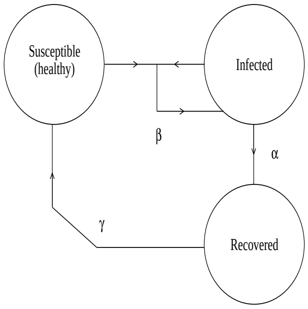

Chapter 1

Partial Differential Equations

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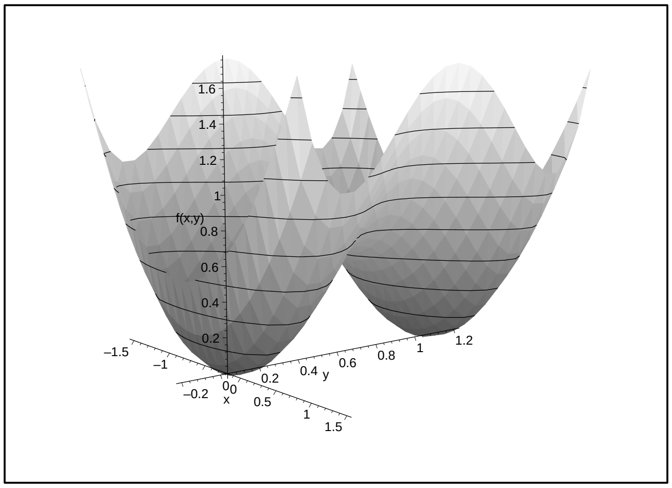

Figure 1.1. *3d01.eps*

1.1 Partial Differential Equations

Partial differential equations occur as soon as more than one independent variable occurs. In this section we give two of the most important examples; an age structured model and reaction-diffusion equations. In the first case, the independent variables are time, t, and age, a. For reaction-diffusion equations we have time, t, and space, x.

We call a differential equation a *partial differential equation* as soon as it involves *partial derivatives*. We recall some basic facts about partial derivatives.

1.1.1 Partial Derivatives

Let $f(x,y)$ be a function which depends on two variables, x and y. A good way to illustrate f is to draw its *graph*. Let $D \subseteq \mathbb{R}^2$ be a domain such that f is defined on D. Then the graph of f is

$$\text{graph}(f) = \{(x, y, f(x,y)) : (x,y) \in D\}$$

Example 1.1.1:

$$f(x,y) = \frac{1}{2}x^2 + y^2(1-y)^2$$

The level sets, or contour lines, are curves in the (x,y) *plane such that* $f(x,y) = k =$ *constant along these lines. In Figure 1.1, we show the graph of* f *and some contour lines.* Since f depends on two variables, we can define two derivatives,

$$\frac{\partial}{\partial x} f(x,y) = \lim_{h \to 0} \frac{f(x+h,y) - f(x,y)}{h}$$
$$\frac{\partial}{\partial y} f(x,y) = \lim_{h \to 0} \frac{f(x,y+h) - f(x,y)}{h}$$

which we call the *partial derivatives* of f.

The partial derivatives as defined above are evaluated at (x,y), hence they are also functions of (x,y).

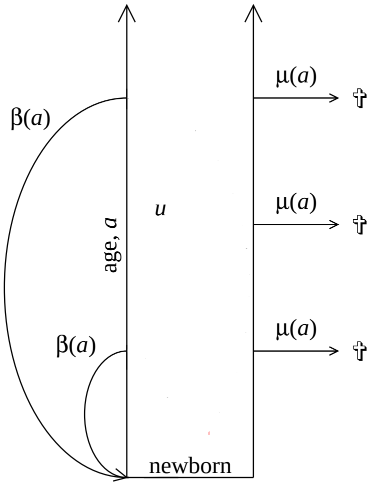

Figure 1.2. *muofa2.eps*

When we arrange these two functions in a vector, then we call it the *gradient* of f:

$$\mathrm{grad} f(x,y) = \begin{pmatrix} \frac{\partial}{\partial x} f(x,y) \\ \\ \frac{\partial}{\partial y} f(x,y) \end{pmatrix}$$

The gradient has a geometric interpretation. The vector $\mathrm{grad} f(x,y)$ always shows into the direction of steepest ascent of the function $f(x,y)$. Equivalently, the vector $\mathrm{grad} f(x,y)$ is always perpendicular to the level curves.

Partial derivatives can be used to find tangent planes, normal lines, etc. We recommend to consult a standard textbook on Calculus for more detailed information about partial derivatives.

1.1.2 An Age-Structured Model

Derivation

Here we study a model for a population which is structured by age. At each time step we would like to know the age-structure of the population. The population density u is the dependent variable, which depends on time, t, and age, a. Then $u(t,a)$ is the population density of age a at time t. Hence,

$$\int_{a_1}^{a_2} u(t,a)da = \text{ number of individuals with age between } a_1 \text{ and } a_2 \text{ at time } t.$$

We sketch the aging population in Figure 1.2. We choose a unit of time Δt. Obviously, individuals age as fast as time progresses. We assume that individuals of age a die in time Δt with probability $q(a)$. A discrete model for aging and death reads

$$u(t+\Delta t, a+\Delta t) = u(t,a) - q(a)\, u(t,a). \tag{1.1}$$

After rearrangements, we can construct differential quotients:

$$\frac{u(t+\Delta t, a+\Delta t) - u(t, a+\Delta t)}{\Delta t} + \frac{u(t, a+\Delta t) - u(t,a)}{\Delta t} = -\frac{q(a)}{\Delta t}\, u(t,a)$$

The death rate is $\mu(a) = \frac{q(a)}{\Delta t}$. Then for $\Delta t \to 0$, we obtain a continuous model

$$\frac{\partial}{\partial t}u(t,a) + \frac{\partial}{\partial a}u(t,a) = -\mu(a)u(t,a) \tag{1.2}$$

Equation (1.2) is a partial differential equation, since it involves derivatives with respect to time, t, and age, a. To be able to solve (1.2), we need boundary and initial conditions:

At $t = 0$, we have an initial age distribution

$$u(0,a) = u_0(a) \tag{1.3}$$

At age $a = 0$, we observe the new born population. Let $\beta(a)$ denote the birth rate of individuals of age a. Then

$$u(t,0) = \int_0^\infty \beta(a)u(t,a)da. \tag{1.4}$$

Solution

To solve equation (1.2) with boundary conditions (1.3) and (1.4), we first introduce the index notation of partial derivatives

$$u_t := \frac{\partial}{\partial t}u(t,a), \qquad u_a := \frac{\partial}{\partial a}u(t,a).$$

A common and powerful method to treat partial differential equations is to write it such that it looks like an ordinary differential equation. Here we write equation (1.2) as

$$u_t = \mathcal{L}u, \quad \text{with} \quad \mathcal{L}u = -u_a - \mu u. \tag{1.5}$$

Now $\mathcal{L}$ is not a number nor a matrix, but it is a linear differential operator which acts on functions. Indeed, for two continuously differentiable functions z_1 and z_2, and for two real constants α_1 and α_2, we obtain

$$\begin{aligned}
\mathcal{L}(\alpha_1 z_1 + \alpha_2 z_2) &= \frac{\partial}{\partial a}(\alpha_1 z_1 + \alpha_2 z_2) - \mu(a)(\alpha_1 z_1 + \alpha_2 z_2) \\
&= \alpha_1 \frac{\partial}{\partial a} z_1 + \alpha_2 \frac{\partial}{\partial a} z_2 - \alpha_1 \mu(a) z_1 - \alpha_2 \mu(a) z_2 \\
&= \alpha_1 \mathcal{L} z_1 + \alpha_2 \mathcal{L} z_2.
\end{aligned}$$

We can treat equation (1.5) similar to a matrix differential equation. We study eigenvalues, λ, and eigenfunctions, $w(a)$, of $\mathcal{L}$:

$$\lambda w(a) = \mathcal{L}w(a)$$

If λ is known, then we can explicitly solve for $w(a)$

$$\begin{aligned}
\lambda w(a) &= -w_a - \mu(a)w \\
\frac{\partial}{\partial a}w = -(\lambda + \mu)w \quad &\Rightarrow \quad w(a) = w_0 e^{-\int_0^a(\lambda + \mu(b))db},
\end{aligned}$$

where the constant w_0 will be specified later.

Another method for solving partial differential equations is *separation of variables.* This expresses the hope that the solution, $u(t,a)$, can be written as a product $u(t,a) = g(t)w(a)$ of one function, $g(t)$, which depends only on t, and another function, $w(a)$, which depends only on age, a. It is not clear, at the beginning, if such a solution exists. We have to try. We consider

$$u(t,a) = g(t)w(a), \tag{1.6}$$

where $w(a)$ is the eigenfunction of $\mathcal{L}$, as identified above. We introduce (1.6) into (1.2) and obtain

$$\begin{aligned} u_t = g'(t)w(a) &= -u_a - \mu u = -g w_a - \mu g w \\ &= g(-w_a - \mu w) = g(\mathcal{L}w) \\ &= \lambda g w \end{aligned}$$

Since $w(a) \neq 0$, we get an equation for $g(t)$:

$$g'(t) = \lambda g(t)$$

with solution

$$g(t) = g_0 e^{\lambda t},$$

where the constant g_0 has to be specified later.

Hence, a general solution is

$$u(t,a) = g_0 w_0 e^{\lambda t} e^{-\int_0^a (\lambda + \mu(b))db.} \tag{1.7}$$

If we introduce another constant $c = g_0 w_0$, then the general solution (1.7) contains two constants which still have to be found, c and the eigenvalue λ. We still have two more conditions, (1.3) and the boundary conditions; (1.4), which we can use to determine c and λ.

At $t = 0$ we have with (1.7)

$$u(0,a) = u_0(a) = c e^{-\int_0^a (\lambda + \mu(b))db} \tag{1.8}$$

This relation can not be valid for all arbitrarily chosen initial conditions $u_0(a)$. This simply means that the separation of variables method works only if (1.8) is satisfied for a constant c. If not, this method does not work, but there might be other methods which do. Here we assume (1.8) is satisfied and we continue with the boundary condition at age $a = 0$:

$$u(t,0) = \int_0^\infty \beta(a) u(t,a) da.$$

We introduce the general solution (1.7) into (1.4) and obtain

$$c e^{\lambda t} e^{-\int_0^0 (\lambda + \mu(b))db} = c e^{\lambda t} = \int_0^\infty \beta(a) c e^{\lambda t} e^{-\int_0^a (\lambda + \mu(b))db} da,$$

$$\Rightarrow \qquad 1 = \int_0^\infty \beta(a) e^{-\int_0^a (\lambda + \mu(b))db} da \tag{1.9}$$

This is a condition to find λ.

If $\beta(a)$ is not zero on an interval, then there is exactly one solution to this equation.

Lemma 1.1. *Assume $\beta(a) \geq \beta_0 > 0$ for some interval $a \in [a_1, a_2]$. Then there is a unique $\bar{\lambda} \in \mathbb{R}$ such that (1.9) holds.*

Proof. The right hand side (r.h.s) of (1.9) is a strictly decreasing function in λ.

We have

$$\lim_{\lambda \to -\infty} \text{r.h.s.} = +\infty, \qquad \lim_{\lambda \to +\infty} \text{r.h.s.} = 0$$

Hence there is exactly one value $\bar{\lambda}$ where the right hand side equals 1 (compare with Figure 1.3). $\square$

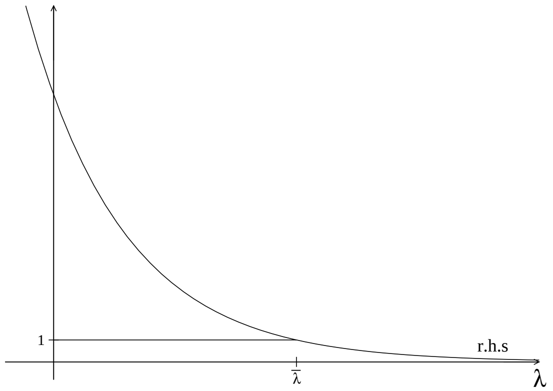

Figure 1.3. *There is exactly one value $\bar{\lambda}$ such that equation (1.9) is satisfied*

Now we find $\bar{\lambda}$ with (1.9) and we know c from (1.8). Then the solution $u(t, a)$ in (1.7) is specified. The time appears only in $e^{\lambda t}$. Hence the sign of λ alone determines the asymptotic behaviour. The following theorem has been proven in Webb [7].

Theorem 1.2.

$$\text{If } \bar{\lambda} < 0, \text{ then } u(t,a) \to 0 \text{ as } t \to \infty.$$
$$\text{If } \bar{\lambda} > 0, \text{ then } u(t,a) \to \infty \text{ as } t \to \infty.$$

For each solution $u(t, a)$ the function $u(t, a)g_0e^{-\lambda t}$ converges to $w(a)$ as $t \to \infty$ for each age a.

1.1.3 Reaction-Diffusion Equations

Another very important class of partial differential equations are *reaction-diffusion equations.* Now the independent variables are time, t, and space, x. Reaction-diffusion equations are used whenever the spatial spread of a population is of importance. Certainly, reaction-diffusion models have their limitations and there are more advanced models of correlated random walks or transport equations, but it is always a good idea to start with a reaction-diffusion model for spatial spread. This has successfully been done in epidemic models, for pattern formation, for predator-prey systems, and in signal transport, to name a few areas. A good overview is given in Murray [5] and in Britton [1].

Derivation of Reaction-Diffusion Equations

Assume a population with density $u(x, t)$ is living and moving in a container. To describe movement, we introduce another dependent quantity, the particle flux, $J(x, t) \in \mathbb{R}^n$. At each location x and at each time, t, the flux $J(x, t)$ is a vector which points into the general direction of movement at that location. Its magnitude, $|J(x, t)|$, is proportional to the amount of particles which flow in that direction per unit time. The flux J plays the role of the heat flux in heat transport or a concentration flux for a chemical reactor.

We consider a test-volumina, Ω, with boundary, Γ, and we balance in and out flux through Γ (see Figure 1.4)

$$\text{Change of } u \text{ in } \Omega = \text{flux through } \Gamma + \text{change due to birth, death, interactions.}$$

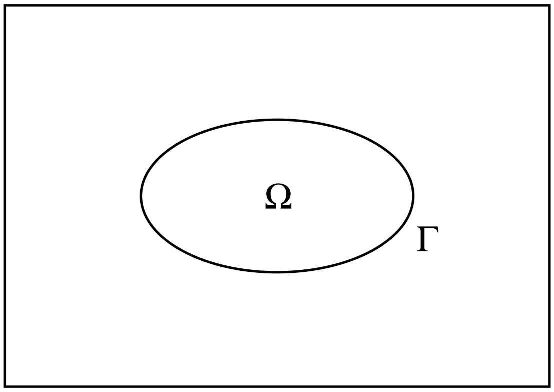

Figure 1.4. *Test area* Ω *with boundary* Γ.

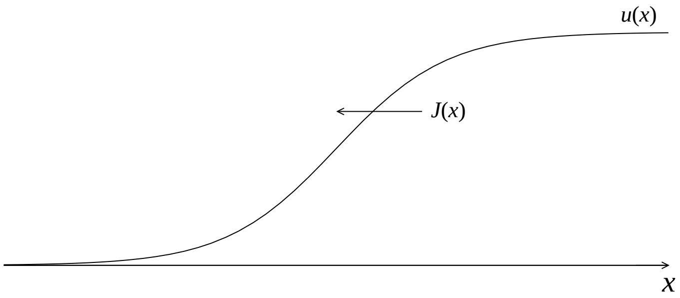

Figure 1.5. *RD.eps*

Written in formulas, this means

$$\frac{d}{dt}\int_{\Omega} u(x,t)dV = -\int_{\Gamma} J(x,t)dS + \int_{\Omega} f(u(x,t))dV,$$

where dV denotes integration in the whole space $\mathbb{R}^n$ and dS denotes surface integration in dimension $\mathbb{R}^{n-1}$.

We use the Divergence Theorem

$$\int_{\Gamma} J(x,t)dS = \int_{\Omega} \mathrm{div} J(x,t)dV$$

and we get

$$\int_{\Omega}\left(\frac{d}{dt}u - f(u) + \mathrm{div}J\right)dV = 0.$$

The above relation is satisfied in all test-volumina Ω. Then (if the measure dV is not degenerate) it follows that

$$\frac{d}{dt}u - f(u) + \mathrm{div}J = 0. \tag{1.10}$$

Next, we need a relation of the flux to the population distribution. As for chemical reactions, we use Fick's second law.

$$J = -D\nabla u \tag{1.11}$$

We assume that the flux J is proportional to the negative gradient of the particle distribution. In Figure 1.5, we find a positive gradient of u ($\frac{\partial}{\partial x}u(x,t) > 0$), and the flux points to the left, trying to equilibrate high and low levels of u. If we combine the balance law (1.10) with Fick's law (1.11), we get a *reaction-diffusion equation*,

$$\frac{d}{dt}u = D\Delta u + f(u), \tag{1.12}$$

where the Laplacian Δu is defined as

$$\Delta u(x,t) = \frac{\partial^2}{\partial x_1^2}u(x,t) + \cdots + \frac{\partial^2}{\partial x_n^2}u(x,t), \quad x = (x_1, \ldots, x_n) \in \mathbb{R}^n.$$

If $f = 0$, then equation (1.12) is simply the *diffusion equation.*

The Fundamental Solution

There is a particular solution of the diffusion equation ((1.12) with $f = 0$), which can be used to find other solutions by convolution (see, for example, Britton [1]). Moreover, this solution shows many of the common properties of solutions of reaction-diffusion equations in general.

The *fundamental solution* appears for a particle which starts at the origin 0. In terms of random walks on a grid (see section **??**), it is straightforward to start with a particle at 0. In the continuous case, however, we use a *δ-distribution* $\delta_0(x)$. The δ-distribution is not a function in the classical sense. It is defined by its action on smooth functions. If $f(x)$ is a smooth function, then $\delta_0(x)$ is the one and only object which satisfies

$$\int_{\mathbb{R}} \delta_0(x) f(x) dx = f(0)$$

and

$$\int_{\mathbb{R}} \delta_0(x) dx = 1.$$

To get an idea about the shape of $\delta_0(x)$ keep in mind that

$$\delta_0(x) = \begin{cases} +\infty & \text{for } x = 0 \\ 0 & \text{for } x \neq 0. \end{cases}$$

The δ-distribution is the prototype of a class of functions which are called *distributions* (we refer to Friedlander [3] for further details on distributions). For now it is sufficient to understand the properties as described above and we consider the *initial value problem* for a particle which diffuses in one dimension and starts with certainty at 0:

$$u_t = Du_{xx}, \quad u(x,0) = \delta_0(x) \tag{1.13}$$

The *fundamental solution* (in one dimension) is

$$u(x,t) = \frac{1}{2\sqrt{\pi D t}} e^{-\frac{x^2}{4Dt}} \tag{1.14}$$

In Figure 1.6, we show this solution for time steps $t = 0$, $t = t_1 > 0$, and $t = t_2 > t_1$, and $D = 1$. Although the initial condition is not continuous, the solution (1.14) is continuous for all $t > 0$. In fact it is infinitely often continuously differentiable, a property which is known as the *regularizing* property of the diffusion equation.

At $t = 0$, we have $\delta_0(x) = 0$ for all $x \neq 0$. However, as soon as $t > 0$, we get $u(x,t) > 0$ for all $x \in \mathbb{R}$. There is a minimal chance to find the particle very far from its start point. The diffusion equation allows for infinitely fast propagation.

Critical Patch Size

Reaction-diffusion equations are used to estimate the size of a habitat such that it can support a population. Obviously, it is not possible to establish a stable surviving rabbit population on an island which

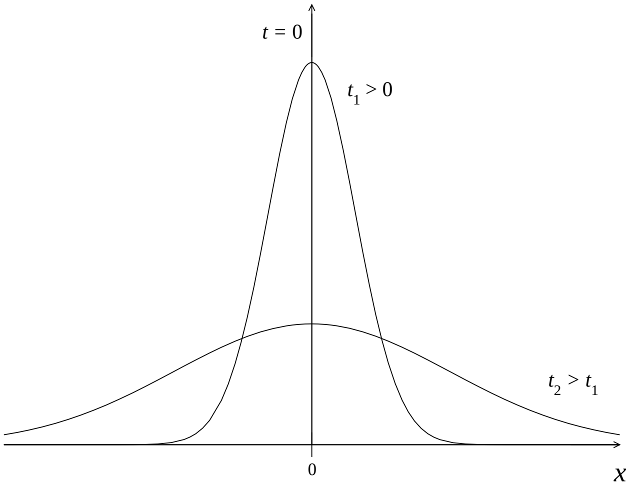

Figure 1.6. *Solutions of the diffusion equation (1.13) for three time values,* $t = 0$, $t = t_1 > 0$, *and* $t = t_2 > t_1$.

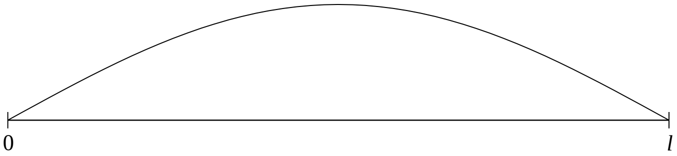

Figure 1.7. *island.eps*

is too small. In other cases, like the spruce budworm (see Murray [5]), the forest management likes to split a woodland into small enough patches as to prevent the budworms from settling in.

To illustrate the use of reaction-diffusion equations in this context, we use Fisher's equation, which shows all necessary features. Fisher [2] proposed the following model for the spread of an advantageous gene in a population.

$$u_t = Du_{xx} + \mu u(1-u) \tag{1.15}$$

The term $\mu u(1-u)$ is already familiar to us; it is Verhulst's law of growth with saturation. The Fisher equation applies also for population growth of randomly moving individuals. We will study this equation on a one-dimensional patch of size l, $I = [0, l]$

A partial differential equation on a bounded interval needs boundary conditions. Here we are guided by the application.

The case of an island as a patch has already been mentioned. Appropriate *island boundary conditions* are

$$u(0,t) = 0, \quad u(l,t) = 0. \tag{1.16}$$

These are also called *homogeneous Dirichlet boundary conditions* (see Figure 1.7). We can also study a valley or a box, or something with sealing walls. Then no individual can leave the patch. Appropriate *box boundary conditions* are

$$u_x(0,t) = 0, \quad u_x(l,t) = 0, \tag{1.17}$$

which are sometimes called *homogeneous Neumann boundary conditions* (see Figure 1.8). Obviously, combinations of island and box boundary conditions can occur, if, for example, the patch is bounded by a wall on the one side and by water on the other. We could also include some semi-permeable walls such that only a fraction of the population can leave the domain etc. We restrict our attention to the two cases given above. And to make it very clear: We need *one set* of boundary conditions; either (1.16) or (1.17), but not both at the same time.

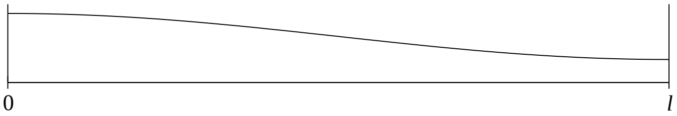

Figure 1.8. *inabox2.eps*

The question we are investigating is:

How large must an island or box be to support a population?

It has been shown in research articles (see, for example, Britton [1]) that it is equivalent to ask when the trivial solution $u(x,t) = 0$ is unstable. If $u(x,t) \equiv 0$ would be stable, then each solution (near 0) would converge to 0, hence the population would die out. Hence, $u(x,t) \equiv 0$ has to be unstable to allow for a surviving population. We are not introducing the notion of *stable* or *unstable* for partial differential equations here, but we can use them in the same way as for ordinary differential equations (see Section **??**).

For the Fisher equation (1.15), the question of stability is equivalent to look for nontrivial stationary solutions (steady states).

A steady state satisfies $u_t = 0$, hence

$$u_{xx} = -\frac{\mu}{D} u(1-u).$$

We are looking for solutions $u(x) \neq 0$ which satisfy the correct boundary conditions. With a new variable, $v = u_x$, we get

$$\begin{aligned} u_x &= v \\ v_x &= -\tfrac{\mu}{D} u(1-u), \end{aligned} \tag{1.18}$$

with Dirichlet boundary conditions

$$u(0) = 0, \quad u(l) = 0,$$

or with Neumann boundary conditions

$$v(0) = 0, \quad v(l) = 0.$$

The key to studying equation (1.18) is to understand x as a "time" variable and to consider

$$\begin{aligned} u' &= v \\ v' &= -\tfrac{\mu}{D} u(1-u) \end{aligned} \tag{1.19}$$

as a 2×2 system of ordinary differential equations. The equilibria of (1.19) are

$$P_1 = (0,0), \quad P_2 = (1,0).$$

The Jacobian of (1.19) is

$$Df(u,v) = \begin{pmatrix} 0 & 1 \\ 2\frac{\mu}{D}u - \frac{\mu}{D} & 0 \end{pmatrix}.$$

The linearization of (1.19) at P_1 is

$$Df(0,0) = \begin{pmatrix} 0 & 1 \\ -\frac{\mu}{D} & 0 \end{pmatrix},$$

which has purely imaginary eigenvalues $\lambda_{1/2} = \pm i\sqrt{\frac{\mu}{D}}$. Hence, $(0,0)$ is a center.

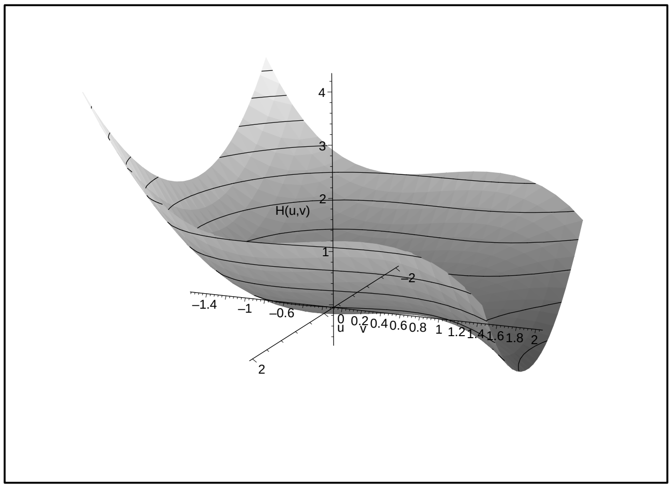

Figure 1.9. *3d02.eps*

At P_2, we find

$$Df(1,0) = \begin{pmatrix} 0 & 1 \\ \frac{\mu}{D} & 0 \end{pmatrix},$$

with eigenvalues $\lambda_{1/2} = \pm\frac{\mu}{D}$. Hence, $(1,0)$ is a saddle.

Since $(1,0)$ is a saddle for the linearization, it is also a saddle for the full, nonlinear system (1.19). This follows from the Hartman-Grobmann Theorem (see, for example, Perko [6]). Unfortunately, the Hartman-Grobmann Theorem does not apply in the center case. We can not decide, yet, if $(0,0)$ is a stable spiral, unstable spiral, or indeed a center for the nonlinear system (1.19).

We get the missing information from a *Hamiltonian function*

$$H(u,v) = \frac{1}{2}v^2 + \frac{\mu}{D}\frac{u^2}{2} - \frac{\mu}{D}\frac{u^3}{3}.$$

We can easily check with the use of (1.19) that

$$\frac{\partial H}{\partial v} = u' \quad \text{and} \quad \frac{\partial H}{\partial u} = -v', \tag{1.20}$$

hence for solutions $(u(x), v(x))$ of (1.19), we get via the chain rule

$$\frac{d}{dx}H(u(x),v(x)) = \frac{\partial H}{\partial u}\cdot u' + \frac{\partial H}{\partial v}\cdot v' = -v'u' + u'v' = 0. \tag{1.21}$$

Condition (1.20) and property (1.21) are the defining properties for H to be a Hamiltonian function of (1.19).

Remember that we understand x as time, hence from (1.21), it follows that the value of H does not change along solution curves $(u(x), v(x))$.

In Figure 1.9, we show H as a function of (u,v). Since H does not change along solution curves, the solution curves must follow the level lines of H. Since we have a Hamiltonian function, it follows that each bounded solution is either

1. an equilibrium point,
2. a connection of equilibrium points, or

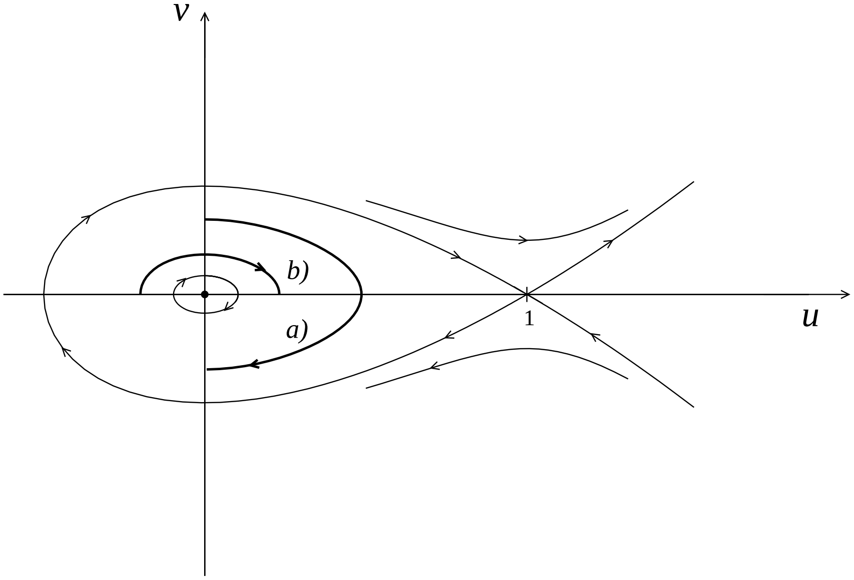

Figure 1.10. *around.eps*

3. a closed orbit.

The phase portrait of (1.19) is given in Figure 1.10. Although the phase portrait includes regions of $u < 0$, we consider only solutions which satisfy $u \geq 0$. Since $u(x)$ is a population density, it can not be negative. We refer to the region $u < 0$ as *not biologically relevant*.

To find solutions, we have to consider the boundary conditions. In the notion of the "time" x, a Dirichlet solution is a solution that starts at 0 ($u(0) = 0$), and it connects to $u(l) = 0$, where $u \geq 0$ all the time. In Figure 1.10 a), we show one such solution. Solutions to Neumann boundary conditions connect $v(0) = 0$ with $v(l) = 0$. A typical solution is indicated in Figure 1.10 b). Of course, this solution is not biologically relevant. The only relevant solutions for the Neumann case are $u \equiv 0$ and $u \equiv 1$.

Hence for a box, we can answer the starting question. A box of any size supports a population up to the carrying capacity (which is 1 in this case).

What is the minimal length for the Dirichlet problem? Let's have a closer look at the Dirichlet solutions. Each solution has a unique u-axis intersection, $\bar{u}$ (see Figures 1.11 and 1.12). As $\bar{u} \to 1$, the solution approaches the saddle point. Very close to the saddle point, it takes longer and longer to move forward. Hence, $l \to \infty$ for $\bar{u} \to 1$.

One could guess that $l \to 0$ for $\bar{u} \to 0$, but this is false. For $\bar{u} \to 0$, we enter the range close to $(0, 0)$, where the linearization describes the behaviour of the solutions. Remember that $(0, 0)$ is a center with eigenvalues $\lambda_{1/2} = \pm i\sqrt{\frac{\mu}{D}}$. Hence the general solution near $(0, 0)$ is given as $(u(x), v(x))^T = \left(c_1 \cos\left(\sqrt{\frac{\mu}{D}}x\right), c_2 \sin\left(\sqrt{\frac{\mu}{D}}x\right)\right)^T$.

A Dirichlet solution corresponds to a half circle starting at $x_0 = 0$, with $\sqrt{\frac{\mu}{D}}l = \pi$, hence $l = \pi\sqrt{\frac{D}{\mu}}$. In the limit $\bar{u} \to 0$, we get a critical patch size of $l^* = \pi\sqrt{\frac{D}{\mu}}$.

If $l > l^*$, we get a population distribution of the form shown in Figure 1.7. If $l < l^*$,the patch cannot support the population.

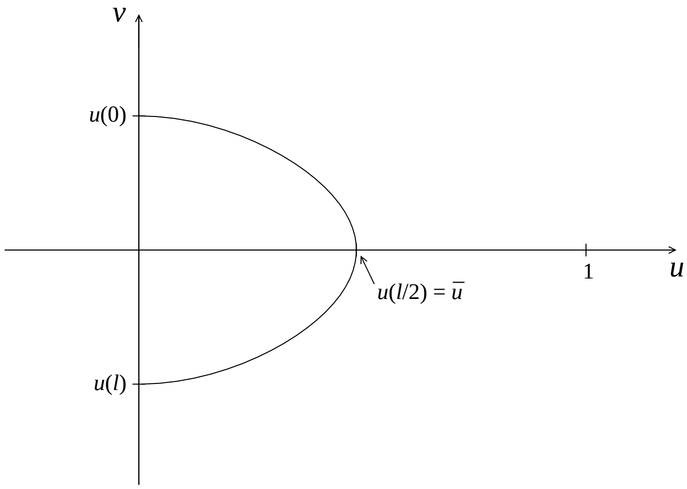

Figure 1.11. *dirichlet.eps*

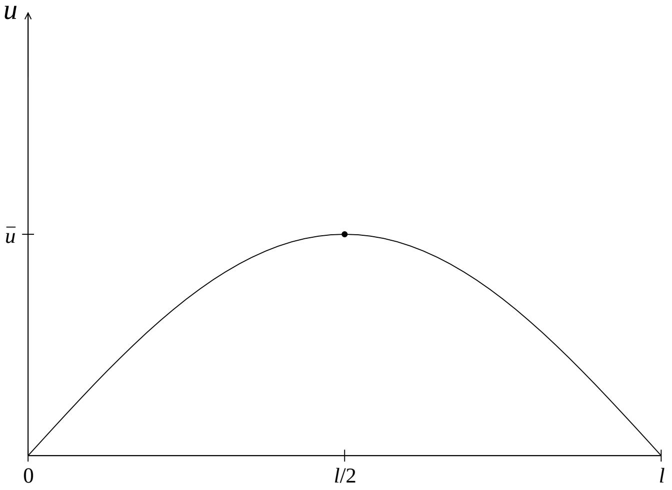

Figure 1.12. *dirichlet2.eps*

Travelling Waves

Another important problem in spatial ecology is if and how species can invade new habitats. Our method for studying this is to look for travelling wave solutions of a reaction-diffusion equation. To illustrate this, we again study the Fisher equation,

$$u_t = Du_{xx} + \mu u(1-u), \tag{1.22}$$

but now on the whole line $\mathbb{R}$. We try to find solutions which describe the invasion of the population into a new habitat, hence $u(x,t)$ should have the form shown in Figure 1.13, and then move with constant speed c. We look for solutions of the form

$$u(x,t) = \phi(x-ct).$$

For $c > 0$, the function $\phi(x-ct)$ appears to be the function $\phi(x)$ shifted to the right by ct, see Figures 1.14 and 1.15. The parameter c is the *wave speed*, the new variable, $z := x - ct$, is called the *wave variable* and the function $\phi(z)$ is called the *wave profile*.

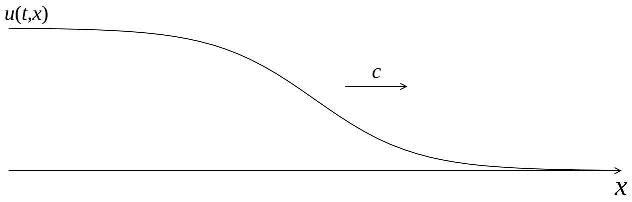

Figure 1.13. *fischer.eps*

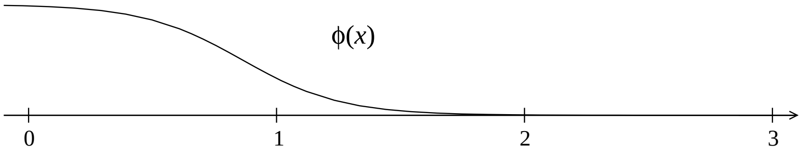

Figure 1.14. *phix.eps*

We make the *travelling wave ansatz*

$$u(x,t) = \phi(x-ct), \quad \phi(-\infty) = 1, \quad \phi(+\infty) = 0, \tag{1.23}$$

where instead of boundary conditions, we now have conditions at $\pm\infty$.

For $x \to -\infty$, the population has already grown to its carrying capacity (1 in this case), and for $x \to +\infty$, the population has not arrived yet.

From (1.23), we obtain

$$\frac{\partial}{\partial t} u(x,t) = -c\phi', \quad \frac{\partial^2}{\partial x^2} u(x,t) = \phi'',$$

hence (1.22) becomes

$$-c\phi' = D\phi'' + \mu\phi(1-\phi). \tag{1.24}$$

As in the previous section, we introduce a new variable, $\psi := \phi'$, and write (1.24) as a 2×2 system

$$\begin{array}{rcl} \phi' & = & \psi \\ \psi' & = & -\frac{c}{D}\psi - \frac{\mu}{D}\phi(1-\phi). \end{array} \tag{1.25}$$

The equilibria of (1.25) are $P_1 = (0,0)$ and $P_2 = (1,0)$. Using the linearization, we find that the point $P_1 = (0,0)$ is stable for $c > 0$. It is a stable spiral for $c < 2\sqrt{D\mu}$, and a stable node for $c > 2\sqrt{D\mu}$. The point $P_2 = (1,0)$ is always a saddle.

As for the critical patch size, we interpret x as a time variable. The boundary conditions for the wave profile are $\phi(-\infty) = 1$ and $\phi(+\infty) = 0$. Moreover, from the form of ϕ as shown in Figure 1.16, it is clear that $\psi(-\infty) = \psi(+\infty) = 0$. Hence in the phase portrait of system (1.25), we have to find a connection from the saddle $(1,0)$ to the stable point $(0,0)$. We show these connections for $c < 2\sqrt{D\mu}$ in Figure 1.17, and for $c > 2\sqrt{D\mu}$ in Figure 1.18. The function ϕ is the profile of the population density; hence it has to be nonnegative. Thus solutions for $c < 2\sqrt{D\mu}$ are not biologically relevant. They correspond to an oscillating front (see Figure 1.19). We obtain that the minimal speed, c^*, for which a wavefront solution exists is given by $c^* = 2\sqrt{D\mu}$ (here we argued graphically; a proof can be found in Källén *et al.* [4]).

General Fisher equation

The above result on minimal wave speed of travelling fronts can be generalized to general Fisher equations

$$u_t = Du_{xx} + f(u),$$

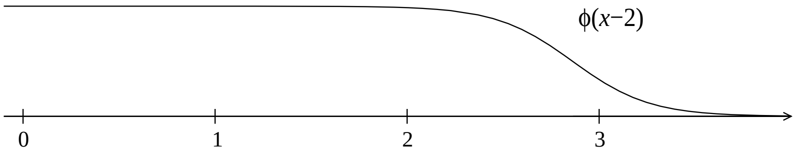

Figure 1.15. *phix-2.eps*

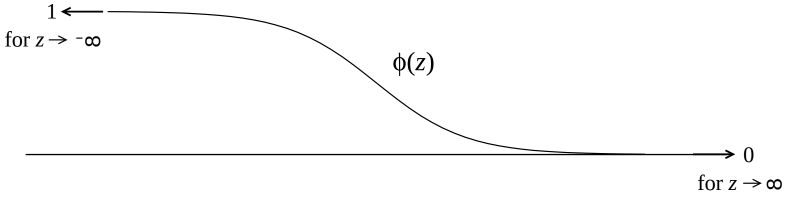

Figure 1.16. *fischer2.eps*

where $f(u)$ "looks like" $\mu u\left(1-\frac{u}{K}\right)$. The exact conditions on f are:

$$f(0)=0,\quad f(K)=0,\ K>0$$

$$f(u)>0,\quad \text{for all }\ 0<u<K$$

$$f'(0)>0,\quad f'(K)<0$$

Then the minimal wave speed is

$$c^*=2\sqrt{Df'(0)}.$$

The Linear Conjecture

As we saw in the previous sections, the minimal wave speed c^* is exactly that value where $(0,0)$ changes from spiral into node (Hopf bifurcation). If we consider the travelling wave solution close to $(0,0)$, then the behaviour is described by the linearization around $(0,0)$. The Jacobian of (1.25) at $(0,0)$ is

$$Df(0,0)=\begin{pmatrix}0 & 1\\ -\frac{\mu}{D} & -\frac{c}{D}\end{pmatrix},$$

which has trace $-c/D$ and determinant μ/D. Hence, $(0,0)$ is a node if and only if

$$c^2-4D\mu>0,$$

or $c>2$. The eigenvalues are then given by

$$\lambda_{1/2}=-\frac{c}{2D}\pm\frac{1}{2}\sqrt{\frac{c^2}{D^2}-4\frac{\mu}{D}},$$

and for $c^*=2\sqrt{D\mu}$, we have an eigenvalue of multiplicity 2:

$$\lambda_1=\lambda_2=-\frac{c^*}{2D}$$

The solution near $(0,0)$ behaves like $e^{-\frac{c^*}{2D}x}$ for $x\to\infty$. Hence, $-\frac{c}{2D}$ is the decay rate at the wave front.

Indeed, in many cases, it is enough to measure the decay rate of the profile for large x to get a good approximation for the minimal wave speed c^* (*linear conjecture*).

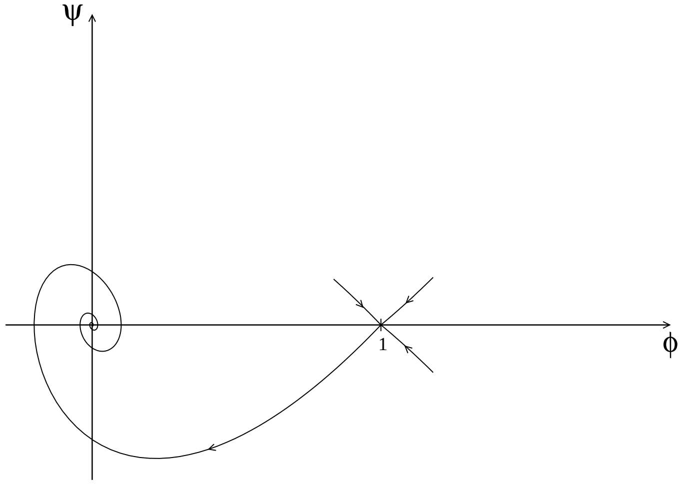

Figure 1.17. *spiral.eps ($c < 2$, no travelling wave) ($\mu = D = 1$)*

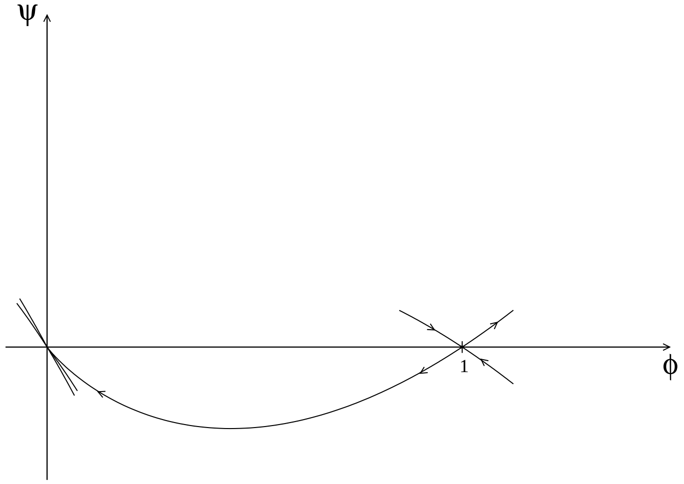

Figure 1.18. *twf.eps ($c > 2$, travelling wave-front) ($\mu = D = 1$)*

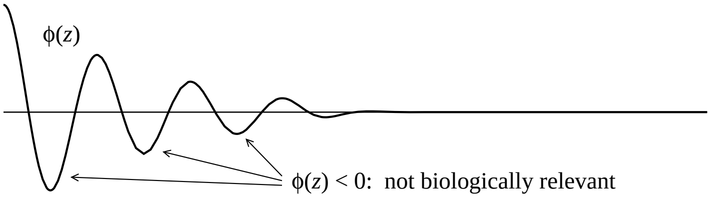

Figure 1.19. *nbr.eps*

1.1.4 Exercises for Partial Differential Equations

Exercise 1.1.1: (Diffusion through a membrane)

This question deals with diffusion through a membrane. We assume that a membrane of width L separates two regions (e.g., the interior and exterior of a cell). Consider a chemical that has a concentration c_1 inside the cell and c_2 outside the cell. The transport through the membrane can be described by a one-dimensional diffusion equation $u_t = Du_{xx}$. We assume that the solution settles onto an equilibrium.

1. Find the equilibrium and sketch the concentration at equilibrium as a function of position.
2. Using Fick's law, the flux across the membrane is given as

   $$J(x,t) = -Du_x(x,t),$$

   where $u(t,x)$ is a solution of the diffusion equation. Find the flux at equilibrium. The quotient D/L is known as the *permeability* of the membrane. Why do you think this is so?

Exercise 1.1.2: (Signalling in ant populations)

Certain ant species (like *Pogonomyrmex badius*) use pheromones as a signal for danger. In experiments Bossert and Wilson released ants in a long tube and they stimulated one ant until it released the chemical signal. They measure in which distance and after which time delay the other ants would react to the signal. A good model for the spread of the pheromones in the tube is the one-dimensional diffusion equation.

We assume that at time $t = 0$ a signal of strength α is released. The diffusion constant is $D = 1$. Other ants react to the stimulus if the concentration they perceive is 10% of α or higher.

1. For each $t > 0$ find the region in the tube $0 \le x \le x(t)$ where the ants would react to the stimulus (*region of influence*).
2. Sketch the time evolution of $x(t)$.
3. Find the time t^* such that the region of influence is empty for all $t > t^*$.

Exercise 1.1.3: (Dingos in Australia)

A Dingo population, which lives in the eastern parts of Australia is prevented from invasion to the west by a fence which runs north-south. In this exercise we study the case that the fence breaks somewhere (at time $t = 0$).

Two farms, A and B, are located on the west side of the fence. The distance of farm A to the fence is 100 miles and the distance from farm A to B is another 100 miles. The farmers like to know how long it takes until the Dingo population reaches their farms. We model the spread of the Dingo population with Fishers equation

$$u_t = Du_{xx} + ku\left(1 - \frac{u}{K}\right),$$

with $k = 1$ (1/month), and $K = 1$ (in the units of u).

1. The region between farm A and the fence is flat and the diffusion constant is $D_1 = 100$ (miles^2/month). When does the Dingo population reach farm A?

2. The region between farm A and B has rocks and slope, hence there the diffusion constant is $D_2 = 50$ (miles^2/month). When does the Dingo population reach farm B?

(Hint: For part a) consider a travelling wave and calculate the wave speed corresponding to D_1 and k. Find the spatial decay rate λ_1 of this wave. For b) take the exponentially decaying wave of part a) and use D_2 to find the wave velocity which corresponds to a decay rate of λ_1.)

Exercise 1.1.4: (Signal transport in the axon)

Fitzhugh and Nagumo derived a model for signal transduction in the axon:

$$u_t = u_{xx} + u(1-u)\left(u - \frac{1}{2}\right),$$

where u represents the membrane potential. We study this model on $0 \le x \le l$ with homogeneous Neumann boundary conditions,

$$u_x(t,0) = 0, \qquad u_x(t,l) = 0.$$

1. Find a system of two ODEs which describe the steady states.
2. Find the equilibrium points of the system of (a) and study their stability.
3. Show that
$$H(u,v) = \frac{1}{2}(u_x)^2 - \frac{1}{4}u^4 + \frac{1}{2}u^3 - \frac{1}{4}u^2$$
is a Hamiltonian function for the system you found in (a).
4. Sketch a phase portrait in the (u, u_x)-plane.
5. Find the steady states which satisfy the Neumann boundary conditions, and sketch the steady states u as a function of x.

Bibliography

[1] N.F. Britton. *Reaction–Diffusion Equations and Their Applications to Biology.* Academic Press, London, 1986.

[2] R.A. Fisher. The advance of advantageous genes. *Ann. Eugenics,* 7:355–369, 1937.

[3] F.G. Friedlander. *Introduction of the theory of distributions. With additional material by M. Joshi.* Cambridge University Press, Cambridge, 2nd edition, 1998.

[4] A. Källén, P. Arcuri, and J.D. Murray. A simple model for the spatial spread and control of rabies. *J. theor. Biol.*, 116:377–393, 1985.

[5] J.D. Murray. *Mathematical Biology.* Springer, Berlin, 1989.

[6] L. Perko. *Differential Equations and Dynamical Systems*, volume 7 of *Texts in Applied Mathematics.* Springer, New York, N.Y., 3rd edition, 2001.

[7] G.F. Webb. *Theory of Nonlinear Age-dependent Population Dynamics.* Marcel Dekker, New York, N.Y., 1985.