

Lecture 6: Dynamical Systems: Equilibrium and Bifurcation

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6.1 Numerical Methods

Mathematical models that are expressed as differential equations involve assumptions about derivatives. In other words, the assumptions often include phrases such as “the rate of change of \dots ” or “the rate of increase of \dots .”

A first order differential equation is of the form

$$\frac{dy}{dt} = f(t, y(t))$$

the purpose is to find function $y(t)$.

An initial-value problem is of the form

$$\frac{dy}{dt} = f(t, y(t)), \quad y(t_0) = y_0$$

A solution to the initial-value problem is a differentiable function $y(t)$ defined on some interval $a < t < b$ containing t_0 such that

1. $\frac{dy}{dt} = f(t, y(t))$ for all t in the interval $a < t < b$ and
2. $y(t_0) = y_0$

A second-order autonomous equation has

- one independent variable (often t) and
- one dependent variable (often x or y).

It has the format

$$\frac{d^2y}{dt^2} = f(y, \frac{dy}{dt})$$

with initial condition: (y_0, y'_0) . Solution to an initial-value problem is a differentiable function $y(t)$ defined on some interval $a < t < b$ containing t_0 that satisfy the system and the initial conditions.

A first-order autonomous system has

1. one independent variable (often t) and
2. two dependent variables.

$$\begin{cases} \frac{dx}{dt} = f(x, y) \\ \frac{dy}{dt} = g(x, y) \end{cases}$$

with *initial condition*: (x_0, y_0) , which is a pair of numbers.

Solution to an initial-value problem: a pair of functions $(x(t), y(t))$ that satisfy the system and the initial conditions.

The existence and the uniqueness of the solutions of ordinary differential equations is guaranteed by the Picard–Lindelöf theorem.

Theorem 6.1 *Consider the initial value problem*

$$\frac{dy}{dt} = f(t, y(t)), y(t_0) = y_0$$

Suppose f is uniformly Lipschitz continuous in y (meaning the Lipschitz constant can be taken independent of t) and continuous in t , then for some value $\epsilon > 0$, there exists a unique solution $y(t)$ to the initial value problem on the interval $[t_0 - \epsilon, t_0 + \epsilon]$

The result can be extended to systems of ordinary differential equations:

Theorem 6.2 *Let*

$$\frac{d\mathbf{Y}}{dt} = \mathbf{F}(\mathbf{t}, \mathbf{Y})$$

be a system of differential equations. Suppose that t_0 is an initial time and \mathbf{Y}_0 is an initial value. Suppose also that the function \mathbf{F} is continuously differentiable. Then there is an $\epsilon > 0$ and a function $\mathbf{Y}(\mathbf{t})$ defined for $t_0 - \epsilon < t < t_0 + \epsilon$, such that $\mathbf{Y}(\mathbf{t})$ satisfies the initial-value problem. Moreover, for t in this interval, this solution is unique.

We can solve ordinary differential equations using Matlab in two ways: numerical and symbolic.

Consider the van der Pol differential equation

$$\frac{d^2y}{dt^2} - (1 - y^2)\frac{dy}{dt} + x = 0$$

first rewrite this equation as a system of first-order ODEs by making the substitution $y' = y_2$ and $y = y_1$. The resulting system of first-order ODEs is

$$\begin{cases} y_1' = y_2 \\ y_2' = (1 - y_1^2)y_2 - y_1 \end{cases}$$

Solve the ODE using the ode45 function on the time interval $[0 \ 20]$ with initial values $[2 \ 0]$:

```
function dydt = vdp1(t, y)
    dydt = [y(2); (1 - y(1)^2) * y(2) - y(1)];
% Solve the differential equation using ode45
[t,y] = ode45(@vdp1,[0 20],[2; 0]);
```

We can also solve differential equations symbolically in Matlab. Consider the second-order differential equation $\frac{d^2y}{dt^2} = a^2y$ with initial conditions $y(0) = b$ and $y'(0) = 1$:

```
syms y(t) a b
eqn = diff(y,t,2) == a^2 * y;
Dy = diff(y,t);
cond = [y(0)==b, Dy(0)==1];
ySol(t) = dsolve(eqn,cond)
```

We can find solutions numerically for any given initial value problem, but a general picture of the behavior of the solutions for all the initial value problem is valuable. Aside from the numerical solutions, we also want to develop a systematic theoretical understanding of the behaviors of dynamic systems.

6.2 Equilibrium Points: One Dimension

For a first-order differential equation $\frac{dy}{dt} = f(x, y)$, $f(x, y)$ defines a slope field, and the graph of a solution must be everywhere tangent to it.

Examples $\frac{dy}{dt} = y - t$

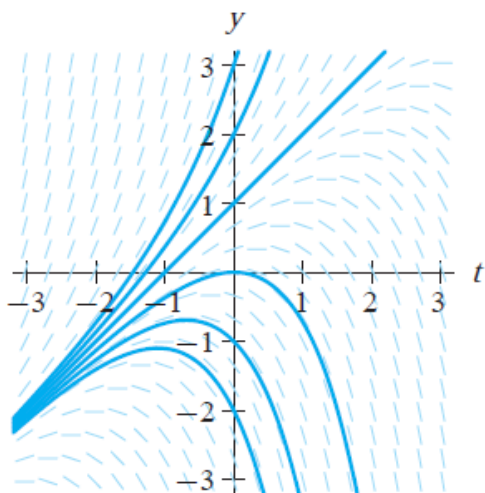


Figure 6.1: Slope field example.

Similarly, a system of first-order differential equations

$$\frac{d\mathbf{Y}}{dt} = \mathbf{F}(\mathbf{Y})$$

define a vector field. We can also define component graphs as graphs of $x(t)$ and $y(t)$; solution curve as the parametrized curve of $(x(t), y(t))$; phase plane as xy -plane; phase portrait as multiple solution curves.

Example Mass spring system again, $\mathbf{F}(\mathbf{y}, \mathbf{v})^T = (\mathbf{v}, -\mathbf{y})^T$

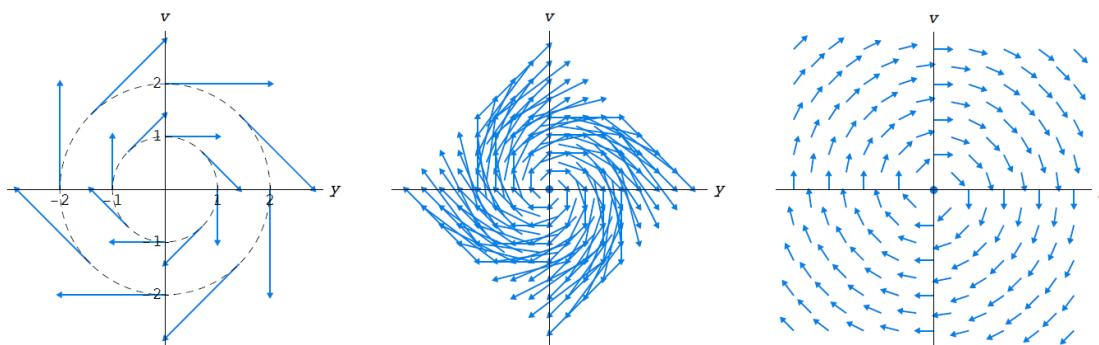


Figure 6.2: Vector field example.

In order to develop a systematic theoretical understanding of the behaviors of dynamic systems, we need to consider **equilibrium solutions**, or solutions for which the derivative functions are constant for all t . Equilibrium points correspond to the equilibrium states of the dynamic system modeled by the differential equation(s).

We have already introduced the logistic model of population growth

$$\frac{dp}{dt} = kp(1 - \frac{p}{N})$$

where k is a growth-rate parameter and N is the carrying capacity. We can draw the phase portrait of the model using test points:



Figure 6.3: Phase portrait of the logistic model.

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 $X = 0$.

According to the fundamental theorem of algebra, the number of roots for the derivative function is the same as the order of the function. Therefore there are only 2 equilibrium points for the logistic population model.

For first order ODEs, there are three types of equilibrium points: stable ones and unstable ones.

- 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. ($x' = x^2$)



Figure 6.4: Stable and unstable equilibria.

For first order ODEs, if the derivative function is linear, then there are only two types of equilibrium points: stable ones and unstable ones.

Definition 6.3 $f(x)$ is linear if and only if

1. $f(x + y) = f(x) + f(y)$
2. $f(ax) = af(x)$

The only functional forms that satisfy the linear conditions are

$$f(x) = kx, f(x) = -kx, k \geq 0$$

For $x' = kx$, the equilibrium point is stable. While for $x' = -kx$, the equilibrium point is unstable.

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.

For a first order ODE $x'(t) = f(x)$, say the logistic population model, consider the graph of $f(x)$ vs. x :

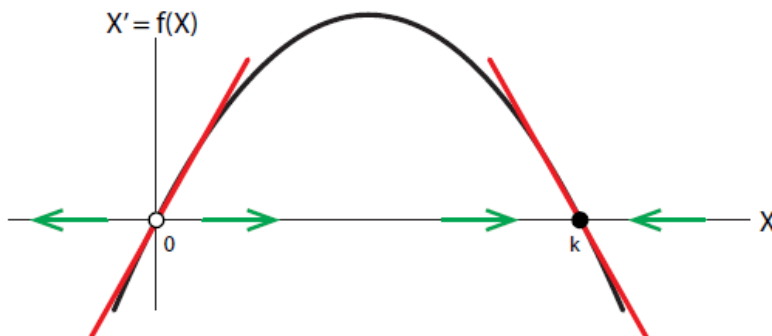


Figure 6.5: Graphical linear stability analysis.

The stable or unstable equilibrium points are characterized by the negative or positive sign of the slope of the tangent of the derivative function f at the point:

$$slope = \left. \frac{dx'}{dx} \right|_{x_0} = \left. \frac{df}{dx} \right|_{x_0}$$

Example The logistic population model $\frac{dp}{dt} = kp(1 - \frac{p}{N})$

6.3 Equilibrium Points: Multiple Dimensions

Consider a system of first order ODEs:

$$\begin{cases} \frac{dx}{dt} = f(x, y) \\ \frac{dy}{dt} = g(x, y) \end{cases}$$

We can find the equilibrium points by setting $x' = f = 0$ and $y' = g = 0$.

Let's first look at two one-dimensional differential equations and mix-match them. See the Matlab code for illustration.

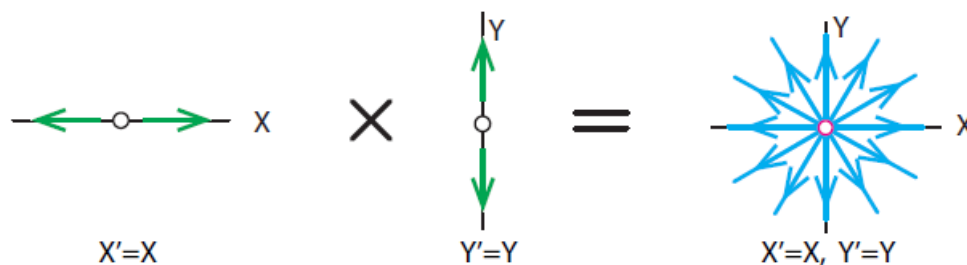


Figure 6.6: Unstable node.

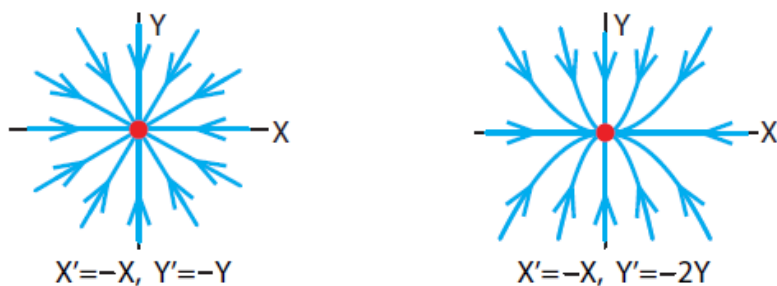


Figure 6.7: Unstable node.

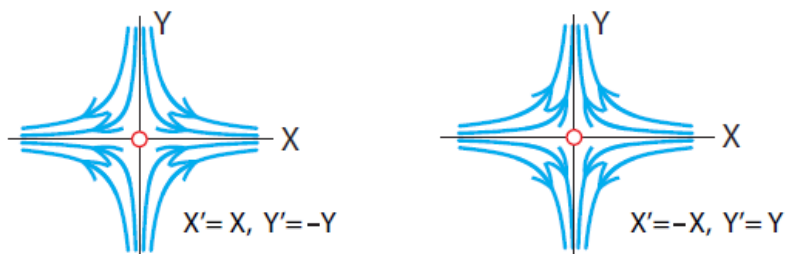


Figure 6.8: Unstable node.

But the mass-spring system is different:

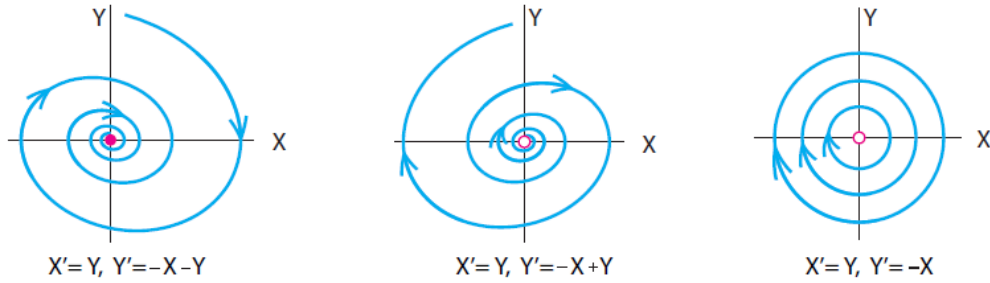


Figure 6.9: Equilibrium points in 2D with rotation.

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).

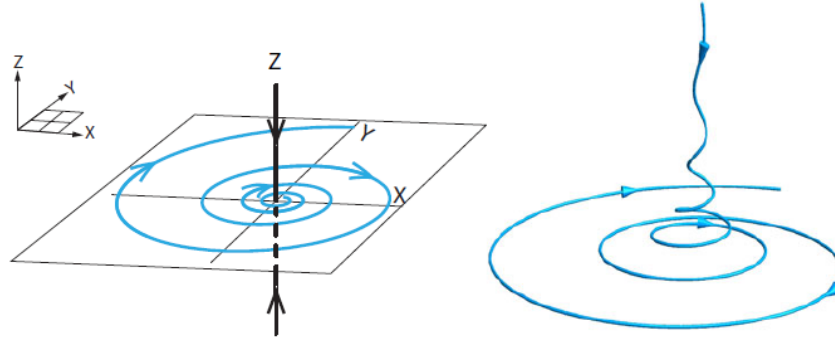


Figure 6.10: Equilibrium points in 3D.

6.4 Multiple Equilibria: The Competition Model

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 . We adopt the following assumptions:

- 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.
- 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:

$$\begin{cases} \frac{dD}{dt} = 3D - MD - D^2 \\ \frac{dM}{dt} = 2M - 0.5MD - M^2 \end{cases}$$

First find the equilibrium points.

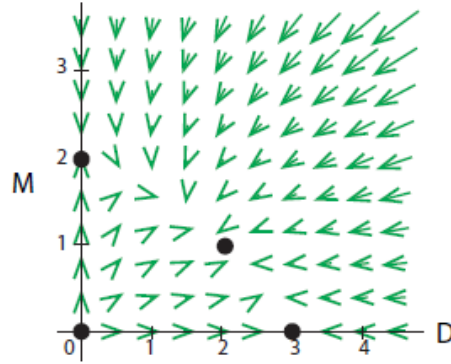


Figure 6.11: Vector field and equilibrium points for the deer-moose competition model.

The line along which $D = 0$ is called the D-nullcline, and similar for M-nullcline. We can use the method of nullcline to find out the stability of the equilibrium points.

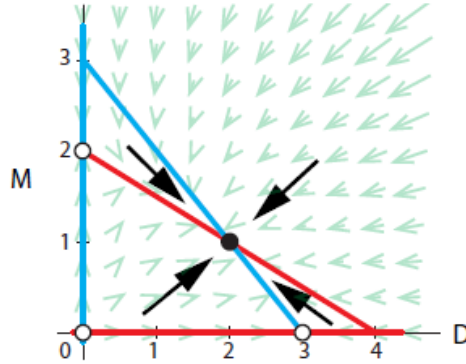


Figure 6.12: Nullclines for the deer-moose model.

Now let's increase the competition between two species:

$$\begin{cases} \frac{dD}{dt} = 3D - 2MD - D^2 \\ \frac{dM}{dt} = 2M - MD - M^2 \end{cases}$$

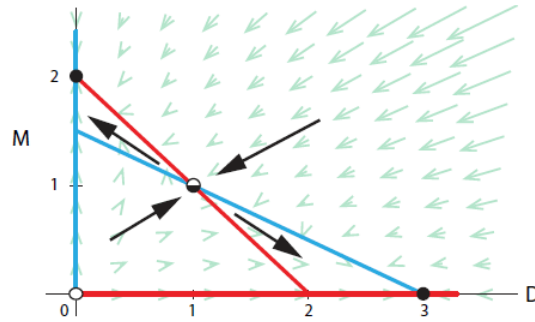


Figure 6.13: Nullclines for the more competitive deer-moose model.

We can use Matlab to find out the phase portrait of the competition model.

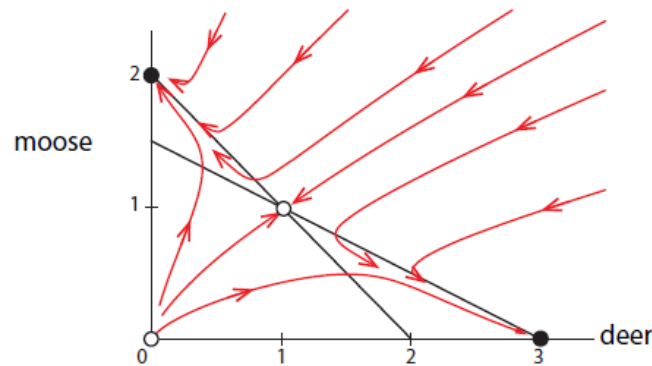


Figure 6.14: Phase portrait and the nullclines for the more competitive deer-moose model.

6.5 Bifurcations of Equilibria: The *lac* Operon

Consider a system with multiple stable equilibrium points. 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.

The terminology “basin” comes from geography. It is also a great illustration of the concept.

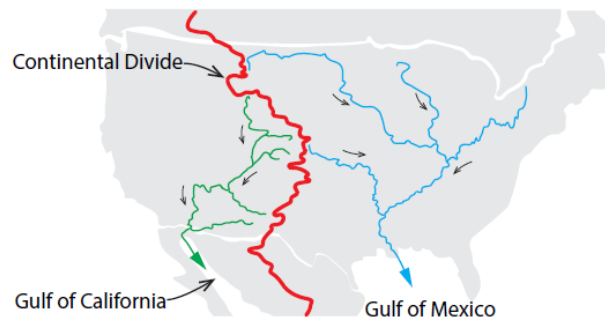


Figure 6.15: The two principal river systems of the United States divide it into two great basins.

Using the concept of basin, we can define the concept of switch. A **switch** is an unstable equilibrium point between two stable equilibrium points. A switch separates two basins.

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*.

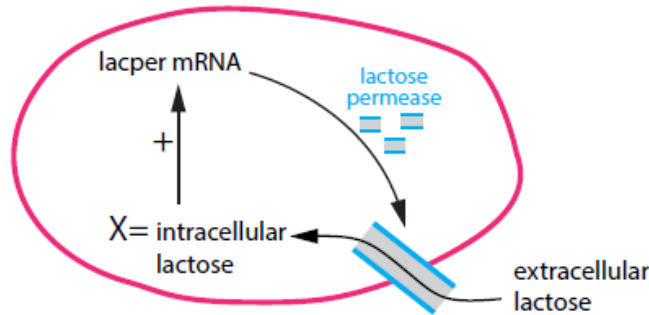


Figure 6.16: Schematic of the lac operon.

Let X equal the intracellular lactose level. We will model the cellular use of lactose by a differential equation:

$$\dot{X} = \text{lactose import (production)} - \text{lactose metabolism (degradation)}$$

We need a sigmoid function to model the lactose import rate. Why?

$$\frac{dX}{dt} = \frac{a + X^2}{1 + X^2} - 0.4X$$

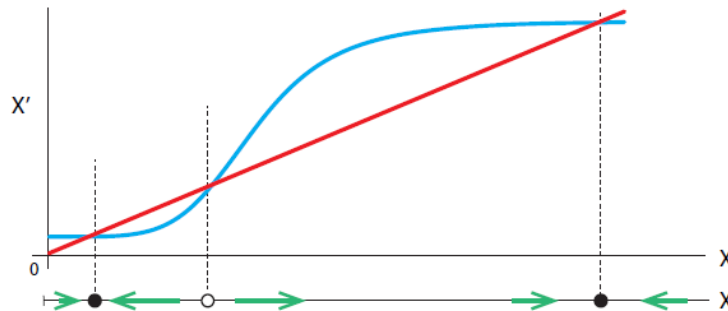


Figure 6.17: Rates of lactose importation (blue) and metabolic degradation (red) as functions of lactose concentration.

In general, we can control the rate of lactose metabolism, which means that we can change the value of 0.4 in the lac operon differential equation.

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

It turns out that r controls the behavior of the lac operon system. We can characterize the relation by the concept of bifurcation.

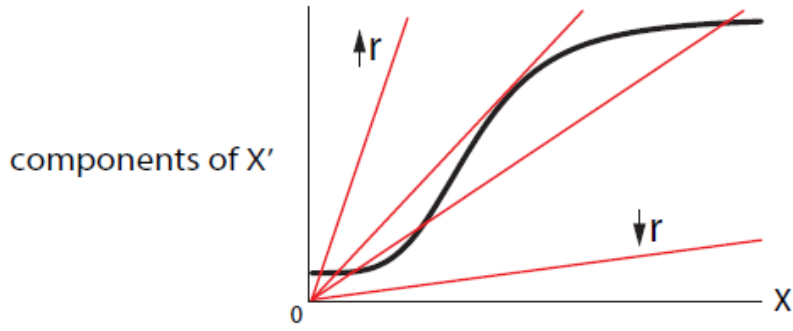


Figure 6.18: The effect of increasing r in the biological switch model.

Bifurcation refers to the phenomenon that a change in parameters can result in a qualitative change in the equilibrium points of a system.

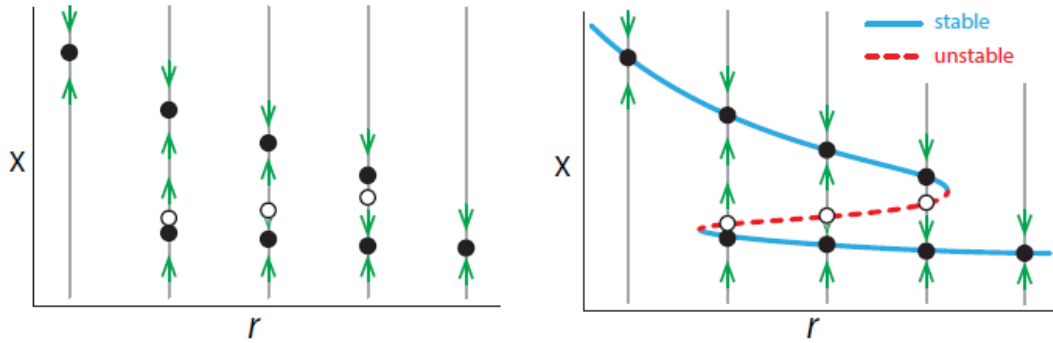


Figure 6.19: Constructing the bifurcation diagram for biological switch model.

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.

There are other two types of bifurcations. let's illustrate them using scientific examples in the next sections.

6.6 Pitchfork Bifurcations: Public Opinion

Pitchfork bifurcations refer to the phenomenon that a stable equilibrium becomes unstable, and two new stable equilibria appear on either side of it.

Let's consider an example from social behavior. Consider a large group of people who may hold one of two opinions, which we will call N (for “negative”) and P (for “positive”).

We make the following two assumptions:

- The total population is fixed at a constant number $2m$
- The bandwagon effect: the larger the per capita conversion rate, the more sensitive it is to the degree of positive tilt.

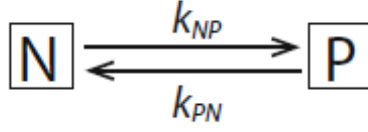


Figure 6.20: Compartmental model of the opinion-flipping game.

From this reaction scheme, we can write the differential equation

$$\begin{cases} \frac{dP}{dt} = k_{NP} \cdot N - k_{PN} \cdot P \\ \frac{dN}{dt} = -k_{NP} \cdot N + k_{PN} \cdot P \end{cases}$$

Define the imbalance toward positive as X

$$X = \frac{P - N}{2m}$$

The differential equations can be transformed into

$$\frac{dX}{dt} = k_{NP}(1 - X) - k_{PN}(1 + X)$$

According to assumption 2,

$$\frac{dk_{NP}}{dx} = a \cdot k_{NP}$$

We get $k_{NP} = v \cdot e^{ax}$. Similarly, $k_{PN} = v \cdot e^{-ax}$. Ultimately we get

$$\frac{dX}{dt} = (1 - X) \cdot v \cdot e^{ax} - (1 + X) \cdot v \cdot e^{-ax}$$

Analyze the stability of the equilibrium points:

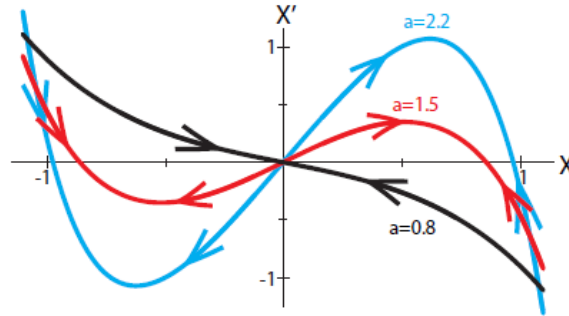


Figure 6.21: Graphs of X' for the opinion-flipping model with three different values of the parameter a .

The bifurcation diagram is called the pitchfork bifurcation.

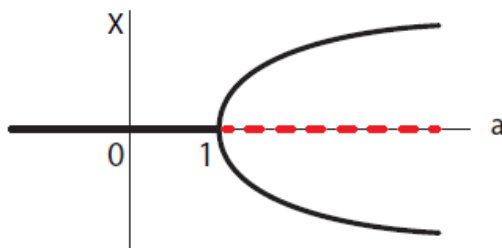


Figure 6.22: Bifurcation diagram for the pitchfork bifurcation in equation.

6.7 Transcritical Bifurcation: 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**.

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

$$\frac{dy}{dt} = ky(1 - \frac{y}{N})(\frac{y}{a} - 1)$$

We can find the equilibrium points by setting $\frac{dy}{dt} = ky(1 - \frac{y}{N})(\frac{y}{a} - 1) = 0$:

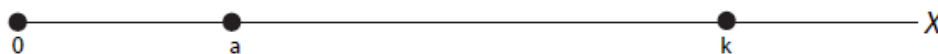


Figure 6.17: State space for the Allee effect model, with its three equilibrium points

Linear stability analysis:

$$\frac{dy'}{dy} = \begin{cases} -k & x = 0, \text{ stable} \\ k - \frac{ka}{N} & x = a, \text{ unstable} \\ k - \frac{kN}{a} & x = N, \text{ stable} \end{cases}$$

The corresponding bifurcation is called the transcritical bifurcation.

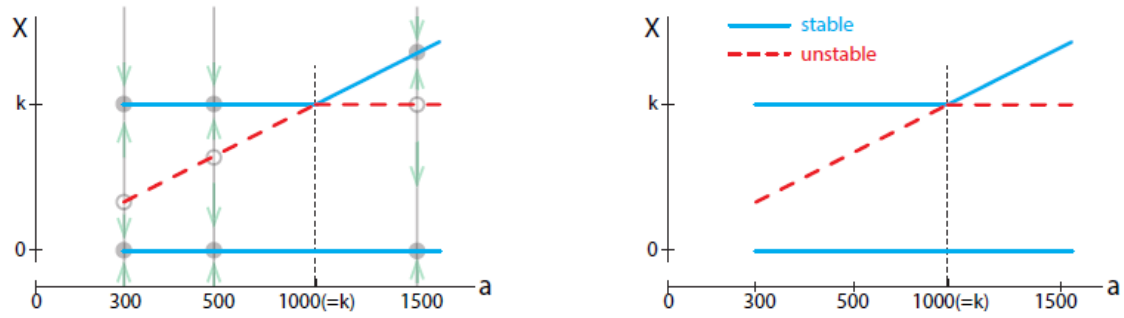


Figure 6.18: A bifurcation diagram for the logistic population model with the Allee Effect

Euler's method is the most basic fixed-step-size algorithm for the numerical approximation of solutions.

References

- [1] A. Garfinkel, J. Shevtsov and Y. Guo, *Modeling Life: The Mathematics of Biological Systems*, Springer International Publishing; 4th edition, 2017.
- [2] P. Blanchard, R.L. Devaney and G. R. Hall, *Differential Equations*, Cengage Learning; 4th edition, 2012.