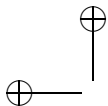


Chapter 3

Ordinary Differential Equations



3.1 Introduction to Ordinary Differential Equations

We have seen in the introductory section (Section 1.2) that the recovery of infected individuals can be modelled by a differential equation (equation (1.2)). In general, differential equations are extremely useful in modelling biological processes. On the one hand, modelling with differential equations is quite transparent, even for complicated biological systems. On the other hand, a powerful mathematical theory is available, including explicit solutions, approximative solutions, numerical solutions, qualitative behaviour, and the theory of dynamical systems. As soon as a model has been derived, it can be treated as a mathematical entity. General theorems and analytical methods can be applied to generate useful results. These results then can be interpreted in biological terms.

The possibility of abstraction is the essential advantage of mathematical modelling. For example, to understand the behaviour of solutions to the equation

$$x'(t) = 2x(t),$$

it does not matter whether $x(t)$ describes a growing fish population, a growing tumor, or the increase in infected individuals. Mathematically, it is just the equation for exponential growth that can be treated and solved without referring to the interpretation at hand. Once the results are established, they need to be understood in biological terms. In this section, we treat differential equations as differential equations, and on the way look at many examples and applications to biological systems.

An *ordinary differential equation* is an equation for an unknown function of one variable, say $x(t)$, which involves the function and some of its derivatives. For example,

$$x'(t) = 2, \quad y'(t) = 3t, \quad z'(t) = \frac{1}{2}z(t), \quad (3.1)$$

are three differential equations. A *solution* is a function that satisfies the differential equation. For the above examples, (3.1), it is easy to check that the solutions are of the form

$$x(t) = 2t + c_1, \quad y(t) = \frac{3}{2}t^2 + c_2, \quad z(t) = c_3 e^{\frac{1}{2}t}, \quad (3.2)$$

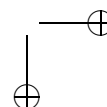
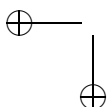
respectively, with constants of integration c_1 , c_2 , and c_3 . The solutions as given in (3.2) are called *general solutions*. If we specify one value for x , y , or z , then the value of c_1 , c_2 , or c_3 is fixed and we obtain a unique solution. In many cases, we specify an *initial condition*, for example,

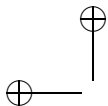
$$x(0) = 1, \quad y(0) = 2, \quad \text{and} \quad z(0) = 1.$$

With use of the above general solutions, we find $c_1 = 1$, $c_2 = 2$, and $c_3 = 1$.

We say that $x(t) = 2t + 1$ solves the *initial-value problem*

$$x'(t) = 2t, \quad x(0) = 1.$$





Similarly, $y(t) = \frac{3}{2}t^2 + 2$ solves the initial value problem $y'(t) = 3t$, $y(0) = 2$, and $z(t) = e^{\frac{1}{2}t}$ solves the initial value problem $z'(t) = \frac{1}{2}z(t)$, $z(0) = 1$.

In general, an ordinary differential equation (ODE),

$$x'(t) = f(x(t), t),$$

for an unknown function, $x(t)$, has the following interpretation. The left hand side, $x'(t)$, describes the *rate of change* of the quantity $x(t)$ over time. The right hand side, $f(x(t), t)$, describes all sources of change in $x(t)$. For the recovery from a disease (equation (1.2)), the change in the amount of infected individuals, $\frac{d}{dt}I(t)$, is given by the recovery rate $-\alpha$ times the number of infected $I(t)$.

To solve a differential equation means to use *local information* (“What happens next?”) to deduce *long time behaviour* (“What happens in the future?”). This interpretation makes ODEs useful for modelling biological processes. If we know all factors of the process at hand, and if we know the rates of change these factors invoke, then we can write down a differential equation. After analyzing and solving the differential equation we seek explanations and predictions for our biological question.

Before we delve into modelling, we will introduce some of the wonderful analytical methods for ODEs, and explain them on the basis of elementary calculus.

3.2 Scalar Equations

We first study *scalar equations of the first order*, that is, equations of the form

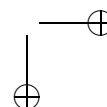
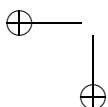
$$x'(t) = f(x(t), t),$$

where $x(t)$ is a scalar function and the equation involves first-order derivatives. If the function $f(x, t)$ does not depend on t , we call the equation *autonomous*. For first-order autonomous scalar ODEs,

$$x' = f(x), \tag{3.3}$$

the *phase-line analysis* explains the qualitative behaviour of solutions without even solving the equation. We consider $f(x) = x(1-x)(2-x)$, for which the graph is shown in Figure 3.1. The function $f(x)$ has zeroes at 0, 1, and 2. We can easily check that $x(t) \equiv 0$, $x(t) \equiv 1$, and $x(t) \equiv 2$ are three constant solutions to the differential equation

$$x' = x(1-x)(2-x). \tag{3.4}$$



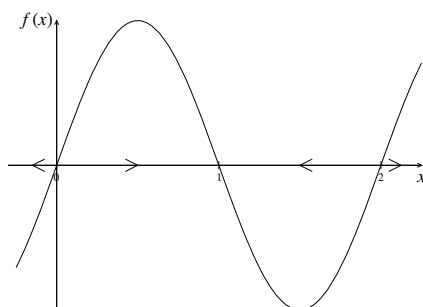


Figure 3.1. Phase-line analysis of $f(x) = x(1-x)(2-x)$. The arrow heads indicate whether the solution of the corresponding ODE is increasing or decreasing.

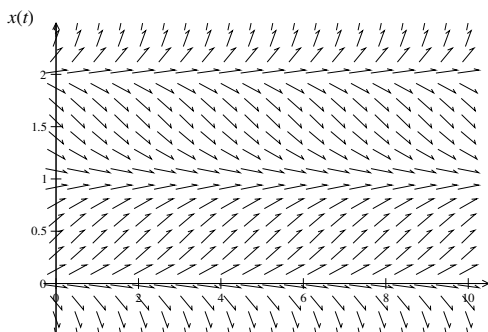


Figure 3.2. Vector field of equation (3.4).

These special solutions are called *equilibria* or *steady states* of (3.4). If initially, at $t = 0$, a solution has the value 0 (or 1 or 2), it remains so for all times $t > 0$. The left hand side of (3.4) describes the change of $x(t)$ over time: the solution $x(t)$ is increasing whenever $f(x) > 0$ and decreasing whenever $f(x) < 0$. In our example, $x(t)$ is increasing in the intervals $(0, 1)$ and $(2, \infty)$; it is decreasing in the intervals $(-\infty, 0)$ and $(1, 2)$. We indicate this behaviour by adding arrow heads to the x -axis in Figure 3.1. If, for instance, the initial condition $x(0)$ is in $(0, 1)$, then the solution will grow and converge to $x = 1$ for $t \rightarrow \infty$.

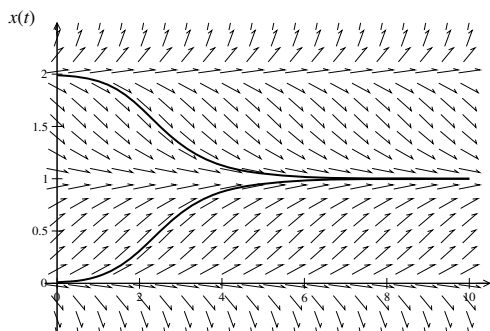


Figure 3.3. Two typical solutions in the vector field of equation (3.4).

To obtain an even better qualitative understanding of the behaviour of the solutions of (3.4), we plot the corresponding *vector field*. For that, we evaluate the *slope* of the solution $x(t)$ for many points (t, x) and draw a short arrow indicating the slope in the (t, x) diagram. Since $x' = f(x)$, the slope is given by $f(x)$. In Figure 3.2, we show the time interval of $[0, 10]$ and the x -interval of $[0, 2.5]$. At approximately 200 points, we have indicated the slope of the solution with a short arrow. Now, solutions $x(t)$ must have slope $x'(t)$, hence solution curves are *tangential* to these short arrows. In Figure 3.3, we show two typical solutions. Note how nicely they follow the vector field. The steady states 0, 1, 2, which we discussed earlier, appear as lines with horizontal arrows, which means the slope is zero ($x'(t) = 0$). Solutions which do not start at 0, 1, or 2 tend to get away from the two equilibria $x = 0$ and $x = 2$, while they converge to $x = 1$. We say that $x = 1$ is a *stable equilibrium*, and $x = 0$ and $x = 2$ are *unstable equilibria*.

With the above *phase-line analysis* and *vector-field analysis* we obtain a very good understanding of the qualitative properties of the solutions *without* solving the equation (3.4). Equation (3.4) can be solved explicitly as well, using separation and partial fractions (compare Exercise 3.9.18). These classical solution techniques can be found in most introductory ODE textbooks (such as Boyce and DiPrima [23]).

Exponential Growth and Exponential Functions.

Solutions to the exponential growth equation

$$N' = rN, \quad (3.5)$$

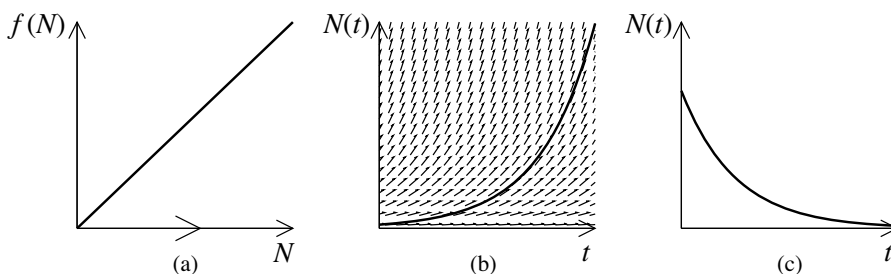


Figure 3.4. (a) Phase-line analysis for equation (3.5) with $r = 2$; (b) vector field and typical solution for $r = 2$; (c) typical solution for $r = -2$.

have the form $N(t) = N_0 e^{rt}$, where $N_0 = N(0)$ is the initial condition. The phase line, the vector field, and a typical solution for $r > 0$ are shown in Figures 3.4 (a) and (b). Figure 3.4 (c) shows a solution for $r < 0$. For $r > 0$, equation (3.5) describes exponential growth, which can be applied to population growth. In the case of $r < 0$, equation (3.5) describes exponential decay, which can be applied to radioactive decay or to the decay of a drug in the blood circulation (see for example Exercise 3.9.1).

Logistic growth

In many cases, exponential growth is not an appropriate model. At a certain size, a growing population will reach a limit where all available resources are used to sustain the high population level, but the habitat will not support any more individuals. Hence, we alter the previous model and consider the logistic equation, also known as the Verhulst equation,

$$N' = rN \left(1 - \frac{N}{K} \right), \quad (3.6)$$

where $r > 0$ is the intrinsic growth rate, and K is the carrying capacity. Compared to the exponential growth model, (3.5), the logistic equation contains the additional term $-(r/K)N^2$. This term can be understood as a competition term of individuals of the same species who compete for the same resources. We use phase-line analysis in Figure 3.5 to obtain the qualitative behaviour of the solution $N(t)$. The population grows and converges to the equilibrium solution $N \equiv K$ for $t \rightarrow \infty$. Note that it will not reach K in finite time, since solutions of ODEs do not intersect (see Theorem 3.2). In Chapter 10.1.5, we use a logistic equation to model growth of cell populations.

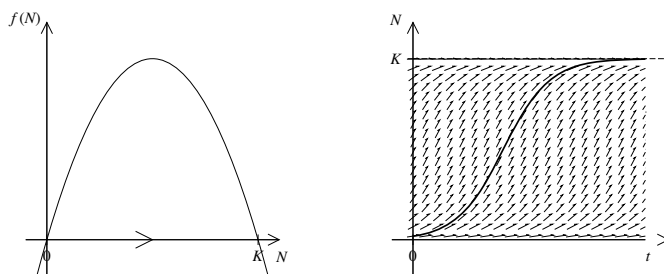


Figure 3.5. (a) Phase-line analysis for equation (3.6); (b) vector field and a typical solution.

3.2.1 The Picard-Lindelöf Theorem

Let us return to the theory of differential equations. There is a general result that states that, under reasonable assumptions, solutions of differential equations do not intersect. To formulate the corresponding theorem, we need the notion of *Lipschitz-continuity*. This means that the function $f(x)$ is continuous and, in addition, it satisfies a growth inequality.

Definition 3.1. A function $f : D \rightarrow \mathbb{R}$ with domain $D \subset \mathbb{R}$ is called Lipschitz continuous if there is a constant $L > 0$ such that $|f(x) - f(y)| \leq L|x - y|$ for all $x, y \in D$.

Theorem 3.2. (Picard-Lindelöf) Assume the function $f : D \rightarrow \mathbb{R}$ is Lipschitz continuous. Let the initial condition x_0 satisfy $x_0 \in D$, $x_0 \notin \partial D$ (boundary of D). Then there is an $\varepsilon > 0$ such that the initial value problem

$$\frac{d}{dt}x = f(x), \quad x(0) = x_0,$$

has a unique solution $x(t)$ for $0 \leq t \leq \varepsilon$.

Remark 3.2.1.

1. Although the theorem is formulated for a small time interval $[0, \varepsilon]$, it implies that solutions to different initial data *never* intersect.

2. The same result holds true for systems of differential equations which can be written in vector notation as

$$\frac{d}{dt} \begin{pmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{pmatrix} = \begin{pmatrix} f_1(x_1, \dots, x_n) \\ \vdots \\ f_n(x_1, \dots, x_n) \end{pmatrix}.$$

In this case, we require that each of the functions $f_1, \dots, f_n$ is Lipschitz continuous in all of its arguments. Qualitative properties of systems of differential equations are more fully covered in the following section.

3. A continuously differentiable function is always Lipschitz continuous (on a bounded domain $D \subset \mathbb{R}$). Hence as soon as $f_1, \dots, f_n$ are differentiable, solutions will never intersect. This includes all differential equations which are built from polynomials, exponentials, sine functions or cosine functions, etc.

3.3 Systems of Equations

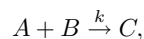
For many biological processes, it is necessary to follow the time evolution of more than one factor or more than one species. For example, a predator-prey system needs at least two dependent variables; predator and prey. Similarly, an epidemic SIR model needs at least three variables; the susceptibles, S , the infected, I , and the recovered, R . We are automatically led to systems of differential equations. To introduce modelling with systems of ordinary differential equations, we study chemical networks, interacting populations, and the spread of an infectious disease in the following sections.

3.3.1 Reaction Kinetics

In this section, we introduce the *law of mass action*, and we show how to use it to model chemical reactions. This method is important for the modelling of many physiological processes. It also serves as a good tool for modelling populations. In fact, as we will see shortly, the epidemic model (3.10) of the following section can be understood in terms of reaction kinetics.

The Law of Mass Action

First, we consider an irreversible reaction process in which reactants A and B produce C :



3.3. Systems of Equations

77

where k is the reaction constant. We are interested in the product C and we argue as follows:

$$\left[\begin{array}{c} \text{change of} \\ \text{the product} \\ \text{over time} \end{array} \right] = \left[\begin{array}{c} \text{number of} \\ \text{collisions of} \\ \text{molecules } A \\ \text{and } B \end{array} \right] \cdot \left[\begin{array}{c} \text{probability that a} \\ \text{collision has enough} \\ \text{kinetic energy to} \\ \text{initiate a reaction} \end{array} \right].$$

Let $a = [A]$, $b = [B]$, and $c = [C]$ denote the concentrations of the reactants A , B , and C , respectively. The product ab is a good approximation for the number of collisions. The probability that a collision has enough energy to overcome the activation energy of this reaction is denoted by a reaction constant $k\Delta t$. If we let ΔC denote the change of the product C over time, then the above word equation can be written as

$$\Delta C = ab(k\Delta t).$$

Dividing both sides by Δt , we obtain

$$\frac{\Delta C}{\Delta t} = k \cdot a \cdot b.$$

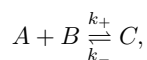
In the limit of $\Delta t \rightarrow 0$, we get

$$\frac{dc}{dt} = k \cdot a \cdot b,$$

which is called the *law of mass action*. Please note that although it is called a *law* of mass action, it is not a physical law; it is indeed a mathematical *model*. For example, it no longer applies if the concentration of one participating factor is many orders of magnitude larger than the other.

Reversible Reactions

For a reversible reaction,



we assume that the molecules of C break apart at a rate that is proportional to the concentration of C molecules (with proportionality constant k_-). If we balance all production and consumption terms for each participating chemical, then we obtain the following system of differential equations

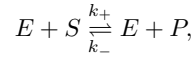
$$\frac{dc}{dt} = k_+ a b - k_- c,$$

$$\frac{da}{dt} = k_- c - k_+ a b,$$

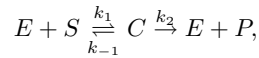
$$\frac{db}{dt} = k_- c - k_+ a b.$$

Michaelis-Menten Kinetics

One situation where the law of mass action is not directly applicable is the enzymatic reaction



involving the reaction of a substrate S with an enzyme E to gain a product P and the enzyme. Note that enzymes are catalyzers. A better description of an enzymatic reaction is the *Michaelis-Menten kinetic*. We assume that substrate S and enzyme E form an intermediate complex, C , which then decays into P and E :



where k_1 , k_{-1} and k_2 are rate constants. Let $s = [S]$, $e = [E]$, $c = [C]$, $p = [P]$. As before, we can describe the process using a system of differential equations, as follows:

$$\begin{aligned} \frac{ds}{dt} &= -k_1 s e + k_{-1} c, \\ \frac{de}{dt} &= -k_1 s e + k_{-1} c + k_2 c, \\ \frac{dc}{dt} &= k_1 s e - k_{-1} c - k_2 c, \\ \frac{dp}{dt} &= k_2 c. \end{aligned} \tag{3.7}$$

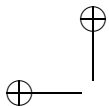
The Michaelis-Menten kinetics model serves as a well-established model for enzyme kinetics, and is used widely in the area of mathematical physiology. For more details on Michaelis-Menten kinetics and related models, we refer to Keener and Sneyd [92].

3.3.2 A General Interaction Model for Two Populations

To further explain modelling with systems of differential equations, we investigate the following general 2-species interaction model :

$$\begin{aligned} \dot{x} &= \alpha x + \beta xy, \\ \dot{y} &= \gamma y + \delta xy, \end{aligned} \tag{3.8}$$

where $x(t)$ and $y(t)$ denote the concentrations (or numbers) of two populations, and α, β, γ , and δ are constant real parameters. In what follows, we will treat all terms of this model and explain the situations they describe. This approach leads to a systematic understanding of typical model ingredients which later can be used and/or modified for specific applications.



The linear terms αx and γy describe the growth or decay of the corresponding population x or y in isolation. For example, if $\alpha > 0$ and $\beta = 0$, then population x will grow like $e^{\alpha t}$; if $\alpha < 0$, it will decay exponentially. Similarly, if $\delta = 0$, then the sign of γ decides whether $y(t)$ is exponentially growing or decaying.

Interaction of the two populations is modelled by the nonlinear terms βxy and δxy . These terms look like “law of mass action” terms. This reflects that two individuals of x and y have to meet before they can interact. If they meet, then β or δ describes the likeliness that an interaction indeed occurs. Alternatively, the term βy can be interpreted as a rate of change of x due to interaction with y . It has turned out that the application of the law of mass action to populations can be very useful.

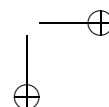
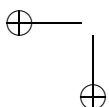
Now, assume $\beta > 0$ and $\delta < 0$. This means that whenever x and y meet, population x grows, while population y declines. Be reminded of the fact that the left hand side of the second equation of (3.8), $\dot{y}$, denotes the change of y with respect to t . The negative term $-|\delta|xy$ on the right hand side contributes negatively to the growth of y . In the case of $\beta > 0$ and $\delta < 0$, population x benefits from interaction and population y suffers. We denote this form of interaction *predator-prey* interaction. In that case, x denotes the predator density (or number) and y denotes the prey.

The situation for $\beta < 0$ and $\delta > 0$ is very similar. In this case x denotes the prey and y the predator. We consider these two cases ($\beta < 0, \delta > 0$ and $\beta > 0, \delta < 0$) as identical. In fact, a switch of notation from (x, y) to (y, x) leads from one case to the other.

Considering the general model (3.8), each of the four parameters can have two signs. Thus, there are $2^4 = 16$ cases to consider. Since we consider the switch of notation as equivalent, there are only 10 qualitatively different cases. These cases are represented by the following sign patterns for $(\alpha, \beta, \gamma, \delta)$:

$$\begin{aligned} &(+ + + +), (+ + + -), (+ + - +), (+ + - -), (+ - + -), \\ &(- + - +), (- + - -), (+ - - -), (- - - -). \end{aligned}$$

The reader might want to verify that the other cases, such as $(+ - - +)$ or $(- - + +)$ are included via a transformation of variables.



α	β	γ	δ	
+	+	+	-	predator (x) – prey (y) models
+	+	-	-	
-	+	+	-	
-	+	-	-	
+	+	+	+	mutualism or symbiosis models
+	+	-	+	
-	+	-	+	
+	-	+	-	competition models
+	-	-	-	
-	-	-	-	

Table 3.1. Classification of the general two-species interaction model, (3.8).

In Table 3.1, we show a summary of these cases. We have seen that the signs of α and γ describe only the growth properties of each species in isolation. We use the interaction terms to classify the cases. All cases with $\beta > 0$ and $\delta < 0$ represent *predator-prey* models. If both $\beta > 0$ and $\delta > 0$, then interactions are beneficial to both populations. We call these models *mutualistic* or *symbiotic* models. Finally, if $\beta < 0$ and $\delta < 0$, then the interaction is disadvantageous for both populations, and the models are called *competition* models.

With the general model (3.8) in hand, it is not difficult to choose the sign pattern of the model for a given situation. For example, in Chapter 10.1.5, we model the competition between two cell populations N_1 and N_2 :

$$\begin{aligned}\dot{N}_1 &= r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{\beta_{12}}{K_1} N_1 N_2, \\ \dot{N}_2 &= r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{\beta_{21}}{K_2} N_1 N_2.\end{aligned}\tag{3.9}$$

The signs of the interaction terms (assuming $K_1, K_2 > 0$ and $\beta_{12}, \beta_{21} > 0$) show that this is indeed a competition model. The difference with model (3.8) is in the growth terms of the species in isolation; we use logistic growth instead of exponential growth.

In Section 3.4.3, we will analyse model (3.8) qualitatively. For further details on predator-prey, competition, and mutualism models, we refer to Murray [114, 115], Edelstein-Keshet [46], or Britton [27].

3.3.3 A Basic Epidemic Model

In this section, we consider the spread of an infectious disease in a host population. Let S , I , and R denote the number of susceptible, infectious, and recovered individuals, respectively. The infection process can be described as shown in Figure 1.1 in Section 1.2. The parameter $\beta > 0$ is the transmission coefficient, $\alpha > 0$ is the recovery rate, and $\gamma > 0$ is the rate for the loss of immunity.

If the disease is transmitted through direct contact, then the new incidences, βIS , are in proportion to the number of susceptible and to the number of infectious individuals, according to the law of mass action. With these assumptions, the disease process shown in Figure 1.1 is described by the following classical SIR model:

$$\begin{aligned} S' &= -\beta IS + \gamma R, \\ I' &= \beta IS - \alpha I, \\ R' &= \alpha I - \gamma R. \end{aligned} \tag{3.10}$$

For simplicity, we assume that $\gamma = 0$. That is, the mean immune period is $\frac{1}{\gamma} = \infty$, namely, the disease confers permanent immunity. The simplified model is known as the Kermack-McKendrick model (although, in the original work of Kermack-McKendrick from 1927 [93], the time since infection was included in the model):

$$\begin{aligned} S' &= -\beta IS, \\ I' &= \beta IS - \alpha I. \end{aligned} \tag{3.11}$$

We will study this model further in Section 3.4.4, after we learn some techniques of qualitative analysis.

3.3.4 Nondimensionalization

Some of the models mentioned above have a large number of free parameters. If the model is used to describe an experiment or an observation, then the values of those parameters might be found in the literature, or by fitting to experiments. With those parameter values at hand one can obtain particular quantitative solutions. Mathematical analysis, however, has the advantage that the qualitative behavior of a model for all possible values of the parameters can be studied. That is, we may understand questions of growth, death, extinctions, epidemic outbreaks, etc., independent of the real values of the parameters, but dependent on their algebraic relationships. In the following sections, we will develop the method of *nondimensionalization*, which is an important technique to reduce the number of free parameters, without losing any properties of the model. Nondimensionalization may significantly reduce the complexity of the model. We give two examples.

Example 3.3.1: In this example we return to the logistic growth model (3.6). The quantity N has the dimension of a population size. We can nondimensionalize if we relate N to some reference population size. In this case, we can choose the carrying capacity K and define $\tilde{N} = N/K$. Then the logistic model reads (divide (3.6) by K):

$$\tilde{N}' = r\tilde{N}(1 - \tilde{N}).$$

In a next step, we transform the time variable and introduce $\tilde{t} = rt$. From the chain rule, we obtain

$$\frac{d\tilde{N}}{dt} = \frac{d\tilde{N}}{d\tilde{t}} \frac{d\tilde{t}}{dt} = r \frac{d\tilde{N}}{d\tilde{t}}.$$

Hence the logistic equation now reads

$$\frac{d}{d\tilde{t}} \tilde{N} = \tilde{N}(1 - \tilde{N}). \quad (3.12)$$

Note that both parameters r and K have disappeared. The transformations used above are all invertible, so that the original quantity $N(t)$ can be generated from $\tilde{N}$, namely

$$N(t) = K\tilde{N}(rt).$$

To understand the qualitative behavior of $N(t)$, it is sufficient to study model (3.12) instead. You will find in the literature that many authors nondimensionalize and then tacitly omit the tilde symbol. Then the nondimensionalized model that corresponds to the logistic equation reads

$$N' = N(1 - N).$$

Example 3.3.2: In this example we consider the general 2-species interaction model (3.8) and reduce the number of parameters for the case of $\alpha, \beta, \delta > 0$. We set

$$\tilde{x} = \frac{\delta}{\alpha}x, \quad \tilde{y} = \frac{\beta}{\alpha}y, \quad \tilde{t} = \alpha t, \quad \mu = \frac{\gamma}{\alpha}.$$

If we apply these transformations to the original equations (3.8) and omit the tilde symbol from the resulting equation, we obtain

$$\begin{aligned} x' &= x + xy, \\ y' &= \mu y + xy. \end{aligned} \quad (3.13)$$

The resulting model depends on a single parameter μ and the qualitative behavior depending on μ can be studied. Also here the transformations are invertible, and the original functions x, y can be generated from (3.13).

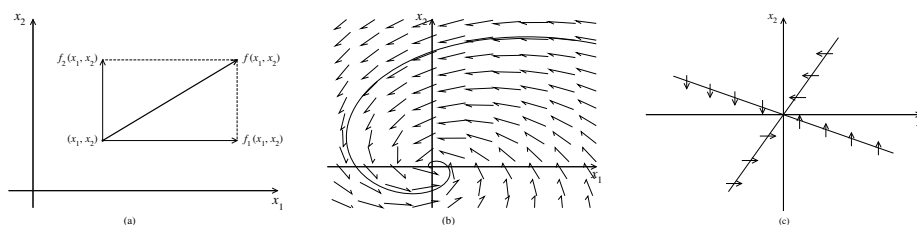


Figure 3.6. (a) Construction of the vector field for (3.14); (b) The vector field for Example 3.4.2 and one typical trajectory; (c) the nullclines with vector field at the nullclines.

3.4 Qualitative Analysis of 2×2 Systems

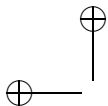
In this section, we develop a qualitative theory for systems of two differential equations, much in the spirit of Section 3.2 where we introduced phase-line and vector-field analyses. Here, we will use *phase-plane* analysis, *vector-field* analysis and the *phase portrait*. With these methods, the qualitative behaviour of a system of equations can be understood without solving the equations explicitly. Explicit solution methods can be found in textbooks on ODEs (such as Boyce and DiPrima [23]).

Consider a system of two differential equations,

$$\begin{aligned} x_1' &= f_1(x_1, x_2), \\ x_2' &= f_2(x_1, x_2). \end{aligned} \quad (3.14)$$

At each $x = (x_1, x_2) \in \mathbb{R}^2$, the *vector field* $f(x) = (f_1(x), f_2(x))$ represents a vector, as shown in Figure 3.6. A solution $x(t) = (x_1(t), x_2(t))$ represents a parametric curve in the (x_1, x_2) plane, called a *trajectory* or an *orbit*, whose tangent vector $x'(t) = (x_1'(t), x_2'(t))$ is specified by the *vector field* $f(x(t)) = (f_1(x_1(t), x_2(t)), f_2(x_1(t), x_2(t)))$. We can obtain a good impression of the overall dynamics if we plot many vectors in the (x_1, x_2) plane. For each chosen point (x_1, x_2) , we calculate $(f_1(x_1, x_2), f_2(x_1, x_2))$ and sketch this vector. We repeat this procedure at many different points until the whole plane is filled with vectors. In Figure 3.6 (a), we show how to calculate one such vector.

Since solution curves are tangential to the vector field, f , we often can follow trajectories just by following the arrows. In Figure 3.6 (b), a typical solution curve is shown (in this case, we have a stable spiral converging at the origin). The vector field can be used to sketch more than one typical solutions, starting at different initial conditions. The sketch of the (x_1, x_2) plane with a number of typical solutions is called a *phase portrait*. Of course, “typical” is a rather vague notion and you need some experience to be able to decide which solutions represent the qualitative behaviour. We will demonstrate and practice this in what follows.



Many computer packages provide a routine to draw the vector field and the phase portrait of an ODE system. In Chapter 8, we will learn how to do this with Maple.

Another helpful tool for obtaining insight into the phase portrait are *nullclines* (or *0-isoclines*). The x_1 -nullcline, n_1 , is the set of points (x_1, x_2) such that $x'_1 = f(x_1, x_2) = 0$, that is,

$$n_1 := \{(x_1, x_2) | f_1(x_1, x_2) = 0\}.$$

Similarly, the x_2 -nullcline, n_2 , is

$$n_2 := \{(x_1, x_2) | f_2(x_1, x_2) = 0\}.$$

On the x_1 -nullcline, n_1 , all vectors of the vector field are vertical (since $x'_1 = 0$). Similarly, on n_2 , all vectors are horizontal (since $x'_2 = 0$). At intersections of n_1 and n_2 , we have $x'_1 = 0$ and $x'_2 = 0$. Hence a *steady state* or *equilibrium point* exists at any intersection of n_1 and n_2 . In Figure 3.6 (c), we show the nullclines corresponding to the vector field of Figure 3.6 (b) and the corresponding steady state at the origin.

In general, *equilibria*, or *steady states* of (3.14) are solutions of

$$f_1(x_1, x_2) = 0, \quad f_2(x_1, x_2) = 0,$$

which we denote by $(\bar{x}_1, \bar{x}_2)$. The steady states play an important role in the understanding of the model dynamics. In many cases, if the behaviour near each steady state is known, then the global behaviour of solutions can be understood quite well. It turns out that we can classify all possible types of behaviour which can occur near a steady state. We will do so in the following two sections. In Section 3.4.1, we first treat specific linear systems. After that, we generalize to arbitrary linear systems. In Section 3.4.2, we consider nonlinear systems. Phase-plane analysis will then be applied to the population interaction model (in Section 3.4.3) and the epidemic model (in Section 3.4.4).

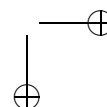
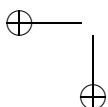
3.4.1 Phase-Plane Analysis: Linear Systems

Step 1: Specific Linear Systems

1a) Real eigenvalues

Consider the simplest linear system,

$$\begin{aligned} x'_1 &= \lambda_1 x_1, \\ x'_2 &= \lambda_2 x_2, \end{aligned} \tag{3.15}$$



3.4. Qualitative Analysis of 2×2 Systems

85

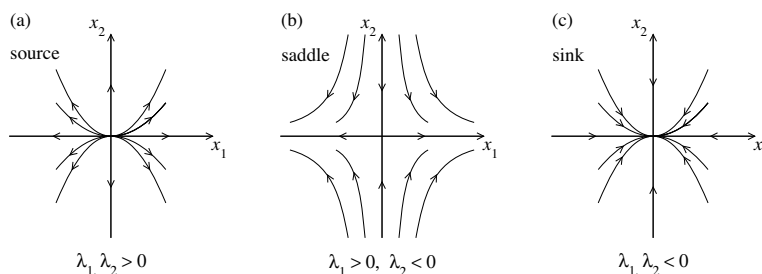


Figure 3.7. Three qualitatively different phase portraits for system (3.15) depending on the sign pattern of λ_1 and λ_2 . (a) $\lambda_1, \lambda_2 > 0$; (b) $\lambda_1 > 0, \lambda_2 < 0$; (c) $\lambda_1, \lambda_2 < 0$.

whose unique steady state is the origin, $(\bar{x}_1, \bar{x}_2) = (0, 0)$. In matrix form, we can write

$$\frac{d}{dt} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

Note that λ_1 and λ_2 are the *eigenvalues* of the matrix

$$A = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}.$$

Solutions to (3.15) are

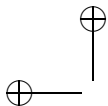
$$x_1(t) = x_1(0)e^{\lambda_1 t}, \quad x_2(t) = x_2(0)e^{\lambda_2 t}.$$

Plotting the parametric curves $(x_1(t), x_2(t))$ for different initial values $(x_1(0), x_2(0))$, we arrive at three distinct phase portraits, depending on the signs of λ_1 and λ_2 , as shown in Figure 3.7.

Case (a): If both eigenvalues λ_1 and λ_2 are positive, then all solutions diverge from the steady state $(0, 0)$. In Figure 3.7 (a), several trajectories are shown for positive, negative, or mixed initial conditions. In this case, the steady state $(0, 0)$ is called a *source* or an *unstable node*.

Case (b): If the eigenvalues have opposite signs, $\lambda_1 > 0$ and $\lambda_2 < 0$, say, then $x_1(t)$ is exponentially increasing, while $x_2(t)$ is decreasing. All solutions approach the x_1 -axis, as shown in Figure 3.7 (b). In this case, the steady state $(0, 0)$ is called a *saddle*.

Case (c): If both eigenvalues are negative, then all solutions converge to the steady state $(0, 0)$, as shown in Figure 3.7 (c). The steady state is called a *sink* or *stable node*.



1b) Complex eigenvalues

Consider the linear system

$$\frac{d}{dt} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}. \quad (3.16)$$

For $\beta \neq 0$, the system has the origin, $(0, 0)$, as its only steady state. The coefficient matrix $A = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}$ has two complex conjugate eigenvalues

$$\lambda_1 = \alpha + \beta i \quad \text{and} \quad \lambda_2 = \alpha - \beta i.$$

We can verify (see Exercise 3.9.8) that (3.16) has two special solutions, namely

$$x^{(1)}(t) = e^{\alpha t} \begin{pmatrix} \cos \beta t \\ -\sin \beta t \end{pmatrix}, \quad x^{(2)}(t) = e^{\alpha t} \begin{pmatrix} \sin \beta t \\ \cos \beta t \end{pmatrix}.$$

The superposition principle of linear systems implies that all solutions to (3.16) are of the form

$$x(t) = c_1 x^{(1)}(t) + c_2 x^{(2)}(t) = a e^{\alpha t} \begin{pmatrix} \cos(\beta t + \phi) \\ -\sin(\beta t + \phi) \end{pmatrix}$$

or

$$\begin{aligned} x_1(t) &= a e^{\alpha t} \cos(\beta t + \phi), \\ x_2(t) &= -a e^{\alpha t} \sin(\beta t + \phi), \end{aligned} \quad (3.17)$$

where a and ϕ are determined by the initial conditions, $(x_1(0), x_2(0))$.

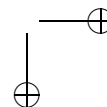
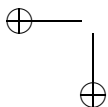
Using (3.17), we can classify three distinct cases, shown in Figure 3.8.

Case (a): $\alpha = 0$, so that both eigenvalues are purely imaginary. All solutions are periodic, and all trajectories are closed orbits surrounding the steady state $(0, 0)$, as shown in Figure 3.8 (a). The steady state is called a *center*.

Case (b): $\alpha > 0$, so that both eigenvalues have positive real parts. The exponential function $e^{\alpha t}$ grows for $t > 0$. All trajectories spiral away from the steady state $(0, 0)$, as shown in Figure 3.8 (b). The steady state is called an *unstable spiral* or a *spiral source*.

Case (c): $\alpha < 0$, so that both eigenvalues have negative real parts. The exponential function $e^{\alpha t}$ decays for $t > 0$. All trajectories spiral towards the steady state $(0, 0)$, as shown in Figure 3.8 (c). The steady state is called a *stable spiral* or a *spiral sink*.

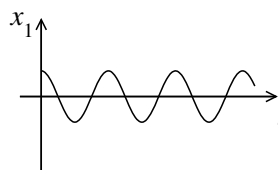
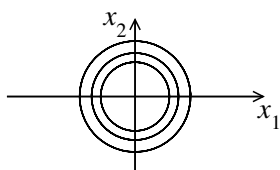
Corresponding solutions $x_1(t)$ for each case are shown in Figure 3.8 as well.



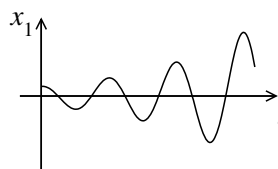
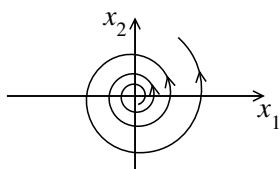
3.4. Qualitative Analysis of 2×2 Systems

87

(a) $\alpha = 0$, center



(b) $\alpha > 0$, unstable spiral



(c) $\alpha < 0$, stable spiral

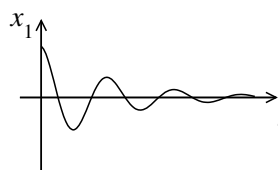
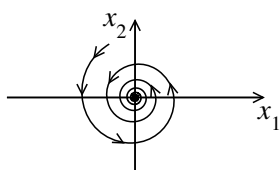


Figure 3.8. Three qualitatively different cases for system (3.16), depending on the value of the parameter α . (a) $\alpha = 0$; (b) $\alpha > 0$; (c) $\alpha < 0$. Graphs in the left column show phase portraits. Graphs in the right column show a typical solution for $x_1(t)$.

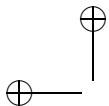
Step 2: General Linear Systems

We now consider a general linear system,

$$\frac{d}{dt} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}, \quad A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}. \quad (3.18)$$

If we make the transformation

$$\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = P^{-1} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix},$$



where P is a 2×2 invertible matrix, then $y = (y_1, y_2)$ satisfies the system

$$\frac{d}{dt} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = B \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}, \quad (3.19)$$

where $B = P^{-1}AP$. Systems (3.18) and (3.19) have the same phase portraits.

It is known from linear algebra (see [99]) that if A has two distinct real eigenvalues λ_1 and λ_2 such that $\lambda_1 \neq \lambda_2$, then we can choose P such that

$$B = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}.$$

If A has two complex conjugate eigenvalues $\lambda_1 = \bar{\lambda}_2 = \alpha + \beta i$, then we can choose P such that

$$B = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}.$$

Thus, we conclude that the phase portraits of (3.18) will be the same as those of systems (3.15) or (3.16), studied earlier. Before presenting a theorem about the stability of the origin, we work out the details of computing the matrix B for two specific examples.

Example 3.4.1: Consider the linear system

$$\begin{aligned} \dot{x} &= 2x - 2y, \\ \dot{y} &= 2x - 3y. \end{aligned} \quad (3.20)$$

In vector matrix notation, we have

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 2 & -2 \\ 2 & -3 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}, \quad A = \begin{pmatrix} 2 & -2 \\ 2 & -3 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

It is straightforward to verify that the eigenvalues and corresponding eigenvectors of A are $\lambda_1 = 1$, $\zeta_1 = \begin{pmatrix} 2 \\ 1 \end{pmatrix}$ and $\lambda_2 = -2$, $\zeta_2 = \begin{pmatrix} 1 \\ 2 \end{pmatrix}$.

The eigenvalues of A are real and distinct. If we use the eigenvectors ζ_1 and ζ_2 as columns of a matrix P , we obtain the transformation

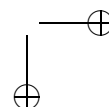
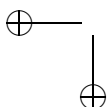
$$P = \begin{pmatrix} 2 & 1 \\ 1 & 2 \end{pmatrix}, \quad P^{-1} = \frac{1}{3} \begin{pmatrix} 2 & -1 \\ -1 & 2 \end{pmatrix},$$

then

$$B = P^{-1}AP = \begin{pmatrix} 1 & 0 \\ 0 & -2 \end{pmatrix}.$$

From the solution of the related linear system

$$\frac{d}{dt} \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & -2 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}, \quad (3.21)$$



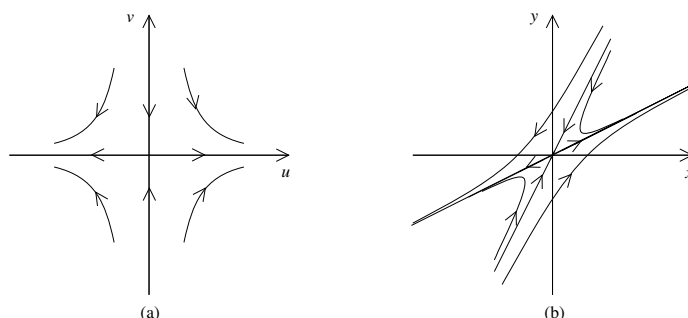


Figure 3.9. The phase portraits of (3.21) (a) and (3.20) (b).

we can recover the solution of (3.20) via

$$\begin{pmatrix} x \\ y \end{pmatrix} = P \begin{pmatrix} u \\ v \end{pmatrix}.$$

The phase portrait of (3.21) is shown in Figure 3.9 (a), and the corresponding phase portrait of (3.20) is shown in Figure 3.9 (b). The transformation P maps the unstable direction $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ of (3.21) onto the unstable direction $\begin{pmatrix} 2 \\ 1 \end{pmatrix}$ of (3.20). Similarly, the stable direction $\begin{pmatrix} 0 \\ 1 \end{pmatrix}$ of (3.21) is mapped onto the stable direction $\begin{pmatrix} 1 \\ 2 \end{pmatrix}$ of (3.20). Note that the phase portrait shown in Figure 3.9 (b) is a compressed and rotated version of the phase portrait shown in Figure 3.9 (a).

Example 3.4.2: We consider the system

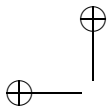
$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -1 & -2 \\ 2 & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

The eigenvalues of the corresponding matrix are $\lambda_1 = -1 + 2i$ and $\lambda_2 = \bar{\lambda}_1 = -1 - 2i$. The corresponding (complex) eigenvectors are $\zeta_1 = \begin{pmatrix} i \\ 1 \end{pmatrix}$ and $\zeta_2 = \begin{pmatrix} -i \\ 1 \end{pmatrix}$. The solution can be written in the general form

$$\begin{pmatrix} x \\ y \end{pmatrix} (t) = e^{-t} \left(c_1 \begin{pmatrix} -\sin(2t) \\ \cos(2t) \end{pmatrix} + c_2 \begin{pmatrix} \cos(2t) \\ \sin(2t) \end{pmatrix} \right)$$

(for a reminder on the details, see Boyce and DiPrima [23] or Hirsch and Smale [80]), which describes a rotation that converges to 0 (because of e^{-t}). The steady state $(0, 0)$ is a stable spiral. The vector field and one solution curve were shown in Figure 3.6 (b).

In all the cases discussed above, solutions only converge to the steady state at $(0, 0)$ when both eigenvalues $\lambda_1, \lambda_2 < 0$ (the origin is a stable node), or when the real part of the eigenvalues satisfies $\alpha < 0$ (the origin is a stable spiral). In these two cases we call the steady state at $(0, 0)$ *asymptotically stable*.



We have seen that we can classify the equilibria of a linear system according to the eigenvalues of the corresponding coefficient matrix,

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

Sometimes it is more convenient to use two other characteristic values of A , namely the *trace*, $\text{tr } A = a + d$, and the *determinant*, $\det A = ad - bc$. It is known that the trace is always the sum of the eigenvalues, $\text{tr } A = \lambda_1 + \lambda_2$, and the determinant is the product, $\det A = \lambda_1 \lambda_2$. Moreover, one can use the trace and determinant to calculate the eigenvalues. In Exercise 3.9.9, the reader is asked to show that

$$\lambda_{1,2} = \frac{\text{tr } A}{2} \pm \frac{1}{2} \sqrt{(\text{tr } A)^2 - 4 \det A}. \quad (3.22)$$

Note that the formula in (3.22) holds only for 2×2 matrices. For higher-order matrices, there is no formula of this form.

From (3.22), we see that it is necessary to have $\text{tr } A < 0$ in order to have a steady state that is asymptotically stable (otherwise at least one eigenvalue would have a positive real part). If $\text{tr } A < 0$, then the discriminant, $(\text{tr } A)^2 - 4 \det A$, is either negative or smaller than $(\text{tr } A)^2$. Hence the real part of the eigenvalues is always negative, and $(0, 0)$ is asymptotically stable. We can summarize our conclusions in the following theorem.

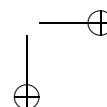
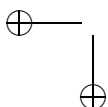
Theorem 3.3. *For a linear system, (3.18), the following are equivalent:*

- the equilibrium $(0, 0)$ is asymptotically stable;
- all eigenvalues of A have negative real parts;
- $\det A = ad - bc > 0$ and $\text{tr } A = a + d < 0$.

We can treat all different combinations for the sign of trace and determinant, and obtain a complete picture of possible behaviour near an equilibrium point. Figure 3.10 shows the “zoo” of all possible types of behaviour for steady states of two-dimensional systems.

We can summarize the possible types of behaviour as follows:

1. Case $\det A < 0$. Then $(\text{tr } A)^2 - 4 \det A > (\text{tr } A)^2$. From formula (3.22), it follows that there is one positive and one negative eigenvalue, $\lambda_1 > 0$ and $\lambda_2 < 0$, say. Hence, $(0, 0)$ is a saddle point. Moreover, solutions grow as $e^{\lambda_1 t}$ in the direction of the eigenvector φ_1 corresponding to λ_1 , and solutions decay as $e^{\lambda_2 t}$ in the direction of the eigenvector φ_2 corresponding to λ_2 . In Figure 3.10, the *stable* and *unstable* eigenvectors are shown.



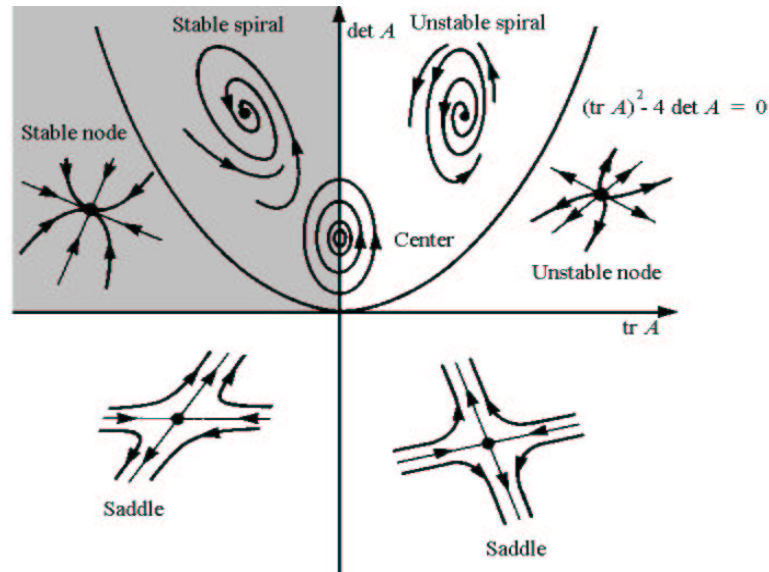


Figure 3.10. The zoo for the general linear system, (3.18). This is a modified version of Figure 5.14 in Edelstein-Keshet [46] used with permission.

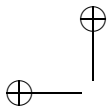
2. Case $\det A > 0$, $\operatorname{tr} A < 0$. If $(\operatorname{tr} A)^2 < 4 \det A$ (above the parabola in Figure 3.10), then λ_1, λ_2 are complex conjugate eigenvalues with real part $\frac{\operatorname{tr} A}{2} < 0$, and $(0, 0)$ is a stable spiral. If $(\operatorname{tr} A)^2 > 4 \det A$ (below the parabola), then λ_1, λ_2 are real, but they have the same sign, and $(0, 0)$ is a stable node.
3. Case $\det A > 0$, $\operatorname{tr} A > 0$. Depending on the sign of $(\operatorname{tr} A)^2 - 4 \det A$, we have either an unstable spiral or an unstable node.
4. Case $\det A > 0$, $\operatorname{tr} A = 0$. In this case we have a center.
5. The remaining cases ($\det A = 0$ and $(\operatorname{tr} A)^2 - 4 \det A = 0$) will not be discussed. We refer to Hirsch and Smale [80] for these cases.

3.4.2 Nonlinear Systems and Linearization

Consider a nonlinear system in $\mathbb{R}^2$,

$$\begin{aligned} x_1' &= f_1(x_1, x_2), \\ x_2' &= f_2(x_1, x_2), \end{aligned} \tag{3.23}$$

where f_1 and f_2 are continuously differentiable functions.



In general, each pair $(\bar{x}_1, \bar{x}_2)$ satisfying $f_1(\bar{x}_1, \bar{x}_2) = f_2(\bar{x}_1, \bar{x}_2) = 0$ is called an equilibrium or a steady state for (3.23). We would like to understand the behaviour of the solutions near equilibria.

For linear systems, we observed that solutions converge to $(0, 0)$, they diverge away from $(0, 0)$, or, in the center case, they stay close by. Before we can generalize these observations to nonlinear systems, we need some definitions from dynamical systems theory (see Perko [127]).

Definition 3.4.

- a) A steady state $(\bar{x}_1, \bar{x}_2)$ is called *stable* if a solution which starts nearby stays nearby.

More formally: $(\bar{x}_1, \bar{x}_2)$ is stable if for all $\varepsilon > 0$, there exists a $\delta > 0$ such that solutions to initial data (x_1^0, x_2^0) with $\|(x_1^0, x_2^0) - (\bar{x}_1, \bar{x}_2)\| < \delta$, satisfy $\|(x_1(t), x_2(t)) - (\bar{x}_1, \bar{x}_2)\| < \varepsilon$ for all time $t > 0$. Here, $\|\cdot\|$ denotes the Euclidean vector norm.

- b) A steady state $(\bar{x}_1, \bar{x}_2)$ which is not stable is called *unstable* (there is at least one solution which diverges from $(\bar{x}_1, \bar{x}_2)$).

- c) A steady state $(\bar{x}_1, \bar{x}_2)$ is called *asymptotically stable* if all solutions near $(\bar{x}_1, \bar{x}_2)$ converge to $(\bar{x}_1, \bar{x}_2)$.

More formally: $(\bar{x}_1, \bar{x}_2)$ is asymptotically stable if $(\bar{x}_1, \bar{x}_2)$ is stable, and there exists a $\delta > 0$ such that all solutions with initial data (x_1^0, x_2^0) , with $\|(x_1^0, x_2^0) - (\bar{x}_1, \bar{x}_2)\| < \delta$, satisfy $\lim_{t \rightarrow \infty} \|(x_1(t), x_2(t)) - (\bar{x}_1, \bar{x}_2)\| = 0$.

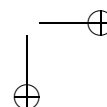
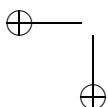
We can determine the stability of a steady state $(\bar{x}_1, \bar{x}_2)$ by linearizing (3.23). The process is similar to the linearization of discrete-time systems, treated in Section 2.3.2.

Let

$$\begin{aligned} x_1(t) &= \bar{x}_1 + z_1(t), \\ x_2(t) &= \bar{x}_2 + z_2(t), \end{aligned}$$

where $z_1(t)$ and $z_2(t)$ are assumed to be small, so that they can be thought of as perturbations to the steady state. We denote $\bar{x} = (\bar{x}_1, \bar{x}_2)$ and $z = (z_1, z_2)$, and write the Taylor expansion of $f = (f_1, f_2)$ about $(\bar{x}_1, \bar{x}_2)$:

$$f(\bar{x} + z) = f(\bar{x}) + Df(\bar{x}) \cdot z + \text{higher-order terms},$$



3.4. Qualitative Analysis of 2×2 Systems

93

where

$$Df(\bar{x}_1, \bar{x}_2) := \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{pmatrix} \bigg|_{(x_1, x_2) = (\bar{x}_1, \bar{x}_2)}$$

contains the partial derivatives of f evaluated at $(\bar{x}_1, \bar{x}_2)$ (for a reminder on partial derivatives, see Section 4.1). The matrix $Df(\bar{x}_1, \bar{x}_2)$ is called the *Jacobian matrix* of f at $(\bar{x}_1, \bar{x}_2)$.

We substitute the Taylor expansion into (3.23) and we drop the higher-order terms. Since $x'_1 = \frac{d}{dt}(\bar{x}_1 + z_1(t)) = z'_1$ and $x'_2 = z'_2$, and since $f(\bar{x}) = 0$, we obtain a linear system governing the dynamics of the perturbation (z_1, z_2) :

$$\frac{d}{dt} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix}. \quad (3.24)$$

We know already from the previous section how to treat linear systems. For most (but not all) steady states, conclusions obtained for the linearized system indeed carry over to the original nonlinear system.

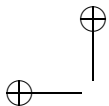
Definition 3.5. $(\bar{x}_1, \bar{x}_2)$ is called *hyperbolic* if all eigenvalues of the Jacobian $Df(\bar{x}_1, \bar{x}_2)$ have nonzero real part.

Theorem 3.6. (Hartman-Grobman) Assume that $(\bar{x}_1, \bar{x}_2)$ is a hyperbolic equilibrium. Then, in a small neighbourhood of $(\bar{x}_1, \bar{x}_2)$, the phase portrait of the nonlinear system, (3.23), is the same as that of the linearized system, (3.24).

Remark 3.4.1.

- 1) By Theorems 3.3 and 3.6, at a hyperbolic equilibrium $\bar{x}$, stability properties are determined by the eigenvalues of the Jacobian matrix, $Df(\bar{x}_1, \bar{x}_2)$. This method of linearization may fail for nonhyperbolic equilibria.
- 2) The phrase “the same as” in the above Theorem refers to *topological equivalence* of vector fields. This means that in a neighbourhood of $(\bar{x}_1, \bar{x}_2)$, there is a homeomorphism (a continuous one-to-one map between open sets) which maps the vector field of the nonlinear system to the vector field of its linearization. In that case, the phase portrait near the stationary point is one of those shown in Figure 3.10. The theory behind the Hartman-Grobman Theorem is beyond the scope of this book, and we refer to Perko [127] for more details.

For example the two phase portraits in Figure 3.9 are topologically equivalent, and the homeomorphism is given by the matrix P from Example 3.4.1.



3.4.3 Qualitative Analysis of the General Population Interaction Model

In this section, we use the qualitative theory developed above to re-examine the general 2-species model, (3.8). From the 10 different cases summarized in Table 3.1, we select one example for predator-prey, one example for mutualism, and one example for competition, and treat these in detail. The other cases are left as exercises. Before we consider specific cases, we determine the steady states and their linearizations.

We begin by writing (3.8) in vector notation:

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} f_1(x, y) \\ f_2(x, y) \end{pmatrix}, \quad (3.25)$$

with $f_1(x, y) = \alpha x + \beta xy$ and $f_2(x, y) = \gamma y + \delta xy$. To find the x -nullcline, n_x , we set $f_1 = 0$. Hence,

$$n_x = \{(x, y) | x = 0, \text{ or } y = -\frac{\alpha}{\beta}\}.$$

Similarly, the y -nullcline is

$$n_y = \{(x, y) | y = 0, \text{ or } x = -\frac{\gamma}{\delta}\}.$$

The steady states $(\bar{x}, \bar{y})$ are intersection points of the nullclines, and they satisfy $f_1(\bar{x}, \bar{y}) = 0$ and $f_2(\bar{x}, \bar{y}) = 0$. We find two steady states, namely

$$P_1 = (0, 0) \quad \text{and} \quad P_2 = \left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right).$$

The linearization of (3.25) is given by

$$\frac{d}{dt} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = Df(\bar{x}, \bar{y}) \begin{pmatrix} z_1 \\ z_2 \end{pmatrix},$$

and

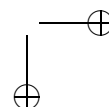
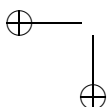
$$Df = \begin{pmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{pmatrix} = \begin{pmatrix} \alpha + \beta y & \beta x \\ \delta y & \gamma + \delta x \end{pmatrix}.$$

We evaluate this matrix at the two steady states, P_1 and P_2 . For P_1 , we find

$$Df(0, 0) = \begin{pmatrix} \alpha & 0 \\ 0 & \gamma \end{pmatrix}, \quad (3.26)$$

which has the two eigenvalues $\lambda_1 = \alpha$ and $\lambda_2 = \gamma$. Similarly for P_2 , we find

$$Df\left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right) = \begin{pmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ -\frac{\alpha\delta}{\beta} & 0 \end{pmatrix} = A.$$



3.4. Qualitative Analysis of 2×2 Systems

95

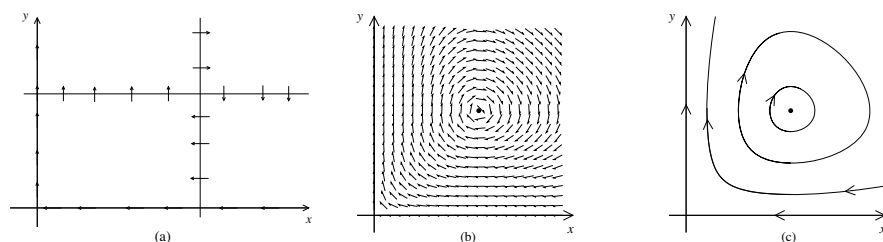


Figure 3.11. (a) Nullclines; (b) Vector field; and (c) phase portrait for the 2-species model, (3.8), with sign pattern $(- + + -)$ (predator-prey).

Since $\text{tr } A = 0$ and $\det A = -\alpha\gamma$, formula (3.22) gives that the eigenvalues are given by

$$\lambda_{1/2} = \pm\sqrt{\alpha\gamma}. \quad (3.27)$$

To identify the type of steady states, we need to have more information. In particular, we need to know the signs of the parameters α , β , γ , and δ . Analysis of three specific cases follows.

Case $(- + + -)$: a predator-prey model

We assume that $\alpha < 0$, $\beta > 0$, $\gamma > 0$, and $\delta < 0$. From (3.26), we see that one eigenvalue is negative ($\lambda_1 = \alpha < 0$), and the other eigenvalue is positive ($\lambda_2 = \gamma > 0$). Hence, $P_1 = (0, 0)$ is a saddle.

Before we study $P_2 = \left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right)$, we have to ensure that it is *biologically relevant*, i.e., $-\frac{\gamma}{\delta} > 0$ and $-\frac{\alpha}{\beta} > 0$. Since γ, δ and α, β have opposite signs, this is indeed true.

In (3.27), the product $\alpha\gamma < 0$, so that the eigenvalues are purely imaginary, namely

$$\lambda_{1/2} = \pm i\sqrt{|\alpha\gamma|}.$$

Hence $\left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right)$ is a center.

Thus, P_2 is not hyperbolic, and the Hartman-Grobman theorem does not apply. We cannot decide the type of steady state: P_2 may be a center, a stable spiral, or an unstable spiral. The theory of Lyapunov functions would help to distinguish between these three possibilities. However, the study of Lyapunov functions is beyond the scope of this text, and we refer to Perko [127]. Accept for now that P_2 is a nonlinear center. The vector field and the phase portrait for the case $(- + + -)$ are shown in Figure 3.11. We observe predator-prey oscillations between periods of high and low population sizes.

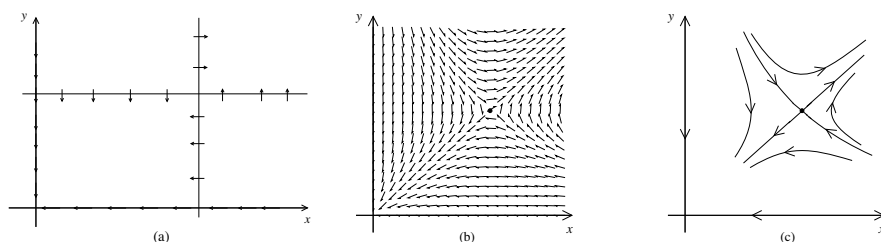


Figure 3.12. (a) Nullclines; (b) Vector field; and (c) phase portrait for the 2-species model, (3.8), with sign pattern $(- + -+)$ (mutualism).

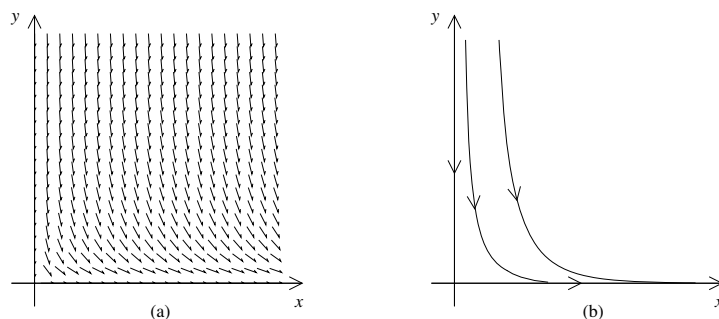


Figure 3.13. (a) Vector field and (b) phase portrait for the 2-species model, (3.8), with sign pattern $(+ - - -)$ (competition).

Case $(- + -+)$: mutualism of two species which cannot survive alone
($\alpha < 0$ and $\gamma < 0$)

The eigenvalues of $Df(0,0)$ are $\alpha < 0$ and $\gamma < 0$ hence $(0,0)$ is a stable node. Also, $-\frac{\alpha}{\beta} > 0$ and $-\frac{\gamma}{\delta} > 0$, hence P_2 is biologically relevant. The product $\alpha\gamma > 0$, hence P_2 is a saddle. The vector field and phase portrait are given in Figure 3.12.

From the phase portrait we see that if the initial populations for x and y are big enough, then both populations can benefit and grow. If one of them is too small initially, then both species go extinct (converge to zero).

Case $(+ - - -)$: a competition model

In this case $(0,0)$ is a saddle and P_2 is not biologically relevant ($-\frac{\gamma}{\delta} < 0$). The vector field and phase portrait are given in Figure 3.13. Population y goes extinct while population x can grow without competition.

See Exercise 3.9.11 for the remaining cases.

3.4.4 Qualitative Analysis of the Epidemic Model

Here, we return to the epidemic model, (3.11), derived in Section 3.3.3. To find steady states, we set $S' = 0$ and $I' = 0$. If $S' = 0$, then either $S = 0$ or $I = 0$. To satisfy $I' = 0$, we must have either $I = 0$ or $S = \frac{\alpha}{\beta}$. Therefore, (3.11) has a ray of steady states along the positive S -axis,

$$\{(S, 0) \mid S \geq 0\}.$$

To find the stability of each steady state $(\bar{S}, 0)$, we examine the Jacobian matrix,

$$\begin{pmatrix} -\beta I & -\beta S \\ \beta I & \beta S - \alpha \end{pmatrix} \Big|_{\substack{S=\bar{S} \\ I=0}} = \begin{pmatrix} 0 & -\beta \bar{S} \\ 0 & \beta \bar{S} - \alpha \end{pmatrix}.$$

The two eigenvalues are $\lambda_1 = 0$ and $\lambda_2 = \beta \bar{S} - \alpha$.

The eigenvalue $\lambda_1 = 0$ corresponds to the neutrally stable direction along the ray of steady states. The second eigenvalue, $\lambda_2 = \beta \bar{S} - \alpha$, is positive if $\bar{S} > \frac{\alpha}{\beta}$ and negative if $\bar{S} < \frac{\alpha}{\beta}$. To construct the phase portrait, we write one unknown, I , as a function of the other, S . This way, we still follow the trajectory of an epidemic, but we forget about the time course for a moment. To achieve this, we use the chain rule. In particular, if $I = I(S(t))$, then

$$\frac{dI}{dt} = \frac{dI}{dS} \cdot \frac{dS}{dt}.$$

Hence,

$$\frac{dI}{dS} = \frac{I'}{S'} = \frac{\beta IS - \alpha I}{-\beta IS} = -1 + \frac{\alpha}{\beta S}.$$

If we regard I as a function of S , and integrate the above equation from S_0 to S , then we obtain

$$I(S) - I(S_0) = -(S - S_0) + \frac{\alpha}{\beta} (\ln S - \ln S_0).$$

Therefore,

$$I(S) = \frac{\alpha}{\beta} \ln S - S + C_1,$$

where the constant C_1 is determined by the initial condition

$$C_1 = I(S_0) + S_0 - \frac{\alpha}{\beta} \ln S_0.$$

To obtain the phase portrait of (3.11), we shift the graph of $\frac{\alpha}{\beta} \ln S - S$ vertically, where the amount of the shift is determined by the values of S_0 and C_1 . As shown in Figure 3.14, steady states to the right of $\frac{\alpha}{\beta}$, namely $\bar{S} > \frac{\alpha}{\beta}$, are unstable in the direction away from the S -axis, and those to the left of $\frac{\alpha}{\beta}$ are stable. This conclusion agrees with our earlier result obtained from local stability analysis.

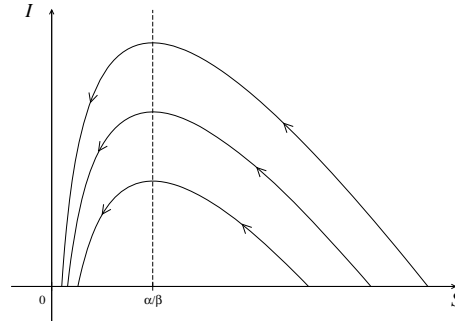


Figure 3.14. Phase portrait of the epidemic model, (3.11).

Biologically, the phase portrait in Figure 3.14 reveals an important fact in epidemiology: $\frac{\alpha}{\beta}$ represents the critical population size to sustain an epidemic. If the initial susceptible population is below $\frac{\alpha}{\beta}$, then no epidemic is possible, and the number of infections decreases, whereas if $S_0 > \frac{\alpha}{\beta}$, then the number of infections initially increases, reaching its maximum when $S = \frac{\alpha}{\beta}$, and then declines.

3.5 General Systems of Three or More Equations

The qualitative theory of linearization, vector fields and phase portraits can be extended easily to systems of 3 or more differential equations, although the graphical illustration can become tricky for higher dimensional systems. Here, we follow the steps of Section 3.4.3, and just indicate how they generalize to higher dimensional systems. For more details, we refer the reader to texts about dynamical systems theory (Perko [127], or Hirsch and Smale [80]).

We write a general system for the n unknowns, $x_1(t), \dots, x_n(t)$, $n \geq 3$, as

$$\dot{x} = f(x), \quad (3.28)$$

where $x(t) = (x_1(t), \dots, x_n(t))^T$, and $f(x) = (f_1(x_1, \dots, x_n), \dots, f_n(x_1, \dots, x_n))^T$.

We can define nullclines in the same way as before. In particular, for $j = 1, \dots, n$, let

$$n_j = \{x | f_j(x) = 0\}.$$

Steady states $\bar{x}$ of (3.28) are solutions of $f(\bar{x}) = 0$ or, equivalently,

$$f_1(\bar{x}_1, \dots, \bar{x}_n) = 0, \dots, f_n(\bar{x}_1, \dots, \bar{x}_n) = 0.$$

The linearization of (3.28) at $\bar{x} = (\bar{x}_1, \dots, \bar{x}_n)$ is given by the Jacobian matrix,

$$Df(\bar{x}) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1}(\bar{x}) & \dots & \frac{\partial f_1}{\partial x_n}(\bar{x}) \\ \vdots & & \vdots \\ \frac{\partial f_n}{\partial x_1}(\bar{x}) & \dots & \frac{\partial f_n}{\partial x_n}(\bar{x}) \end{pmatrix}.$$

As before, the eigenvalues of $Df(\bar{x})$ determine the stability of $\bar{x}$. Suppose, for example, that we have a 6-dimensional problem, and that we find two positive real eigenvalues ($\lambda_1, \lambda_2 > 0$), one negative real eigenvalue ($\lambda_3 < 0$), one zero eigenvalue ($\lambda_4 = 0$) and a pair of complex conjugate eigenvalues ($\lambda_5 = \bar{\lambda}_6$) with negative real part. Let $\zeta_1, \dots, \zeta_6$ denote the corresponding eigenvectors. Solutions which start close to $\bar{x}$ will grow in the ζ_1 and ζ_2 direction, and they will decay along the ζ_3 direction. Since $\lambda_4 = 0$, we cannot conclude from linearization whether the solutions grow or decay in the ζ_4 direction. The two complex eigenvalues λ_5 and λ_6 indicate rotations in the plane which is spanned by $\text{Re } \zeta_5$ and $\text{Im } \zeta_5$. Since the real parts of λ_5 and λ_6 are negative, solutions will spiral towards $\bar{x}$ in this plane.

We call the plane spanned by ζ_1 and ζ_2 which goes through $\bar{x}$ the (local) *unstable manifold*, $M^u(\bar{x})$. The 3-dimensional space spanned by $(\zeta_2, \text{Re } \zeta_5, \text{Im } \zeta_5)$ is called the (local) *stable manifold*, $M^s(\bar{x})$. The line through $\bar{x}$ in direction ζ_4 is called the (local) *center manifold*.

Visualizing the phase portrait in 6-dimensional space is difficult, if not impossible. Even though the graphical analysis is limited, it is important to know the dimensions of the stable, unstable, and center manifolds. This can be used to understand the stability of steady states, to prove or disprove the existence of limit cycles, or to predict the existence of complicated dynamics. A detailed study of stable/unstable/center manifolds is out of reach of this textbook. For further treatment of manifolds, we refer to Perko [127], or Hirsch and Smale [80].

3.6 Discrete-Time Models from Continuous-Time Models

There are important connections between discrete-time and continuous-time models. We have seen already that linearization and linear stability analysis play a dominant role for ODEs as well as for discrete models. There are other connections. In this section, we will discuss two approaches by which to derive discrete-time equations corresponding to a given ODE. In Section 3.6.1, we discuss *numerical methods*, and in Section 3.6.2, we discuss the derivation of *time-one maps*.