In the application of ODEs to model biological processes it is always useful to have a computer language available that can solve ODEs numerically. In this textbook we present Maple as a modeling tool. Equally useful are languages and software packages like *Mathematica*, MATLAB, or XPP-AUT.

3.9 Exercises for ODEs

Exercise 3.9.1: The C^{14}-method. *The C^{14}-method is used to estimate the age of archaeological objects. It is known that living objects accumulate the radioactive C^{14}-isotope during their lifetime, to a certain concentration c_0. If the organism dies, then the radioactive C^{14} decays with a half-life of $T_{1/2} = 5760$ years.*

Archaeologists found a piece of wood in the Nile delta which showed a concentration of 75% of c_0. Estimate the age of this piece of wood. Could Tutankhamen have been sitting in a boat made from the same tree as the one from which this piece of wood came?

Exercise 3.9.2: Learning curves. *Psychologists interested in learning theory study learning curves. A learning curve is the graph of a function $P(t)$, the performance of someone learning a skill as a function of the training time t.*

(a) *What does dP/dt represent?*

(b) *Discuss why the differential equation*

$$\frac{dP}{dt} = k(M - P),$$

where k and M are positive constants, is a reasonable model for learning. What is the meaning of k and M? What would be a reasonable initial condition for the model? Include a graph of dP/dt versus P as part of your discussion.

(c) *Make a qualitative sketch of solutions to the differential equation.*

Exercise 3.9.3: Harvesting. *The Verhulst (logistic) model for population growth reads*

$$\dot{u} = au\left(1 - \frac{u}{K}\right),$$

where K denotes the carrying capacity and a is a reproduction rate. We assume that the amount harvested is proportional to population size, with proportionality constant c. The modified model then reads

$$\dot{u} = au\left(1 - \frac{u}{K}\right) - cu.$$

Plot the vector field and find the steady states. For what values of c does the population die out? When does the population persist? Give a biological explanation.

Exercise 3.9.4: Fishing. *In this exercise, you will be considering three simple models of a fishery. Let $N(t)$ be the population of fish at time t. In the absence of fishing, the population* *is assumed to grow logistically, that is,*

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

where $r > 0$ is the intrinsic growth rate of the population, and $K > 0$ is the carrying capacity for the fish population. The effects of fishing are modeled with an additional term in the equation for $\dot{N}$. The three models are as follows:

$$\textbf{Model 1: } \dot{N} = rN\left(1 - \frac{N}{K}\right) - H_1;$$

$$\textbf{Model 2: } \dot{N} = rN\left(1 - \frac{N}{K}\right) - H_2 N;$$

$$\textbf{Model 3: } \dot{N} = rN\left(1 - \frac{N}{K}\right) - H_3 \frac{N}{A + N},$$

where H_1, H_2, H_3, and A are positive constants.

(a) *For each model, give a biological interpretation of the fishing term. How do they differ? What is the meaning of the constants H_1, H_2, H_3, and A?*

(b) *Critique Model 1. Why is it not biologically realistic?*

(c) *Which of Models 2 or 3 do you think is best and why?*

Exercise 3.9.5: A metapopulation model. *Levins* [107] *suggested modeling not the number of individuals but the fraction of patches that a population occupies. He suggested the following equation:*

$$P' = cP(h - P) - \mu P,$$

where $P(t)$ denotes the fraction of occupied patches. The number h denotes the fraction of patches that is actually habitable for the population and, hence, $h - P$ is the number of empty but habitable patches. Note that $0 \le P \le h \le 1$. The population colonizes empty patches with rate c. Occupied patches become empty with rate μ.

(a) *Find the steady states of the system.*

(b) *Assume that h can be varied (e.g., construction takes up habitable patches). Draw the bifurcation diagram with h as the parameter. Do all the habitable patches have to be destroyed before the population dies out?*

Exercise 3.9.6: Gene activation. *Consider a gene that is activated by the presence of a biochemical substance S. Let $g(t)$ denote the concentration of the gene product at time t, and assume that the concentration of S, denoted by s_0, is fixed. A model describing the dynamics of g is as follows:*

$$\frac{dg}{dt} = k_1 s_0 - k_2 g + \frac{k_3 g^2}{k_4^2 + g^2}, \tag{3.36}$$

where the k's are positive constants.

(a) *Interpret each of the three terms on the right-hand side of the equation (be sure to mention the meaning of the k's).*

(b) *Show that* (3.36) *can be put in the dimensionless form*

$$\frac{dx}{d\tau} = s - rx + \frac{x^2}{1+x^2}, \tag{3.37}$$

where $r > 0$ *and* $s \geq 0$ *are dimensionless groups. What are r and s in terms of the original model parameters?*

(c) *A graph of* $\frac{dx}{d\tau}$ *versus x is shown in Figure* 3.24 *for the case* $s = 0$ *and* $r = 0.4$. *On the same set of axes, sketch graphs of* $\frac{dx}{d\tau}$ *versus x for various values of* $s > 0$. *We will keep r fixed at* 0.4 *throughout the remainder of this question.*

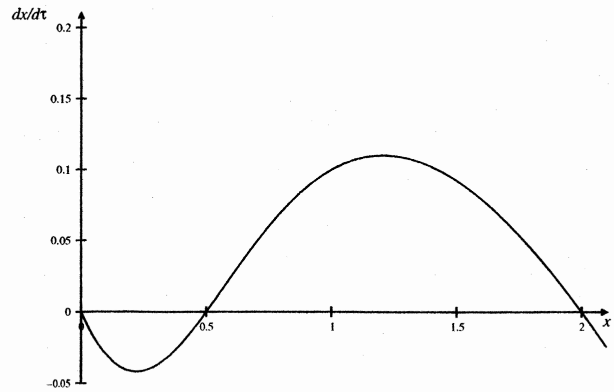

Figure 3.24. *Graph of* $\frac{dx}{d\tau}$ *versus x for* (3.37).

(d) *Make a* qualitative *sketch of the bifurcation diagram, showing the location and stability of the steady states of* (3.37) *as a function of the parameter s. Identify any bifurcation(s).*

(e) *Assume that initially there is no gene product, that is,* $x(0) = 0$, *and suppose that s is slowly increased from zero (i.e., the biochemical substance S is slowly introduced).*

(f) *What happens to* $x(\tau)$? *Why?*

(g) *What happens if s then goes back to zero? Does the gene turn off again? Why?*

Exercise 3.9.7: Linear systems. *We study* 2×2 *systems of linear ODEs:*

$$y' = Ay, \quad y = \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}, \quad A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

Classify the origin $\binom{0}{0}$ *as a stable/unstable spiral, node, or saddle, and plot (or sketch) the phase portrait for each of the following cases:*

$$A = \begin{pmatrix} 1 & 1 \\ 3 & -1 \end{pmatrix}, \begin{pmatrix} 2 & 1 \\ 2 & 3 \end{pmatrix}, \begin{pmatrix} -1 & -2 \\ 2 & -1 \end{pmatrix}, \begin{pmatrix} 1 & 2 \\ -2 & 1 \end{pmatrix}, \begin{pmatrix} 0 & -2 \\ 2 & 0 \end{pmatrix}.$$

Exercise 3.9.8: A linear system with complex eigenvalues. *Show that*

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

are two solutions of the linear differential equation (3.16).

The superposition principle for linear equations (see Boyce and DiPrima [25]*) ensures that each solution can be written as a linear combination of* $x^{(1)}$ *and* $x^{(2)}$*:*

$$x(t) = c_1 x^{(1)}(t) + c_2 x^{(2)}(t).$$

Write $x(t)$ *in the following form:*

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

with $a = \sqrt{c_1^2 + c_2^2}$. *The parameter* ϕ *in the solution is called the phase. Find an expression for the* phase ϕ *depending on* c_1 *and* c_2.

Exercise 3.9.9: The trace-determinant formula. *Prove formula* (3.22).

Exercise 3.9.10: Using the trace-determinant formula. *Use formula* (3.22) *to classify the stability of* $\binom{0}{0}$ *with* A *given by*

$$A = \begin{pmatrix} 1 & 5 \\ 3 & 2 \end{pmatrix}, \begin{pmatrix} 0 & -2 \\ 1 & -3 \end{pmatrix}, \begin{pmatrix} -2 & 4 \\ -3 & 4 \end{pmatrix},$$

$$\begin{pmatrix} 2 & 1 \\ 1 & 3 \end{pmatrix}, \begin{pmatrix} -2 & -1 \\ 1 & 2 \end{pmatrix}, \begin{pmatrix} -1 & -2 \\ 2 & 1 \end{pmatrix}.$$

Exercise 3.9.11: Two-population model. *For the two-population model,* (3.8), *sketch the phase portraits for the remaining sign patterns:*

$$(+++-), (++--), (-+--), (++++), (++-+), (+-+-), (----).$$

Give a biological interpretation for each case.

Exercise 3.9.12: Predator–prey model. *Suppose that an insect population,* $x(t)$*, is controlled by a natural predator population,* $y(t)$.

(a) *Write down a model describing the interaction of these two populations.*

(b) *Suppose an insecticide is used to reduce the population of insects, but it is also toxic to the predators; hence, the poison kills both predator and prey at rates proportional to their respective populations. Modify your model from* (a) *to take this into account.*

Exercise 3.9.13: Inhibited enzymatic reaction. *Write down the differential equations describing the following enzymatic reaction, where enzyme* E *is inhibited by inhibitor* I*:*

$$S + E \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} B_1 \overset{k_2}{\rightarrow} E + Q,$$

$$E + I \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} B_2.$$

Exercise 3.9.14: A feedback mechanism for oscillatory reactions. *Write down a differential equation model for the following pathway:*

$$A \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} B \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} C \underset{k_{-3}}{\overset{k_3}{\rightleftharpoons}} A.$$

Exercise 3.9.15: Enzymatic reaction with two intermediate steps. *Write down the equations describing the following reaction:*

$$S + E \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C_1 \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} C_2 \underset{k_{-3}}{\overset{k_3}{\rightleftharpoons}} E + P.$$

Exercise 3.9.16: Self-intoxicating population. *Some populations produce waste products, which in high concentrations are toxic to the population itself. For example, algae or bacteria show the structure in Figure* 3.25.

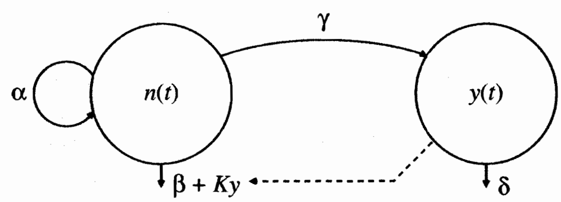

Figure 3.25. *Arrow diagram for a self-intoxicating population.*

Let the population density be denoted by $n(t)$ *and the toxin concentration by* $y(t)$. *Then*

$$\dot{n} = (\alpha - \beta - Ky)n,$$
$$\dot{y} = \gamma n - \delta y,$$

with $\alpha, \beta, \gamma, \delta, K \geq 0$.

(a) *Explain each term of the above system.*

(b) *Find the nullclines, the steady states, and sketch a phase portrait.*

(c) *Sketch the vector field.*

(d) *Linearize the system and characterize each of the steady states (stable/unstable, saddle, node, spiral, center, etc.). Find the regions in parameter space such that the nontrivial (coexistence) equilibrium is either a node or a spiral.*

(e) *Sketch some trajectories for the case of* $\delta < 4(\alpha - \beta)$, *and explain what you see in terms of the biology.*

(f) *Consider the case of higher dilution:* $\delta \gg 1$, $\gamma/\delta < \infty$.

Exercise 3.9.17: Fish populations in a pond. *Imagine a small pond that is mature enough to support wildlife. We desire to stock the pond with game fish, say trout and bass. Let* $T(t)$ *denote the population of the trout at any time* t, *and let* $B(t)$ *denote the bass population.*

(a) *Initially, assume that the pond environment can support an unlimited number of trout in isolation (i.e., growth of the trout population is exponential). Write down an equation that describes the evolution of the trout population in the absence of competition.*

(b) *Modify the equation to account for competition of the trout with the bass population for living space and a common food supply. You may assume that the growth rate of the trout population depends linearly on the bass population.*

(c) *Repeat* (a) *and* (b) *for the bass population.*

(d) *Explain the meaning of the parameters you introduced into the model.*

(e) *What are the steady states of the system? Determine the stability of the steady states using linearization.*

(f) *Perform a graphical analysis of the model. That is, find the nullclines, and sketch the phase portrait, taking into account the information obtained in* (e).

(g) *Is coexistence of the two species in the pond possible? If so, how sensitive is the final solution of the population levels to the initial stocked levels and external perturbations? Explain.*

(h) *Replace the exponential growth term in each equation with a logistic growth term. Use r_t and r_b to denote the intrinsic growth rate of the trout and bass, respectively, and K_t and K_b to denote the respective carrying capacities. Analyze the following specific case: $K_t > r_b/I_b$ and $K_b > r_t/I_t$, where I_t (I_b) represents the strength of the effect of the bass (trout) population on the rate of change of the trout (bass) population. How does the final outcome differ from before? Explain.*

(i) *The second model is a lot more realistic than the first model, as it no longer assumes unlimited growth in the absence of competition. Think of at least one further improvement to the model. How would the equations be affected? You should write down the equations, but you do not have to analyze them.*

Exercise 3.9.18: Exact solution for the logistic equation.

(a) *Develop the solution of the initial value problem for the logistic equation,*

$$N' = \mu N\left(1 - \frac{N}{K}\right), \qquad N(0) = N_0.$$

Note that the differential equation is separable, and use the method of partial fractions to find

$$N(t, N_0) = \frac{e^{\mu t} N_0}{1 + \frac{e^{\mu t}-1}{K} N_0}.$$

Alternatively, you can linearize the differential equation using the transformation $u = 1/N$.

(b) *Compare the solution obtained above to the solution of the Beverton–Holt model, developed in Exercise* 2.4.8.