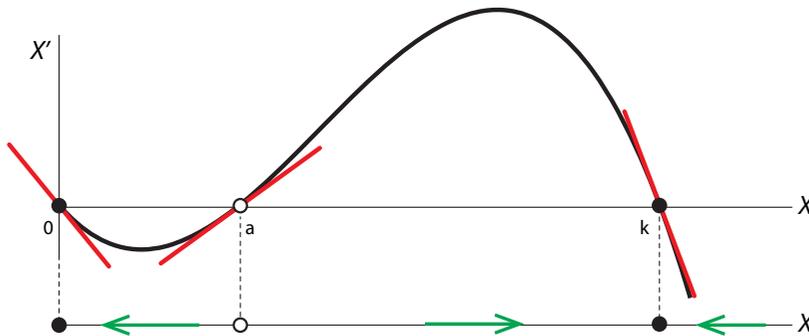


Figure 3.11: Graphical linear stability analysis for the Allee effect model.

We can confirm this by a calculation. In order to calculate $\frac{dX'}{dX}$, the easiest method is to multiply out the terms in

$$X' = rX\left(1 - \frac{X}{k}\right)\left(\frac{X}{a} - 1\right) = -\frac{r}{ak}X^3 + \frac{r}{a}X^2 + \frac{r}{k}X^2 - rX$$

and then use the power rule to differentiate X' , giving

$$\frac{dX'}{dX} = -\frac{3r}{ak}X^2 + \frac{2r}{a}X + \frac{2r}{k}X - r$$

If we then plug the three values $X = 0$, $X = a$, and $X = k$ into this expression, we get

$$\left.\frac{dX'}{dX}\right|_{X=0} = -r$$

$$\left.\frac{dX'}{dX}\right|_{X=a} = r\left(1 - \frac{a}{k}\right)$$

$$\left.\frac{dX'}{dX}\right|_{X=k} = r\left(1 - \frac{k}{a}\right)$$

Since we are assuming that a is less than k , these values are negative, positive, and negative. Therefore, we have confirmed the results obtained by looking at the vector field.

Exercise 3.2.13 Carry out the same analysis for the example you chose in Exercise 3.2.12.

Example: Game Theory Models in Evolution and Social Theory

Much significant modeling has been done using models of the dynamics of games, with applications to evolution and also to social theory.

Game theory was introduced into evolution as a way of talking about how different genes might succeed or fail in various environments. For example, suppose you are a bird that can have a gene for oily feathers *or* a gene for dry feathers.

Which is better? It depends! If it is going to rain, then you would definitely prefer oily feathers that can shed the rain, but if it is going to be dry, then you would prefer dry feathers. So we can

view the choice as a game: you, as the bird, are the gambler. You can bet on “oily feathers” or “dry feathers.” Every individual in the population makes such a bet. The croupier spins the wheel, and it comes up “rain,” with probability X , or “dry,” with probability $1 - X$. When it comes up “rain,” she pays the bet on “oily feathers” and rakes in the chips from the bet on “dry feathers,” and when the wheel comes up “dry,” she does the opposite.

In social theory, game theory models are used to explain how various patterns of behaviors can evolve in society, such as how cooperation develops among self-interested individuals (for example, in the game called “prisoners’ dilemma”).

These games are all described by differential equations. We will study a simple model here. The basic idea is really already familiar to you. We will imagine two strategies, call them A and B ; we will use the letters A and B as state variables to represent the numbers of people (or animals) currently playing each strategy. Which strategy you play is determined by whether you have the A or B genotype.² Thus, these are basically population dynamics models like the shark–tuna model of Chapter 1.

The basic idea is to write

$$\begin{aligned}A' &= r_A \cdot A \\B' &= r_B \cdot B\end{aligned}$$

where r_A and r_B are the reproductive rates of individuals carrying the two genotypes. Only now r_A and r_B are not going to be constant, but will vary: the reproductive rate will be a direct outcome of success in previous encounters. More specifically, r_A is proportional to A ’s success in recent encounters, and r_B is proportional to B ’s success in recent encounters:

$$\begin{aligned}r_A &\propto A\text{'s success in recent encounters} \\r_B &\propto B\text{'s success in recent encounters}\end{aligned}$$

(The sign “ \propto ” is read “proportional to.”)

The Replicator Equation

Instead of looking at the raw numbers of individuals playing A or B , we will look at the fraction of the population that each group represents. These are

$$X = \frac{A}{A+B} \quad \text{and} \quad Y = \frac{B}{A+B}$$

Let’s form a differential equation for X by differentiating this expression.

$$X' = \left(\frac{A}{A+B} \right)'$$

Now we need the quotient rule, which gives us

$$\begin{aligned}\left(\frac{A}{A+B} \right)' &= \frac{(A+B)A' - A(A+B)'}{(A+B)^2} \\ &= \frac{AA' + BA' - AA' - AB'}{(A+B)^2}\end{aligned}$$

But $A' = r_A A$ and $B' = r_B B$, so

$$X' = \frac{r_A AB - r_B BA}{(A+B)^2}$$

²For simplicity, we assume that all individuals are haploid.

Recall that $X = \frac{A}{A+B}$ and $Y = \frac{B}{A+B} = 1 - X$, so this gives us

$$X' = (r_A - r_B)X(1 - X)$$

This is called the *replicator equation*.

Payoffs

Now we need to find a model for the reproductive rates r_A and r_B . We said that

reproductive rate \propto previous success

But what is previous success? It consists in the success of encounters with individuals of the same genotype and encounters with individuals of the other genotype. So the payoff to r_A is

$$\left(\begin{array}{c} \text{the payoff for} \\ X-X \text{ encounters} \end{array} \right) \cdot X + \left(\begin{array}{c} \text{the payoff for} \\ X-Y \text{ encounters} \end{array} \right) \cdot Y$$

What is the payoff for these encounters? It varies from game to game! A number of different games have been proposed as evolutionary models. Here we will study one of them.

Hawks and Doves

We will now apply stability analysis to a classic problem in the evolution of behavior. This example will illuminate why different genotypes can persist in a population.

Suppose that an animal population consists of individuals of two genotypes, "hawks" (A) and "doves" (B). These individuals compete for access to a resource, such as mates or food. Hawks always fight when they encounter a competitor, while doves share the resource equally on encountering another dove and bow out on encountering a hawk.

Fighting carries a substantial cost for the loser. In this example, the cost of losing a fight is 3, so its payoff value is -3 , while the value of the resource gained is $+2$. All hawks have the same fighting ability, so the probability of a hawk winning a fight with another hawk is 50%. Therefore, the expected payoff to a hawk when it encounters another hawk is a 50% chance of $+2$ and a 50% chance of -3 , giving a total expected value of $0.5 \cdot (+2) + 0.5 \cdot (-3) = -0.5$.

Doves never fight. When a dove encounters another dove, they split the resource, whose value is still $+2$, so the outcome for a dove encountering another dove is $+1$.

When a hawk encounters a dove, the hawk takes the resource, but the dove doesn't risk fighting. Therefore, the benefit to the hawk is $+2$, while the dove incurs neither a cost nor a benefit.

The costs and benefits of various encounters are summarized in the *payoff table* (or *payoff matrix*) in Table 3.1.

	Hawk(A)	Dove(B)
Hawk(A)	$(-0.5, -0.5)$	$(+2, 0)$
Dove(B)	$(0, +2)$	$(+1, +1)$

Table 3.1: Payoff table describing the costs and benefits to participants in hawk–dove interactions.

We want to know what will happen to the prevalence of hawk and dove genotypes over time. We will denote the fraction of the population consisting of hawks as X . Since all individuals are either hawks or doves, the fraction of the population that consists of doves is $1 - X$.

Next, we define the per capita growth rate of each genotype as the sum of the outcomes of its interactions with members of the same and the other genotype. For example, if r_A is the per capita growth rate of hawks, then

$$r_A = \underbrace{-0.5}_{\text{payoff when a hawk encounters another hawk}} \cdot \underbrace{X}_{\text{frequency of encountering another hawk}} + \underbrace{2}_{\text{payoff when a hawk encounters a dove}} \cdot \underbrace{(1-X)}_{\text{frequency of encountering a dove}}$$

$$= 2 - 2.5 \cdot X$$

Similarly, the per capita growth rate of doves is

$$r_B = \underbrace{0}_{\text{payoff when a dove encounters a hawk}} \cdot \underbrace{X}_{\text{frequency of encountering a hawk}} + \underbrace{1}_{\text{payoff when a dove encounters another dove}} \cdot \underbrace{(1-X)}_{\text{frequency of encountering another dove}}$$

$$= 1 - X$$

Substituting for r_A and r_B in the replicator equation, which we derived earlier, gives

$$X' = \frac{dX}{dt} = (r_A - r_B)X(1 - X)$$

$$= (2 - 2.5X - (1 - X))X(1 - X)$$

$$= (1 - 1.5X)X(1 - X)$$

So the **hawk–dove differential equation** is

$$X' = (1 - 1.5X)X(1 - X) \tag{3.2}$$

where X is the fraction of the population who are hawks.

Exercise 3.2.14 Explain the values in the payoff table of Table 3.1.

Exercise 3.2.15 Derive a similar equation for the payoff table.

	Hawk(A)	Dove(B)
Hawk(A)	(-1, -1)	(+3, 0)
Dove(B)	(0, +3)	(+0.5, +0.5)

Equilibrium Points

How will this system behave? Let's begin by finding equilibrium points. If we set $X' = 0$, two of the equilibria of this equation, $X = 0$ and $X = 1$, can be immediately found by inspection of the equation. We find the third one by solving the equation

$$1 - 1.5X = 0$$

which gives the third equilibrium point (Figure 3.12),

$$X = \frac{2}{3}$$



Figure 3.12: Equilibrium points of the hawk–dove differential equation.

Stability 1: Method of Test Points

To find the stability of these equilibria, we need to know the sign of X' on the intervals $0 < X < \frac{2}{3}$ and $\frac{2}{3} < X < 1$. One easy way to do this is to pick a value in each interval and plug it into the hawk–dove differential equation (equation (3.2)).

For the interval $0 < X < \frac{2}{3}$, we can use $X = 0.5$. Then $X > 0$, $1 - X > 0$, and $1 - 1.5 \times 0.5 > 0$, so $X' > 0$ in the left-hand interval.

For the interval $\frac{2}{3} < X < 1$, we can use the point $X = 0.8$. For this value of X , X and $1 - X$ remain positive, but $1 - 1.5 \times 0.8 < 0$, so $X' < 0$.

Thus, the method of test points tells us that $X = 0$ and $X = 1$ are unstable equilibrium points, while $X = \frac{2}{3}$ is stable (Figure 3.13).



Figure 3.13: Stability of equilibria for the hawk–dove model, by the method of test points.

Stability 2: Linear Stability Analysis

To use linear stability analysis, we first plot $X' = f(X)$, giving us the black curve in Figure 3.14. Note the three places the curve intersects the $X' = 0$ axis, representing the three equilibrium points. The tangents to the curve at the three points are shown in red. Their slopes are obviously positive, negative, and positive, indicating that the equilibrium points are unstable, stable, and unstable.

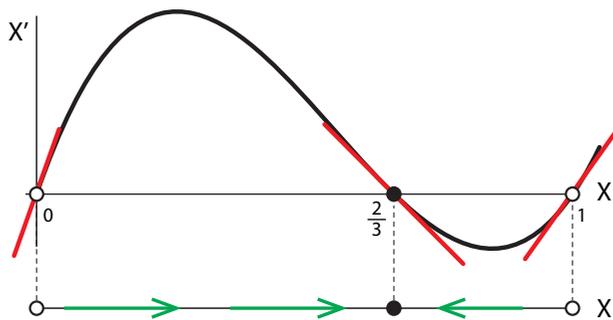


Figure 3.14: Linear stability analysis of the hawk–dove differential equation.

Finally, we confirm the linear stability analysis by calculating the sign of the derivatives at the three equilibrium points. First, we multiply out the X' equation,

$$X' = (1 - 1.5X)X(1 - X)$$

to give

$$X' = 1.5X^3 - 2.5X^2 + X$$

Then we use the polynomial rule to differentiate this expression,

$$\begin{aligned} \frac{dX'}{dX} &= \frac{d}{dX}(1.5X^3 - 2.5X^2 + X) \\ &= 4.5X^2 - 5X + 1 \end{aligned}$$

evaluated at $X_0 = 0$,

$$\left. \frac{dX'}{dX} \right|_{X_0=0} = +1$$

evaluated at $X_0 = \frac{2}{3}$,

$$\left. \frac{dX'}{dX} \right|_{X_0=\frac{2}{3}} = -\frac{1}{3}$$

and evaluated at $X_0 = 1$,

$$\left. \frac{dX'}{dX} \right|_{X_0=1} = +0.5$$

Therefore, we have confirmed that the three equilibrium points are unstable, stable, and unstable.

Exercise 3.2.16 Redo this stability analysis for the model you obtained in Exercise 3.2.15. Use both methods.

So the overall conclusion of our analysis of the hawk–dove game is that the two populations, hawks and doves, will evolve to a stable equilibrium at $X = \frac{2}{3}$. In other words, the population will evolve to a stable state in which there are two hawks for every dove.

Notice that this conclusion is far from obvious. This is why we model. It would be very easy to wave our hands, consult our personal intuition, and say “Oh, the hawks will prevail; it will be all hawks,” or “Oh, the hawks will kill each other and the doves will prevail.” It turns out that neither scenario is true. The model predicts the coexistence of the two genotypes, in the ratio 2:1.

Other evolutionary games include “stag hunt,” which is a model of group collective behavior, “prisoners’ dilemma,” which is a model of cooperation and competition, and “rock/paper/scissors,” which is a model of cyclic population dynamics.

Further Exercises 3.2

1. A kayaker is paddling directly into the wind but the kayak keeps veering either left or right.
 - a) Use your physical intuition to explain why the kayaker is having difficulty going straight.
 - b) Describe this situation in terms of equilibria and stability. (*Hint: Sketch a vector field. No equations are necessary.*)

2. The spread of a genetic mutation in a population of mice can be modeled by the differential equation

$$P' = 2P \cdot (1 - P) \cdot (1 - 3P)$$

where P is the fraction of the mice that have the new gene. (This means that $0 \leq P \leq 1$.)

- a) Find the equilibrium points of this model and determine the stability of each one.
- b) If 10% of the mice have the new gene (so $P = 0.1$) initially, what fraction of the population will have the new gene in the long run?
- c) What if the initial fraction is 90% of the mice?

3. The von Bertalanffy growth model, which can be used to model the growth of individual organisms, is given by

$$L' = r \cdot (k - L)$$

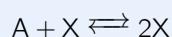
where L is the length of the organism, and r and k are positive constants. Find the equilibrium point(s) for this model and determine their stability. How large will the organism eventually grow?

4. The Gompertz growth model, which is sometimes used to model the growth of tumors, is given by

$$X' = X \cdot \left(k - \alpha \ln \left(\frac{X}{X(0)} \right) \right)$$

where X is the mass of the tumor, and k and α are positive constants. Find the equilibrium points for this model and determine the stability of each one. How large will the tumor eventually grow?

5. (Modified from Strogatz) Consider a system of two chemical compounds, A and X. One molecule of A and one of X react to produce two molecules of X, with rate constant 0.1. Also, two molecules of X can react to form one molecule of X and one molecule of A, with rate constant 0.05.



The amount of A is much larger than that of X, so its concentration can be thought of as a constant, 2.

- a) Write a differential equation for the concentration of X. (*Hint: Look back at the predator–prey and disease models studied in earlier sections.*)
 - b) Find the equilibria of this system and describe their stability.
6. This problem will look at equilibria in chemistry more generally. You may find it helpful to review Section 1.4 on page 34.
- a) In the chemical equation $A \xrightleftharpoons[k_b]{k_f} B$, what do k_f and k_b mean in dynamical terms?
 - b) Write models for the following chemical reactions:
 1. $A \xrightarrow{k} B$
 2. $A + B \xrightarrow{k} C$
 3. $A \xrightleftharpoons[k_b]{k_f} B$
 - c) Look back at all the models you just wrote. Do you notice anything unusual about the equations?
 - d) Use the observation you just made to help you find an expression for the equilibrium of the reaction $A \xrightleftharpoons[k_b]{k_f} B$. (Solve for $\frac{k_f}{k_b}$.) The expression you get is called an *equilibrium constant*.
 - e) Do the same thing for $A + B \xrightleftharpoons[k_b]{k_f} C + D$.
 - f) Write a model for the reaction $2A \xrightarrow{k} B$. (*Hint: Keep the coefficients in mind.*)
 - g) Write a model for $2A + B \xrightleftharpoons[k_b]{k_f} C + 3D$ and find the equilibrium constant. (*Hint: How many molecules of each substance are coming together in each reaction?*)
 - h) Write a model for $aA + bB \xrightleftharpoons[k_b]{k_f} cC + dD$ and find the equilibrium constant. If the result doesn't look familiar, it should after you take more chemistry.
7. Is it possible for a one-dimensional system to have two stable equilibria without an unstable one between them? Explain. (*Hint: Try drawing the situation.*)
8. How could you use simulation (numerical integration) to determine whether an equilibrium point of a differential equation is stable or unstable?
9. In the text, we said that linear stability analysis fails if $\frac{df}{dX}|_{X_0} = 0$. Here, we will see why.
- a) All of the following differential equations have an equilibrium point at $X = 0$. By looking at the vector field, determine the stability of this equilibrium point for each equation.

a) $X' = X^3$	b) $X' = -X^3$	c) $X' = X^2$	d) $X' = -X^2$
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b) Now find $\left. \frac{df}{dX} \right|_{X=0}$ for each function. What do you notice?

10 The text said that semistable equilibrium points are rare. Here, we will see why.

- $X' = X^2$ has an equilibrium point at $X = 0$. Determine the stability of this equilibrium point.
- Use graphical methods to find the equilibria of $X' = X^2 + a$ for at least one positive and two negative values of a . For each value of a , determine the stability of the equilibria.
- Use your findings to explain why semistable equilibria rarely occur in real life.

3.3 Equilibrium Points in Higher Dimensions

In one dimension, the only possible types of long-term behavior are perpetual growth and movement toward an equilibrium point.

In multivariable systems, much more complex behaviors are possible, but equilibria are still important, both as forms of behavior and as landmarks that help determine system behavior.

Finding Equilibrium Points

The definition of an equilibrium point in a multivariable system is a point at which *all* changes vanish.

In order to find the equilibrium points of a system of differential equations in several variables, we solve for values of the state variables at which *all* the equations are equal to zero.

An equilibrium point of the differential equation,

$$X' = f_1(X, Y, \dots, Z)$$

$$Y' = f_2(X, Y, \dots, Z)$$

$$\vdots$$

$$Z' = f_n(X, Y, \dots, Z)$$

is a point (X^*, Y^*, \dots, Z^*) for which

$$f_1(X^*, Y^*, \dots, Z^*) = 0$$

$$f_2(X^*, Y^*, \dots, Z^*) = 0$$

$$\vdots$$

$$f_n(X^*, Y^*, \dots, Z^*) = 0$$

Exercise 3.3.1 Find the equilibrium point of the system of equations $X' = -0.5X, Y' = -Y$.

Types of Equilibrium Points in Two Dimensions

Equilibrium Points Without Rotation

One way to make equilibrium points in 2D is to take two 1D equilibria and put them together. Recall from Chapter 1 that if we have two 1D spaces X and Y , then we can make the 2D space $X \times Y$, called the *Cartesian product* of X and Y , which is the set of all pairs (x, y) with x in X and y in Y . Geometrically, this corresponds to using X and Y as the two perpendicular axes in our new 2D space.

We will now use a similar technique, mixing and matching pairs of state points and change vectors to generate a series of 2D phase portraits. Look at Figure 3.15. For every point in the state space X , there is a change vector in the tangent space X' , and for every point in the state space Y , there is a change vector in the tangent space Y' . Since both spaces are one-dimensional, both the state and the change vectors can be thought of simply as real numbers.

Now let's say that $X' = X$ and $Y' = Y$. Suppose $X = 1$ and $Y = 2$. Then, in this particularly simple example, at the point $(1, 2)$, we have $(X', Y') = (1, 2)$. We obtain the whole vector field in the same way, mixing and matching.

Exercise 3.3.2 What is the change vector at the point $(3, -4)$?

We can also look at the whole vector field at once. For example, let's take the 1D phase portrait for $X' = X$. This has an unstable equilibrium point at $X = 0$. Then we take a second 1D phase portrait, for $Y' = Y$. This has a second unstable equilibrium point at $Y = 0$. If we take these two 1D phase portraits and join them together, we get a 2D unstable equilibrium point at $(X, Y) = (0, 0)$ (Figure 3.15).

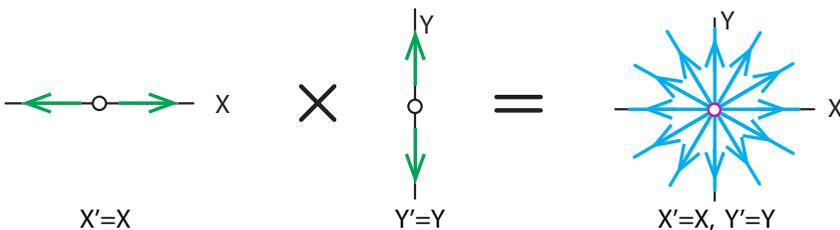


Figure 3.15: Unstable node.

This type of unstable equilibrium is called an *unstable node* (Figure 3.16).

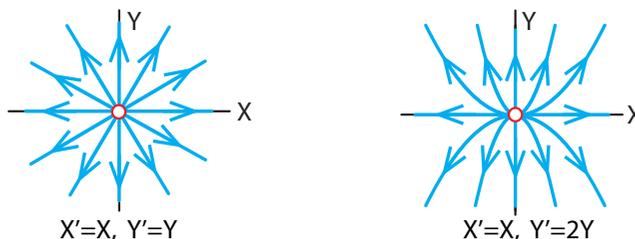


Figure 3.16: Unstable nodes.

Similarly, we can take a stable equilibrium point in X and combine it with a stable equilibrium point in Y to get a stable equilibrium in 2D, called a *stable node* (Figure 3.17).

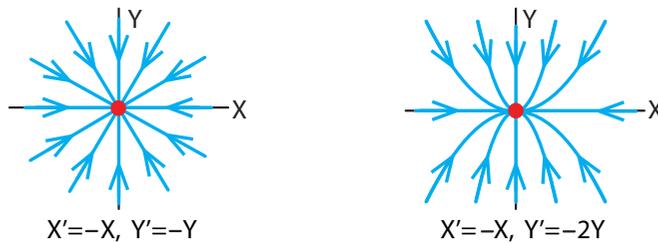


Figure 3.17: Stable nodes.

Stable and unstable nodes are essentially similar to stable and unstable equilibrium points in one dimension, not exhibiting any really new features.

Another type of equilibrium point can be created by taking a stable equilibrium point in X and an unstable equilibrium point in Y (or vice versa) and joining them to make a new kind of equilibrium point.

This new type of equilibrium point, called a *saddle point*, is more interesting (Figure 3.18).

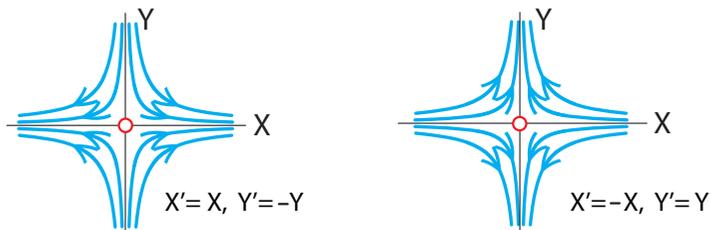


Figure 3.18: Saddle points. Left: X -axis is unstable, Y -axis is stable. Right: X -axis is stable, Y -axis is unstable.

A saddle point has a stable direction and an unstable direction. The typical state point will move under the influence of both, that is, it will move in the stable direction (toward the unstable axis), as well as in the unstable direction (away from the stable axis). The only way to approach the equilibrium point in the long run is to start *exactly* on the stable axis. Since the typical trajectory does not lie *exactly* on the stable axis, a saddle point is considered unstable.

Exercise 3.3.3 Sketch time series (for both X and Y) corresponding to two trajectories in Figure 3.18.

Nodes and saddle points are important examples of 2D equilibrium points. We should mention that sometimes it is possible to get nonisolated equilibria. For example, there may be a line completely made up of equilibrium points. Such situations are mathematically pathological and require special handling.

Equilibrium Points with Rotation

So far, we have been taking two 1D equilibrium points and joining them together to make a 2D equilibrium point. Now we will consider a new kind of equilibrium point that is irreducibly two-dimensional, not made up of two one-dimensional systems. These equilibrium points all involve rotation, which is impossible in one dimension because there is no room for it.

Recall the spring with friction:

$$\begin{aligned}X' &= V \\V' &= -X - V\end{aligned}$$

It has an equilibrium point at $(X, V) = (0, 0)$. What kind of equilibrium point is this? If we plot a trajectory, it looks like Figure 3.19, left.

Notice that the point $(0, 0)$ meets the definition of a stable equilibrium point: if we perturb the system a little bit from the equilibrium point, it returns to it. So $(0, 0)$ is a stable equilibrium point of this system. It is called a *stable spiral*.

Similarly, if we consider the spring with “negative friction,”

$$\begin{aligned}X' &= V \\V' &= -X + V\end{aligned}$$

we get the equilibrium point in Figure 3.19, middle, which is called an *unstable spiral*.

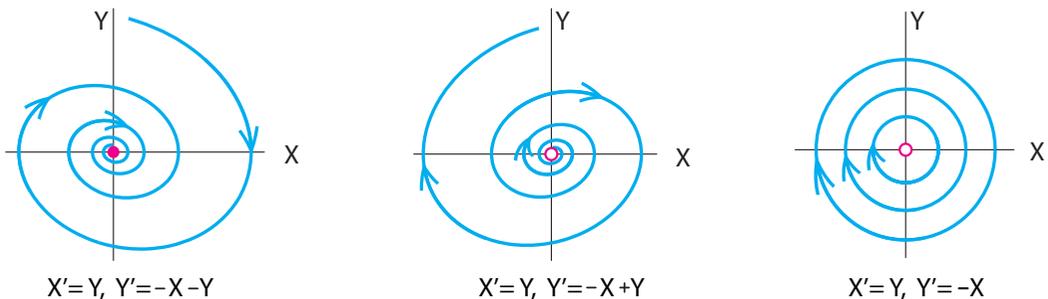


Figure 3.19: Equilibrium points in 2D with rotation. Left: stable spiral. Middle: unstable spirals. Right: center.

Finally, there is one more kind of 2D equilibrium point. We saw it in the predator–prey model and the frictionless spring:

$$\begin{aligned}X' &= V \\V' &= -X\end{aligned}$$

Here, the equilibrium point (Figure 3.19, right) is clearly not stable, but neither is it clearly unstable. A small perturbation from the equilibrium point does not go far away, and neither does it return to the equilibrium point. Instead, it hangs around the neighborhood of the equilibrium point and oscillates in a new trajectory nearby. This type of equilibrium point is called a *neutral equilibrium point* or a *center*.

We have now classified all the equilibrium points that can occur robustly in a 2D system.

Equilibrium Points in n Dimensions

The generalization to n dimensions is straightforward: to make an n -dimensional equilibrium point, we simply take as many 1D equilibrium points as we like (stable or unstable nodes), and as many 2D equilibrium points as we like (stable or unstable spirals or centers), and mix and match them to make an n -dimensional equilibrium point (of course, the total number of dimensions has to add up to n).

These equilibrium points will be studied systemically in Chapter 6. They are all the equilibrium points of linear vector fields in n dimensions.

Here let's look at an example in three dimensions. Let's take an unstable spiral in X and Y , and a stable node in Z , giving us a 3D unstable equilibrium point.

A trajectory near this equilibrium point will spiral out in the X - Y plane, while it heads toward $Z = 0$ (Figure 3.20).

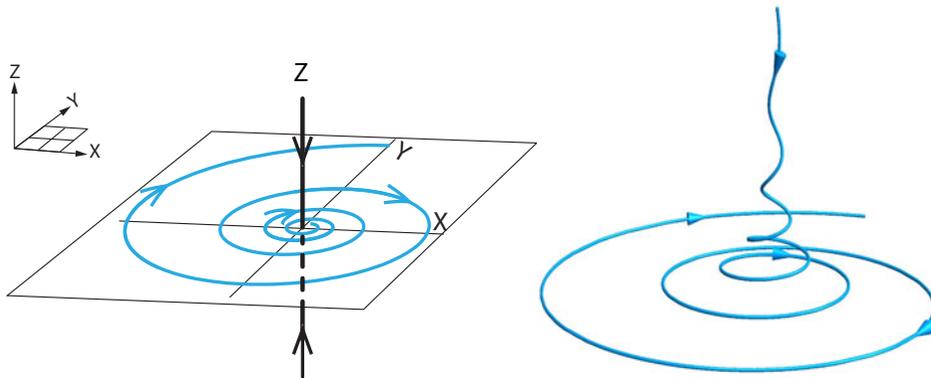


Figure 3.20: Left: unstable equilibrium point in 3D, composed of one stable dimension (Z) and a 2D unstable spiral in X and Y . Right: a trajectory near this equilibrium point.

Further Exercises 3.3

1. Consider the following Romeo and Juliet model, in which (as usual) R represents Romeo's love for Juliet, and J represents Juliet's love for Romeo (recall that these variables can be positive or negative):

$$R' = J - 0.1R$$

$$J' = -R$$

- a) Verify that this system has one equilibrium point and it is at the origin.
- b) Sketch the vector field for this system, using eight to ten change vectors.
- c) What can you say about the equilibrium point at the origin?
- d) Plot the vector field in SageMath. Can you determine the type of equilibrium point at the origin now?

- e) Choose some initial conditions and use SageMath to simulate this system and plot (at least) one trajectory. Can you determine the type of equilibrium point at the origin now?
2. Repeat the same analysis as in the previous problem, but with the following differential equations:

$$\begin{aligned}R' &= J \\J' &= -R + 0.1J\end{aligned}$$

3. Create a SageMath interactive that allows you to explore the effects of parameters on the vector field of the Romeo–Juliet system $R' = aR + bJ$, $J' = cR + dJ$. Use parameter values ranging between -2 and 2 in steps of 0.5 , using the syntax $a = (-2, 2, 0.5)$ in your function definition. (This will allow you to control parameter values more precisely.) Then, do the following exercises, supplementing the vector field with simulations when necessary.
- a) Set b and c to zero and d to -1 . Classify the equilibrium point at $(0, 0)$ for $a < -1$, $a = -1$, $-1 < a < 0$, $a = 0$, and $a > 0$. Do you get the same results if you switch the roles of a and d ?
- b) Set a and d to zero and manipulate b and c . What happens to the equilibrium when both a and d are negative? When both are positive? When they are of opposite signs?
- c) How is each type of equilibrium point you found in the previous part affected by manipulating b and c ?

3.4 Multiple Equilibria in Two Dimensions

We have now seen all the types of simple equilibrium points that can occur in two dimensions. (Later, we will see that these are exactly the *linear* equilibrium points.) A typical *nonlinear* vector field will have multiple equilibrium points.

Example: Competition Between Deer and Moose

Consider two populations of deer and moose, which compete with each other for food. The deer population is denoted by D , and the moose population is denoted by M . If there were no environmental limitations, the deer population would grow at a per capita rate 3, and the moose population would grow at a per capita rate 2. Each animal competes for resources within its own species, giving rise to the $-D^2$ and $-M^2$ intraspecies crowding terms. In addition, deer compete with moose and vice versa, although the impact of the deer on the moose is only 0.5, giving rise to the cross species term $-0.5MD$ in the M' equation, while the impact of the moose on the deer is harsher, and has value 1, giving rise to the $-MD$ term in the D' equation.

These assumptions make up the *Lotka–Volterra competition model*.

$$\begin{aligned}D' &= 3D - MD - D^2 \\M' &= 2M - 0.5MD - M^2\end{aligned}\tag{3.3}$$

What are the equilibria of this system? Clearly, one is $(D^*, M^*) = (0, 0)$, often called the *trivial equilibrium*.

Also, notice that if the population of one species is equal to zero, the other can be nonzero. If $D = 0$ and M is nonzero, we can divide the $M' = 0$ equation by M to get

$$2 - 0.5D - M = 0$$

Since we specified that $D = 0$, we have $2 - 0.5D - M = 0$ and thus $M = 2$. Therefore, $(D^*, M^*) = (0, 2)$ is also an equilibrium point.

Similarly, if $M = 0$ and D is nonzero, we can divide the $D' = 0$ equation by D to get

$$3 - M - D = 0$$

Since $M = 0$, we have $3 - M - D = 0$ and thus $D = 3$. Therefore, $(D^*, M^*) = (3, 0)$ is a third equilibrium point.

So far, we have calculated three equilibrium points of the deer–moose dynamical system. They are

$$(D^*, M^*) = (0, 0)$$

$$(D^*, M^*) = (0, 2)$$

$$(D^*, M^*) = (3, 0)$$

At all three of these equilibrium points, at least one population has the value zero, which means that that species went extinct. Is there an equilibrium at which the deer and moose coexist? In this case,

$$\left. \begin{aligned} 3D - DM - D^2 &= 0 \\ 2M - 0.5DM - M^2 &= 0 \end{aligned} \right\} \text{It's an equilibrium point}$$

$$\left. \begin{aligned} D &\neq 0 \\ M &\neq 0 \end{aligned} \right\} \text{neither species is extinct}$$

Since neither M nor D is 0, we can divide the first equation by D and the second by M , getting

$$\begin{aligned} 3 - M - D &= 0 \\ 2 - 0.5D - M &= 0 \end{aligned}$$

We will solve one of these equations and substitute the result into the other one. Let's start with $3 - M - D = 0$. Solving for D gives $D = 3 - M$. Substituting this result into $2 - 0.5D - M = 0$ gives $2 - 0.5(3 - M) - M = 2 - 1.5 + 0.5M - M = 0$, so $-0.5M + 0.5 = 0$ and $M = 1$. We can now substitute $M = 1$ into $D = 3 - M$, which gives $D = 2$.

Therefore, the equilibrium point we are seeking at which the deer and moose can coexist is

$$(D^*, M^*) = (2, 1)$$

Exercise 3.4.1 Find the equilibria for the shark–tuna model $\begin{cases} S' = 0.01ST - 0.2S \\ T' = 0.05T - 0.01ST \end{cases}$

Stability

We have found the four equilibria for the deer–moose model (equation (3.3) on the preceding page). But how are we to determine their stability? In Chapter 7, we will study this model using higher-dimensional linearization techniques. Right now, all we have is simulation. So let's simulate the deer–moose equation. If we plot the vector field at many points, the stability becomes obvious (Figure 3.21). The only stable equilibrium point is the one at $(D, M) = (2, 1)$.

Nullclines

An important technique for finding equilibrium points and determining their stability in two dimensions is called the *method of nullclines*.

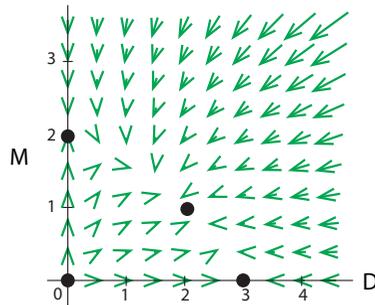


Figure 3.21: Vector field and equilibrium points for the deer–moose competition model.

Consider the vector field for the deer–moose competition model, Figure 3.21. A close look at this vector field reveals that some change vectors look almost completely horizontal or vertical. When a change vector is purely horizontal, it means that at that point in state space, only the population of the X axis species is changing, while that of Y axis species remains constant. Similarly, if a change vector attached to some point is purely vertical, only the population of the Y axis species is changing at that point; that of the X axis species is not changing.

We can plot the curve along which the X axis species is not changing and the curve along which the Y axis species is not changing and use them to study stability. The line along which $X' = 0$ is called the X -nullcline, and the line along which $Y' = 0$ is called the Y -nullcline.

So now let's consider the case of the deer–moose vector field. Since nullclines are curves on which $D' = 0$ or $M' = 0$, they are found by setting one differential equation equal to zero and rearranging to obtain one variable in terms of the other. For example, in order to find the D -nullcline (the curve on which $D' = 0$) for the deer–moose competition model, we set the D' differential equation to zero:

$$D' = 3D - MD - D^2 = D(3 - M - D) = 0$$

This equation has two solutions. One immediately evident one is $D = 0$, the vertical axis. To find the other one, we solve $3 - M - D = 0$ for M , which gives

$$M = 3 - D$$

Note that this is a straight line. It is the blue slanted line in Figure 3.22.

Exercise 3.4.2 Find the M -nullcline for the first deer-moose competition model, $D' = D(3 - M - D)$, $M' = M(2 - M - 0.5D)$.

If we plot the nullclines $D' = 0$ and $M' = 0$, we see the result in Figure 3.22.

You can see that vectors crossing the D -nullclines (blue) are vertical and those crossing the M -nullclines (red) are horizontal. Equilibrium points are the points at which nullclines cross. For example, an equilibrium at which the two species coexist exists only if the nullclines cross at a point away from the axes.

Exercise 3.4.3 Why do equilibria occur where nullclines cross? Can they occur anywhere else?

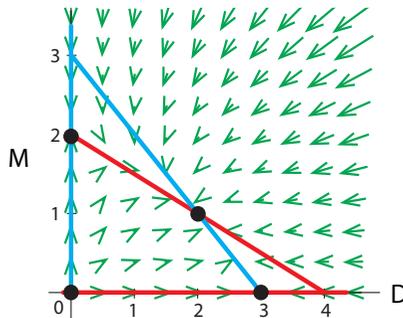


Figure 3.22: Nullclines for the first deer-moose model (equation (3.3)).

By studying the nullclines, we can actually determine the stability of the four equilibrium points. Note that the nullclines divide the state space into four sectors. Within each sector, the change vectors point in a consistent direction. For example, all change vectors in the lower left-hand sector are pointing up and to the right. If we summarize these changes sector by sector (black arrows in Figure 3.23), we see that the equilibrium point at the center, for example, must be stable.

Similarly, the other three equilibrium points all have net change vectors pointing away from the point; therefore, they must be unstable.

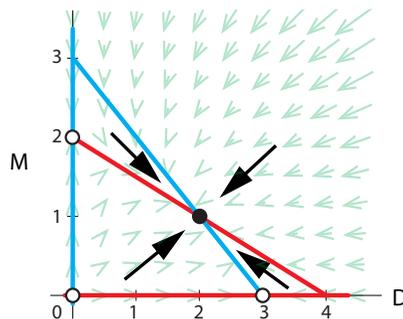


Figure 3.23: Nullclines determine the stability of equilibrium points in the first deer-moose model (equation (3.3)).

A Detailed Example

Now let's consider a new version of the deer–moose competition model with different parameters:

$$\begin{aligned} D' &= 3D - 2MD - D^2 \\ M' &= 2M - DM - M^2 \end{aligned} \quad (3.4)$$

As before, we find the D -nullcline by setting the equation for D' equal to zero and solving

$$0 = 3D - 2MD - D^2$$

Factoring out D gives

$$0 = D(3 - 2M - D)$$

This has two solutions: $D = 0$ and $3 - 2M - D = 0$. Solving the latter equation for M gives

$$M = -\frac{1}{2}D + \frac{3}{2}$$

(It doesn't matter which variable you solve for. You can pick the one that's easier, or if both are about the same, the one you plan to plot on the vertical axis.) Therefore,

$$D\text{-nullclines} \quad \begin{cases} D = 0 \\ M = -\frac{1}{2}D + \frac{3}{2} \end{cases}$$

Exercise 3.4.4 Find the M -nullclines for this model.

Exercise 3.4.5 Find the model's equilibria.

Plotting the nullclines gives Figure 3.24.

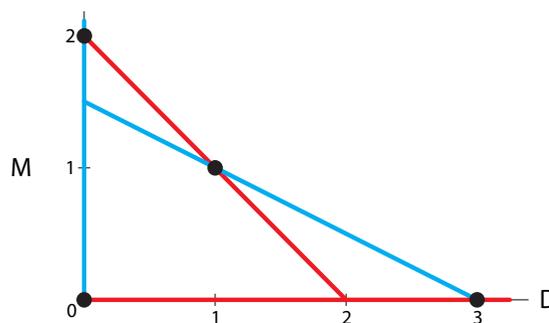


Figure 3.24: Nullclines for the second deer–moose model (equation (3.4)).

We now want to use the nullclines to sketch the vector field. First, we recall that on the D -nullcline, $D' = 0$, so D is not changing. Since we put D on the horizontal axis, this means that the change vectors on the D -nullclines will be vertical. We don't yet know whether they're going up or down, but they have to be vertical. Similarly, the change vectors on the M -nullcline must be horizontal. We can now draw dashes on the nullclines to represent this (Figure 3.25).

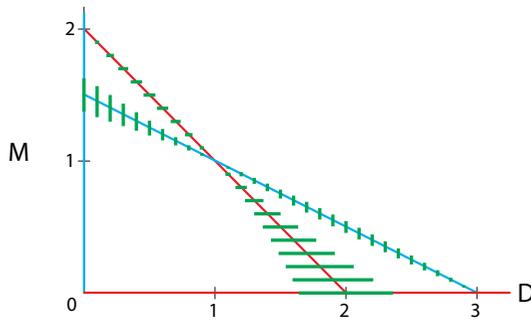


Figure 3.25: Nullclines for the second deer–moose model with horizontal and vertical dashes drawn in.

Now we need to figure out which way the change vectors are actually pointing. In order to do this, we’ll need one piece of information about change vectors on nullclines. These change vectors can flip their direction (left/right or up/down) only when the nullcline passes through an equilibrium point. (The reason for this is similar to the reason that change vectors in one-dimensional systems can change direction only on either side of an equilibrium point; you can’t go from negative to positive, or vice versa, without passing through zero.) Thus, equilibrium points break up nullclines into pieces on which all change vectors point in the same direction.

The result is that *the nullclines divide the state space quiltlike, into regions within which the vector field has the same up/down and left/right directions* (Figure 3.26). We just need to find out which region is which, and for that we use the nullclines with the horizontal and vertical lines.

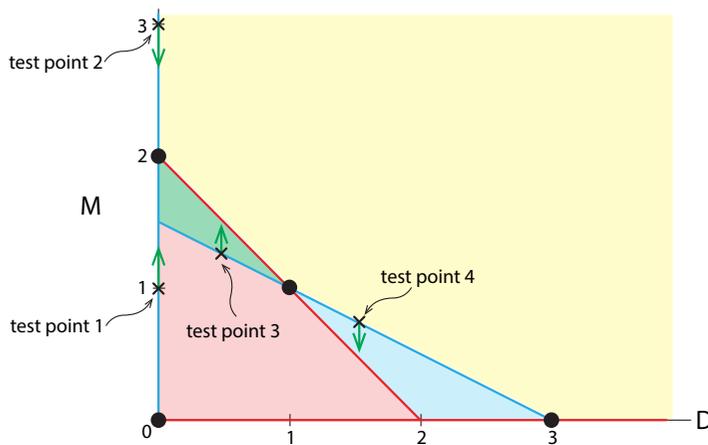


Figure 3.26: Nullclines for the second deer–moose model separate state space into four regions within which the behavior is consistent. Change vectors are not drawn to scale.

We now have to do some calculations. We have to pick test points on the nullclines and find the corresponding change vectors. Let’s start with the first part of the D -nullcline, $D = 0$, the vertical axis. The change vector on it is purely vertical. The question is: pointing up or down? Since we know that the vertical change vectors can flip only at an equilibrium point, we can go to the nonzero equilibrium point on this branch of the D -nullcline, which is $(0, 2)$, and pick test points on either side of it, say $(D, M) = (0, 1)$ and $(D, M) = (0, 3)$. The change vectors at

those two test points are

test point 1	$(D', M') _{(0,1)} = (0, 1)$	change vector points up
test point 2	$(D', M') _{(0,3)} = (0, -3)$	change vector points down

Now let's look at the other part of the D -nullcline, which is the line $M = -\frac{1}{2}D + \frac{3}{2}$. Since this nullcline passes through an equilibrium point at $(1, 1)$, we will choose two points on either side of this equilibrium point, say $D = 0.5$ and $D = 1.5$. We now need to find the corresponding values of M by plugging these values of D into the nullcline equation $M = -\frac{1}{2}D + \frac{3}{2}$. We get the two test points as $(D, M) = (0.5, 1.25)$ and $(D, M) = (1.5, 0.75)$. Now we need to determine whether the change vectors at those test points are pointing up or down:

test point 3	$(D', M') _{(0.5,1.25)} = (0, 0.3125)$	change vector points up
test point 4	$(D', M') _{(1.5,0.75)} = (0, -0.1875)$	change vector points down

Exercise 3.4.6 Use this procedure to sketch the change vectors on the M -nullclines.

The nullclines with change vectors are shown in Figure 3.27.

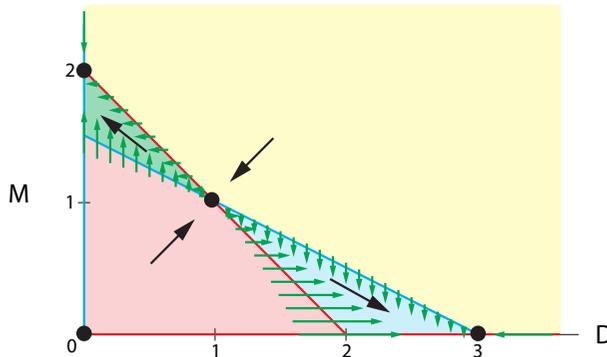


Figure 3.27: Nullclines with change vectors for the second deer–moose model.

We can use the change vectors on the nullclines to sketch the rest of the vector field. The key fact that will allow us to do this is that *vector fields change gradually*. Look at the pink region in Figure 3.27. Notice that the change vectors in that region are pointing *up and to the right*. (The ones closer to the nullclines on which change vectors point up will be nearly vertical, while the ones close to the horizontal change vectors will be nearly horizontal.) Using the same reasoning, we can sketch the general direction of the change vectors in each of the four regions.

pink region	<i>up and to the right</i>
blue region	<i>down and to the right</i>
yellow region	<i>down and to the left</i>
green region	<i>up and to the left</i>

The equilibrium point in the middle is clearly a saddle point. If we want to, we can sketch the vector field in more detail, as in Figure 3.28.

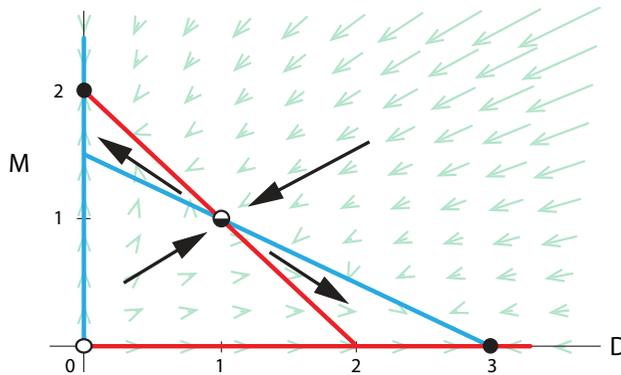


Figure 3.28: Nullclines with change vectors for the second deer–moose model.

Exercise 3.4.7 What is the biological significance of the fact that this equilibrium is a saddle point?

Exercise 3.4.8 Find the nullclines and equilibrium points of the Lotka–Volterra predation model, $N' = 0.05N - 0.01NP$, $P' = 0.005NP - 0.1P$. Then, sketch the vector field.

Why Bother with Nullclines?

When we have a vector field, plotting nullclines may seem redundant. However, a computer can plot a vector field only when numbers are available for all parameter values. On the other hand, it is often possible to work with nullclines without specifying exact parameter values. For example, we can rewrite the deer–moose competition model in the symbolic general form

$$D' = D(r_D - k_D M - c_D D)$$

$$M' = M(r_M - k_M D - c_M M)$$

Then the D -nullcline is

$$D' = D(r_D - k_D M - c_D D) = 0$$

which gives us

$$D = 0 \quad \text{or} \quad M = -\frac{c_D}{k_D} D + \frac{r_D}{k_D}$$

which is, of course, a vertical line ($D = 0$) and a straight line going from $(0, \frac{r_D}{k_D})$ to $(\frac{r_D}{c_D}, 0)$ that has slope $-\frac{c_D}{k_D}$.

In this way, plotting nullclines can allow us to sketch an approximate vector field and get a sense of the system's dynamics without having numerical parameter values.

Exercise 3.4.9 Calculate the M -nullcline symbolically.

Equilibria of Nonlinear Systems

If we calculate trajectories for the second deer–moose model, we see clearly that there are four equilibrium points (Figure 3.29). It is especially important to note that *each one of them is of one of the simple types described above*: there are two purely stable equilibria, one purely unstable equilibrium, and one unstable saddle point.

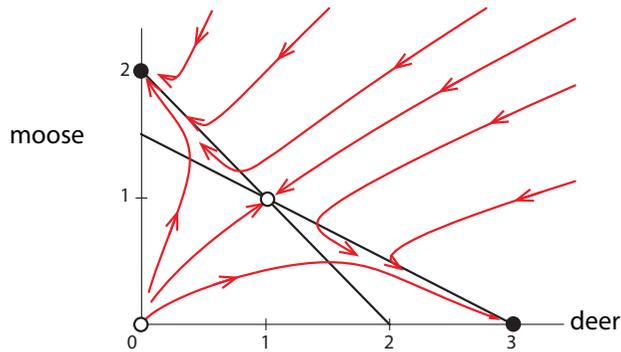


Figure 3.29: Phase portrait and nullclines of the second deer–moose model.

As we will see in Chapter 7, this is always the case: complex systems can have many equilibrium points, but each one is one of the simple types above. (These simple types are the equilibrium points of linear vector fields. We will pursue this in Chapter 6.) This is a consequence of the *Hartman–Grobman theorem*, or the *principle of linearization*.

The Hartman–Grobman theorem guarantees that while a nonlinear vector field may have many equilibrium points, each robust equilibrium point is of one of the simple types.

Two-dimensional nonlinear systems can also give us examples of biological switches.

Further Exercises 3.4

1. Consider the Lotka–Volterra predation model, $N' = rN - aNP$, $P' = caNP - \delta P$, with N the number of prey and P the number of predators.
 - a) Without doing any algebra, explain why there are no equilibria at which one species has a nonzero population and the other does not.
 - b) Find the equilibria.
2. The growth of a population in the absence of predators is described by the logistic equation with $r = 0.1$ and $K = 5000$. To model the predation, we add a term representing the consumption of prey by the predators. We assume that a single predator consumes prey at a per prey individual rate of 0.01. We also assume that the contribution of the prey to the predator birth rate is small, and has coefficient 0.001, and that the

predator per capita death rate is 0.001. If the prey population size is N and the predator population size is P , we have the differential equations $N' = rN(1 - \frac{N}{5000}) - 0.01NP$, $P' = 0.001NP - 0.001P$. Find the equilibria of this system.

3. Using SageMath, plot the vector field of the predator–prey system described in Further Exercise 3.4.2 and classify the equilibria. How do they differ from those in the Lotka–Volterra model?
4. Consider the following Romeo and Juliet model:

$$R' = J - 0.25R^2$$

$$J' = R + J$$

- a) Plot the nullclines of this system. (Recall that both R and J can be negative!)
 - b) Use the nullclines and/or algebra to find the equilibrium points of the system.
 - c) Sketch the direction of the change vectors along each nullcline. Then, fill in the change vectors in the rest of the vector field.
 - d) Use your sketch of the vector field to determine the type of each equilibrium point.
5. Let R be the size of a population of rabbits, and S the population of sheep in the same area. The Lotka–Volterra competition model for these species might look like the following:

$$R' = 24R - 2R^2 - 3RS$$

$$S' = 15S - S^2 - 3RS$$

(Refresh your memory about what each of the six terms in the equations above represents.)

- a) Plot the nullclines of this system.
 - b) Use the nullclines and/or algebra to find the equilibrium points of the system.
 - c) Sketch the direction of the change vectors along each nullcline. Then, fill in the change vectors in the rest of the vector field.
 - d) Use your sketch of the vector field to determine the type of each equilibrium point.
 - e) How many stable equilibrium points are there? Draw a *rough estimate* of the basin of attraction of each one. Based on this, what one-word description could you give to this system?
6. Let D be the size of a population of deer, and M the population of moose in the same area. The Lotka–Volterra competition model for these species might look like the following:

$$D' = 0.3D - 0.02D^2 - 0.05DM$$

$$M' = 0.2M - 0.04M^2 - 0.02DM$$

- a) Plot the nullclines of this system.

- b) Use the nullclines and/or algebra to find the equilibrium points of the system.
- c) Sketch the direction of the change vectors along each nullcline. Then fill in the change vectors in the rest of the vector field.
- d) Use your sketch of the vector field to determine the type of each equilibrium point.
- e) What will happen to these two populations in the long run? Can they coexist?
7. Repeat the same analysis as in the previous problem, but with the following differential equations:

$$D' = 0.3D - 0.05D^2 - 0.03DM$$

$$M' = 0.2M - 0.04M^2 - 0.02DM$$

- a) Plot the nullclines of this system.
- b) Use the nullclines and/or algebra to find the equilibrium points of the system.
- c) Sketch the direction of the change vectors along each nullcline. Then, fill in the change vectors in the rest of the vector field.
- d) Use your sketch of the vector field to determine the type of each equilibrium point.
- e) What will happen to these two populations in the long run? Can they coexist?

3.5 Basins of Attraction

Let's consider a system with multiple stable equilibrium points. Consider one of those points. There is a region around this equilibrium point in which every initial condition approaches the equilibrium point. The set of all such points that approach a given equilibrium point is called the *basin of attraction*, or simply *basin* of that equilibrium point.

For example, in the Allee effect, the basin of attraction of the equilibrium point $X = 0$ consists of all population sizes less than a , while the basin of attraction of the equilibrium point $X = k$ consists of all populations sizes greater than a (Figure 3.30).

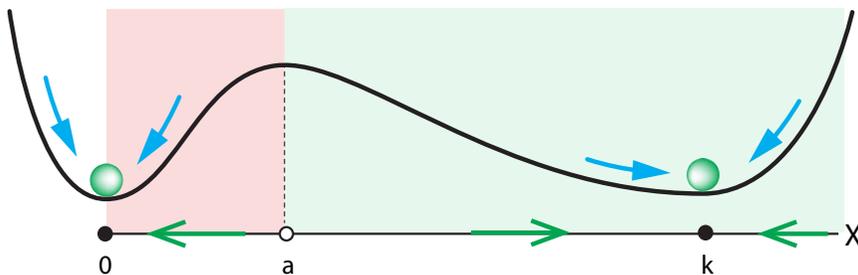


Figure 3.30: Schematic illustrating the basins of attraction in the Allee effect equation.

Exercise 3.5.1 What is the basin of attraction for $X = 0$?

Exercise 3.5.2 Does $X = a$ belong to either basin of attraction? (*Hint: Where does a system starting exactly at $X = a$ go?*)

The terminology “basin” comes from geography. Think about the two principal river systems of the United States (Figure 3.31). In the west, water flows into the Colorado River system and into the Gulf of California. In the east, water flows into the Mississippi River system and into the Gulf of Mexico. Separating the two is the crest line of the Rocky Mountains, which is known as the Continental Divide. The Continental Divide therefore separates North America into the two great basins of the Colorado and Mississippi Rivers. Theoretically, a drop of water to the west of the Continental Divide flows down the Colorado to the Gulf of California, and a drop of water to the east of the Continental Divide flows down the Mississippi down to New Orleans, and then into the Gulf of Mexico.

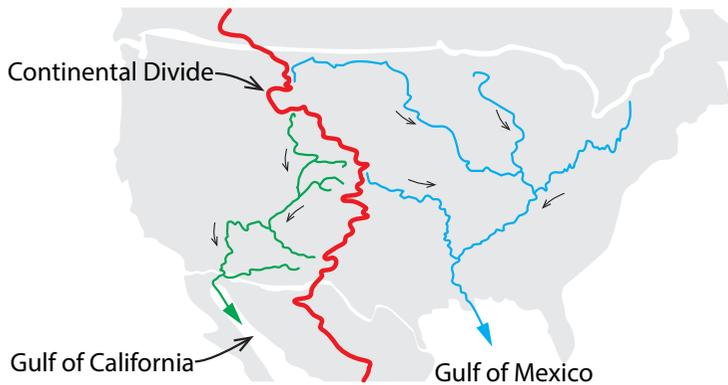


Figure 3.31: The two principal river systems of the United States divide it into two great basins.

Biological Switches: The lac Operon

The concept of a “switch” plays an important role in many biological processes, often together with the related concept of a “threshold.”

- Hormone or enzyme production is “switched on” by regulatory mechanisms when certain signals pass “threshold” values.
- Cells in development pass the switch point, after which they are irreversibly committed to developing into a particular type of cell (say, a neuron or a muscle cell). This is of critical importance in both embryonic development and in the day-to-day replacement of cells.
- In neurons and cardiac cells, the voltage V is stable unless a stimulus causes V to pass a “threshold,” which switches on the action potential.

A famous example of a biological switch can be found in the bacterium *E. coli*. *E. coli* can use the sugar lactose for energy, but in order to import extracellular lactose into the cell, the cell needs a transport protein, called lactose permease, to transport the extracellular lactose across the cell boundary (Figure 3.32). Making lactose permease costs a lot of resources. Thus, it would be advantageous to the cell to make this protein in large amounts only when lactose concentrations are high. In that case, it wants to “switch on” lactose permease production.

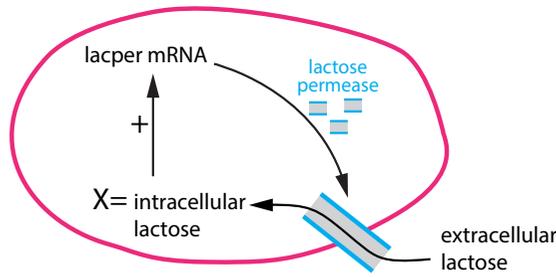


Figure 3.32: Schematic of the lac operon. Lactose permease is the enzyme that carries lactose into the cell, where it activates messenger RNA to produce more lactose permease.

This is what the cell, in fact, does. Let X equal the intracellular lactose level. We will model the cellular use of lactose by a differential equation,

$$X' = \text{lactose import} - \text{lactose metabolism}$$

The rate of lactose import is proportional to the amount of lactose permease. When lactose levels X are low, so is the production of lactose permease. We will assume there is a constant background low-level production of lactose permease, at a rate a .

As lactose levels rise, the production of lactose permease increases rapidly, but then levels off at high lactose concentrations. The blue curve in Figure 3.33 shows a function that roughly describes the rate of lactose permease production as a function of lactose concentration. A curve having this shape is called a *sigmoid*. Since the rate at which the cell imports lactose is proportional to the amount of lactose permease the cell makes, we can model it with the simple sigmoidal function

$$\text{lactose import rate} = \text{amount of lactose permease} = f(X) = \frac{a + X^2}{1 + X^2}$$

For simplicity, we are making the constant of proportionality 1.

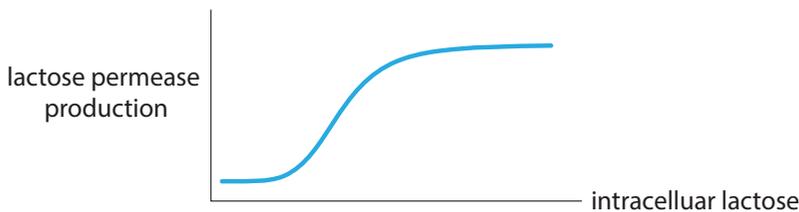


Figure 3.33: A sigmoidal curve relating lactose permease production to intracellular lactose levels.

In this particular case, we use a classical linear degradation term $g(X) = kX$, where k is the degradation rate of lactose. Here we choose $k = 0.4$. The expression for the lactose metabolism can be written as

$$\text{lactose metabolism} = g(X) = k(\text{amount of intracellular lactose}) = 0.4X$$

Therefore, the overall equation for the rate of change of lactose concentration is

$$\underbrace{X'}_{\text{change in lactose}} = \underbrace{\frac{a + X^2}{1 + X^2}}_{\text{lactose import}} - \underbrace{0.4X}_{\text{lactose metabolic degradation}}$$

System Behavior

How will this system behave? Let's begin by finding equilibrium points. We could multiply out the terms in the X' equation to give us a cubic equation and then find the roots of the cubic equation. However, in this case, there is a much more intuitive approach. Note that the X' equation says that X' is equal to a positive term $f(X)$ minus another positive term $g(X)$.

Therefore, the equilibrium points are those points where the two terms are equal, that is, where $f(X) = g(X)$. We can easily find those points by plotting $f(X)$ and $g(X)$ separately and seeing where they cross (Figure 3.34). There are clearly three equilibrium points, one at a very low X value, one at a medium X value, and one at a high X value.

Next, we find the stability of these equilibrium points. In order to read off stability from the vector field, we simply need to know whether X is increasing or decreasing, in other words, whether $X' > 0$ or $X' < 0$.

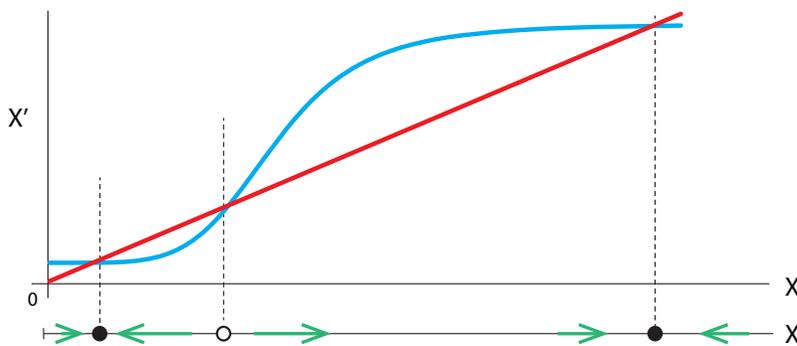


Figure 3.34: Rates of lactose importation (blue) and metabolic degradation (red) as functions of lactose concentration.

But X' , the rate of change of lactose concentration, is just the import rate $f(X)$ minus the degradation rate $g(X)$. If the import rate is higher than the degradation rate, X' is positive, and if the import rate is lower than the degradation rate, X' is negative.

Consider Figure 3.34, where $f(X)$ is shown in blue and $g(X)$ is shown in red. Therefore, when the blue curve is above the red curve, $X' > 0$, and when the blue curve is below the red curve, $X' < 0$.

Exercise 3.5.3 How is the lactose concentration changing when the red and blue curves cross?

Thus, the left-hand equilibrium point $X = low$ and the right-hand equilibrium point $X = high$ are stable, while the middle equilibrium point $X = medium$ is unstable. (This method of determining vector direction, and thus equilibrium stability, is sometimes called the *over-under method*.)

We now see how this system can function as a “switch.” As long as lactose concentrations are low, enzyme production stays low. However, if the amount of lactose in the environment rises past the critical middle value (the threshold), the cell snaps to the stable equilibrium at $X = high$, manufacturing large amounts of lactose permease.

Dynamics of Gene Expression: The Phage Lambda Decision Switch

In the 1940s and 1950s, scientists confirmed earlier speculation that the compound DNA contained in the cell nucleus carries genetic information, and they worked out its 3D structure. They also learned that genes code for proteins. (When a cell uses a gene to make a protein, we say that the gene is *expressed*.) Soon after that, other scientists realized that it was of great importance to understand how gene expression is regulated. For example, how is a gene “turned on”? How can we get long-lasting changes in gene expression from single stimuli? In 1961, the biologists Monod and Jacob published an influential paper arguing that in order to understand gene regulation, we needed to understand feedback loops (Monod and Jacob 1961).

Monod and Jacob identified feedback loops, both positive and negative, that regulate gene expression. They won the Nobel Prize in 1965 for identifying the positive feedback loop that underlies the “turning on” of the *lac* operon (see 147).

Here we will talk about another example of the dynamics of gene regulation, the phage lambda decision switch. We will follow the excellent account in *Mathematical Modeling in Systems Biology: An Introduction*, by Brian P. Ingalls. A *phage* (short for bacteriophage) is a virus that preys on bacteria, which are much larger.

When the phage lambda infects the bacterium *E. coli*, it faces an uncertain environment. Ordinarily, in a healthy cell, the virus would incorporate itself into the genome of the bacterium and get passed along to all the new progeny of the host cell. This is called lysogenic growth, and is the default mode of the virus. But if the cell is sick or damaged, the virus turns on another program, and the virus goes instead into a mode called lytic growth, where it hijacks the host cell machinery to produce hundreds of copies of the virus, which then burst the cell.

The question is then, how does the viral cell sense the health of the host, and then, how does sensing the unhealthy state turn on the lytic growth program?

The key is that there are two genes in the phage DNA, called *repressor* and *control of repressor*. These two genes produce proteins, called R and C, respectively, that form feedback loops that inhibit their own production as well as that of the other.

We won’t go into the molecular biology details here (see Ingalls (2013)), but the bottom line from the dynamics point of view is that drawing on the biology, we can form a model for the concentrations of R and C:

$$R' = F_R - d_R \cdot R \quad (3.5a)$$

$$C' = F_C - d_C \cdot C \quad (3.5b)$$

where

$$F_R = \frac{a + 10 \cdot a \cdot k_1 \cdot \left(\frac{R}{2}\right)^2}{1 + k_1 \cdot \left(\frac{R}{2}\right)^2 + k_1 \cdot k_2 \cdot \left(\frac{R}{2}\right)^3 + k_3 \cdot \frac{C}{2} + k_4 \cdot k_3 \cdot \left(\frac{C}{2}\right)^2}$$

$$F_C = \frac{b + b \cdot k_3 \cdot \frac{C}{2}}{1 + k_1 \cdot \left(\frac{R}{2}\right)^2 + k_2 \cdot k_1 \cdot \left(\frac{R}{2}\right)^3 + k_3 \cdot \frac{C}{2} + k_4 \cdot k_3 \cdot \left(\frac{C}{2}\right)^2}$$

In each equation, the negative term represents classic degradation $-d_R \cdot R$ and $-d_C \cdot C$. The two positive terms have complex forms, but we can see what they are saying qualitatively. Each term has the concentration of the protein itself in the numerator, which means that the protein spurs its own production. But each one also has its own concentration in the denominator, which means that each can inhibit its own production. And then each protein has the other protein’s

concentration in the denominator of its own production term, meaning that the other protein decreases, that is, inhibits, its production.

First let's look at the nullclines for this system; see Figure 3.35, left. Note that they intersect in three places, shown by the large dots. Those are the equilibrium points. The leftmost is stable, the middle one is unstable, and the right-hand one is stable, as can be confirmed by running a number of simulations from different initial conditions (see Figure 3.35, right). Thus, we can see a perfect example of a saddle point (middle) flanked by two stable equilibria.

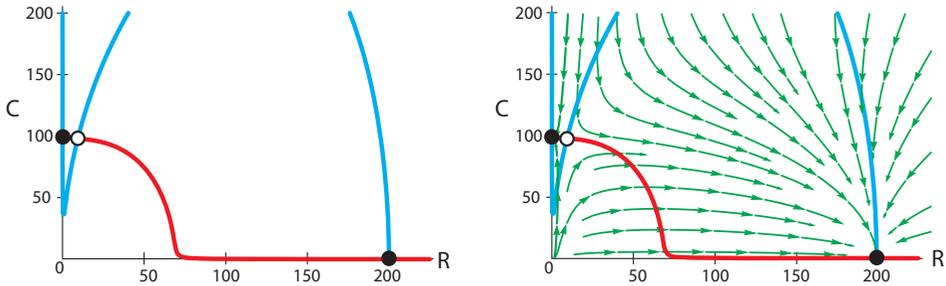


Figure 3.35: Nullclines and phase portrait for Ingalls's model (equation (3.5)). Parameters are $a = 5$, $b = 50$, $k_1 = 1$, $k_2 = 0.1$, $k_3 = 5$, $k_4 = 0.5$, $d_R = 0.02$, and $d_C = 0.02$.

What does this saddle point mean biologically? Note that the left equilibrium point is a low R /high C state. This is the lytic state, the disruptive state that kills the host cell. The right equilibrium point is the opposite, a high R /low C state. This is the lysogenic state. Thus, the saddle point is a switch between the two behaviors. With normal parameters (see Ingalls (2013)), the nullclines of the system look like Figure 3.35, left, and the behavior like Figure 3.35, right. Note that the basin of the high R /low C (lysogenic) state is very large compared to the basin of the high C /low R lytic state. Almost all initial conditions flow to it. Thus, we can conclude that the cell is typically going to be at the high R /low C equilibrium point, that is, in the lysogenic mode.

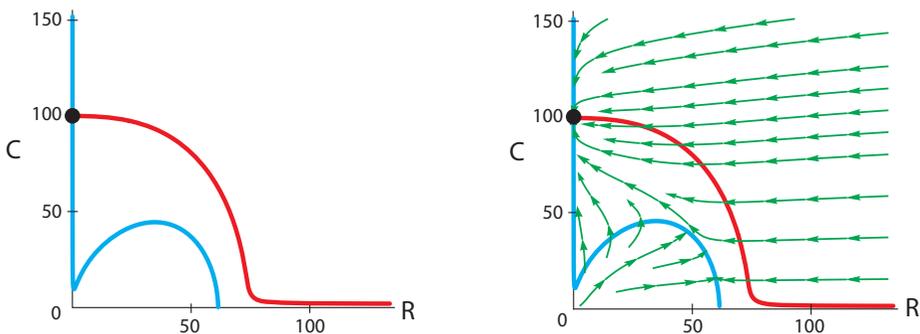


Figure 3.36: When d_R is increased to 0.2, the nullclines intersect only once, and all initial conditions flow to the stable equilibrium point at $R = 0$, $C = 100$ (black dot).

But now if circumstances change, the basins can change also. Suppose now that the host cell is damaged. When the cell's DNA is damaged, cell repair proteins are released. These repair proteins greatly increase the degradation rate of the R protein. We can see the effect of this

(Figure 3.36) by increasing d_R from 0.02 to 0.2. The effect is dramatic: now the system becomes monostable, with just a single equilibrium point at the low R /high C state. This is the lytic mode. Thus, increased degradation of R flips the system from one mode to the other.

The Collins Genetic Toggle Switch

Building on this work, in 2000, a group at Boston University led by James Collins used nonlinear dynamics to devise a version of the genetic switch that was reversible and fully bistable. Then, using genetic engineering techniques in the bacterium *E. coli*, they actually constructed two genes that neatly repressed each other. They showed that the inhibition took a very simple form of a downward-going sigmoid:

$$\frac{k}{1+x^n} \quad \text{where } n = 4$$

This inhibition gives rise to an elegant differential equation,

$$\begin{aligned} R' &= \frac{k}{1+C^4} - R \\ C' &= \frac{k}{1+R^4} - C \quad \text{where } k = 5 \end{aligned}$$

The resulting nullclines look like Figure 3.37, left, and the resulting predicted behavior is perfectly bistable (Figure 3.37, right). Note the two stable equilibrium points flanking the unstable one.

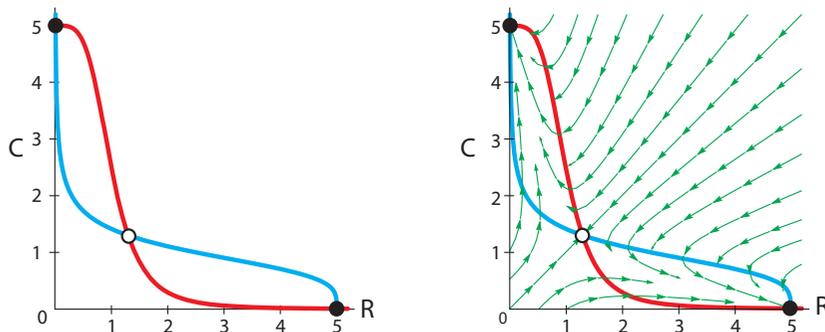


Figure 3.37: Left: Nullclines for the Collins genetic switch. Right: Every initial condition flows to one of the two stable equilibrium points.

Exercise 3.5.4 In Figure 3.37, what kind of equilibrium point is the middle one?

The paper by Collins et al. goes on to demonstrate experimentally that the system they engineered does indeed have the bistable switch property. They used two types of “signals.” One, the chemical IPTG, is a molecular mimic of allolactose, a lactose metabolite, the same kind that triggers the *lac* operon. The other signal is heat: the system is briefly subjected to a temperature of 42°C.

The upper panel of Figure 3.38 shows the result of applying each of the two signals. On the left, a dose of IPTG, after a few hours, takes the population of cells from 0% in the high state to 100%, while on the right, a pulse of higher temperature takes the population from 100%

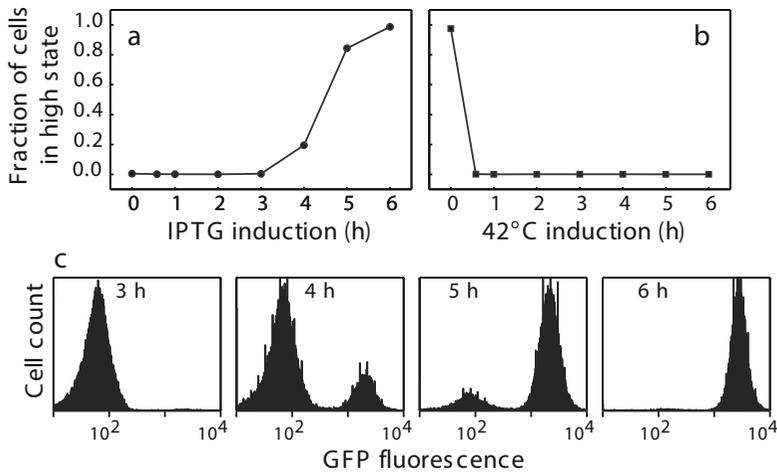


Figure 3.38: Results from Gardner et al. (2000). Experimental results demonstrating switchlike behavior in a genetically engineered circuit. Reprinted by permission from Macmillan Publishers Ltd: Nature “Construction of a genetic toggle switch in *Escherichia coli*,” by T.S. Gardner, C.R. Cantor, and J.J. Collins, 2000, *Nature* 403(6767):339–342, copyright 2000.

high state to 0%. The lower panel shows the populations changing over time after the IPTG administration. The authors distinguished the two cell populations by the fact that they had different levels of green fluorescent protein (GFP).

The authors point out that this represents a very general archetype: a system with clear “on/off” behavior, serving as a kind of biological “memory unit.” The two stable states, which can be thought of as “0” and “1,” are tolerant to noise: small fluctuations will not cause switching. They also observe that their work “represents a significant departure from traditional genetic engineering in that we rely primarily on the manipulation of network architecture, rather than the engineering of proteins and other regulatory elements, to obtain desired behaviour.” It is extremely important for molecular biology to recognize that the emphasis on the structure and engineering of protein molecules needs to be extended to a recognition of the importance of biological circuits and their resulting dynamical properties.

Further Exercises 3.5

1. What do basins of attraction have to do with black holes? Specifically, what famous concept associated with black holes describes a basin of attraction?
2. How could you use simulation to (approximately) map the basin of attraction of a stable equilibrium?
3. The over–under method can be applied whenever we have one curve representing an inflow and one representing an outflow. Sketch three sets of such curves. For each set, mark the equilibria on the horizontal axis and find their stability. No equations are necessary.

4. Sketch a pair of input and output functions that would create a switch with three or more positions.
5. Determine the stability of equilibrium points to the *lac* operon equation using the method of linearization:

$$X' = \frac{0.01 + X^2}{1 + X^2} - 0.4X$$

Plot the equation and calculate the derivatives $\frac{dX'}{dX}$ at each equilibrium point.

6. Use the over–under method to find equilibria and assess their stability if the importation rate is a hump-shaped function of the lactose concentration and the breakdown rate is proportional to concentration, as above. (Assume that the line representing lactose breakdown crosses the importation curve.)

3.6 Bifurcations of Equilibria

In the two deer–moose models, we saw an interesting contrast: for two different sets of parameters, the model gives two qualitatively different scenarios. In the first model, coexistence is a stable equilibrium, while in the second model, coexistence is unstable. So we see that *a change in parameters can result in a qualitative change in the equilibrium points of a system*. This general phenomenon is called *bifurcation*.³

Bifurcations are extremely important clues for the explanation and control of a system's behavior. For example, in the two deer–moose cases, we can say that the coexistence equilibrium became stable *because* certain parameters changed their values. In particular, a decrease in the interspecies competition terms *caused* a change from competition to coexistence. And if we wished to intervene in this ecosystem, the bifurcation structure would show us what parameters had to be changed to bring about a desired conclusion.

A **bifurcation** of an equilibrium point is a change in the number or stability of equilibrium points in a differential equation as a parameter changes its value.

Changes in Parameters: Transcritical Bifurcation

Suppose a population exhibits logistic growth with an Allee effect,

$$X' = 0.1X\left(1 - \frac{X}{k}\right)\left(\frac{X}{a} - 1\right)$$

where a is the minimum population size necessary for the population to be able to grow. Now suppose that due to changes in the environment, this threshold gradually increases over time. How will this affect the population?

We begin to answer this question by finding the model's equilibrium points. These are 0, a , and k . When $a < k$, k is a stable equilibrium point and a is an unstable one. However, when $a > k$, k becomes an unstable equilibrium point and a becomes stable.

³Bifurcations of equilibrium points are called *local* bifurcations.

Exercise 3.6.1 Draw phase portraits to confirm what was said about the stabilities of a and k , both when $a < k$ and when $a > k$.

In order to represent this change, we are going to use a new kind of diagram, called a *bifurcation diagram*. A bifurcation diagram shows how the existence and stability of equilibrium points depend on the value of a given parameter. Here, we will construct a bifurcation diagram for the Allee equation. First, we will plot different phase portraits at different values of the parameter a , say 300, 500, and 1500. Then we will stack these phase portraits vertically, each corresponding to its a value (Figure 3.39).

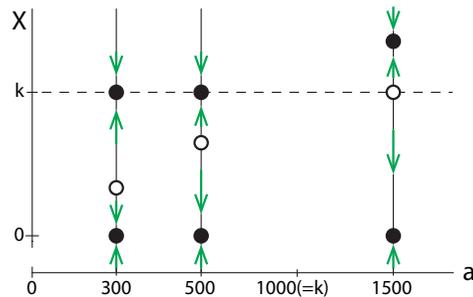


Figure 3.39: At selected values of the parameter a (the horizontal axis), we construct a one-dimensional state space shown vertically with its equilibrium points and their stability indicated.

Now if we imagine many many of these state spaces stacked side by side, we can draw lines connecting the equilibrium points at adjacent a values. This is the bifurcation diagram (Figure 3.40).

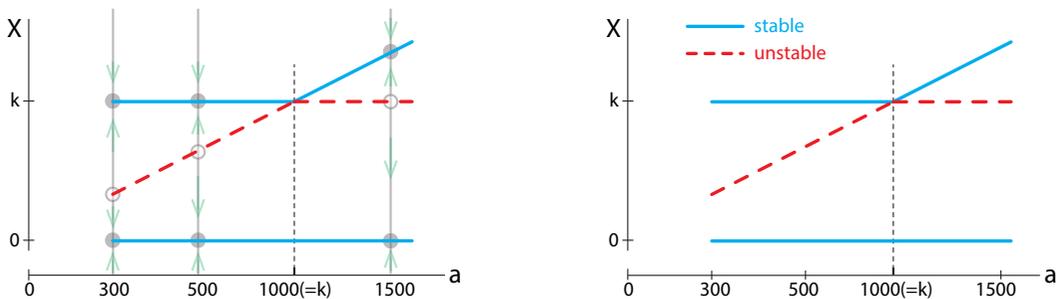


Figure 3.40: A bifurcation diagram of the equation $X' = 0.1X\left(\frac{X}{a} - 1\right)\left(1 - \frac{X}{k}\right)$. Solid lines represent stable equilibria, while dashed lines represent unstable ones.

The horizontal axis of this figure shows values of a , and the vertical axis shows values of X . For each value of a , the diagram shows the corresponding equilibrium points. (It is common to show stable equilibria as solid lines and unstable ones as dashed lines.)

Exercise 3.6.2 Use the bifurcation diagram in Figure 3.40 to find the equilibrium population levels at $a = 600$, $a = 900$, and $a = 1200$. Describe the stability of each equilibrium point.

One way to summarize what happens in Figure 3.40 is to say that the two equilibria collide and exchange stabilities. This particular bifurcation, in which a pair of equilibrium points approach each other, collide, and exchange stability as a parameter smoothly varies, is called a *transcritical bifurcation*.

Changes in Parameters: Saddle Node Bifurcations

The lac Operon

In an earlier section, we introduced a model of a biological switch in the *lac* operon. If X is the intracellular lactose level, then

$$X' = \frac{a + X^2}{1 + X^2} - rX$$

Note that we have left the degradation rate as r instead of stating a numerical value. We now want to study what happens as r varies. We will plot the lactose importation term and lactose metabolism term on the vertical axis as before.

If we plot the degradation term rX for several values of r , we see that as r increases, the red line representing degradation gets steeper, and the locations at which it intersects the black curve representing importation gradually change (Figure 3.41). Recall that points where the red line intersects the black curve are the equilibrium points of the system.

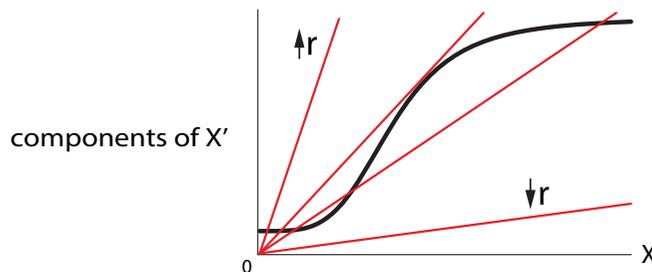


Figure 3.41: The effect of increasing r in the biological switch model. The black curve is a schematic: we have compressed the actual function for graphic effect.

When r is large, the slope of the red line is steep, and the line crosses the curve only once, at a low value of X . As r decreases, there is one mathematical point at which the straight line is tangent to the curve, and then as r decreases further, a pair of equilibrium points are born, one stable and the other unstable, giving us three equilibria. As r declines even further, the new unstable equilibrium gets closer and closer to the old stable equilibrium, until finally, for very small values of r , a reverse bifurcation occurs as the two equilibrium points coalesce and destroy each other, leaving only one stable equilibrium at a high value of X .

In order to construct a bifurcation diagram for this system, we will use the same technique of stacking up phase portraits. For each value of r , we will place a vertical copy of the state space, with filled dots representing the stable equilibrium points and hollow dots representing unstable ones (Figure 3.42).

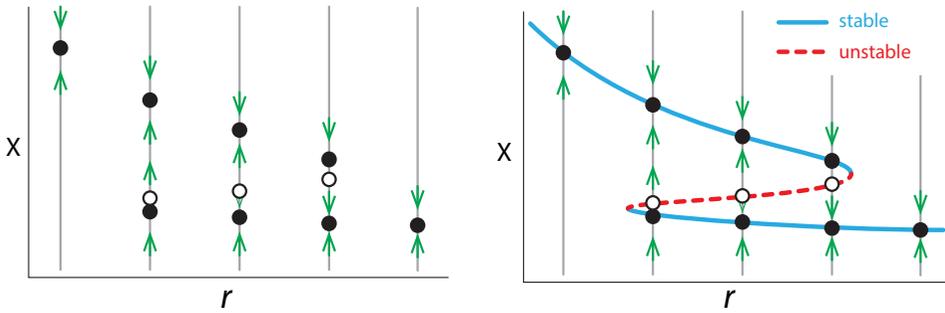


Figure 3.42: Constructing the bifurcation diagram for biological switch model. Left: Representative examples of one-dimensional state spaces and vector fields, erected vertically over the corresponding parameter value r . Right: If we could do this for infinitely many values of r , the equilibrium points would form the blue and red lines.

Then we remove the state space construction lines, and the result is the bifurcation diagram for the *lac* operon (Figure 3.43).

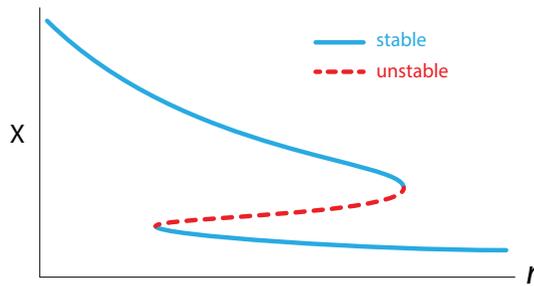


Figure 3.43: Eliminating the construction lines gives us the bifurcation diagram for the *lac* operon, showing the location of the equilibrium points and their stability for any value of the parameter r .

Plotting this system’s equilibria against r gives the bifurcation diagram in Figure 3.43. Reading the diagram from right to left, we see that at first, for large values of r , there is only one equilibrium point, with X at a very small value. When r reaches a critical value, however, a new equilibrium point is born and immediately splits into two, one stable and one unstable.

This type of bifurcation, in which a gradual change in a parameter results in the sudden appearance of a pair of equilibria, is called a *saddle-node bifurcation*.

Exercise 3.6.3 Does the pair of equilibria produced by a saddle-node bifurcation have to consist of one that is stable and one that is unstable?

The sequence of changes as the degradation rate r increases can be visualized using our analogy of

- stable equilibrium point = ball in a bowl
- unstable equilibrium point = ball on a hill

We can combine this into a picture of the existence and stability of the equilibrium points at various values of r (Figure 3.44).

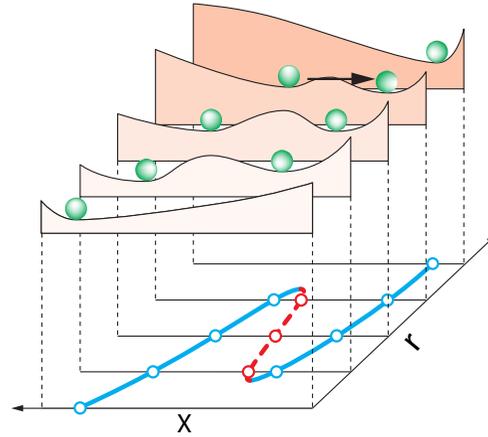


Figure 3.44: Existence and stability of equilibrium points as degradation rate r increases. In the bistable region, a significant push is required to move from one basin to the other. (Adapted from Scheffer et al. (2001).)

Outbreak: The Spruce Budworm

Another important example of a saddle-node bifurcation comes up in ecology. The spruce budworm is a caterpillar that inhabits the forests of the northeastern United States. Typically, the spruce budworm is present in low numbers, but sometimes its populations increase dramatically, to the point of defoliating large tracts of forest. Why do these outbreaks happen?

To answer this question, we start by setting up a model. (We follow the treatment in Strogatz (2014).) Let's let X equal the budworm population. We assume that in the absence of predators, the budworm population undergoes logistic growth with carrying capacity k ,

$$\text{growth of budworm} = rX\left(1 - \frac{X}{k}\right)$$

However, they are preyed upon by birds. When there are very few budworms around, the birds don't hunt them much because they are focusing on other prey. As budworm abundance rises, so does predation, unless there are so many budworms that all the birds have eaten their fill, and an increase in budworm abundance does not bring about an increase in predation. This describes a sigmoidal curve, as in the previous example. Here,

$$\text{predation of budworm by birds} = \frac{X^2}{1 + X^2}$$

Thus, we have the overall equation

$$X' = \underbrace{rX\left(1 - \frac{X}{k}\right)}_{\text{growth of budworm}} - \underbrace{\frac{X^2}{1 + X^2}}_{\text{predation of budworm by birds}}$$

We now turn to the equilibria of this system. One obvious one is $X = 0$. What about others? To make finding them easier, we assume $X \neq 0$, and divide the equation for X' by X and then

set the two terms equal to each other:

$$\begin{aligned}
 X' &= 0 \\
 \implies rX\left(1 - \frac{X}{k}\right) &= \frac{X^2}{1 + X^2} \\
 \text{dividing by } X \text{ gives } r\left(1 - \frac{X}{k}\right) &= \frac{X}{1 + X^2}
 \end{aligned}$$

So now we want to know where the curves described by $r\left(1 - \frac{X}{k}\right)$ and $\frac{X}{1 + X^2}$ intersect. Let's study this graphically.

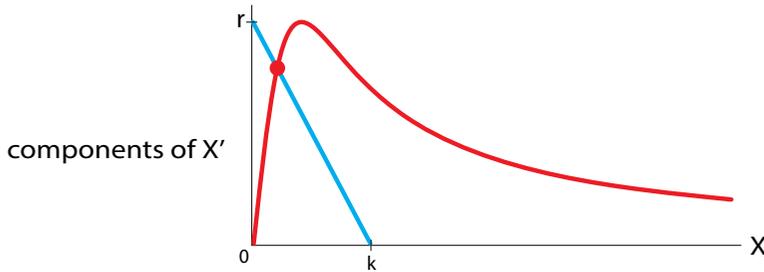


Figure 3.45: Graphical solution of the equilibrium point problem for the low- k Spruce Budworm model. Non-zero equilibrium points exist wherever the red curve and the blue line meet (the red dot).

When k is low, the curves intersect only at one low (but nonzero) value of X (Figure 3.45). The biological interpretation of this fact is that for a low carrying capacity (k), the system can support only one stable equilibrium, at a low value of X .

But for larger values of k , we can have multiple equilibria (Figure 3.46). Note first that if r is low, there is only one equilibrium point, at a low value of X . In this situation, the spruce budworm population is tightly controlled by predators. However, as the forest matures, it becomes a better budworm habitat, and r increases, approaching the situation shown in Figure 3.46. Now there are three equilibria: a stable one at low population density, called “refuge,” an unstable one at intermediate density, and another stable one at high density, called “outbreak.” Thus, the spruce budworm model exhibits the birth of a pair of equilibria, which is the signature of a saddle-node bifurcation.

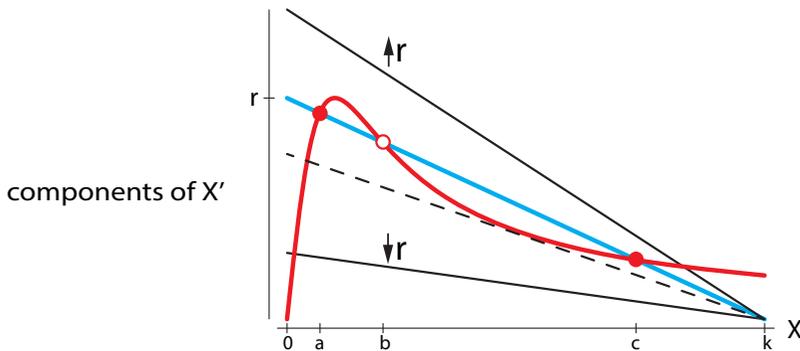


Figure 3.46: Equilibrium points for the high- k Spruce Budworm model as parameter r is varied. For intermediate values of r , for example, the blue line crosses the red curve three times, resulting in three equilibrium points, at $X = a, b$, and c .

Exercise 3.6.4 Using the over–under method, confirm the above statements about the stability of the model’s equilibria.

Exercise 3.6.5 You can also get these results without dividing by X . Pick a value for k and plot $rX(1 - \frac{X}{k})$ and $\frac{X^2}{1+X^2}$ in SageMath. Describe how varying r affects the system’s equilibria.

There are two parameters in this model, r and k . Therefore, we can make a 2-parameter bifurcation diagram, showing us, for each pair of values (k, r) , what the equilibrium point structure is (Figure 3.47 on the following page). This diagram can be thought of as summarizing the results of millions of simulations, one for each pair (k, r) , and that is indeed one way of generating Figure 3.47. However, using some math, we can actually calculate the curves that define the bifurcation regions. We have done that here, following Strogatz (2014). See that excellent treatment for more details.

Exercise 3.6.6 For each of the (k, r) pairs below, describe how many equilibria the system has, whether they’re high or low, and what their stability is.

a) $k = 10, r = 0.1$

b) $k = 25, r = 0.6$

c) $k = 20, r = 0.4$

This two-parameter bifurcation diagram gives us a powerful roadmap that shows us how to change parameters to convert the system from one type of behavior to another. We could imagine three different kinds of interventions that could be made in the spruce budworm system.

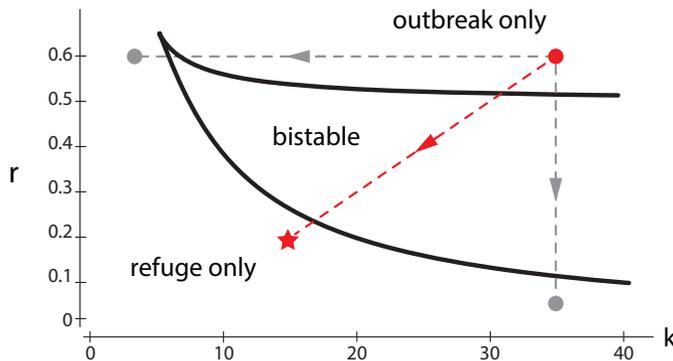


Figure 3.47: Two-parameter bifurcation diagram for the Spruce Budworm model. The diagram shows, for any pair (k, r) , the type of equilibria that the model displays for that pair of parameter values.

- We could lower r , the reproductive rate of the insect, by preventing them from mating successfully.
- We could lower k by spraying defoliants, because the carrying capacity k depends on the amount of total leaf space available.
- We could directly lower X by spraying insecticide.

Obviously, each strategy has social and environmental costs associated with it. The optimal strategy is the one that moves us from “outbreak” to “refuge” at the lowest cost.

Which strategy is best? The bifurcation diagram shows us that the best strategy is a combination one. For example, suppose we are in an “outbreak” state, with, say, $k = 35$ and $r = 0.6$ (the red dot). We would like to get back to the low- X “refuge” state. The bifurcation diagram shows us that a pure- r strategy, moving straight downward in the diagram (vertical gray arrow), would be very difficult. Lowering r alone would require a drastic change down to $r < 0.1$. Similarly, a pure- k strategy, spraying defoliant (horizontal gray arrow), also wouldn’t work well, since we would be moving to the left, and would have to lower k drastically to see any effect.

However, a combined r -and- k strategy would work better than either alone. Moving along the red arrow, say to $k = 15$ and $r = 0.2$, would successfully bring us back to the refuge state.

There is another, even more interesting, intervention strategy. In order to best visualize it, let’s expand the bifurcation diagram to make it into a 3D figure. We will keep (k, r) space as the base of our 3D space, and now, instead of just saying how many equilibrium points there are, we will actually plot where they are in the third dimension, which is X -space.

Now we will make another bifurcation diagram. Only now we have two parameters, not one. We will make our two-parameter space (k, r) the base plane, and at every point (k_0, r_0) in this plane, we will erect a copy of the phase portrait for the differential equation with parameter values $k = k_0, r = r_0$, using green balls to denote stable equilibrium points and red balls to denote unstable ones (Figure 3.48).

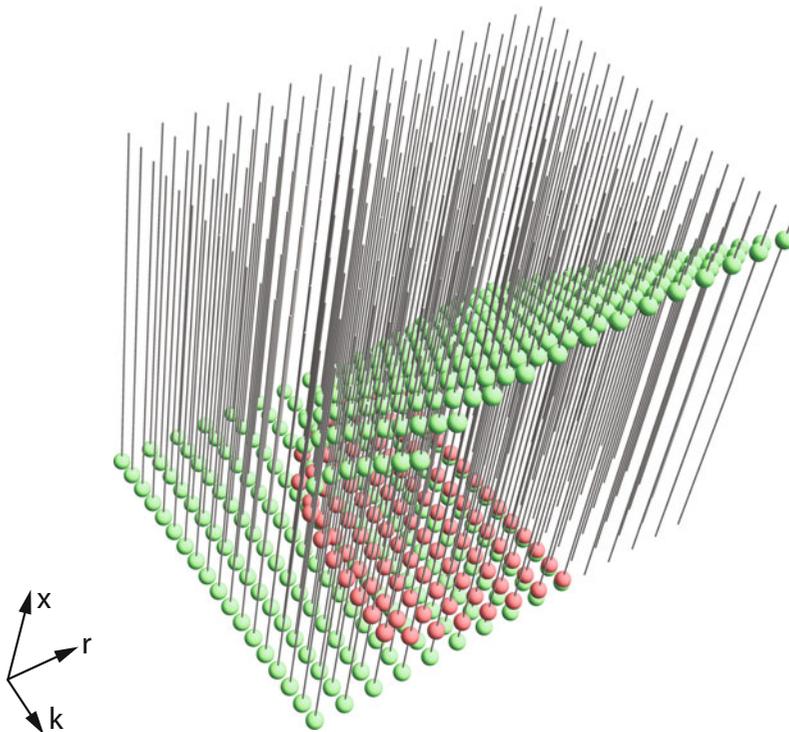


Figure 3.48: Construction of the bifurcation diagram for the spruce budworm model.

Then we remove the state space construction lines, and the resulting figure is a pleated surface over (r, k) space (Figure 3.49).

This amounts to solving the equilibrium point condition

$$X' = rX\left(1 - \frac{X}{k}\right) - \frac{X^2}{1 + X^2} = 0$$

and plotting these results for many values of k and r . The resulting plot is intriguing.

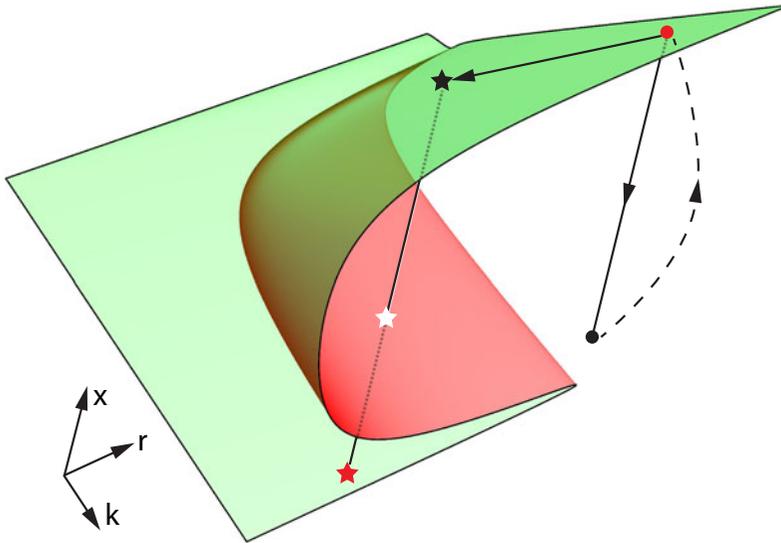


Figure 3.49: Equilibrium points ($X' = 0$) for the spruce budworm model, for many values of r and k . Stable equilibria are in green; unstable equilibria are in red.

We can clearly see that there is another strategy available. First, suppose we are at the red dot, in outbreak. Someone proposes massive insecticide use to lower X . It is obvious from the diagram that if we simply lower X , that moves us down in the 3D space to a low X state. But there is no stable equilibrium there, so the system will not stay there. The only stable equilibrium is the high- X outbreak state, and therefore the system will immediately bounce back to it after our intervention.

Instead, if we lower k and r together just a little to get us into the bistable region (black star), and then lower X just a little, to just below the unstable equilibrium (white star), then the system will go by itself to the low- X equilibrium (red star). This equilibrium is stable, so the system will stay there with no further intervention.

In this way, the bifurcation diagram gives us a kind of “master view” of the possibilities of intervention in a system. There are many interesting applications of this bifurcation diagram. Search online for “cusp bifurcation” for more examples.

Changes in Parameters: Pitchfork Bifurcations

There is another type of bifurcation that is less common in biology than saddle-node bifurcations, but is still worth knowing about. In this kind of bifurcation, termed a *pitchfork bifurcation*, a stable equilibrium becomes unstable, and two new stable equilibria appear on either side of it.

Let's consider an example from social behavior. Our account follows the very interesting paper called *Herd Behaviour, Bubbles and Crashes* by Lux (1995).

Consider a large group of people who may hold one of two opinions, which we will call N (for "negative") and P (for "positive"). For example, the individuals might be investors deciding whether the price of a particular stock will go up (P) or down (N). Individuals change their minds by following the opinions of others.

Let N be number of people who hold the negative opinion (at time t), and let P be the number of people who hold the positive opinion (at time t). We assume that the total population is fixed at a constant number $2m$ (the reason for this somewhat unusual choice will soon become clear):

$$N + P = 2m \quad (3.6)$$

We then write our basic model as a compartmental model (Figure 3.50). (You can also think of this as being similar to a chemical reaction.)

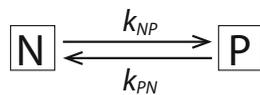


Figure 3.50: Compartmental model of the opinion-flipping game. N denotes the number of people who hold the Negative opinion and P denotes the number of people who hold the Positive opinion.

From this reaction scheme, we can write the differential equation

$$\begin{aligned} P' &= k_{NP} \cdot N - k_{PN} \cdot P \\ N' &= -k_{NP} \cdot N + k_{PN} \cdot P \end{aligned}$$

Now although there are apparently two variables in this differential equation, in fact there is really only one, since the sum of N and P is constant at $2m$. Therefore, we can define a new single variable X by

$$X = \frac{P - N}{2m} \quad (3.7)$$

Thus X measures the imbalance toward positive; when $X = 0$, then the positive and negative people exactly balance. When $X = 1$, everyone holds the P opinion, while when $X = -1$, everyone holds the N opinion.

Now let's write the differential equation in terms of the single variable X . Recalling that X , N , and P are all functions of t and differentiating equation (3.7) with respect to t , we get

$$\begin{aligned} X' &= \left(\frac{1}{2m}\right) \cdot (P' - N') \\ &= \left(\frac{1}{2m}\right) \cdot (2k_{NP} \cdot N - 2k_{PN} \cdot P) \\ &= \left(\frac{1}{m}\right) \cdot (k_{NP} \cdot N - k_{PN} \cdot P) \end{aligned}$$

Now we use equation (3.6) and equation (3.7) to get

$$X = \frac{P - (2m - P)}{2m}$$

so

$$P = m(1 + X)$$

Similarly,

$$N = m(1 - X)$$

so now we can write the differential equation as

$$X' = k_{NP} \cdot (1 - X) - k_{PN} \cdot (1 + X)$$

Now we have to propose expressions for the rate constants k_{NP} and k_{PN} . For example, k_{NP} is the rate of change to positive. Let's look at the quantity

$$\frac{d(k_{NP})}{dX}$$

which measures how sensitive k_{NP} is to the degree of positive tilt. One plausible answer for this is that there is a bandwagon effect:

$$\frac{d(k_{NP})}{dX} \text{ is proportional to } k_{NP}$$

This says that the larger the per capita conversion rate, the more sensitive it is to the degree of positive tilt. We will let that constant of proportionality be a . So a measures the strength of the bandwagon effect:

$$\frac{d(k_{NP})}{dX} = a \cdot k_{NP}$$

As we saw in Chapter 2, this differential equation has an explicit solution, whose formula is

$$k_{NP} = v \cdot e^{ax}$$

Similarly, we also assume that

$$\frac{d(k_{PN})}{dX} = -a \cdot k_{PN}$$

yielding

$$k_{PN} = v \cdot e^{-ax}$$

Here v is a constant representing the speed of opinion changing. (Note that at $X = 0$, $v = k_{PN} = k_{NP}$), and a is the parameter representing the strength of the contagion factor. It measures how strongly individuals' opinions are influenced by the opinions of those around them.

We then get

$$X' = \underbrace{(1 - X) \cdot v \cdot e^{ax}}_{\text{increases } X} - \underbrace{(1 + X) \cdot v \cdot e^{-ax}}_{\text{decreases } X} \quad (3.8)$$

The stability analysis of this equation is shown in Figure 3.51. Note that for values of $a < 1$ (black), there is only one equilibrium point, at $X = 0$. It is stable. But for $a > 1$ (red and blue), the formerly stable equilibrium point at 0 becomes unstable, and two new stable equilibria appear, at positive and negative values of X .

This is called a *pitchfork bifurcation* (Figure 3.52). When $a \leq 1$, the system has a single stable equilibrium at $X = 0$. However, when $a > 1$, the equilibrium at $X = 0$ becomes unstable, and two new stable equilibria emerge.

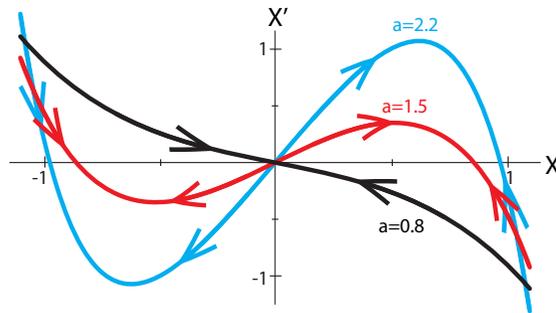


Figure 3.51: Graphs of X' for the opinion-flipping model with three different values of the parameter a .

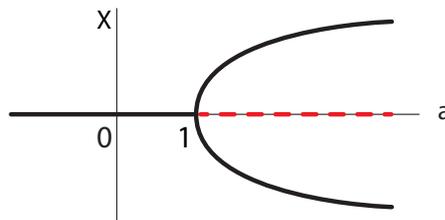


Figure 3.52: Bifurcation diagram for the pitchfork bifurcation in equation (3.8).

Exercise 3.6.7 Use SageMath to plot the two parts of equation (3.8) (increases and decreases) for three values of a . Find the resulting equilibria and determine their stability.

The interpretation of this bifurcation gives us insight into the dynamics. Recall what the key terms mean: X is the “tilt toward P ,” and the bifurcation parameter is a , which measures how strongly individuals are influenced by the opinions of others (the bandwagon effect). We saw that if a is low, there is only one stable equilibrium point, at $X = 0$. But $X = 0$ is the “no tilt” state, so a stable equilibrium at $X = 0$ means that the population will achieve a stable balance of N and P views. But if $a > 1$, then the bandwagon effect becomes so strong that the “evenly balanced” equilibrium is no longer stable, and the system instead has two new stable equilibria, which are “all N ” and “all P .” The middle is unstable.

The interesting thing to note is that once the $X = 0$ equilibrium loses its stability, which new equilibrium the system ends up at can be determined by the tiniest of fluctuations. Thus, we can observe big differences arising for trivial reasons.

Bifurcation: Qualitative Change

Perhaps the most important lesson to take from these discussions of bifurcations is the idea of explaining qualitative changes in the behavior of systems. People often think of math as “quantitative.” With that mindset, it can seem strange to talk about “qualitative mathematics.” Yet in a way, that’s exactly what bifurcation theory is.

It’s important to realize that very often in science, we really are asking why a system has the qualitative behavior it does:

- Why does the deer–moose system have a stable coexistence equilibrium (or not)?
- Why does the *lac* operon have a bistable switch? What causes it to flip from mode A to mode B?

- In the model of public opinion, why did the middle “balanced opinions” equilibrium become unstable and the two extremes become stable?
- Why does the spruce budworm have outbreaks?

This concept of bifurcation theory as providing a qualitative dynamics originates with Poincaré, who studied qualitative changes in the orbits of the planets in models of the solar system. It was further developed in the twentieth century by pioneers like René Thom and Ralph Abraham.

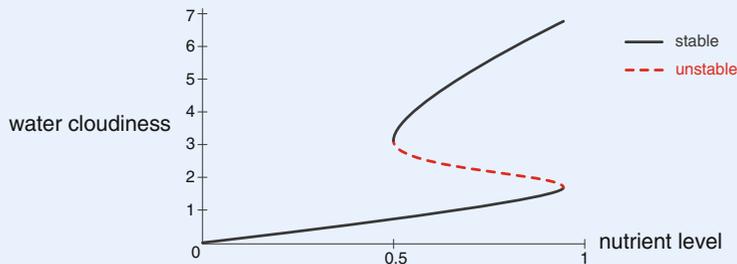
Further Exercises 3.6

1. We saw that in the model of logistic growth with an Allee effect,

$$X' = rX\left(1 - \frac{X}{K}\right)\left(\frac{X}{A} - 1\right)$$

A , the growth threshold, becomes a stable equilibrium point, and K , the carrying capacity, becomes an unstable one when $A > K$. Does this make biological sense? For what ranges of parameter values does the model behave reasonably?

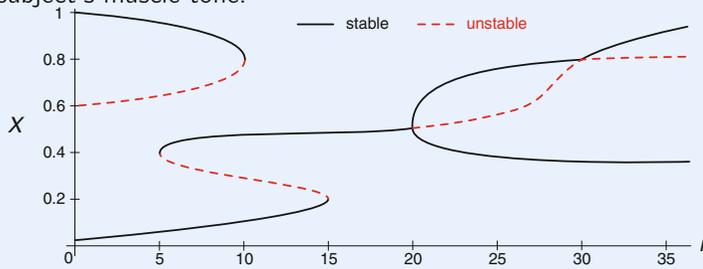
2. The figure below shows a possible relationship between nutrient levels and water turbidity in a lake.



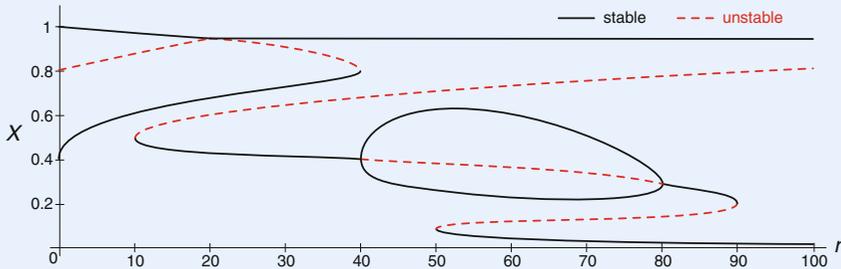
- a) If the nutrient level is 0.2, approximately what will the water turbidity level be?
- b) If the nutrient level then increases to 0.8, approximately what will the water turbidity level be?
- c) Suppose the nutrient level increases further, to 1.0. What will the water turbidity be?
- d) You are in charge of water quality for this lake. Your predecessor on the job decided that lowering nutrient levels to 0.8 would be sufficient to restore clear water. What happened to the water turbidity when this was done? Why?
- e) How low do nutrient levels need to be for the water to become clear again?
- f) The main source of nutrients in the lake is fertilizer washed off from local lawns and gardens. Although people want clear water, significantly reducing fertilizer use is not initially a popular proposal. Explain your nutrient reduction goal in a way community members can understand.

Note: The phenomenon illustrated here, in which a change in state caused by a parameter change cannot be reversed by undoing the parameter change, is known as *hysteresis*. Scheffer et al. (2001) provides excellent explanations and examples.

3. You are studying the effects of psychological stress on movement. Suppose you generated the following bifurcation diagram, where r is the stress level felt by the subject, and X is the subject's muscle tone.



- List the bifurcations that occur in this diagram. For each one, state what type of bifurcation it is and at what value of r it occurs.
 - How many stable equilibrium points are there when $r = 25$?
 - Suppose that initially, $r = 8$ and $X = 0.1$. What happens if r is increased to 18?
 - What could happen if f was increased to 22?
4. Suppose that the bass population in a lake is affected by terrestrial carbon input (falling leaves, etc.) in a way portrayed in the bifurcation diagram below, with r the carbon input and X the bass population density.



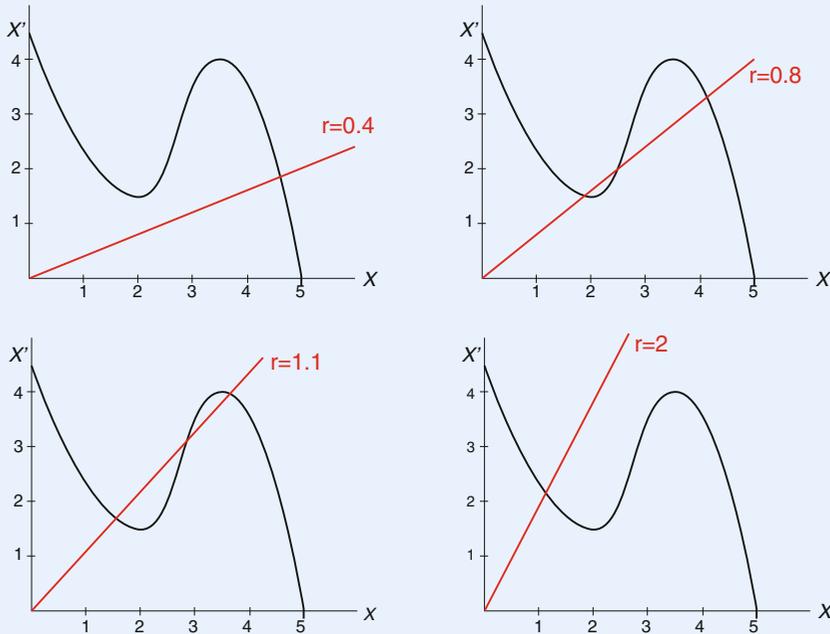
- List the bifurcations that occur in this diagram. For each one, state what type of bifurcation it is and at what value of r it occurs.
 - How many equilibria are there when $r = 60$? Say which are stable and which are unstable.
 - Explain the meaning of the loop in the middle of the diagram. (*Hint: Suppose r is increasing.*)
 - Suppose you can manipulate the carbon inputs to this system. If initially, $r = 70$ and $X = 0.05$, how could you manipulate r to raise X to approximately 1? Describe how X will change during the manipulations.
5. Let X be the concentration of a certain protein in the bloodstream. The protein is produced at a rate $f(X)$, and it degrades at a rate rX (see graphs below). In other

words, X satisfies the differential equation

$$X' = f(X) - rX$$

where $f(X)$ is the function shown in black in the graphs below.

- a) Use the “over–under” method to find the equilibrium points of this system, and determine their stability, for the following values of r :



- b) Draw a bifurcation diagram for this system as r varies from 0 to 3. How many bifurcations occur, and what type is each one? You may want to trace or copy the graph of $f(X)$.

6. Suppose that in the absence of predators, a population grows logistically with $r = 0.75$ and $k = 1$. Also, a fraction h of the population is hunted each year.
- Write the differential equation for this system.
 - Construct a bifurcation diagram for this system with h as the parameter. What kind(s) of bifurcation(s) do you observe?
 - Change r to 0.5. At what value of h does the bifurcation now occur?
7. Create a SageMath animation similar to Figure 3.46. Your animation should vary r and show how this affects where and whether the line and curve cross.
8. Create a SageMath interactive of the spruce budworm system. Manipulate r to approximate the value at which the bifurcation takes place.
9. Using SageMath and the over–under method, create plots that show how the number and stability of equilibria of the model $x' = (1 - x)e^{ax} - (1 + x)e^{-ax}$ vary with a .