1

Introduction

1.1 Introductory Remarks

A fundamental goal of theoretical ecology is to understand how the interactions of individual organisms with each other and with the environment determine the distribution of populations and the structure of communities. Empirical evidence suggests that the spatial scale and structure of environments can influence population interactions (Gause, 1935; Huffaker, 1958) and the composition of communities (MacArthur and Wilson, 1967). In recent decades the role of spatial effects in maintaining biodiversity has received a great deal of attention in the literature on conservation; see for example Soulè (1986) or Kareiva et al. (1993). One of the most common ways that human activities alter environments is by fragmenting habitats and creating edges. Some habitat fragments may be designated as nature reserves, but they are fragments nonetheless.

One way to try to understand how spatial effects such as habitat fragmentation influence populations and communities is by using mathematical models; see Tilman and Kareiva (1997), Tilman (1994), Molofsky (1994), Holmes et al. (1994), Goldwasser et al. (1994). In this book we will examine how one class of spatial population models, namely reaction-diffusion equations, can be formulated and analyzed. Our focus will be primarily on models for populations or communities which occupy an isolated habitat fragment. There are several other types of spatial population models, including cellular automata, interacting particle systems, metapopulation models, the ideal free distribution, and dispersal models based on integral kernels. Each type of model is based on some set of hypotheses about the scale and structure of the spatial environment and the way that organisms disperse through it. We describe some of these types of models a bit later in our discussion of model formulation; see also Tilman and Kareiva (1997). Some of the ideas used in analyzing reaction-diffusion systems also can be applied to these other types of spatial models. We also describe a few of the connections between different types of models and some unifying principles in their analysis.

Reaction-diffusion models provide a way to translate local assumptions or data about the movement, mortality, and reproduction of individuals into global conclusions about the persistence or extinction of populations and the coexistence of interacting species. They can be derived mechanistically via rescaling from models of individual movement which are based on random walks; see Turchin (1998) or Durrett and Levin (1994). Reaction-diffusion models are spatially explicit and typically incorporate quantities such as dispersal rates, local growth rates, and carrying capacities as parameters which may vary with location or time.

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Thus, they provide a good framework for studying questions about the ways that habitat geometry and the size or variation in vital parameters influence population dynamics.

The theoretical advances in nonlinear analysis and the theory of dynamical systems which have occurred in the last thirty years make it possible to give a reasonably complete analysis of many reaction-diffusion models. Those advances include developments in bifurcation theory (Rabinowitz 1971, 1973; Crandall and Rabinowitz 1971, 1973), the formulation of reaction-diffusion models as dynamical systems (Henry 1981), the creation of mathematical theories of persistence or permanence in dynamical systems (Hofbauer and Sigmund 1988, Hutson and Schmitt 1992), and the systematic incorporation of ideas based on monotonicity into the theory of dynamical systems (Hirsch 1982, 1985, 1988a,b, 1989, 1990, 1991; Hess 1991; Smith 1995). One of the goals of this book is to show how modern analytical approaches can be used to gain insight into the behavior of reaction-diffusion models.

There are many contexts in which reaction-diffusion systems arise as models, many phenomena that they support, and many ways to approach their analysis. Existing books on reaction-diffusion models reflect that diversity to some extent but do not exhaust it. There are three major phenomena supported by reaction-diffusion models which are of interest in ecology: the propagation of wavefronts, the formation of patterns in homogeneous space, and the existence of a minimal domain size that will support positive species density profiles. In this book we will focus our attention on topics related to the third of those three phenomena. Specifically, we will discuss in detail the ways in which the size and structure of habitats influence the persistence, coexistence, or extinction of populations. Some other treatments of reaction-diffusion models overlap with ours to some extent, but none combines a specific focus on issues of persistence in ecological models with the viewpoint of modern nonlinear analysis and the theory of dynamical systems. The books by Fife (1979) and Smoller (1982) are standard references for the general theory of reaction-diffusion systems. Both give detailed treatments of wave-propagation, but neither includes recent mathematical developments. Waves and pattern formation are treated systematically by Grindrod (1996) and Murray (1993). Murray (1993) discusses the construction of models in considerable detail, but in the broader context of mathematical biology rather than the specific context of ecology. Okubo (1980) and Turchin (1998) address the issues of formulating reaction-diffusion models in ecology and calibrating them with empirical data, but do not discuss analytic methods based on modern nonlinear analysis. Hess (1991) uses modern methods to treat certain reaction-diffusion models from ecology, but the focus of his book is mainly on the mathematics and he considers only single equations and Lotka-Volterra systems for two interacting species. The book by Hess (1991) is distinguished from other treatments of reaction-diffusion theory by being set completely in the context of time-periodic equations and systems. The books by Henry (1981) and Smith (1995) give treatments of reaction-diffusion models as dynamical systems, but are primarily mathematical in their approach and use specific models from ecology or other applied areas mainly as examples to illustrate the mathematical theory. Smith (1995) and Hess (1991) use ideas from the theory of monotone dynamical systems extensively. An older approach based on monotonicity and related ideas is the method of monotone iteration. That method and other methods based on sub- and supersolutions are discussed by Leung (1989) and Pao (1992) in great detail. However, Leung (1989) and Pao (1992) treat reaction-diffusion models in general without a strong focus on ecology, and they do not discuss ideas and methods that do not involve sub- and supersolutions in much depth. One such idea, the notion of permanence/uniform persistence, is discussed by Hofbauer and Sigmund (1988, 1998) and in the survey paper by Hutson and Schmitt (1992). We will use that idea fairly extensively but our treatment differs from those

given by Hofbauer and Sigmund (1988, 1998) and Hutson and Schmitt (1992) because we examine the specific applications of permanence/uniform persistence to reaction-diffusion systems in more depth, and we also use other analytic methods. Finally, there are some books on spatial ecology which include discussions of reaction-diffusion models as well as other approaches. Those include the volumes on spatial ecology by Tilman and Kareiva (1997) and on biological invasions by Kawasaki and Shigesada (1997). However, those books do not go very far with the mathematical analysis of reaction-diffusion models on bounded spatial domains.

We hope that the present volume will be interesting and useful to readers whose backgrounds range from theoretical ecology to pure mathematics, but different readers may want to read it in different ways. We have tried to structure the book to make that possible. Specifically, we have tried to begin each chapter with a relatively nontechnical discussion of the ecological issues and mathematical ideas, and we have deferred the most complicated mathematical analyses to Appendices which are attached to the ends of chapters. Most chapters include a mixture of mathematical theorems and ecological examples and applications. Readers interested primarily in mathematical analysis may want to skip the examples, and the readers interested primarily in ecology may want to skip the proofs. We hope that at least some readers will be sufficiently interested in both the mathematics and the ecology to read both.

To read this book effectively a reader should have some background in both mathematics and ecology. The minimal background needed to make sense of the book is a knowledge of ordinary and partial differential equations at the undergraduate level and some experience with mathematical models in ecology. A standard introductory course in ordinary differential equations, a course in partial differential equations from a book such as Strauss (1992), and some familiarity with the ecological models discussed by Yodzis (1989) or a similar text on theoretical ecology would suffice. Alternatively, most of the essential prerequisites with the exception of a few points about partial differential equations can be gleaned from the discussions in Murray (1993). Readers with the sort of background described above should be able to understand the statements of theorems and to follow the discussion of the ecological examples and applications.

To follow the derivation of the mathematical results or to understand why the examples and applications are of interest in ecology requires some additional background. To be able to follow the mathematical analysis, a reader should have some knowledge of the theory of functions of a real variable, for example as discussed by Royden (1968) or Rudin (1966, 1976), and some familiarity with the modern theory of elliptic and parabolic partial differential equations, as discussed by Gilbarg and Trudinger (1977) and Friedman (1976), and dynamical systems as discussed by Hale and Koçak (1991). To understand the ecological issues behind the models, a reader should have some familiarity with the ideas discussed by Tilman and Kareiva (1997), Soulè (1986), Soulè and Terborgh (1989), and/or Kareiva et al. (1993). The survey articles by Tilman (1994), Holmes et al. (1994), Molofsky (1994), and Goldwasser et al. (1994) are also useful in that regard. For somewhat broader treatments of ecology and mathematical biology respectively, Roughgarden et al. (1989) and Levin (1994) are good sources.

1.2 Nonspatial Models for a Single Species

The first serious attempt to model population dynamics is often credited to Malthus (1798). Malthus hypothesized that human populations can be expected to increase geometrically

with time but the amount of arable land available to support them can only be expected to increase at most arithmetically, and drew grim conclusions from that hypothesis. In modern terminology the Malthusian model for population growth would be called a density independent model or a linear growth model. In nonspatial models we can describe populations in terms of either the total population or the population density since the total population will just be the density times the area of the region the population inhabits. We will typically think of the models as describing population densities since that viewpoint still makes sense in the context of spatial models. Let $P(t)$ denote the density of some population at time t. A density independent population model for $P(t)$ in continuous time would have the form

$$\frac{dP}{dt} = r(t)P(t); \tag{1.1}$$

in discrete time the form would be

$$P(t+1) = R(t)P(t). \tag{1.2}$$

These sorts of models are linear in the terminology of differential or difference equations, which is why they are also called linear growth models. In the discrete time case we must have $R(t) \geq 0$ for the model to make sense. If r is constant in (1.1) we have $P(t) = e^{rt}P(0)$; if $R(t)$ is constant in (1.2) we have $P(t) = R^t P(0)$. In either case, the models predict exponential growth or decay for the population. To translate between the models in such a way that the predicted population growth rate remains the same we would use $R = e^r$ or $r = \ln R$.

The second major contribution to population modeling was the introduction of population self-regulation in the logistic equation of Verhulst (1838). The key element introduced by Verhulst was the notion of density dependence, that is, the idea that the density of a population should affect its growth rate. Specifically, the logistic equation arises from the assumption that as population density increases the effects of crowding and resource depletion cause the birth rate to decrease and the death rate to increase. To derive the logistic model we hypothesize that the birthrate for our population is given by $b(t) - a(t, P)$ and the death rate by $d(t) + e(t, P)$ where b, a, d, and e are nonnegative and a and e are increasing in P. The simplest forms for a and e are $a = a_0(t)P$ and $e = e_0(t)P$ with $a_0, e_0 \geq 0$. The net rate of growth for a population at density P is then given by

$$\begin{aligned} \frac{dP}{dt} &= ([b(t) - a_0(t)P] - [d(t) + e_0(t)P])P \\ &= ([b(t) - d(t)] - [a_0(t) + e_0(t)]P)P \\ &= (r(t) - c(t)P)P, \end{aligned} \tag{1.3}$$

where $r(t) = b(t) - d(t)$ may change sign but $c(t) = a_0(t) + e_0(t)$ is always nonnegative. We will almost always assume $c(t) \geq c_0 > 0$. If r and c are constant we can introduce the new variable $K = r/c$ and write (1.3) as

$$\frac{dP}{dt} = r\left(1 - \left[\frac{P}{K}\right]\right)P. \tag{1.4}$$

Equation (1.4) is the standard form used in the biology literature for the logistic equation. The parameter r is often called the intrinsic population growth rate, while K is called

the carrying capacity. If $r(t) > 0$ then equation (1.3) can be written in the form (1.4) with K positive. However, if K is a positive constant then letting $r = r(t)$ in (1.4) with $r(t)$ negative some of the time leads to a version of (1.3) with $c(t) < 0$ sometimes, which contradicts the underlying assumptions of the model. We will use the form (1.4) for the logistic equation in cases where the coefficients are constant, but since we will often want to consider situations where the intrinsic population growth rate r changes sign (perhaps with respect to time, or in spatial models with respect to location) we will usually use the form (1.3). Note that by letting $p = P/K$ and $\tau = rt$ we can rescale (1.4) to the form $dp/d\tau = p(1 - p)$. We sometimes assume that (1.4) has been rescaled in this way. A derivation along the lines shown above is given by Enright (1976). The specific forms $a = a_0(t)P$, $e = e_0(t)P$ are certainly not the only possibilities. In fact, the assumptions that increases in population density lead to decreases in the birth rate and increases in the death rate may not always be valid. Allee (1931) observed that many animals engage in social behavior such as cooperative hunting or group defense which can cause their birth rate to increase or their death rate to decrease with population density, at least at some densities. Also, the rate of predation may decrease with prey density in some cases, as discussed by Ludwig et al. (1978). In the presence of such effects, which are typically known as Allee effects, the model (1.3) will take a more general form

$$\frac{dP}{dt} = g(t, P)P \tag{1.5}$$

where g may be increasing for some values of P and decreasing for others. A simple case of a model with an Allee effect is

$$\frac{dP}{dt} = r(P - \alpha)(K - P)P \tag{1.6}$$

where $r > 0$ and $0 < \alpha < K$. The model (1.6) implies that P will decrease if $0 < P < \alpha$ or $P > K$ but increase if $\alpha < P < K$.

The behavior of (1.4) is quite simple. Positive solutions approach the equilibrium K monotonically as $t \to \infty$ at a rate that depends on r, so that the equilibrium $P = 0$ is unstable and $P = K$ is stable. The behavior of (1.6) is slightly more complicated. Solutions which start with $0 < P < \alpha$ will approach 0 as $t \to \infty$; solutions starting with $P > \alpha$ will approach K monotonically as $t \to \infty$. Thus, the equilibrium $P = \alpha$ is unstable but $P = 0$ and $P = K$ are stable.

There are various ways that a logistic equation can be formulated in discrete time. The solution to (1.4) can be written as $P(t) = e^{rt}P/(1 + [(e^{rt} - 1)/K]P)$. If we evaluate $P(t)$ at time $t = 1$ we get $P(1) = e^r P(0)/(1 + [(e^r - 1)/K]P(0))$; by iterating we obtain the discrete time model

$$P(t + 1) = e^r P(t)/(1 + [(e^r - 1)/K]P(t)). \tag{1.7}$$

The model (1.7) is a version of the Beverton-Holt model for populations in discrete time (see Murray (1993), Cosner (1996)). A different formulation can be obtained by integrating the equation $dP/dt = r[1-(P(0)/K)]P(t)$; that yields $P(1) = \exp(r[1-(P(0)/K)])P(0)$ and induces an iteration

$$P(t + 1) = \exp(r[1 - (P(t)/K)])P(t). \tag{1.8}$$

This is a version of the Ricker model (see Murray (1993), Cosner (1996)). The difference in the assumptions behind (1.7) and (1.8) is that in (1.7) intraspecific competition is assumed to occur throughout the time interval (t, t_1) while in (1.8) the competitive effect is only based on conditions at time t. The behaviors of the models (1.7) and (1.8) are quite different. Model (1.7) behaves much like the logistic model (1.4) in continuous time. Solutions that are initially positive converge to the equilibrium $P = K$ monotonically (see Cosner (1996)). On the other hand, (1.8) may have various types of dynamics, including chaos, depending on the parameters (see Murray (1993)). In most of what follows we will study continuous time models which combine local population dynamics with dispersal through space, and we will describe dispersal via diffusion. Some of the ideas and results we will discuss can be extended to models in discrete time, but the examples (1.7), (1.8) show that models in discrete time may or may not behave in ways that are similar to their continuous time analogues, so some care is required in going from continuous to discrete time.

In many populations individuals are subject to different levels of mortality and have different rates of reproduction at different ages or stages in their lives. Models which account for these effects typically classify the population by developmental stage, age, or size and specify the rates at which individuals move from one stage to another, what fraction survive each stage of their life history, and the rates at which individuals at each of the stages produce offspring. The type of models which have been used most frequently to describe age or stage structured populations are discrete time matrix models of the sort introduced by Leslie (1948) and treated in detail by Caswell (1989). These models divide a population into n classes, with the population in each class denoted by P_i. Usually the class P_0 represents eggs, seeds, or recently born juveniles. The total population is then given by $\sum_{i=0}^{n} P_i$. The models typically specify the fraction S_i of individuals in class i that survive and enter class $i+1$ at each time step, the fraction S_{n+1} that survive and remain in class n, and the number of offspring R_i of class $i = 0$ produced in each time step by an individual of class i. The models then take the form

$$\vec{P}(t) = M\vec{P}(t) \tag{1.9}$$

where $\vec{P} = (P_0, \ldots, P_n)$ and M is the matrix

$$M = \begin{pmatrix} R_0 & R_1 & R_2 & \ldots & R_n \\ S_1 & 0 & 0 & \ldots & 0 \\ 0 & S_2 & \ddots & \ddots & \ldots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \ldots & 0 & S_n & S_{n+1} \end{pmatrix}.$$

Models of the form (1.9) are discussed at length by Caswell (1989). In general the entries in the matrix M may depend on $\vec{P}$ in various ways. A key property of matrices of the form shown for M with constant positive entries is that M^n has all its entries positive. It follows from the theory of nonnegative matrices that M has a positive eigenvalue λ_1 whose corresponding eigenvector $\vec{v}$ is componentwise positive. (This is a consequence of the Perron-Frobenius theorem. See Caswell (1989), Berman and Plemmons (1979), or the discussion of positivity in Chapter 2.) The eigenvalue λ_1 is called the principal eigenvalue

of M, and it turns out that λ_1 is larger than the real part of any other eigenvalue of M. If $\lambda_1 > 1$ then the population will increase roughly exponentially; specifically, if $\vec{v}$ is the componentwise positive eigenvector of unit length corresponding to λ_1 we will have $P(t) \approx \lambda_1^t(\vec{P}(0) \cdot \vec{v})\vec{v}$ for t large. (See Caswell (1989).) Similarly, if $\lambda_1 < 1$ then the population will decline roughly exponentially. Thus, λ_1 plays the same role as R plays in (1.2). If we viewed λ_1 as giving an overall growth rate for the entire population $\sum_{i=0}^{n} P_i$, which is reasonable in view of the asymptotic behavior of (1.9), we would use $r = \ln \lambda_1$ in the corresponding continuous model. In this case $r > 0$ if and only if $\lambda_1 > 1$. Because they break down the life history of an organism into simpler steps, models of the form (1.9) are useful in deriving population growth rates from empirical data on survivorship and fecundity; again, see Caswell (1989). The principal eigenvalue of M in effect averages population growth rates over the age or stage classes of a structured population. The use of eigenvalues to obtain something like an average growth rate for a structured population will be a recurring theme in this book. However, the populations we consider will usually be structured by spatial distribution rather than age, and the eigenvalues will generally correspond to differential operators rather than matrices. If the entries in the matrix M depend on $\vec{P}$ then the model (1.9) can display the same types of behavior as (1.7) and (1.8). See Caswell (1989) or Cosner (1996) for additional discussion of density dependent models of the form (1.9).

It is also possible to formulate age structured population models in continuous time. The simplest formulation of such models describes a population in terms of $P(a, t)$ where a is a continuous variable representing age, so that the number of individuals in the population at time t whose ages are between a_1 and a_2 is given by $\int_{a_1}^{a_2} P(a, t)da$. The basic form of a linear (or density independent) model for a population with a continuous age structure consists of an equation describing how individuals age and experience mortality, and another equation describing the rate at which new individuals are born. The equation describing how individuals age is the McKendrick-Von Foerster equation

$$\frac{\partial P}{\partial t} + \frac{\partial P}{\partial a} = -d(a)P \tag{1.10}$$

where $d(a)$ is a age-specific death rate. The equation describing births is the birth law

$$P(0, t) = \int_0^{\infty} b(a)P(a, t)da \tag{1.11}$$

where $b(a)$ is an age dependent birth rate. Density dependent models arise if d or b depends on P. Age structured models based on generalizations of (1.10) and (1.11) are discussed in detail by Webb (1985).

Our main goal is to understand spatial effects, so we will usually assume that the population dynamics of a given species at a given place and time are governed by a simple continuous time model of the form (1.5). We will often consider situations where the population dynamics vary with location, and we will typically model dispersal via diffusion. Before we discuss spatial models, however, we describe some models for interacting populations which are formulated in continuous time via systems of equations analogous to (1.5).

The population models described above are all deterministic, and all of them can be interpreted as giving descriptions of how populations behave as time goes toward infinity.

It is also possible to construct models based on the assumption that changes in population are stochastic. Typically such models predict that populations will become extinct in finite time, and often the main issue in the analysis of such models is in determining the expected time to extinction. We shall not pursue that modeling approach further. A reference is Mangel and Tier (1993).

1.3 Nonspatial Models For Interacting Species

1.3.1 Mass-Action and Lotka-Volterra Models

The first models for interacting species were introduced in the work of Lotka (1925) and Volterra (1931). Those models have the general form

$$\frac{dP_i}{dt} = \left(a_i + \sum_{j=1}^{n} b_{ij} P_j \right) P_i, \quad i = 1, \ldots, n, \tag{1.12}$$

where P_i denotes the population density of the ith species. The coefficients a_i are analogous to the linear growth rate $r(t)$ in the logistic model (1.3). The coefficients b_{ii} represent intraspecies density dependence, in analogy with the term $c(t)P$ in (1.3), so we have $b_{ii} \leq 0$ for all i. The coefficients b_{ij}, $i \neq j$, describe interactions between different species. The nature of the interaction–competition, mutualism, or predator-prey interaction–determines the signs of the coefficients b_{ij}. If species i and j compete then b_{ij}, $b_{ji} < 0$. If species i preys upon species j, then $b_{ij} > 0$ but $b_{ji} < 0$. If species i and j are mutualists, then b_{ij}, $b_{ji} > 0$. (In the case of mutualism Lotka-Volterra models may sometimes predict that populations will become infinite in finite time, so the models are probably less suitable for that situation than for competition or predator-prey interactions.) Usually Lotka-Volterra competition models embody the assumption that $b_{ii} < 0$ for each i, so the density of each species satisfies a logistic equation in the absence of competitors. In the case where species i preys on species j, it is often assumed that $b_{jj} < 0$ (so the prey species satisfies a logistic equation in the absence of predation), but that $b_{ii} = 0$ while $a_i < 0$. Under those assumptions the predator population will decline exponentially in the absence of prey (because $a_i < 0$), but the only mechanism regulating the predator population is the availability of prey (because $b_{ii} = 0$, implying that the growth rate of the predator population does not depend on predator density). If the predator species is territorial or is limited by the availability of resources other than prey, it may be appropriate to take $b_{ii} < 0$. Lotka-Volterra models are treated in some detail by Freedman (1980), Yodzis (1989), and Murray (1993).

The interaction terms in Lotka-Volterra models have the form $b_{ij} P_i P_j$. If species i and species j are competitors then the equations relating P_i and P_j in the absence of other species are

$$\begin{aligned} \frac{dP_i}{dt} &= (a_i - b_{ij} P_j - b_{ii} P_i) P_i \\ \frac{dP_j}{dt} &= (a_j - b_{ji} P_i - b_{jj} P_j) P_j. \end{aligned} \tag{1.13}$$

In the context of competition, the interaction terms appear in the same way as the self-regulation terms in the logistic equation. Thus, if b_{ii} is interpreted as measuring the extent to which members of species i deplete resources needed by that species and thus reduce the

net population growth rate for species i, then b_{ij} can be interpreted as measuring the extent to which members of species j deplete the same resources. This interpretation can be used to study the amount of similarity in resource utilization which is compatible with coexistence; see MacArthur (1972) or Yodzis (1989). The interpretation in the context of predator-prey interaction is more complicated. The interaction rate $b_{ij}P_iP_j$ can be interpreted as a mass-action law, analogous to mass-action principles in chemistry. The essential idea is that if individual predators and prey are homogeneously distributed within some region, then the rate at which an individual predator searching randomly for prey will encounter prey individuals should be proportional to the density of prey, but predators will search individually, so that the number of encounters will be proportional to the prey density times the predator density. Another assumption of the Lotka-Volterra model is that the birth rate of predators is proportional to the rate at which they consume prey, which in turn is directly proportional to prey density. Both of these assumptions are probably oversimplifications in some cases.

1.3.2 Beyond Mass-Action: The Functional Response

A problem with the mass-action formulation is that it implies the rate of prey consumption by each predator will become arbitrarily large if the prey density is sufficiently high. In practice the rate at which a predator can consume prey is limited by factors such as the time required to handle each prey item. This observation leads to the notion of a functional response, as discussed by Holling (1959). Another problem is that predators and prey may not be uniformly distributed. If predators search in a group then the rates at which different individual predators encounter prey will not be independent of each other. Finally, predators may spend time interacting with each other while searching for prey or may interfere with each other, so that the rate at which predators encounter prey is affected by predator density. These effects can also be incorporated into predator-prey models via the functional response.

We shall not give an extensive treatment of the derivation of functional response terms, but we shall sketch how functional responses can be derived from considerations of how individuals utilize time and space. We begin with a derivation based on time utilization, following the ideas of Holling (1959) and Beddington et al. (1975). Suppose a predator can spend a small period of time ΔT searching for prey, or consuming captured prey, or interacting with other predators. (The period of time ΔT should be short in the sense that the predator and prey densities remain roughly constant over ΔT.) Let P_1 denote the predator density and P_2 the prey density. Let ΔT_s denote the part of ΔT that the predator spends searching for prey. Let ΔT_1 denote the part of ΔT the predator spends interacting with other predators and let ΔT_2 denote the part of ΔT the predator spends handling prey. We have $\Delta T = \Delta T_s + \Delta T_1 + \Delta T_2$, but ΔT_1 and ΔT_2 depend on the rates at which the predator encounters other predators and prey, and on how long it takes for each interaction. Suppose that during the time it spends searching each individual predator encounters prey and other predators at rates proportional to the prey and predator densities, respectively (i.e. according to mass action laws.) The number of prey encountered in the time interval ΔT will then be given by $e_2P_2\Delta T_s$, while the number of predators encountered will be $e_1P_1\Delta T_s$, where e_1 and e_2 are rate constants that would depend on factors such as the predator's movement rate while searching or its ability to detect prey or other predators. If h_1 is the length of time required for each interaction between predators and h_2 is the length of time required for each interaction between a predator and a prey item, then $\Delta T_1 = e_1h_1P_1\Delta T_s$ and $\Delta T_2 = e_2h_2P_2\Delta T_s$. Using the relation $\Delta T = \Delta T_s + \Delta T_1 + \Delta T_2$,

we have $\Delta T = (1 + e_1h_1P_1 + e_2h_2P_2)\Delta T_s$. Also, the predator encounters $e_2P_2\Delta T_s$ prey items during the period ΔT, so the overall rate of encounters with prey over the time interval ΔT is given by

$$\begin{aligned} e_2P_2\Delta T_s/\Delta T &= e_2P_2\Delta T_s/(1 + e_1h_1P_1 + e_2h_2P_2)\Delta T_s \\ &= e_2P_2/(1 + e_1h_1P_1 + e_2h_2P_2). \end{aligned} \tag{1.14}$$

The expression $g(P_1, P_2) = e_2P_2/(1 + e_1h_1P_1 + e_2h_2P_2)$ is a type of functional response, introduced by Beddington et al. (1975) and DeAngelis et al. (1975). Under the assumption that predators do not interact with each other, so that $h_1 = 0$, it reduces to a form derived by Holling (1959), known as the Holling type 2 functional response. If we maintain the assumption that the rate at which new predators are produced is proportional to the per capita rate of prey consumed by each predator, and assume the prey population grows logistically in the absence of predators, the resulting model for the predator-prey interaction is

$$\begin{aligned} \frac{dP_1}{dt} &= \frac{ae_1P_2P_1}{1 + e_1h_1P_1 + e_2h_2P_2} - dP_1 \\ \frac{dP_2}{dt} &= r\left(1 - \left[\frac{P_2}{K}\right]\right)P_2 - \frac{e_2P_1P_2}{1 + e_1h_1P_1 + e_2h_2P_2}. \end{aligned} \tag{1.15}$$

(The coefficient a represents the predator's efficiency at converting consumed prey into new predators, while d represents the predator death rate in the absence of prey.) Note that if the prey density is held fixed at the level P_2^* the predator equation takes the form

$$\frac{dP_1}{dt} = \frac{AP_1}{B + CP_1} - dP_1 = \left[\frac{A}{B + CP_1} - d\right]P_1, \tag{1.16}$$

where $A = ae_2P_2^*$, $B = 1 + e_2h_2P_2^*$, and $C = e_1h_1$. If $A/B > d$ and $C > 0$ the function $[A/(B+CP_1)]-d$ is positive when $P_1 > 0$ is small but negative when P_1 is large. Thus, the model (1.16) behaves like the logistic equation in the sense that it includes self-regulation.

The derivation of the Beddington-DeAngelis (and Holling type 2) functional response in the preceding paragraph from considerations of time utilization retained the assumption that the total rate of encounters between searching predators and items of prey should follow a mass-action law. Other types of encounter rates can arise if predators or prey are not homogeneously distributed. This point is discussed in some detail by Cosner et al. (1999). Here we will just analyze one example of how spatial effects can influence the functional response and then describe the results of other scenarios. Let E denote the total rate of encounters between predators and prey per unit of search time. The rate at which prey are encountered by an individual predator will then be proportional to E/P_1 where P_1 is the predator density. The *per capita* encounter rate E/P_1 reduces to e_2P_2 if $E = e_2P_1P_2$, as in the case of mass action. Substituting the form $E/P_1 = e_2P_2$ into the derivation given in the preceding paragraph yields the Holling type 2 functional response if we assume that predators do not interact with each other. However, the mass action hypothesis $E = e_2P_1P_2$ is based on the assumption that predators and prey are homogeneously distributed in space. Suppose instead that the predators do not search for prey independently but form a group in a single location and then search as a group. In that case, increasing the number of predators in the system will not increase the area searched per unit time and thus the number of encounters with prey will not depend on predator density. (This assumes that

adding more predators to the group does not significantly increase the distance at which predators can sense prey or otherwise increase the searching efficiency of the predators.) In that case we would still expect the rate of encounters to depend on prey density, so that $E = e^* P_2$. Since E represents the total encounter rate between all predators and all prey, the per capita rate at which each individual predator encounters prey will be given by $e_2^* P_2/P_1$. (We are assuming that predators and prey inhabit a finite spatial region so that the numbers of predators and prey are proportional to their densities.) Since we are assuming that all the predators are in a single group, they will not encounter any other predators while searching for prey. Using the *per capita* encounter rate with prey $e_2^* P_2/P_1$ instead of $e_2 P_2$ in the derivation of (1.14) leads to

$$(e_2^* P_2/P_1)/(1 + e_2^* h_2(P_2/P_1)) = e^* P_2/(P_1 + e_2^* h P_2). \tag{1.17}$$

The corresponding predator-prey model is

$$\begin{aligned} \frac{dP_1}{dt} &= \frac{ae_2^*(P_2/P_1)P_1}{1 + e_2^* h_2(P_2/P_1)} - dP_1 = \left[\frac{ae_2^* P_2}{P_1 + e_2^* h_2 P_2} - d\right] P_1 \\ \frac{dP_2}{dt} &= r\left(1 - \left[\frac{P_2}{K}\right]\right) P_2 - \frac{e_2^* P_1 P_2}{P_1 + e_2^* h_2 P_2}. \end{aligned} \tag{1.18}$$

The model (1.18) is said to be ratio-dependent, because the functional response depends on the ratio P_2/P_1. Other types of functional responses arise from other assumptions about the spatial grouping of predators. These include the Hassell-Varley form $eP_2/(P_1^\gamma + ehP_2)$ where $\gamma \in (0, 1)$, among others; see Cosner et al. (1999). In the ratio-dependent model (1.18) the functional response is not smooth at the origin. For that reason the model can display dynamics which do not occur in predator-prey models of the form

$$\begin{aligned} \frac{dP_1}{dt} &= \left[ag(P_1, P_2) - d\right] P_1 \\ \frac{dP_2}{dt} &= r\left(1 - \left[\frac{P_2}{K}\right]\right) P_2 - g(P_1, P_2) P_1 \end{aligned} \tag{1.19}$$

with $g(P_1, P_2)$ smooth and $g(P_1, 0) = 0$. In particular, the ratio-dependent model (1.18) may predict that both predators and prey will become extinct for certain initial densities; see Kuang and Beretta (1998).

There are several other forms of functional response which occur fairly often in predator-prey models. Some of those arise from assumptions about the behavior or perceptions of predators. An example, and the last type of functional response we will discuss in detail, is the Holling type 3 functional response $g(P_2) = eP_2^2/(1 + fP_2^2)$. The key assumption leading to this form of functional response is that when the prey density becomes low the efficiency of predators in searching for prey is reduced. This could occur in vertebrate predators that have a "search image" which is reinforced by frequent contact with prey, or that use learned skills in searching or in handling prey which deteriorate with lack of practice; i.e. when prey become scarce. It will turn out that the fact that the Holling type 3 functional response tends toward zero quadratically rather than linearly as $P_2 \to 0$ can sometimes be a significant factor in determining the effects of predator-prey interactions.

There are many other forms of functional response terms that have been used in predator-prey models. Some discussion and references are given in Getz (1994) and Cosner et al. (1999). The various specific forms discussed here (Holling type 2 and type 3, Beddington-DeAngelis, Hassell-Varley, etc.) are sometimes classified as prey dependent ($g = g(P_2)$ in

our notation), ratio-dependent ($g = g(P_2/P_1)$) and predator dependent ($g = g(P_1, P_2)$). There has been some controversy about the use of ratio-dependent forms of the functional response; see Abrams and Ginzburg (2000) for discussion and references. In a recent study of various data sets, Skalski and Gilliam (2001) found evidence for some type of predator dependence in many cases. In what follows we will often use Lotka-Volterra models for predator-prey interactions, but we will sometimes use models with Holling type 2 or 3 functional response or with Beddington-DeAngelis functional response, depending on the context. Our main focus will generally be on understanding spatial effects, rather than exhaustively exploring the detailed dynamics corresponding to each type of functional response, and the forms listed above represent most of the relevant qualitative features that occur in standard forms for the functional response. We will not consider the ratio dependent case. That case is interesting and worthy of study, but it presents some extra technical problems, and it turns out that at least some of the scaling arguments which lead to diffusion models can destroy ratio dependence.

1.4 Spatial Models: A General Overview

The simple models we have described so far assume that all individuals experience the same homogeneous environment. In reality, individual organisms are distributed in space and typically interact with the physical environment and other organisms in their spatial neighborhood. The most extreme version of local interaction occurs among plants or sessile animals that are fixed in one location. Even highly mobile organisms encounter only those parts of the environment through which they move. Many physical aspects of the environment such as climate, chemical composition, or physical structure can vary from place to place. In a homogeneous environment any finite number of individuals will necessarily occupy some places and not others. The underlying theoretical distribution of individuals may be uniform, but each realization of a uniform distribution for a finite population will involve some specific and nonuniform placement of individuals. These observations would not be of any great interest in ecology if there were no empirical reasons to believe that spatial effects influence population dynamics or if simple models which assume that each individual interacts with the average environment and the average densities of other organisms adequately accounted for the observed behavior of populations and structure of communities. However, there is considerable evidence that space can affect the dynamics of populations and the structure of communities. An early hint about the importance came in the work of Gause (1935). Gause conducted laboratory experiments with *paramecium* and *didnium* and found that they generally led to extinction of one or both populations, even though the same species appear to coexist in nature. In a later set of experiments Huffaker (1958) found that a predator-prey system consisting of two species of mites could collapse to extinction quickly in small homogeneous environments, but would persist longer in environments that were subdivided by barriers to dispersal. Another type of empirical evidence for the significance of spatial effects comes from observations of natural systems on islands and other sorts of isolated patches of favorable habitat in a hostile landscape. There are many data sets which show larger numbers of species on larger islands and smaller numbers of species on smaller islands. These form the basis for the theory of island biogeography introduced by MacArthur and Wilson (1967); see also Williamson (1981) or Cantrell and Cosner (1994). A different sort of empirical evidence for the importance of space is that simple nonspatial models for resource competition indicate that in competition for a single limiting resource the strongest competitor should exclude

all others (MacArthur, 1972; Yodzis, 1989), but in natural systems many competitors coexist (see Hutchinson (1961)). This point has been studied systematically from both empirical and theoretical viewpoints by Tilman (1994, 1982). Finally, there are some biological phenomena, such as invasions by exotic species, which are intrinsically spatial in nature and thus require models that involve space. In recent years the amount of attention given to issues of biological conservation has greatly increased. A major reason why many species are threatened or endangered is the destruction or fragmentation of their habitats; see for example Pimm and Gilpin (1989), Quinn and Karr (1986), McKelvey et al. (1986), Groom and Schumaker (1990). The goal of understanding how patterns of habitat destruction and fragmentation affect the persistence of populations provides a strong motivation to develop models for spatial effects.

There are many ways that space and the organisms inhabiting it can be represented in models. Some models treat space explicitly, that is, they incorporate something analogous to a map of a spatial region and they give some sort of description of what is happening at each spatial location at any given time. Other models treat space implicitly, perhaps by incorporating parameters that correlate with spatial scale or by describing what fraction of an environment is occupied by some species without specifying how that fraction of the environment is actually arranged in physical space. Among the models that treat space explicitly, some treat space as a continuum and others treat space as a discrete collection of patches. Similarly, some models explicitly keep track of individuals; others represent populations in terms of densities, and others describe only the probability that a given location is inhabited by a given species. Finally, some models treat the birth, movement, and/or death of individuals as stochastic phenomena, while others are completely deterministic. (Some models can be viewed as giving deterministic predictions for the mean, expected value, or some other attribute of a random variable.) We shall briefly describe a number of representative approaches to spatial modeling before we narrow our focus to the reaction-diffusion models that are the main topic of this book. Our goal is not to give a systematic survey of spatial modeling, but rather to place reaction-diffusion models in a broader context of spatial models and to delineate to some extent the circumstances under which reaction-diffusion models provide an appropriate modeling approach. Other discussions of similarities, differences, and relationships among different types of spatial models are given by Durrett and Levin (1994) and Tilman et al. (1997).

Models that treat both space and population dynamics implicitly include the MacArthur-Wilson (1967) models for island biogeography and the classical metapopulation model of Levins (1969). Both models describe populations strictly in terms of their presence or absence and account for patterns of occupancy in terms of a balance between colonizations and extinctions, which are assumed to occur stochastically. The MacArthur-Wilson model in its simplest form envisions a single island and a collection of species which may colonize the island or, if already present, may become extinct. Let S_0 denote the total number of species that might colonize the island and let S be the number present on the island. If species not already on the island immigrate to it at rate I and species inhabiting the island experience local extinctions at rate E, then an equilibrium value for S is obtained by balancing immigrations and extinctions so that $I(S_0 - S) = ES$. This leads to the formula $S = IS_0/(I + E)$ (see MacArthur and Wilson 1967). If I and E are assumed to depend on the area, location, and other attributes of the island then the model can yield species-area relationships. The model of Levins (1969) describes a species which inhabits an environment consisting of discrete sites, and which may colonize empty sites or experience local extinctions in occupied sites. Let p represent the fraction of sites which are occupied

(so $0 \leq p \leq 1$). Let c be the rate at which colonists are produced if all sites are occupied, so if a fraction p of sites are occupied then the rate at which colonists are produced is cp. All sites are assumed to be equally accessible to colonists, so the fraction of sites which are unoccupied when colonists reach them is $1 - p$; thus the total rate of colonization of empty sites is $cp(1-p)$. Let e be the rate of local extinctions on occupied sites. The model for the fraction of sites occupied is then $dp/dt = cp(1-p) - ep = (c-e)p - cp^2$. This model behaves just like a logistic equation, predicting that the fraction of sites occupied will approach zero as $t \to \infty$ if $c \leq e$ and will approach the equilibrium $1 - (e/c)$ as $t \to \infty$ if $c > e$. (See Levins (1969), Tilman et al. (1997), Tilman (1994).) The model can be extended to multispecies systems; see Tilman (1994).

The Levins model can be modified to treat space in a more explicit way. That is an essential theme in recent work by Hanski and his colleagues (Hanski, 1997, 1999; Hanski and Ovaskainen, 2000, 2001). A key idea is to think of the quantity p as the probability that a patch is occupied rather than the fraction of patches that are occupied. This interpretation makes sense because if a patch is chosen at random from a collection of patches where a fraction p are occupied then the probability of selecting an occupied patch is equal to p. The important thing about interpreting p as a probability of occupancy is that it can be allowed to vary from patch to patch, along with probabilities of colonization or extinction. Thus, Hanski's formulation of metapopulation models envisions a collection of n patches and describes the probability p_i that each patch is occupied in terms of the occupancy of other patches. Assume that a patch can only be colonized if it is empty, that when patch j is occupied colonists from patch j arrive at patch i at a rate c_{ij}, and that when patch i is occupied the population inhabiting it experiences a local extinction in unit time with probability e_i. The formulation of metapopulation models given by Hanski (1997, 1999) then describes the probability p_i that the ith patch is occupied by the equation

$$\frac{dp_i}{dt} = \sum_{\substack{j=1 \\ j \neq i}}^{n} c_{ij} p_j (1 - p_i) - e_i p_i. \tag{1.20}$$

The terms c_{ij} and e_i can be used to incorporate some aspects of the spatial structure of the patch network into the model. Specifically, Hanski and his colleagues use $c_{ij} = cA_j \exp(-\alpha d_{ij})$ and $e_i = e/A_i$, where A_i is the area of the ith patch, d_{ij} is the distance between patch i and patch j, exp denotes the natural exponential, α is a parameter describing the hostility of landscape between patches (which is sometimes called the matrix between patches), and c and e are parameters describing properties of the species which are related to the likelihood of colonizations or extinctions.

The model (1.20) incorporates some aspects of space explicitly in the sense that spatial attributes of the environment appear in the model, but it is not spatially explicit in the sense of keeping track of the locations of individuals as they move through space or of population density as a function of spatial location. Following the terminology of fluid mechanics, models that track the location of individuals within some explicit representation of a spatial region are sometimes called Lagrangian, while models that describe the variations of population density over some explicit representation of a spatial region are sometimes called Eulerian. Lagrangian models are often called individual based because they keep track of individuals. In practice, individual based models have been used primarily in computer simulations. They can capture enough details of behavior and life history to make predictions about the behavior of natural systems, but they do not seem to be amenable to mathematical analysis via existing analytic methods. For a discussion of individual based models and

modeling, see DeAngelis et al. (1994). It is sometimes possible to calibrate Eulerian models precisely enough to make useful predictions, but a major reason for using them is that they often can be analyzed mathematically in ways that lead to broad insights about general systems, as opposed to precise predictions about specific systems. Both specific prediction and general understanding are worthy goals, but it is not always feasible to achieve both with the same model. Our discussion in most of this book will focus on reaction-diffusion models, which constitute a particular type of Eulerian model, but for now we will describe some other types of Eulerian models, and in the next section we will explore connections between different types of models.

Eulerian models for the dynamics of spatially distributed populations can incorporate various assumptions about the structure of space, the measurement of time, and the dispersal of organisms through space over time. Specifically, they can treat space and time as continuous or discrete, and they can treat dispersal and population dynamics as stochastic or deterministic.

The simplest widely used population model that can incorporate space explicitly is probably the ideal free distribution of Fretwell (1972); see also Fretwell and Lucas (1970). In its original form, the model simply describes the equilibrium distribution of a population of fixed size dispersing through a spatially discrete environment in a deterministic way. The essential idea is that in an environment which is spatially heterogeneous, individuals will position themselves in the most favorable locations, but the favorability of any location is reduced by crowding. To be more specific, the model envisions an environment divided into n habitats, with P_i denoting the population in the nth habitat. Let $P = \sum_{i=1}^{n} P_i$ denote the total population. Each habitat is assumed to have an intrinsic "fitness" a_i which is reduced logistically by crowding to $a_i - b_i P_i$. The habitats are arranged in order of their intrinsic fitness, so that $a_1 > a_2 > a_3 \cdots > a_n$. The model is given by the rule that if $a_1 - b_1 P > a_2$, then $P_1 = P$, $P_i = 0$ for $i = 2, \ldots, n$. When P is large enough that $a_1 - b_1 P \leq a_2$, individuals distribute themselves so that $a_1 - b_1 P_1 = a_2 - b_2 P_2$ with $P_1 + P_2 = P$, and with $P_i = 0$ for $i = 3, \ldots, n$ as long as $a_1 - b_1 P_1 = a_2 - B_2 P_2 > a_3$, etc. In words, individuals distribute themselves deterministically so that each individual's fitness is maximized. The theory simply describes the equilibrium distribution that develops when the population follows that rule. The model assumes that individuals can assess environmental quality and move deterministically in response to it. A version of the ideal free distribution that treats space as a continuum is formulated in Kshatriya and Cosner (2002).

A class of models that assume space to be discrete and movement to be deterministic (at least at the population level) but which include population dynamics are known as discrete diffusion or island chain models. These models treat space as a discrete set of patches and describe how the population (or density) P_i on each patch varies with time. These models can be set in either discrete or continuous time. Suppose that in each patch the population grows or declines according to a population dynamical equation $dP_i/dt = f_i(P_i)$, and that individuals disperse from patch i at a rate $D_i \geq 0$ and arrive at patch j at a rate $d_{ji} \geq 0$ with $\sum_{\substack{j=1 \\ j \neq i}}^{n} d_{ji} \leq D_i$. (If there is no mortality in transit, $\sum_{\substack{j=1 \\ j \neq i}}^{n} d_{ji} = D_i$.) The model then takes the form

$$\frac{dP_i}{dt} = \sum_{\substack{j=1 \\ j \neq i}}^{n} d_{ij} P_j - D_i P_i + f(P_i), \quad i = 1, \ldots, n. \tag{1.21}$$

Models of the form (1.21) can be extended to include density-dependent dispersal and multispecies interactions. If Q_i denotes the population (or density) of another species on patch i, an extension of (1.21) which allows density-dependent dispersal and describes interspecific interactions is

$$\begin{aligned}\frac{dP_i}{dt} &= \sum_{\substack{j=1\\ j\neq i}}^{n} d_{ij}(P_i, P_j, Q_i, Q_j)P_j - D_i(P_i, Q_i)P_i + f_i(P_i, Q_i)\\ \frac{dQ_i}{dt} &= \sum_{\substack{j=1\\ j\neq i}}^{n} \tilde{d}_{ij}(P_i, P_j, Q_i, Q_j)Q_j - \tilde{D}_i(P_i, Q_i)Q_i + \tilde{f}_i(P_i, Q_i),\\ & i = 1, \ldots, n.\end{aligned} \tag{1.22}$$

An analogous formulation can be given in discrete time. To see how such a model should be formulated, consider a two-patch dispersal model

$$\frac{dP_1}{dt} = D_2P_2 - D_1P_1, \quad \frac{dP_2}{dt} = D_1P_1 - D_2P_2.$$

Adding the two equations shows that for $P = P_1 + P_2$ we have $dP/dt = 0$ so $P_1 + P_2 = P = P(0)$ so that $P_2 = P(0) - P_1$; then $dP_1/dt = D_2(P(0) - P_1) - D_1P_1$. This is a simple linear first order equation. Solving for P_1 and then P_2 yields

$$\begin{aligned}P_1(t) &= [(D_2 + D_1e^{-Dt})/D]P_1(0) + [D_2(1 - e^{-Dt})/D]P_2(0)\\ P_2(t) &= [D_1(1 - e^{-Dt})/D]P_1(0) + [(D_1 + D_2e^{-Dt})/D]P_2(0)\end{aligned}$$

where $D = D_1 + D_2$. If we set $t = 1$, we arrive at a model of the form

$$\begin{aligned}P_1(1) &= d_{11}P_1(0) + d_{12}P_2(0)\\ P_2(1) &= d_{21}P_1(0) + d_{22}P_2(0)\end{aligned}$$

where $d_{11} + d_{21} = d_{12} + d_{22} = 1$ and $0 \leq d_{ij} \leq 1$ for all i, j. This last model can be interpreted as saying that at each time step a fraction d_{ii} of the population of patch i remains there and a fraction d_{ji} move to the other patch. Combining the dispersal models with population dynamics gives

$$\begin{aligned}P_1(t+1) &= f_1(d_{11}P_1(t) + d_{12}P_2(t))\\ P_2(t+1) &= f_2(d_{21}P_1(t) + d_{22}P_2(t))\end{aligned}$$

(if we assume that at each time step dispersal occurs first, then population dynamics take effect) or as

$$\begin{aligned}P_1(t+1) &= d_{11}f_1(P_1(t)) + d_{12}f_2(P_2(t))\\ P_2(t+1) &= d_{21}f_1(P_1(t)) + d_{22}f_2(P_2(t))\end{aligned}$$

(if we assume population dynamics act first and dispersal follows). Models of this type can be extended to systems involving several patches and several interacting species.

Two other types of spatially explicit models which treat space as a discrete grid are interacting particle systems (Durrett and Levin, 1994) and cellular automata (Comins et al. 1992; Hassell et al., 1994); see also Tilman and Kareiva (1997). These sorts of models keep track of what happens at each point of the spatial grid. Typically, the state space for such models consists of integer valued functions (or vectors of such functions, if the model describes more than one species) defined on the grid points which give the population at each grid point at any given time. In some cases the function may take on just the values zero and one, indicating whether a given site is empty or occupied. A key feature of cellular automata and interacting particle systems is that the transitions between states at a given grid point are not described by deterministic equations but by rules which may include logical alternatives or may be stochastic. This feature allows for a relatively high degree of realism but can make the mathematical analysis of such models difficult. Interacting particle systems have stochastic rules for transitions between states and usually are set in continuous time; cellular automata may have deterministic or stochastic rules for transitions and often are set in discrete time. We will not try to describe these types of models further here, but discuss interacting particle systems in more detail in the next section, when we explore the connections between reaction-diffusion models and other spatial models.

The last major class of spatial models are those that treat space as a continuum and describe the distribution of populations in terms of densities that vary deterministically in time (but which may sometimes have close connections to stochastic processes). These models include the reaction-diffusion models which are the main subject of this book, along with more general types of models based on partial differential equations and discrete-time models based on integral kernels. We shall discuss the derivation of such models in more detail in the next section, but the essential idea is to envision individuals dispersing via random walks, so that at large spatial scales a collection of dispersing individuals will behave analogously to a collection of particles diffusing under the action of Brownian motion. For simplicity, suppose the spatial environment is one dimensional. If we ignore population dynamics, we can describe the density of a population dispersing via diffusion as $u(x, t)$ where

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2}. \tag{1.23}$$

(In (1.23) the coefficient d describes the rate of movement.) To get a full model we augment (1.23) with population dynamical terms:

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + f(x, t, u). \tag{1.24}$$

This type of model describes local population interactions in the same way as the nonspatial models treated in sections 1.2 and 1.3. Models of the form (1.24) were introduced into ecology by Skellam (1951) and Kierstead and Slobodkin (1953). They extend readily to more space dimensions and to several interacting species. They can also be extended to account for dispersal behavior that is more complex than simple diffusion, specifically advection or taxis, and dispersal in response to densities of conspecifics, prey, or predators; see for example Belgacem and Cosner (1995), Kareiva and Odell (1987) or the discussion of chemotaxis and cross-diffusion in Murray (1993). In principle, models such as (1.24) can be deduced from assumptions about the local dispersal behavior and life history of individuals and can be analyzed to give insights about the dynamics of a population at a

larger scale. If we start with the dispersal model (1.23) and allow it to act on an initial density $u(x, 0)$ for unit time, we obtain

$$u(x, 1) = \int_{-\infty}^{\infty} K(x - y, 1)u(y, 0)dy \tag{1.25}$$

where $K(x, t)$ is the integral kernel giving the fundamental solution of the diffusion equation (1.23): $K(x, t) = \exp(-x^2/4dt)/\sqrt{4\pi dt}$ (Strauss, 1992). If we assume that a population engages in reproduction and then disperses via diffusion for a unit time, we can construct a discrete-time population model

$$u(x, t + 1) = \int_{-\infty}^{\infty} K(x - y, 1) f(u(y, t))dy. \tag{1.26}$$

Other forms of the integral kernel $K(x, t)$ can be used to describe models of dispersal other than simple diffusion. This approach is discussed by Lewis (1997); see also Van Kirk and Lewis (1997), and Hardin et al. (1988b, 1990).

The sorts of models we have described all combine some description of dispersal with some type of population dynamics (perhaps only a specification of the probability of local extinctions) so that they can be used directly to address questions about the persistence of populations. There are also models that only describe movement, specifically the formation of schools or swarms. We shall not discuss those further (see Grünbaum (1994, 1999), Flierl et al. (1999)).

We have described a variety of types of spatial models, but how can we decide which to use in a given situation? The key factors in choosing a type of model are the biology of the organisms being modeled and the structure of the spatial environment they inhabit, the goal of the modeling effort, and the spatial scale of the system. For organisms which have nonoverlapping generations (such as animals that breed once a year) or which disperse only as seeds or juveniles and then remain in one place, so that dispersal occurs via reproduction, models that operate on short to moderate time scales should generally be cast in discrete time. Over longer time scales and for large populations, even these types of organisms can often be adequately described via continuous time models. Different types of models make different assumptions about dispersal. The ideal free distribution assumes that individuals assess environmental quality and locate themselves deterministically to maximize their fitness. Thus, it is suitable as a model only for fairly complex organisms that can monitor environmental quality and move in response to it. In contrast, reaction-diffusion models and interacting particle systems, and many models based on integral kernels, assume that dispersal has a random component. (These types of models can incorporate some directed movement along with random dispersal.) Individual based models can incorporate essentially any type of dispersal, so they may be needed for organisms with highly complex dispersal behavior. At the other extreme, metapopulation models do not describe dispersing individuals at all, only the probability that a patch will be colonized given the current pattern occupancy of patches. Since plants occupy fixed sites and disperse by colonizing empty sites, metapopulation models may be especially suitable for plant populations; see Tilman (1994).

A single patch of habitat, possibly with some internal heterogeneity, can often be viewed as a continuum, so that it is appropriate to use reaction-diffusion models or models based on integral kernels to describe the density of a population inhabiting it. A landscape viewed at a moderately large scale may also be a continuum, or it may be better described as a

network of discrete habitat patches within a (possibly hostile) matrix of habitat of other types. In the first case, a reaction-diffusion or integral kernel model might be appropriate, but in the second a patch model such as (1.21) or some type of metapopulation model would probably be more suitable. If a network of patches is viewed on a sufficiently large scale, patch models such as (1.21) may be well approximated by reaction-diffusion models, so those may again be appropriate at large spatial scales.

The scale of the underlying spatial environment can affect the choice of models. So can scaling by the level of detail a model should capture. Interacting particle systems can capture a large amount of detail but are difficult to analyze. Moving to a larger spatial scale reduces the resolution of the models, but in some cases interacting particle systems can be rescaled into reaction-diffusion models which are easier to analyze.

Usually models that incorporate a significant level of detail or account for many factors that might affect population dynamics are difficult to analyze mathematically, although they can often be used in computer simulations. Thus we encounter a trade-off between the resolution of models in making specific predictions and their amenability to analytic approaches which can lead to general insights. Individual based models, cellular automata, and interacting particle systems provide a significant level of detail but are hard to analyze. Thus, they are good choices for doing computer experiments. Metapopulation models, reaction-diffusion models, discrete diffusion or patch models, and models based on integral kernels all provide less detail but are easier to analyze, so they are good candidates for mathematical analysis aimed at gaining general insights. Finally, there is the issue of robustness of conclusions. If similar conclusions follow from diverse models, we can be somewhat confident that those conclusions describe some actual phenomenon that might occur in biological systems. (Clearly, deciding whether or not phenomena that *might* occur actually *do* occur and determining how important they are require data as well as models.) On the other hand, if different models lead to different results, that suggests that the phenomena they propose to describe are not adequately understood and that new empirical data or a different conceptual framework will be needed for the theory to progress further.

1.5 Reaction-Diffusion Models

1.5.1 Deriving Diffusion Models

Diffusion models can be derived as the large scale limits of dispersal models based on random walks. Such derivations are discussed by Okubo (1980) and Turchin (1998). They can also be derived from Fick's law (which describes the flux of a diffusing substance in terms of its gradient), as discussed by Okubo (1980) and Murray (1993), or from stochastic differential equations, as discussed by Gardiner (1985). Finally, they can be derived from interacting particle systems. We will describe the derivation from interacting particle systems in some detail later in this section, but first we sketch some of the other derivations. As we shall see, scaling turns out to be a crucial issue in the derivation of diffusion models.

Suppose we think of an individual (organism or particle) that moves along a line in discrete time steps by jumping one spatial step to the right with probability α or one step to the left with probability $(1-\alpha)$. Let Δt denote the time step and Δx denote the space step, and let $p(x,t)$ denote the probability that the individual is at location x at time t. The probability $p(x,t+\Delta t)$ that the individual is at location x at time $t+\Delta t$ can be computed by observing that to get to position x at time $t+\Delta t$ the individual must either be at position $x-\Delta x$ at time t and move to the right or be at position $x+\Delta x$ at time t and move to the

left. Thus, we have

$$p(x, t + \Delta t) = \alpha p(x - \Delta x, t) + (1 - \alpha) p(x + \Delta x, t) \tag{1.27}$$

which we can also write as

$$\begin{aligned} \frac{p(x, t + \Delta t) - p(x, t)}{\Delta t} &= \frac{1}{2\Delta t}[p(x + \Delta x, t) - 2p(x, t) + p(x - \Delta x, t)] \\ &\quad + \frac{\beta}{\Delta t}[p(x + \Delta x, t) - p(x - \Delta x, t)] \end{aligned} \tag{1.28}$$

where $\beta = (1/2) - \alpha$. To obtain a diffusion equation from (1.28) we must relate $(1/2\Delta t)$ and $(\beta/\Delta t)$ to Δx via scaling. If we let $d = (\Delta x)^2/2\Delta t$ and let $v = -2\beta\Delta x/\Delta t$ then $1/2\Delta t = d/(\Delta x)^2$ and $\beta/\Delta t = -v/2\Delta x$ so that (1.28) becomes

$$\begin{aligned} \frac{p(x, t + \Delta t) - p(x, t)}{\Delta t} &= d\left[\frac{p(x + \Delta x, t) - 2p(x, t) + p(x - \Delta x, t)}{(\Delta x)^2}\right] \\ &\quad - v\left[\frac{p(x + \Delta x, t) - p(x - \Delta x, t)}{2\Delta x}\right]. \end{aligned} \tag{1.29}$$

We can now pass to the limit as Δt and Δx approach zero as in (Okubo, 1980, p. 68) to obtain

$$\frac{\partial p}{\partial t} = d\frac{\partial^2 p}{\partial x^2} - v\frac{\partial p}{\partial x}. \tag{1.30}$$

If there is no preferred direction of motion then $\beta = 0$, so $v = 0$. Thus, the term $d\partial^2 p/\partial x^2$ describes the aspect of movement coming from symmetric random displacements, i.e. the aspect due to diffusion. If we return to equation (1.27) and let $\alpha = 1$ we obtain $p(x, t + \Delta t) = p(x - \Delta x, t)$ which reflects a deterministic movement to the right. We can rewrite this last relation as $\dfrac{p(x, t + \Delta t) - p(x, t)}{\Delta t} = \dfrac{p(x - \Delta x, t) - p(x, t)}{\Delta t}$. When $\alpha = 1$, $\beta = -1/2$, so the scaling $-2\beta\Delta x/\Delta t = v$ becomes $v = \Delta x/\Delta t$, so that (1.28) becomes $\left[\dfrac{p(x, t + \Delta x) - p(x, t)}{\Delta t}\right] = -v\left[\dfrac{p(x, t) - p(x - \Delta x, t)}{\Delta x}\right]$ which has the limiting equation

$$\frac{\partial p}{\partial t} = -v\frac{\partial p}{\partial x}. \tag{1.31}$$

The equation (1.31) has solution $p(x, t) = p_0(x - vt)$ where $p(x, 0) = p_0(x)$. Thus, it indeed describes motion to the right with velocity $\Delta x/\Delta t = v$. The interpretation of the coefficient d in (1.30) is more subtle, but the relation $(\Delta x)^2/\Delta t = 2d$ suggests that d can be viewed as being half of the square of the distance that is traversed by an individual in unit time by symmetric random movements to the left or right.

The random walk described above can also be analyzed in terms of probability distributions. For simplicity, assume that an individual starts at $x = 0$ and at each time step Δt the individual moves a distance Δx to the right with probability $1/2$ or moves to the left with a distance Δx with probability $1/2$. After n time steps, the probability that the object has moved to the right r times (and thus to the left $n - r$ times) is $(1/2)^n n!/r!(n - r)!$. Assume, again for simplicity, that $-n \leq m \leq n$ and that m and n are both even or both odd. To arrive at position $m\Delta x$ at time $n\Delta t$, the individual must move so that $r - (n - r) = m$,

that is, the difference in the numbers of steps to the right and to the left must be m. Thus, $r = (n+m)/2$ so $n - r = (n-m)/2$, so the probability $p(m\Delta x, n\Delta t)$ that the object is at position $m\Delta x$ at time $n\Delta t$ is

$$p(m\Delta x, n\Delta t) = (1/2)^n n!/[(n+m)/2]![(n-m)/2]!. \tag{1.32}$$

The distribution in (1.32) is a type of binomial distribution. This distribution can be well approximated by the normal (i.e. Gaussian) distribution for n and m large; see for example Dwass (1970). To determine the coefficients in the limiting Gaussian distribution for (1.32), we observe that the position of the individual at time $n\Delta t$ is the sum of n jumps to the right or left, each with probability 1/2. Thus, we can describe the position of the individual at time $n\Delta t$ as arising from the sum $X_1 + \cdots + X_n$ of n independent random variables, each having the value $-\Delta x$ with probability 1/2 or Δx with probability 1/2. Thus, X_k has mean 0 and variance $\sigma^2 = (1/2)(-\Delta x)^2 + (1/2)(\Delta x)^2 = (\Delta x)^2$. Let $Y_n = (X_1 + \cdots + X_n)/\sigma\sqrt{n} = (X_1 + \cdots + X_n)/\Delta x\sqrt{n}$, and let $P(X \le z)$ denote the probability that $X \le z$, where X is any random variable. By the central limit theorem (Dwass 1970) (and using the fact that the mean of X_k is 0 for each k) we have

$$\lim_{n\to\infty} P(Y_n \le z) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{z} e^{-r^2/2} dr. \tag{1.33}$$

Since $t = n\Delta t$ is the total time for n steps,

$$P(X_1 + \cdots + X_n \le x) = P(Y_n \le x/\Delta x\sqrt{t/\Delta t}) = P(Y_n \le x/\sqrt{2dt}) \tag{1.34}$$

where we have used the scaling $(\Delta x)^2/\Delta t = 2d$, as before. Thus, we obtain from (1.33) and (1.34),

$$\lim_{n\to\infty} P(X_1 + \cdots + X_n \le x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x/\sqrt{2dt}} e^{-r^2/2} dr. \tag{1.35}$$

Making the substitution $y = (\sqrt{2dt})r$ in (1.35) yields

$$\lim_{n\to\infty} P(X_1 + \cdots + X_n \le x) = \frac{1}{\sqrt{4\pi dt}} \int_{-\infty}^{x} e^{-y^2/4dt} dy. \tag{1.36}$$

The expression $(1/\sqrt{4\pi dt})e^{-y^2/4dt}$ on the right side of (1.36) is the fundamental solution of the diffusion equation (1.30) in the case $v = 0$, i.e. in the case where there is no bias in the direction of motion; see Strauss (1992). If we use that as a model for the probability distribution $p(y,t)$ for the position of an individual at time t, then $p(y,0) = \delta(y)$, that is, $p(y,0)$ is a point-mass or delta distribution at zero. Furthermore, $\partial p/\partial t = d\partial^2 p/\partial x^2$. If a single particle starts at a point z then the distribution after time t should be $(1/\sqrt{4\pi dt})e^{-(y-z)^2/4dt}$. If we start with a collection of particles with density at time zero given by $u_0(x)$ then at time t the density should be given by

$$u(x,t) = \frac{1}{\sqrt{4\pi dt}} \int_{-\infty}^{\infty} e^{-(y-x)^2/4dt} u_0(y) dy, \tag{1.37}$$

which is equivalent to

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2}, \quad u(x,0) = u_0(x). \tag{1.38}$$

The notion of a random walk can be extended to more space dimensions and to more complex types of movement. We shall not explore those extensions further here, except to note that if there is no bias in the direction of a random walk and no correlation between successive steps, the distribution for an individual starting at the origin in $\mathbb{R}^n$ after time t is well approximated by $(1/(4\pi dt)^{n/2})e^{-r^2/4dt}$, where $r = \sqrt{x_1^2 + \cdots + x_n^2}$; this form is the fundamental solution to the equation

$$\frac{\partial u}{\partial t} = d\left(\frac{\partial^2 u}{\partial x_1^2} + \cdots + \frac{\partial^2 u}{\partial x_n^2}\right) = d\nabla \cdot \nabla u \tag{1.39}$$

which is the n-dimensional diffusion equation. In any dimension, $d = \sigma^2/2$ where σ^2 is the variance of the distribution $(1/(4\pi dt)^{n/2})e^{-r^2/4dt}$ when $t = 1$. Since the distribution at $t = 1$ describes the probability that an individual has moved a distance r from its starting point at time 1, the quantity σ^2 can be calculated from data obtained, e.g., via mark-recapture experiments. See Okubo et al. (1989), Andow et al. (1990) and Turchin (1998) for more discussion of how to calibrate diffusion models from data.

Random walks can be described in other ways. One approach is to describe movement in terms of stochastic differential equations, where the position $x(t)$ of an individual is determined by

$$dx = b(x, t)dt + \sigma(x, t)dW \tag{1.40}$$

where dx and dt can be viewed as ordinary differentials and $dW = \xi(t)dt$, where $\xi(t)$ is a random variable describing white noise. One typically requires $\xi(t)$ to have mean zero and $\xi(t_1)$, $\xi(t_2)$ to have covariance $\delta(t_1 - t_2)$. The diffusion equation can be obtained as a partial differential equation for the distribution of x at time t, known as the Fokker-Plank equation. See Gardiner (1985), Okubo (1980) or Belgacem (1997) for some additional discussion of stochastic differential equations. (Note that the stochastic differential equation is a Lagrangian description of movement; the Fokker-Plank equation translates it into an Eulerian form.) A reason to mention stochastic differential equations is that they make explicit the notion that steps are not correlated. If one assumes that the probability of moving a given direction at a certain time step is correlated with the direction moved in the previous time step, derivations similar to those given above lead to the equation

$$a\frac{\partial^2 u}{\partial t^2} + b\frac{\partial u}{\partial t} = c\frac{\partial^2 u}{\partial x^2} \tag{1.41}$$

where a, b, and c are positive constants related to the spatial and temporal scales of the random walk; see Okubo (1980). Equation (1.41) is called the telegraph equation. It has some features that differ from those of the diffusion equation, but it turns out that for our purposes the differences usually will not be too important. We return to that point later.

A completely different approach to deriving diffusion equations is based on Fick's law and the notion of flux. This approach is analogous to some standard derivations of the heat equation. Fick's law, in the one-dimensional case, is the empirically derived hypothesis that diffusion transports particles or individuals across a specified point at a rate which is proportional to the spatial derivative of the concentration or density at that point, and in the direction of decreasing concentration. In higher space dimensions the situation is slightly more complicated, because the transport rate across a surface element is proportional to the directional derivative of the concentration or density in the direction normal to the

surface, that is, the component of the gradient of the concentration or density in the normal direction. Again, the direction of transport is in the direction of decreasing concentration, so the constant of proportionality is negative. This leads to the formulation of the diffusive flux as $\vec{J}_D = -d\nabla u$, where u represents a density or concentration. If S is a flat surface element, such as a line segment in the plane or a finite subset of a plane in three-dimensional space, and $\vec{N}$ is a unit normal vector to S, the total rate of diffusive transport across S is $|S|(\vec{J}_D \cdot \vec{N})$ where $|S|$ is the size (length, area, etc. depending on dimension) of S. If Ω is a region with boundary $\partial\Omega$ and $\vec{n}$ denotes the outer unit normal vector to $\partial\Omega$, the total rate of transport *into* Ω by diffusion is given by the surface integral

$$\int_{\partial\Omega} [(-\vec{n}) \cdot \vec{J}_D] dS = \int_{\partial\Omega} d\nabla u \cdot \vec{n} dS.$$

The rate of transport into Ω equals the rate of change in the total number of individuals (or amount of diffusing substance) in Ω, so we have

$$\frac{\partial}{\partial t} \int_{\Omega} u dx = \int_{\partial\Omega} d\nabla u \cdot \vec{n} dS. \tag{1.42}$$

Assume that u and $\partial\Omega$ are smooth enough that we can bring the derivative inside the integral on the left side of (1.42) and apply the divergence theorem to the right side; doing those things and dividing by $|\Omega|$ (the volume of Ω) we obtain

$$\frac{1}{|\Omega|} \int_{\Omega} \left(\frac{\partial u}{\partial t} \right) dx = \frac{1}{|\Omega|} \int_{\Omega} (\nabla \cdot d\nabla u) dx. \tag{1.43}$$

Equation (1.43) says that the average of $\partial u/\partial t$ over any set Ω is the same as the average of $\nabla \cdot d\nabla u$, which we often denote as $d\nabla^2 u$ if d is constant. Since Ω could be any set, we can try to take the limit of those averages as $|\Omega| \to 0$, and if $\partial u/\partial t$ and $d\nabla^2 u$ are continuous we obtain

$$\frac{\partial u}{\partial t} = d\nabla^2 u, \tag{1.44}$$

which is the diffusion equation. The notion of flux extends to advective transport or directed motion; the flux $\vec{J}_{\vec{v}}$ arising from advective or directed motion with velocity $\vec{v}$ is simply $\vec{J}_{\vec{v}} = \vec{v}u$, where u is the concentration or density. If we let $\vec{J} = \vec{J}_D + \vec{J}_{\vec{v}}$, and allow d and $\vec{v}$ to depend on x and repeat the calculations (1.42), (1.43) leading to (1.44) we obtain

$$\frac{\partial u}{\partial t} = \nabla \cdot [d(x)\nabla u - \vec{v}u] = \nabla \cdot d(x)\nabla u - \nabla \cdot (\vec{v}u). \tag{1.45}$$

(We could also allow d and $\vec{v}$ to depend on t, but then we would have to go through a similar calculation based on taking integrals over $\Omega \times (t, t + \Delta t)$.)

Finally, diffusion equations can be derived via scaling of deterministic spatially discrete models. If we begin with the model

$$\frac{dU_i}{dt} = D(U_{i+1} - 2U_i + U_{i-1}), \tag{1.46}$$

use $D = d/(\Delta x)^2$, let $x = m\Delta x$, and make the identification $u(x, t) = u(m\Delta x, t) = U_m(t)$, then taking the limit as $\Delta x \to 0$ of (1.46) yields the diffusion equation (1.38). The same

is true if we identify $u(m\Delta x,\ n\Delta t) = U_{m,n}$ and let $\Delta x,\ \Delta t \to 0$ with $(\Delta x)^2/\Delta t = s < 1/2$ in

$$\frac{U_{m,n+1} - U_{m,n}}{\Delta t} = d\left[\frac{U_{m+1,n} - 2U_{m,n} + U_{m-1,n}}{(\Delta x)^2}\right]. \tag{1.47}$$

(See Strauss (1992) and John (1982)). The same sort of results apply to systems in more space dimensions. If the plane is divided into a square grid and the density at point $(i\Delta x,\ j\Delta y)$ is denoted U_{ij}, the system

$$\frac{\partial U_{ij}}{\partial t} = D\left(U_{i+1j} + U_{i-1j} + U_{ij+1} + U_{ij-1} - 4U_{ij}\right) \tag{1.48}$$

will approximate the diffusion equation (1.44) under an appropriate scaling as the mesh size $\Delta x, \Delta y \to 0$. If (1.46) is modified to $dU_i/dt = D_1U_{1+i} - (D_1 + D_2)u_i + D_2u_{i-1}$ with $D_1 \neq D_2$, the limiting equation will have a drift term as in (1.30) or (1.45).

It follows from the above discussion that island chain models such as (1.21) where the dispersal coefficients d_{ij} are zero unless patches i and j are nearest neighbors will behave approximately like reaction-diffusion models if viewed on a sufficiently large spatial scale. The same turns out to be true for some interacting particle systems, but for those systems the scaling can also affect the interaction terms. We discuss that topic in detail next.

1.5.2 Diffusion Models Via Interacting Particle Systems: The Importance of Being Smooth

Interacting particle systems treat space as a discrete set of points upon which particles move and interact stochastically. Typically they keep track of the presence or absence of a particle at each point, or the number of particles at each point. The formulation we present here is essentially the one given by Durrett and Levin (1994); various mathematical treatments are given by Liggett (1985), Spohn (1991), DeMasi and Presutti (1991), and Kipnis and Landim (1999). In the systems we consider, space is identified with $\mathbb{Z}^2$, i.e. the set of points in the plane with integer coordinates. The state space for the model is the set of nonnegative integer valued functions on $\mathbb{Z}^2$, so the states specify the number of individuals at each point on the lattice. The dynamics of the model are specified by the rates at which individuals move and die or reproduce. (To say that something happens at a given rate R in this context typically means that it occurs at times which are determined by an exponentially distributed random variable with mean $1/R$.) The rates at which an individual gives birth or dies may be affected by the presence of other individuals at or near its location. If we rescale the grid $\mathbb{Z}^2$ by ϵ (so that each grid point has the form $(m\epsilon, n\epsilon)$ for integers m and n) and rescale the movement rate appropriately, solutions to the interacting particle system can sometimes be shown to converge to solutions to a related reaction-diffusion model via a process known as taking hydrodynamic limits (Durrett and Levin, 1994; DeMasi and Presutti, 1991; Spohn, 1991; Levin and Pacala, 1997; Kipnis and Landim, 1999). There are many technical difficulties connected with proving that interacting particle systems do indeed converge to reaction-diffusion models, but since we are primarily interested in reaction-diffusion models we limit our discussion to calculations of what the hydrodynamic limits would be for certain systems if the limits do indeed exist.

To specify an interacting particle system model we need to describe dispersal, interactions between individuals at a given location, and interactions between individuals in a local neighborhood. The distinction between location and neighborhood makes it possible to account for interactions between individuals at neighboring sites. The nearest neighbors of a point (m, n) are $(m+1, n)$, $(m-1, n)$, $(m, n+1)$, and $(m, n-1)$. A local neighborhood would consist of all points $(m, n) + (p, q)$ where (p, q) belongs to some neighborhood $\mathcal{N}$ of $(0, 0)$. The neighborhood $\mathcal{N}$ might consist only of $(0, 0)$, or of $(0, 0)$ and its nearest neighbors, or might be larger. We denote the number of grid points in $\mathcal{N}$ by $|\mathcal{N}|$. Suppose that individuals

(i) move to a randomly chosen nearest neighbor of their location at rate D, and

(ii) reproduce or die at rates which depend on the number of individuals at the same location, or in the local neighborhood of that location.

To give a specific example for ii), let $\eta_t(x)$ denote the number of individuals at point $x = (m, n)$ at time t. Suppose that for each individual the birth rate is decreased (or death rate increased) logistically by other individuals at the same location; then the *per capita* birth/death rate is given by $a - b(\eta_t(x) - 1)$. (The fact that b multiplies $\eta - 1$ instead of η reflects the idea that individuals do not compete with themselves.) The overall birth/death rate at location x and time t is then $\eta_t(x)(a - b(\eta_t(x) - 1))$. The hydrodynamic limit for the system defined above arises by scaling the grid as $(\epsilon m, \epsilon n)$ and scaling $D = 4d/\epsilon^2$. (The 4 enters the scaling because each site has 4 nearest neighbors, so that the rate of dispersal into a given neighboring site is $D/4$.) Notice that $1/D$ represents a time scale and that $1/D$ scales as ϵ^2, where ϵ represents the spatial scaling. Thus, once again, the diffusion model arises from a scaling where Δt is proportional to $(\Delta x)^2$. Let $\eta_t^\epsilon(x)$ denote the number of individuals at point x at time t in the scaled system, and let $u^\epsilon(x, t) = E(\eta_t^\epsilon(x))$, that is, let $u^\epsilon(x, t)$ be the mean of $\eta_t^\epsilon(x)$. If the hydrodynamic limit can indeed be taken, then $u^\epsilon(x, t) \to u(x, t)$ where the dispersal equation for $u(x, t)$ is

$$\frac{\partial u}{\partial t} = d\nabla^2 u. \tag{1.49}$$

Under some technical assumptions (see Durrett and Levin (1994), Spohn (1991), DeMasi and Presutti (1991), Kipnis and Landim (1999)), the joint distribution for the number of individuals at any finite set of sites converges to independent Poisson distributed random variables at each point, each with mean $u(x, t)$. Thus, to compute the reaction terms, we would calculate the expected birth or death rate by computing $E([a - b(U-1)]U)$ where U is a Poisson distributed random variable with mean u. The Poisson distribution with mean u has $P(U = k) = e^{-u}u^k/k!$ so that $E(f(U)) = \sum_{k=0}^{\infty} e^{-u} f(k) u^k/k!$. If we compute this expression for aU we simply recover au since $u = E(U)$ is the mean of U. For $U(U-1)$ we have

$$\begin{aligned} E(U(U-1)) &= e^{-u}\sum_{k=0}^{\infty} k(k-1)u^k/k! = e^{-u}\sum_{k=2}^{\infty} u^k/(k-2)! \\ &= u^2 e^{-u}\sum_{k=2}^{\infty} u^{k-2}/(k-2)! = u^2 e^{-u}\sum_{j=0}^{\infty} u^j/j! = u^2. \end{aligned} \tag{1.50}$$

Thus, $E(aU - bU(U-1)) = au - bu^2$, so the hydrodynamic limit for this system is the diffusive logistic model

$$\frac{\partial u}{\partial t} = d\nabla^2 u + (a - bu)u. \tag{1.51}$$

This hydrodynamic limit can be derived rigorously; see DeMasi and Presutti (1991).

If we wanted to consider interactions between two species and to allow interactions to occur in the local neighborhood of each point, we would need to introduce variables $\xi_t(x)$ and $\hat{\xi}_t(x)$, where $\xi_t(x)$ denotes the number of individuals of the second species at location x at time t, and $\hat{\xi}_t(x)$ denotes the numbers of individuals in the local neighborhood of x at time t. In the hydrodynamic limit, these quantities would converge to independent Poisson random variables with the means corresponding to $\xi, \hat{\eta}$, and $\hat{\xi}$ being $v, |\mathcal{N}|u, |\mathcal{N}|v$ respectively, where v represents a density of the second species and $|\mathcal{N}|$ the size of the interaction neighborhood. If a birth (or death) rate is given by $f(\xi, \eta, \hat{\xi}, \hat{\eta})$ in the interacting particle system, the corresponding term in the reaction-diffusion model arising as the hydrodynamic limit should be $E(f(U, V, \hat{U}, \hat{V}))$ where $U, V, \hat{U}$, and $\hat{V}$ are independent Poisson random variables with means $u, v, |\mathcal{N}|u$, and $|\mathcal{N}|v$. In principle this expectation can be calculated via computations along the lines of (1.50); however, in practice, the result can be represented in terms of elementary functions only for certain fairly simple forms of f. A consequence of the independence of the random variables is that, for example, $E(\hat{U}V) = E(\hat{U})E(V) = |\mathcal{N}|uv$. It follows that scaling by hydrodynamic limits has no qualitative effect on the interaction terms in Lotka-Volterra models. It turns out that if $f(U) = U/(U+1)$, as might be encountered in a model with a Holling type 2 functional response, $E(f(U)) = 1 - [(1 - e^{-u})/u]$. On the other hand, $E(U/(U+2)) = 1 - 2[u - 1 + e^{-u}]/u^2$ and $E(U/(U+\sqrt{2}))$ does not appear to have a simple representation. Some properties can be deduced from the general form $E(f(U)) = \sum_{k=0}^{\infty} e^{-u} f(k) u^k / k!$. Clearly if $|f(k)| \le M^k$ for some M then $E(f(U))$ is an analytic function, since the power series for $E(f(U))$ will converge. It is less obvious but still true that if $f(U)$ is increasing then so is $E(f(U))$ as a function of u. These and other properties are derived in Cantrell and Cosner (in press). Because most of the models we will consider involve Lotka-Volterra interactions, or other smooth interaction terms such as the Holling type 2 response, we usually simply augment the original interaction terms with diffusion rather than attempting to calculate hydrodynamic limits. This is certainly justified in the Lotka-Volterra case, since in that case the hydrodynamic limit is still Lotka-Volterra. In most of the other models we will consider, we will be concerned with qualitative effects that depend more on general properties of interaction terms such as monotonicity rather than on details of their algebraic form. Thus, using the original form of a Holling type 2 functional response rather than the form arising from hydrodynamic limits (which may not have a representation in terms of elementary functions) usually would not affect the qualitative properties of a model very much. There are, however, some important classes of models where the smoothing property of hydrodynamic limits, i.e. the fact that $E(f(U))$ is an analytic function as long as $f(U)$ does not grow faster than exponentially in U, has significant qualitative effects. These include ratio-dependent models and the hawk-dove game discussed by Durrett and Levin (1994). We will discuss the hawk-dove game in some detail and then describe briefly the analogous effects in ratio-dependent models.

The hawk-dove game is a model for evolution of a pair of strategies that individuals might use for interacting with conspecifics, in a context where the results of using a given strategy

depend on the fraction of the local population that is using each of the two strategies. The payoff in this case is interpreted as a birth/death rate. The interactions between individuals using different strategies are assumed to occur in the local neighborhood of each location. Recall that we denoted the number of individuals of each type at x by $\eta_t(x)$ and $\xi_t(x)$, and the numbers in the local neighborhood of x by $\hat{\eta}_t(x)$ and $\hat{\xi}_t(x)$. For the moment we refer to the first type as "hawks" and the second as "doves". Let $\hat{p}_t(x) = \hat{\eta}_t(x)/(\hat{\eta}_t(x)+\hat{\xi}_t(x))$, that is, $\hat{p}_t(x)$ is the fraction of hawks among individuals in the local neighborhood of x at time t. Suppose that hawks at the location x have the birth (or death) rate $a\hat{p}_t(x) + b(1 - \hat{p}_t(x))$; similarly, suppose that doves at x have birth (death) rate $c\hat{p}_t(x) + d(1 - \hat{p}_t(x))$. Finally, suppose that all individuals at x have a logistic death rate proportional to the total number of individuals at x; that is, the death rate is $k(\eta_t(x) + \xi_t(x))$. If we simply treat $\eta, \hat{\eta}, \xi$, and $\hat{\xi}$ as densities u, v then a nonspatial model with interaction terms corresponding to the rates shown above would be

$$\begin{aligned} \frac{du}{dt} &= \left[\frac{au}{u+v} + \frac{bv}{u+v} - k(u+v)\right]u \\ \frac{dv}{dt} &= \left[\frac{cu}{u+v} + \frac{dv}{u+v} - k(u+v)\right]v. \end{aligned} \tag{1.52}$$

The traditional way to obtain a spatial model from (1.52) would be to simply add diffusion to obtain

$$\begin{aligned} \frac{\partial u}{\partial t} &= d\nabla^2 u + \left[\frac{au}{u+v} + \frac{bv}{u+v} - k(u+v)\right]u \\ \frac{\partial v}{\partial t} &= d\nabla^2 v + \left[\frac{cu}{u+v} + \frac{dv}{u+v} - k(u+v)\right]u. \end{aligned} \tag{1.53}$$

In the case $a = -0.6,\ b = 0.9,\ c = -0.9,\ d = 0.7$, both (1.52) and (1.53) can be shown to predict that $(u, v) \to (0, 0)$ as $t \to \infty$; see Durrett and Levin (1994). On the other hand, the interacting particle system itself predicts that the hawks and doves will coexist (Durrett and Levin, 1994). Computing the hydrodynamic limit for the interacting particle system via computations analogous to (1.50) yields the system

$$\begin{aligned} \frac{\partial u}{\partial t} &= d\nabla^2 u + \left[a\left(h + (1-h)\frac{u}{u+v}\right) + b(1-h)\frac{u}{u+v} - k(1+u+v)\right]u \\ \frac{\partial u}{\partial t} &= d\nabla^2 v + \left[c\left(h + (1-h)\frac{u}{u+v}\right) + d(1-h)\frac{v}{u+v} - k(u+v+1)\right]v \end{aligned} \tag{1.54}$$

where $h(u, v) = [1 - e^{-|\mathcal{N}|(u+v)}]/|\mathcal{N}|(u + v)$; recall that $|\mathcal{N}|$ is the size of the local neighborhood. See Durrett and Levin, (1994), and Perrut (2000). (If we were to assume that individuals do not interact with themselves, then the rate terms in the original interacting particle system would be modified and the form of the hydrodynamic limit would be slightly different, but the general qualitative features of the models would be very similar.) It turns out that (1.54) has an equilibrium with u and v both positive which is globally attracting for positive solutions (Durrett and Levin, 1994). Thus, in this case, taking the hydrodynamic limit of the interacting particle system yields a prediction which is opposite to what is obtained by just using the rates in that system directly, with or without diffusion. This is quite different form the cases of logistic or Lotka-Volterra models. For those, taking hydrodynamic limits typically has no effect at all on the form of the interaction terms,

and the only quantitative effect is that some terms may be multiplied by $|\mathcal{N}|$ (Cantrell and Cosner in press.) What is the difference between these cases? The key observation is that the terms $u^2/(u+v)$, $uv/(u+v)$, etc. in (1.52) and (1.53) are not smooth at $(0,0)$; that is, they have partial derivatives which are not continuous at $(0,0)$. The corresponding terms in the hydrodynamic limit are smooth. (This can be seen by expanding $h(u,v)$ in a power series or by recalling that all hydrodynamic limits arise from convergent power series as in (1.50), and that functions with convergent power series representations are smooth.) When the interaction terms are not smooth, pairs of ordinary differential equations can have equilibria of types that are different than the usual stable and unstable nodes, saddles, spiral points, etc. which occur in smooth systems. This point has been explored in some detail in the context of ratio-dependent predator-prey models (Kuang and Berreta, 1998). In smooth systems with two components, there is only a single direction along which a trajectory can approach a saddle point. In predator-prey models the origin is often a saddle point, and in smooth systems the only direction from which trajectories approach the origin is generally along the predator axis. In similar models with ratio-dependent interaction terms there can be a whole sector, that is, a range of values of the ratio of the two components, within which trajectories can enter the origin. Taking the hydrodynamic limit of such a ratio-dependent system generally leads to a smooth system where the region is again an ordinary saddle point. It is not surprising that the model (1.52) supports phenomena similar to those seen in ratio-dependent predator-prey models, because the terms $u/(u+v)$ and $v/(u+v)$ are ratio dependent. If we derive a reaction-diffusion model for a system where the local interaction rates are given by functions that are not smooth, then the results obtained by simply adding diffusion may not accurately reflect the behavior of the interacting particle system. Deriving the reaction-diffusion model via hydrodynamic limits smooths out the interaction terms and thus seems to capture more accurately the behavior of the original system in some cases.

Many of the systems we will study are based on Lotka-Volterra models, and essentially all of them are based on smooth interaction terms whose key properties (e.g. monotonicity) are preserved by hydrodynamic limits. Thus, we usually just add diffusion to the terms describing local interactions, because in the cases we will consider taking hydrodynamic limits has few if any qualitative effects on the structure of the model. This approach would not be appropriate for deriving diffusion models for systems where the local interactions are not smooth, such as ratio-dependent models or variations on the hawk-dove game. For those systems it may be necessary to use hydrodynamic limits if the resulting reaction-diffusion model is supposed to display the same behavior as the underlying interacting particle system.

1.5.3 What Can Reaction-Diffusion Models Tell Us?

Reaction-diffusion models can explain three types of spatial phenomena that are relevant in ecology: waves of invasion by exotic species, the formation of patterns in homogeneous space, and the effects of the size, shape, and heterogeneity of the spatial environment on the persistence of species and the structure of communities. These ideas were introduced in four classic papers on diffusion theory. The idea that reaction-diffusion models can support traveling waves was introduced by Fisher (1937) in the context of models for the spatial spread of an advantageous gene. The idea that adding diffusion to a nonspatial model (with two or more components) can destabilize spatially homogenous equilibria and lead to the formation of patterns was introduced by Turing (1952) in the context of models for morphogenesis. The idea that reaction-diffusion models predict the minimal

patch size needed to sustain a population was introduced by Skellam (1951) and Kierstead and Slobodkin (1953), specifically in the context of spatial ecology. (Skellam also extended Fisher's idea of a traveling wave to the spread of populations, as opposed to genes within a population.) In what follows we focus our attention almost exclusively on the effects of habitat geometry and heterogeneity on the persistence, coexistence, and extinction of species in finite habitats. We have chosen to pursue that topic in this book (and the research leading to it) in part because some good treatments of traveling waves (and invasions in general) and pattern formation are already available. Traveling waves in reaction-diffusion models are discussed from a mathematical viewpoint by Fife (1979), Smoller (1982), and Grindrod (1996). They are discussed from the viewpoint of biological applications by Murray (1993). Models for biological invasions, including but not limited to reaction-diffusion models, are discussed by Kawasaki and Shigesada (1997). Pattern formation is discussed by Grindrod (1996) and, again in the biological context, by Murray (1993). There are some general treatments of reaction-diffusion systems in bounded spatial domains, including Lotka-Volterra models with diffusion, for example Leung (1989) and Pao (1992), and in the time periodic case (Hess, 1991), but those treatments are essentially mathematical in nature and generally do not attempt to make close connections with specific applications in ecology. Also, the material we present includes a number of methods and applications which to our knowledge have only appeared in journal articles.

The phenomena that can be described via reaction-diffusion models can often be treated via other types of models. If highly detailed specific predictions are required, it is probably best to use simulations, perhaps via individual based models, cellular automata, or interacting particle systems. Some of these sorts of approaches are discussed by Tilman et al. (1997). A limitation of simulation models is that it is usually difficult to analyze them mathematically and extract general properties which can provide insights into the mechanisms underlying their predictions. However, they can be used in numerical experiments to construct artificial data sets from which general properties can be inferred. In particular, cellular automata models have been observed to generate spatial patterns analogous to those produced by reaction-diffusion models (Comins et al., 1992; Hassell et al., 1994). It is sometimes possible to obtain information about the rate at which a population expands its range from interacting particle systems; see Ellner and et al. (1998). Traveling waves can be shown to exist in island chain models; see Zinner (1991,1992). A limitation of reaction-diffusion models for the propagation of traveling waves is that diffusion equations on unbounded domains predict that an initial density which is zero except on some bounded set will be positive everywhere for all positive times. This seems to be at odds with the notion that organisms move with finite speed. That could be resolved by replacing reaction-diffusion models with models based on the telegraph equation $\epsilon^2 \partial^2 u/\partial t^2 + \partial u/\partial t = d\partial^2 u/\partial x^2 + f(u)$. However, it turns out that for parameter values that occur in natural systems, the predictions of the telegraph equation are very close to those of the corresponding reaction diffusion model (Holmes, 1993). A more serious problem is that diffusion models do not account for long-distance movement, e.g. for the movement of an insect that "hitch-hikes" on a car or truck instead of crawling on its own. More generally, diffusion predicts that a population which is initially concentrated at a single point will develop a normal (i.e. Gaussian) distribution in space as time passes. Other patterns are certainly possible, and these can be examined by using models based on integral kernels. It turns out that the details of how the kernel decays at infinity can have profound effects on wave propagation; see Lewis (1997). Thus, there are sometimes good reasons to use such models instead of reaction-diffusion models in the study of biological invasions.

However, in a finite habitat patch the issue of long distance dispersal is much less important, especially if the primary goal is to understand the long term effects of local dispersal and habitat geometry on population dynamics. Thus, while it is possible to use integral kernels to study long term persistence in habitat patches (Hardin et al., 1988a,b 1990; VanKirk and Lewis, 1997, 1999), it is also reasonable to use reaction-diffusion models. Metapopulation models, especially as formulated by Hanski and his co-workers (1997, 1999) and Tilman (1994) can address the issue of persistence in finite habitats, but those models treat networks of patches and treat local population dynamics implicitly, in terms of presence or absence of populations. Thus, they are typically appropriate models for spatial effects on a different set of spatial scales than reaction-diffusion models. Discrete diffusion models, i.e. island chain models, can also be used to model patch networks. To describe systems where different species operate on different spatial scales, it may be necessary to combine reaction-diffusion models and patch network models. An example is discussed in Cantrell and Cosner (1996).

The phenomena of traveling waves and pattern formation differ from that of minimal patch in a fundamental way: they can occur in homogeneous space, while the very notion of "patch" requires at least enough spatial heterogeneity to distinguish the patch from its surroundings. A defining feature of any finite habitat is that it has a boundary, or edge. Edges can mediate numerous effects in population dynamics (Fagan et al., 1999). Habitat edges can be created by physical features such as rivers, roads, or (for aquatic systems) shorelines; they can also arise from interfaces between different types of ecological communities such as forests and grasslands. Edges can influence population dynamics in various ways. They can affect movement patterns, act as a source of mortality or resource subsidy, or function as a unique environment with its own rules for population interactions (Fagan et al., 1999). Edges can have different effects on different species; for example, a road may act as a barrier for some species and a source of mortality for others. Thus, because edges can exert different effects on different species, the presence of edges can influence community structure in ways that are not completely obvious from the ways in which they affect each species. Reaction-diffusion models provide a natural framework for the study of edge effects, because to correctly formulate a reaction-diffusion model in a finite patch it is necessary to specify boundary conditions. In other words, we must describe not only how individuals disperse throughout a patch, but also what they do when they reach the edge of the patch. An advantage of reaction-diffusion models is that they can readily incorporate simple rules about the effects of edges. They can also incorporate effects of internal heterogeneity within a patch. We will use those features of reaction-diffusion models to study how environmental heterogeneity affects populations.

1.5.4 Edges, Boundary Conditions, and Environmental Heterogeneity

The simplest way to formulate boundary conditions for reaction-diffusion models is probably via Fick's law. Recall that Fick's law is based on the idea that the rate of diffusion across an interface is given by $\vec{J} \cdot \vec{n}$ where $\vec{n}$ is the unit normal vector to the interface. If we are describing the density u of a population of individuals that diffuse at a rate $d(x)$ and are advected or engage in directed movement with velocity $\vec{v}(x)$, then $\vec{J} = -d(x)\nabla u + \vec{v}(x)u$ and the diffusion equation for u is (1.45), repeated here for convenience: $\partial u/\partial t = -\nabla \cdot \vec{J} = \nabla \cdot d(x)\nabla u - \nabla \cdot (\vec{v}(x)u)$. The standard boundary conditions for (1.45) relate the flux of individuals across a boundary to the density at the boundary. Specifically, let Ω be a bounded region with smooth boundary $\partial\Omega$, and let $\vec{n}$ denote the outward pointing unit normal. Then the flux across the boundary $\partial\Omega$ at any given

point is proportional to the density with constant of proportionality $\beta(x)$ if $\vec{J} \cdot \vec{n} = \beta u$, i.e. $[-d(x)\nabla u + \vec{v}(x)u] \cdot \vec{n} = \beta(x)u$. The quantity $\nabla u \cdot \vec{n}$ is the directional derivative of u in the direction of the outward normal vector to $\partial\Omega$; it is often denoted by $\partial u/\partial \vec{n}$, and we will use that notation. The boundary condition for the diffusion model (1.45) would typically be expressed as

$$d(x)\frac{\partial u}{\partial \vec{n}} + [\beta(x) - \vec{v}(x) \cdot \vec{n}(x)]u = 0. \tag{1.55}$$

To understand what the boundary condition means, it is useful to return to the form $\vec{J} \cdot \vec{n} = \beta u$. If $\beta = 0$ then the condition says that there is no flux across $\partial\Omega$, so that $\partial\Omega$ acts as a perfect barrier to dispersal. As β increases, a larger proportion of individuals who encounter the boundary will cross it in the outward direction. Finally, if we write the condition as $u = (1/\beta)\vec{J} \cdot \vec{n}$, then as $\beta \to \infty$ the boundary condition becomes $u = 0$ on $\partial\Omega$, indicating that individuals who encounter the boundary cross it immediately and thereby maintain the density on the boundary at zero. It we want to compare boundary conditions within a single model it may be convenient to write the boundary condition as

$$\alpha[d(x)\partial u/\partial \vec{n} - \vec{v} \cdot \vec{n}u] + (1 - \alpha)u = 0 \tag{1.56}$$

with $0 \leq \alpha \leq 1$. In that formulation, α measures the fraction of individuals which do not cross the boundary when they encounter it. Thus, $\alpha = 1$ corresponds to a situation where no individual crosses $\partial\Omega$, $\alpha = 0$ corresponds to one where all individuals who encounter $\partial\Omega$ cross it, and $0 < \alpha < 1$ corresponds to intermediate situations. The boundary conditions (1.55) or (1.56), along with other sorts of boundary conditions, can be obtained from the theory of stochastic processes (Gardiner, 1985). The interpretation of conditions (1.55), (1.56) is the same as in the derivation from Fick's law, but cast in terms of the probability of an individual crossing $\partial\Omega$ as opposed to the rate at which individuals cross. There is some standard terminology that is used to specify boundary conditions. The condition $u = 0$ on $\partial\Omega$ is sometimes called "absorbing" because under that condition $\partial\Omega$ effectively absorbs all individuals encountering it. That boundary condition is typically called a Dirichlet condition in the mathematical literature. In population dynamics, the boundary condition $u = 0$ is sometimes said to correspond to a lethal boundary, because it can be interpreted as meaning that all individuals who encounter $\partial\Omega$ die. (For purposes of analyzing what happens inside Ω it doesn't usually matter whether individuals encountering $\partial\Omega$ die or simply leave and don't return.) The boundary condition $d(x)\partial n/\partial \vec{n} - \vec{v} \cdot \vec{n}u = 0$ is called a no-flux or reflecting boundary condition, since it means that individuals encountering $\partial\Omega$ are always "reflected" back into Ω so they do not leave. In the mathematical literature the boundary condition $\partial u/\partial \vec{n} = 0$ is called a Neumann condition. It corresponds to a reflecting or no-flux boundary condition *if* $\vec{v} = 0$, but not otherwise. Boundary conditions of the form $\alpha(x)\partial u/\partial \vec{n} + \beta(x)u = 0$ with both α and β positive are called Robin conditions in the mathematical literature.

In some cases individuals may have a preference for crossing a habitat edge in a particular direction. Models for movement which incorporate a preferred direction of motion at an interface have been studied in the context of stochastic processes under the name "skew Brownian motion." The basic process of skew Brownian motion is formulated as a random walk in one dimension, analogous to those described in (1.27)–(1.30), but with $\alpha = 1/2$ *except* at a single point where in general $\alpha \neq 1/2$; see Walsh (1978), and Harrison and Shepp (1981). (Recall that α is the probability that an individual moves to the right at any given time step.) According to Walsh (1978) and Harrison and Shepp (1981), the scaling

used in (1.27)–(1.30) where $\Delta x, \Delta t \to 0$ with $(\Delta x)^2/2\Delta t = d$ can be applied to this type of motion. If $\alpha = 1/2$ except at $x = 0$, the process is described by a diffusion equation of the form

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} \quad \text{on} \quad (-\infty, 0) \cup (0, \infty) \\ &\lim_{x\to 0+} \alpha \frac{\partial u}{\partial x}(x,t) = \lim_{x\to 0-} (1-\alpha)\frac{\partial u}{\partial x}(x,t) \\ &\lim_{x\to 0+} \frac{\partial^2 u}{\partial x^2}(x,t) = \lim_{x\to 0-} \frac{\partial^2 u}{\partial x^2}(x,t); \end{aligned} \tag{1.57}$$

see Walsh (1978). The first equation in (1.57) is the same diffusion equation we derived earlier in this section. The next equation implies a discontinuity in the flux at the point zero if $\alpha \neq 1/2$ and $\lim_{x\to 0+} \partial u/\partial x$ or $\lim_{x\to 0-} \partial u/\partial x$ is nonzero. The third equation requires that $\partial^2 u/\partial x^2$ can be extended continuously across the interface at $x = 0$. In Cantrell and Cosner (1998, 1999) we considered models based on skew Brownian motion. In Chapter 2 we discuss them in some detail. The models are set on an interval containing 0; they have the form

$$\begin{aligned} &\frac{\partial u}{\partial t} = D_1\frac{\partial^2 u}{\partial x^2} + su \quad \text{for} \quad x < 0 \\ &\frac{\partial u}{\partial t} = D_2\frac{\partial^2 u}{\partial x^2} + ru \quad \text{for} \quad x > 0 \\ &\lim_{x\to 0+} \alpha D_2 \frac{\partial u}{\partial x} = \lim_{x\to 0-} (1-\alpha) D_1 \frac{\partial u}{\partial x} \\ &\lim_{x\to 0+} D_2\frac{\partial^2 u}{\partial x^2} + ru = \lim_{x\to 0-} D_1\frac{\partial^2 u}{\partial x^2} + su. \end{aligned}$$

The equations above extend those of Walsh (1978) in a fairly natural way, but the model has some peculiar features. In Cantrell and Cosner (1998) we show that to conserve total population in Walsh's model, which has no explicit birth or death rate, the population distribution must sometimes include a multiple of the Dirac delta, i.e. a point mass, at $x = 0$. In other words, the pure dispersal model for skew Brownian motion derived by Walsh (1978) implies that there may be a nonzero number of individuals *on* the interface at $x = 0$. There are other possible formulations for models with a preferred direction of movement at an interface. One that involves a discontinuity in density but keeps flux continuous has been derived by Ovaskainen (preprint). The general problem of correctly formulating and analyzing models where individuals have a directional preference at an interface deserves further study.

Once we have specified a patch Ω, the dispersal properties and local population dynamics of a species inhabiting Ω, and the behavior (or fate) of individuals encountering the boundary of Ω, we can assemble a complete reaction-diffusion model. A typical example would be a model for the density u of a population whose members disperse throughout Ω by diffusion at a rate $d(x)$ which may vary in space, reproduce (or die) logistically with a net birth or death rate $a(x) - b(x)u$, and leave Ω when they encounter $\partial\Omega$. The model for

the population density would then be

$$\frac{\partial u}{\partial t} = \nabla \cdot d(x)\nabla u + [a(x) - b(x)u]u \text{ in } \quad \Omega \times (0, \infty)$$
$$u = 0 \qquad\qquad\qquad\qquad\qquad \text{on } \quad \partial\Omega \times (0, \infty).$$

To obtain a specific solution, we would also have to know the initial state of the system as given by the initial density $u(x, 0)$. In his pioneering work on diffusion models in ecology, Skellam (1951) said of models such as the preceding that "orthodox analytical methods appear inadequate." Much of the remainder of this book is devoted to the presentation of "analytical methods" which have been developed in the half century since Skellam made that remark, and to discussions of how to apply those methods to such models. Although many questions remain open, the new mathematical methods are somewhat closer to being adequate for the treatment of such models than those available in 1951.

1.6 Mathematical Background

1.6.1 Dynamical Systems

The basic units of information about a group or collection of species that we will keep track of in this volume are population counts or population densities for the species in question. The very simplest example imaginable would be to keep track of either the total population of some species over some spatial region or its average population density over the region as time varies. In this case a single nonnegative number $y(t)$ is adequate to designate the total population or the average population density at time t. However, if we want to subdivide the population in some way (e.g., by life stages) and track the total population or average density for each of the divisions over time, or if we want to track the total population or average population density for more than one species simultaneously, a single number for each value of time is inadequate to convey this information. Obviously, a nonnegative number is needed for each distinct subdivision we want to consider in the first instance and for each individual species in question in the second. The most suitable way to encode such information mathematically is to use an *ordered n-tuple* or *vector* of numbers $(y_1(t), y_2(t), \ldots, y_n(t))$ for each value of time.

There are three basic properties of n-vectors that pertain to the analyses of this volume. First of all, two n-vectors $(y_1, y_2, \ldots, y_n)$ and $(y_1^*, y_2^*, \ldots, y_n^*)$ may be added by adding components and an n-vector $(y_1, \ldots, y_n)$ may be multiplied by a scalar c componentwise; i.e.,

$$(y_1, y_2, \ldots, y_n) + (y_1^*, y_2^*, \ldots, y_n^*) = (y_1 + y_1^*, y_2 + y_2^*, \ldots, y_n + y_n^*) \tag{1.58}$$
$$c(y_1, \ldots, y_n) = (cy_1, \ldots, cy_n). \tag{1.59}$$

We say that (1.58) and (1.59) endow the collection of all such n-tuples of real numbers with a *linear structure*, and this structure permits us to do arithmetic on the collection. Of course, since for our purposes the components are always nonnegative, we usually want c in (1.59) to be nonnegative. The second feature of n-vectors that we employ is that we can measure the distance between $(y_1, \ldots, y_n)$ and $(y_1^*, \ldots, y_n^*)$. To this end, we have the formula

$$d((y_1, \ldots, y_n), (y_1^*, \ldots, y_n^*)) = \left(\sum_{i=1}^{n} (y_i - y_i^*)^2 \right)^{1/2}, \tag{1.60}$$

where d in (1.60) stands for distance and the formula is the natural extension of the Pythagorean theorem to n-vectors. It is immediate from (1.60) that

$$\begin{aligned} &d((y_1, \ldots, y_n), (y_1^*, \ldots, y_n^*)) \geq 0 \quad \text{with} \quad d((y_1, \ldots, y_n), (y_1^*, \ldots, y_n^*)) \\ &= 0 \quad \text{only if} \quad (y_1, \ldots, y_n) = (y_1^*, \ldots, y_n^*), \end{aligned} \tag{1.61}$$

and

$$d((y_1, \ldots, y_n), (y_1^*, \ldots, y_n^*)) = d((y_1^*, \ldots, y_n^*), (y_1, \ldots, y_n)). \tag{1.62}$$

It may not be so immediate but it is nevertheless also the case that if $(y_1^{**}, \ldots, y_n^{**})$ represents some other n-vector, then

$$\begin{aligned} d((y_1, \ldots, y_n), (y_1^*, \ldots, y_n^*)) &\leq d((y_1, \ldots, y_n), (y_1^{**}, \ldots, y_n^{**})) \\ &+ d((y_1^{**}, \ldots, y_n^{**}), (y_1^*, \ldots, y_n^*)). \end{aligned} \tag{1.63}$$

Note that (1.63) can be interpreted as saying that the length of one side of a triangle is less than or equal to the sum of the lengths of the other two sides and hence is known as the *triangle inequality*. Being able to equip the collection of n-vectors with (1.58)–(1.60) enables us to employ methods of real analysis such as calculus on the collection. The third feature of significance in the collection of n-vectors is that there is sometimes a natural way to order two vectors. The most usual choice is to say that

$$(y_1, \ldots, y_n) \leq (y_1^*, \ldots, y_n^*) \Leftrightarrow y_i \leq y_i^* \quad \text{for} \quad i = 1, \ldots, n, \tag{1.64}$$

i.e., the ordering between components of the n-vectors is consistent from one component of the n-tuple to the next. Of course, not all n-vectors are so ordered once $n > 1$ (e.g., (1,2) and (2,1)). Consequently, (1.64) is called a *partial ordering* on the collection of n-vectors.

Of course, our principal aim in this volume is to employ reaction-diffusion models to model and analyze the interaction of biological species in isolated bounded spatial habitats. To do so, we must consider pointwise population densities in place of average densities. So our state spaces are now n-tuples of nonnegative functions $(y_1(x), \ldots, y_n(x))$, where $x \in \overline{\Omega}$, the habitat patch in question, instead of n-tuples of nonnegative numbers $(y_1, \ldots, y_n)$. Of course, to track changes over time in an n-tuple of population densities requires us to consider n-tuples of the form $(y_1(x, t), \ldots, y_n(x, t))$.

Now two functions $y(x)$ and $y^*(x)$ on $\overline{\Omega}$ may be added together in a natural way to form a function $(y + y^*)(x)$ via the formula

$$(y + y^*)(x) = y(x) + y^*(x) \tag{1.65}$$

and a function $y(x)$ may be multiplied by a scalar c to form a function $(c \cdot y)(x)$ in a natural way via the formula

$$(c \cdot y)(x) = c \cdot y(x). \tag{1.66}$$

It follows from (1.65) and (1.66) that just as in the case of the collection of n-tuples of average population densities we can impose a linear structure on the collection of n-tuples of pointwise population densities on the habitat $\overline{\Omega}$ so that we can do arithmetic

on the collection. So the first of the three aforementioned features of the collection of n-tuples of average population densities carries over to the collection of n-tuples of pointwise population densities on $\overline{\Omega}$ in a straightforward manner.

The second feature of the collection of n-tuples of average population densities, namely the ability to measure the distance between two such n-tuples, also carries over to the collection of n-tuples $(y_1(x), \ldots, y_n(x))$ of pointwise population densities. However, the inclusion of explicit spatial structure complicates the issue. Should having $(y_1(x), \ldots, y_n(x))$ be close to $(y_1^*(x), \ldots, y_n^*(x))$ mean that the two n-tuples are close in some sense at every point $x \in \overline{\Omega}$ or need they only be close in some way on the average over $\overline{\Omega}$? Should only the values of the population densities matter or should we take into account their spatial derivatives to some order and, if so, to what order? All these possibilities give rather different but nevertheless valid notions of "closeness" in the context of n-tuples of pointwise population densities on the habitat $\overline{\Omega}$. Consequently, we should define distance in enough generality so as to accommodate any of them. We do so via the notion of *metric space* from topology. By a *metric space*, we mean a collection or set Y of objects or points y and a *distance function* or *metric* d to measure distance between points of Y. Mathematically, d is a map that assigns a nonnegative number $d(y, y^*)$ to every ordered pair (y, y^*) of points y, y^* in Y. We require that d satisfy (1.61)–(1.63); i.e., two points at zero distance from each other must coincide, the distance from y to $y^*(d(y, y^*))$ must be the same as the distance from y^* to $y(d(y^*, y))$, and the triangle inequality must hold.

For our purpose, Y will usually be *some* collection of n-tuples of pointwise population densities on $\overline{\Omega}$. The most appropriate collection of such n-tuples in any given situation depends on the choice of the metric d. We will be tracking configurations of population densities as they evolve over time and necessarily will be interested in their limits. We will frequently want a limiting configuration of population densities to inherit the properties of the configurations that approach it. For instance, we may want to insist that all the densities that we consider be continuous on $\overline{\Omega}$. To see why there is an issue as regards the choice of metric, let us look at a specific example. For simplicity, we will consider just a single species distributed across the one-dimensional habitat $[0, 2]$. A possible family of continuous population densities for the species is given by the sequence of functions $f_k(x),\ x \in [0, 2]$, where

$$f_k(x) = \begin{cases} x^k & 0 \le x \le 1 \\ 1 & 1 \le x \le 2. \end{cases}$$

Clearly the pointwise limit of this family of densities is the function $f_0(x)$ with

$$f_0(x) = \begin{cases} 0 & 0 \le x < 1 \\ 1 & 1 \le x \le 2 \end{cases}$$

which is clearly not continuous on $[0, 2]$. If we define $d_1(f, g)$ for real valued functions f, g defined on $[0, 2]$ by

$$d_1(f, g) = \int_0^2 |f(x) - g(x)| dx,$$

then it is easy to establish that d_1 satisfies (1.61)–(1.63). So d_1 is a perfectly acceptable metric. Moreover, the sequence $\{f_k\}$ converges to f_0 under this metric since $d_1(f_k, f_0) = \int_0^1 x^k = 1/(k+1) \to 0$ as $k \to \infty$. So under the metric d_1 the limit of continuous densities on $[0, 2]$ need not be continuous. If preserving continuity in the limiting density is important to us, we need to change the metric. If d_1 is the metric we want, we need to expand the class of density functions we consider beyond continuous ones. The mathematical method of dealing with this issue is to refine the notion of metric space by defining the term *complete metric space*. A metric space Y is complete if all sequences in Y whose elements become arbitrarily close together converge to an element in Y. The technical word mathematicians use for a sequence whose elements become arbitrarily close together is *Cauchy*. A Cauchy sequence $\{y_n\} \subseteq Y$ is one so that given any positive number ε, there will correspond an index N so that for indices $n, m \geq N$ the distance $d(y_n, y_m) < \varepsilon$. Completeness of Y is the property that all Cauchy sequences have limits in Y. In our example, if we switched from d_1 to d_∞ where $d_\infty(f, g)$ is defined by

$$d_\infty(f, g) = \max_{x \in [0,2]} |f(x) - g(x)|$$

for continuous real valued functions f, g defined on $[0, 2]$, a basic result in real analysis (see, e.g., Rudin 1976) is that a Cauchy sequence of such functions converges to a unique continuous real value function defined on $[0, 2]$. So under d_∞, the continuous real-valued functions on $[0, 2]$ are complete. The sequence $\{f_k\}$ simply fails to be Cauchy under the metric d_∞.

A metric space Y does not require a linear structure, only a means of measuring distances between points that satisfies (1.61)–(1.63). However, when there is a linear structure on Y, this feature can be employed in the construction of the metric. To this end, if y and y^* are vectors in Y, $y - y^*$ can be viewed either as a point or vector in its own right or as a line segment joining y and y^*. Consequently, it is natural to suppose that $d(y, y^*) = d(y - y^*, 0)$. In such a case, one need only measure distance to the zero vector of Y. The notation $||y||$ is usually used for this purpose. If $||y||$ has the properties that

$$\begin{aligned} &||y|| \geq 0 \quad \text{and} \quad ||y|| = 0 \Leftrightarrow y = 0, \\ &||cy|| = |c|||y|| \quad \text{for all scalars} \quad c, \\ &||y + y^*|| \leq ||y|| + ||y^*|| \quad \text{for all} \quad y, y^* \in Y, \end{aligned} \tag{1.67}$$

then $d(y, y^*) = ||y - y^*||$ defines a metric on Y. The number $||y||$ is referred to as the *norm* of the vector. A linear space Y which is complete as a metric space under such a metric is called a *Banach space*.

The n-tuples of pointwise population densities on the habitat patch $\overline{\Omega}$ that are the primary concern of this volume all belong to Banach spaces. Later in this section we discuss the various Banach spaces that arise in our discussion, including the definition of the norm in each case. For now, we want to make two additional observations. First, Banach spaces are primary objects of study in the branch of mathematics known as *functional analysis*, which provides a collection of very powerful mathematical results for use in analyzing models for several interacting biological species in an isolated bounded habitat. Secondly as noted previously, since our interest is in population densities, we will usually confine ourselves to n-tuples the components of which are nonnegative functions. As a result, we will usually be

examining closed subsets of a Banach space rather than the entire space. It is a basic result of functional analysis that closed subsets of Banach spaces are complete metric spaces.

As noted, our primary interest in this volume is to track the predictions of reaction-diffusion models about the long term behavior of the densities for several interacting biological species on an isolated bounded habitat $\overline{\Omega}$. If u_i denotes the density of species i (say i runs from 1 to n), then in most of the models we consider, the time rate of change $\frac{\partial u_i}{\partial t}$ does not explicitly depend upon time; i.e. the growth law is *autonomous*. (Of course, $\frac{\partial u_i}{\partial t}$ does depend upon u_i and its spatial derivatives and may also depend explicitly upon the spatial coordinate x and some or all of the remaining densities.) In the next subsection, we review the basic theory of systems of reaction-diffusion equations. We note there that in all the examples of such systems that we consider, the time evolution of species densities so governed is uniquely determined for all times $t \geq 0$ by the initial configuration of the densities; i.e. $(u_1(x,t), \ldots, u_n(x,t)) = \varphi(u_1(x,0), \ldots, u_n(x,0), t)$ for $t \geq 0$. Moreover, φ is continuous when viewed as a function from $Y \times [0,\infty)$ into Y, where the complete metric space Y is some suitable prespecified collection of n-tuples of possible species densities on an underlying habitat $\overline{\Omega}$. When the reaction-diffusion system is autonomous, the basic theory then guarantees that the configuration to which $(u_1(x,0), \ldots, u_n(x,0))$ evolves after $t + t'$ units of time where $t, t' > 0$ is the same configuration as arises when $\varphi(u_1(x,0), \ldots, u_n(x,0), t)$ is viewed as an initial configuration and then evolves for t' units of time; i.e.,

$$\varphi(u_1(x,0), \ldots, u_n(x,0), t + t') = \varphi(\varphi(u_1(x,0), \ldots, u_n(x,0), t), t'). \tag{1.68}$$

These features mean that the solution trajectories to such autonomous reaction-diffusion models are examples of *continuous time semi-dynamical systems*.

A (*continuous time*) *dynamical system* or *flow* is a continuous function π defined on $Y \times \mathbb{R}$ and taking values in Y, where for our purposes Y is a metric space, so that

$$\pi(u, 0) = u \tag{1.69}$$

for all $u \in Y$ and

$$\pi(u, t + t') = \pi(\pi(u, t), t') \tag{1.70}$$

for all t, t' in $\mathbb{R}$ so that $\pi(u, t + t')$ and $\pi(u, t)$ are defined. (We refer to (1.70) as the semi-group property.) When the set of real numbers $\mathbb{R}$ in the preceding is replaced by the set $[0,\infty)$, π is called a *semi-dynamical system* or *semiflow*.

If π is a dynamical system and $u \in Y$, then the solution $\pi(u,t)$ exists for all t in some maximal open interval $(t_-(y), t_+(y))$, with $-\infty \leq t_-(y) < 0 < t_+(y) \leq \infty$. The set of points

$$\gamma(u) = \{\pi(u,t) : t_-(y) < t < t_+(y)\} \tag{1.71}$$

is called the *orbit* of π through u. The set of points

$$\gamma^+(u) = \{\pi(u,t) : 0 \leq t < t_+(y)\} \tag{1.72}$$

is called the *positive semi-orbit* of π through u. Of course, in case π is a semi-dynamical system that does not extend to be a dynamical system, only positive semi-orbits are guaranteed to exist for all $u \in Y$.

In order to consider long term behavior of a dynamical or semi-dynamical system, it is legitimate to require at a minimum that the system be such that

$$t_+(u) = +\infty \quad \text{in (1.71) or (1.72) for all } u \in Y. \tag{1.73}$$

Of course, not all dynamical or semi-dynamical systems have this property. For example, in the ordinary differential equation

$$\frac{dy}{dt} = (y - K)^2$$

with $K > 0$, $t_+(m) = \dfrac{1}{m - K}$ for all $m > K$, and the corresponding orbit "blows up" in finite time.

Certainly most ecological models for interacting biological species do not envision orbits that "blow up" in finite time. Moreover, when ecological models are used to describe the long-term interactions for biological species (we are specifically excluding linear models at this point), they usually include mechanisms which preclude unbounded growth in species densities in the long term. Consequently, the hypotheses that we impose on a dynamical or semi-dynamical system to obtain (1.73) will actually restrict the systems much more stringently. Namely, we require that the systems be *dissipative*, by which we mean that there is a bounded subset U of Y so that for any $u \in Y$, $\pi(u, t) \in U$ for all sufficiently large t. (Recall that Y will usually be a closed subset of a Banach space with norm $||\cdot||$. Having U be bounded means that there is a positive number M so that if $v \in U$, $||v|| \leq M$. For an individual element $u \in Y$, how large t must be in order for $\pi(u, t) \in U$ is allowed to depend on u.)

Let us now note a consequence of the dissipativity assumption in the context of the most basic example of a continuous time dynamical system, namely the collection of all solution trajectories (based at $t = 0$) of a system or ordinary differential equations of the form

$$y_i' = f_i(y_1, \ldots, y_n), \tag{1.74}$$

$i = 1, 2, \ldots, n$. Let $(y_1^0, \ldots, y_n^0)$ represent an arbitrary initial configuration for, say, the average population densities of species 1 to n. Assuming (1.74) is dissipative, then the sequence of configurations $\{\pi((y_1^0, \ldots, y_n^0), t_j)\}$ for $j = 1, 2, 3, \ldots$ is contained in the bounded set $U_R = \{(y_1, \ldots, y_n) : ||(y_1, \ldots, y_n)|| \leq R\}$ for some $R > 0$ for any collection of distinct times t_j such that $t_j \to +\infty$ as $j \to +\infty$. If U_R is expressed as the union of some *finite* collection of subsets of itself, at least one of these subsets must contain $\pi((y_1^0, \ldots, y_n^0), t_j)$ for *infinitely* many distinct values of t_j. It follows from this observation that there must be at least one point $(\overline{y}_1, \ldots, \overline{y}_n) \in U_R$ so that some subsequence $\pi((y_1^0, \ldots, y_n^0), t_{j_k})$ of $\pi((y_1^0, \ldots, y_n^0), t_j)$ converges to $(\overline{y}_1, \ldots, \overline{y}_n)$ as the index $k \to \infty$. (This result is one of the main results of advanced calculus and is known as the Bolzano-Weierstrass Theorem (see, e.g., Apostol (1974)). A set P with the property that any sequence of points in P has a convergent subsequence is called *precompact*. If the limit of the subsequence is always actually in P, then P is said to be *compact*. In particular $\{\pi((y_1^0, \ldots, y_n^0), t_j)\}$ is precompact for any distinct collection of times t_j such that $t_j \to \infty$.) Consequently, dissipativity in the context of (1.74) means there will be a bounded subset that attracts the orbits of (1.74) as time tends toward $+\infty$. In the semi-dynamical system context of reaction-diffusion models for interacting biological species in an isolated bounded habitat, the underlying state space Y is infinite

dimensional. Consequently, dissipativity by itself does not guarantee precompactness of positive semi-orbits. Rather, dissipativity must be used in conjunction with the smoothing action associated to the elliptic operators in the system to draw this conclusion. This issue is discussed in detail in the next subsection.

In the preceding example (1.74) dissipativity allowed us to conclude that orbits tend toward a bounded attracting set. Of course, if we want to interpret (1.74) as a model describing the temporal evolution of the average population densities of species 1 to n, it must be the case for all $t \neq 0$ that if $(y_1(t), \ldots, y_n(t)) = \pi((y_1^0, \ldots, y_n^0), t)$, then $y_i(t)$ is nonnegative. A condition on (1.74) that guarantees such is the case is for f_i to satisfy

$$f_i(y_1, \ldots, y_n) = y_i \tilde{f}_i(y_1, \ldots, y_n) \tag{1.75}$$

for $i = 1, \ldots, n$. If (1.75) holds, then the principle of the uniqueness of solutions to initial value problems guarantees that $y_i(t) \geq 0$ for all $t \neq 0$ and $i = 1, \ldots, n$ so long as $y_i^0 \geq 0$ for $i = 1, \ldots, n$. Moreover, it also guarantees that $y_i(t)$ can equal 0 for some $i \in \{1, \ldots, n\}$ and some $t \neq 0$ only when $y_i^0 = 0$ and that in such case $y_i(t) = 0$ for all $t \in \mathbb{R}$. We then say that the sets $\{(y_1, \ldots, y_n) : y_i \geq 0 \quad \text{for} \quad i = 1, \ldots n\}$, $\{(y_1, \ldots, y_n) : y_i > 0 \quad \text{for} \quad i = 1, \ldots, n\}$ and $\{(y_1, \ldots, y_n) : y_i \geq 0 \quad \text{for} \quad i = 1, \ldots, n \quad \text{and} \quad y_i = 0 \quad \text{for at least one} \quad i \in \{1, \ldots, n\}\}$ are invariant under π.

Precompactness of orbits or positive semi-orbits and invariance of a set under π are essential notions in the analysis of the asymptotic behavior of dynamical and semi-dynamical systems. In general, if we assume that (Y, π) is a dissipative dynamical or semi-dynamical system, we say that a subset U of Y is *forward invariant* under π if $\gamma^+(u) \subseteq U$ for all $u \in U$. If $t_-(u) = -\infty$ in (1.71) and $\gamma(u) \subseteq U$ for all $u \in U$, we say that U is *invariant* under π. (Notice that in the case that (Y, π) is a semi-dynamical system but not a dynamical system Y may nevertheless contain invariant subsets. In general, when backward continuation of an orbit is possible, the continuation may not be uniquely determined. However, it is in the case of the semi-dynamical systems associated with reaction-diffusion models for several interacting biological species on an isolated bounded habitat, so we shall not delve further into this topic.) Now if for $u \in Y$, $\gamma^+(u)$ is precompact, then there is a bounded set in Y which attracts points on the positive semi-orbit of u. This set is referred to as the *omega limit set of* u, denoted by $\omega(u)$ and is defined by

$$\omega(u) = \bigcap_{t \geq 0} \overline{\bigcup_{s \geq t} \{\pi(u, r) : r \geq s\}} \tag{1.76}$$

where $\overline{V}$ denotes the closure of set V. The set $\omega(u)$ consists of all limits of all sequences $\{\pi(u, t_n)\}$ where $t_n \to +\infty$ as $n \to \infty$. It is well-known (e.g. Saperstone, 1981) that $\omega(u)$ is nonempty, compact, connected and invariant under π. (The term *alpha limit set of* u, denoted $\alpha(u)$, consists of all limits of all sequences $\{\pi(u, t_n)\}$ where $t_n \to -\infty$ as $n \to \infty$.) If now for a set U, the set $\{\pi(u, r) : u \in U, \ r \geq s \quad \text{for some} \quad s \geq 0\}$ is precompact, there is a companion notion of the *omega limit set of* U, denoted $\omega(U)$, with $\omega(U)$ defined by

$$\omega(U) = \bigcap_{t \geq 0} \overline{\bigcup_{s \geq t} \{\pi(u, r) : u \in U, r \geq s\}}.$$

The set $\omega(U)$ is the set of all limits of all sequences $\{\pi(u_n, t_n)\}$ where $u_n \in U$ and $t_n \to \infty$ as $n \to \infty$. Notice that $\bigcup_{u \in U} \omega(u) \subseteq \omega(U)$, but that in general $\omega(U)$ is much

larger. However, we shall need to use $\bigcup_{u\in U}\omega(u)$ at several places in our discussion. At those places, we denote this set as $\omega(U)$ but make clear that the usage is nonstandard.

A *global attractor* for a dynamical or semi-dynamical system π on the metric space (Y, d) is a set $\mathcal{A}$ which is compact, invariant under π and such that for all bounded subsets V of Y

$$\lim_{t\to\infty}\sup_{v\in V}\inf_{u\in\mathcal{A}} d(\pi(v,t),u)=0. \tag{1.77}$$

A fundamental result of Bilotti and La Salle (1971) (see Theorem 4.1) says that if (Y, d) is complete, π is dissipative and for all $t > t_0 \geq 0$, the set $\pi(U,t) = \{\pi(u,t) : u \in U\}$ is precompact if U is bounded, then π has a nonempty global attractor. (The function $\pi(\cdot,t) : Y \to Y$ is said to be *compact* if $\pi(U,t)$ is precompact whenever U is bounded. In particular, the image $\{\pi(u_n,t)\}$ of a bounded sequence $\{u_n\}$ is precompact if $\pi(\cdot,t) : Y \to Y$ is compact.) Notice that if $\mathcal{A}$ is a global attractor, $\varepsilon > 0$ is given and $\mathcal{B}(\mathcal{A},\varepsilon)$ is defined by $\mathcal{B}(\mathcal{A},\varepsilon) = \{y \in Y : d(y,u) < \varepsilon \quad \text{for some} \quad u \in \mathcal{A}\}$, then (1.77) implies that if $V \subseteq Y$ is bounded,

$$\pi(V,t) \subseteq \mathcal{B}(\mathcal{A},\varepsilon)$$

for all $t \geq t_0$, where t_0 depends upon V.

A point $u \in Y$ such that $\pi(u,t) = u$ for $t \in \mathbb{R}$ is called an *equilibrium* or *equilibrium point* for π. Equilibria play a large role in our discussion of the asymptotic predictions of reaction-diffusion models for interacting biological species in an isolated bounded habitat. Indeed, the most basic example of a global attractor is a *globally attracting equilibrium.* There are two special classes of dynamical or semi-dynamical systems in which the omega limit set $\omega(u)$ for all or almost all $u \in Y$ is an equilibrium. These are *gradient systems* and *monotone dynamical systems*. (We pause to note that a system can be both of gradient type and monotone.) Suppose that π is dissipative and $\gamma^+(u)$ is precompact for every u in Y, where Y is a closed subset of a Banach space. Then π is a gradient system (see, e.g., Henry 1981, Hale (1988)) if there is a *Lyapunov function* for π. By a Lyapunov function we mean a continuous function $V : Y \to \mathbb{R}$ so that

(i) V is bounded below;

(ii) $V(u) \to +\infty$ as $||u|| \to +\infty$;

(iii) $V(\pi(u,t))$ is nonincreasing in t for each $u \in Y$; (1.78)

(iv) If $V(\pi(u,t)) = V(u)$ for all $t \in \mathbb{R}$, then u is an equilibrium for π.

We show in Section 3.1 that many of the reaction-diffusion models for a single biological species an isolated bounded habitat that we consider in this volume may be formulated as gradient systems. In a gradient system, $\omega(u)$ is an equilibrium for all $u \in Y$. (See, e.g., Hale (1988).)

The third feature of the collection of n-tuples of average population densities for species 1 to n that we noted earlier was the partial ordering given by (1.64). The notion of a monotone dynamical or semi-dynamical system is a possibility when Y admits a partial ordering. In the examples we consider Y is a closed subset of a Banach space, and the

partial ordering in Y is induced by a closed subset K of the Banach space called a *positive cone* via the equivalence

$$u_1 \leq u_2 \quad \text{in} \quad Y \Leftrightarrow u_2 - u_1 \in K. \tag{1.79}$$

To be a positive cone K must satisfy

$$\begin{aligned} &\text{(i)} \quad \text{If} \quad c \quad \text{is a nonnegative scalar and} \\ &\qquad u \in K, \quad \text{then} \quad cu \in K; \\ &\text{(ii)} \quad \text{If} \quad u_1, u_2 \in K, \quad \text{then} \quad u_1 + u_2 \in K; \\ &\text{(iii)} \quad \text{If} \quad u, -u \in K, \quad \text{then} \quad u = 0. \end{aligned} \tag{1.80}$$

In the case where Y is the collection of all n-tuples of nonnegative numbers partially ordered via (1.64), K may be taken equal to Y, and it is then clear that (1.80) holds and that (1.64) is equivalent to (1.79). However, if we consider the collection of all ordered pairs of nonnegative numbers (y_1, y_2) we may define a partial ordering via

$$(y_1, y_2) \leq (y_1^*, y_2^*) \Leftrightarrow y_1 \leq y_1^* \quad \text{but} \quad y_2 \geq y_2^*.$$

In this case (1.79) holds provided we define the positive cone K by

$$K = \{(u_1, u_2) : y_1 \geq 0, y_2 \leq 0\}.$$

So Y need not equal K. This last example will be relevant when we consider two species competition in Sections 4.4 and 5.2.

Once a partial ordering has been established in Y, π will be *monotone* provided

$$u_1 \leq u_2 \quad \text{in} \quad Y \Rightarrow \pi(u_1, t) \leq \pi(u_2, t) \quad \text{in} \quad Y \tag{1.81}$$

for all $t \neq 0$ when π is a dynamical system and for all $t > 0$ when π is a semi-dynamical system. A positive semi-orbit $\gamma^+(u)$ of π is said to be *increasing* provided

$$\pi(u, t_1) \leq \pi(u, t_2) \quad \text{for} \quad 0 \leq t_1 < t_2 \tag{1.82}$$

with an analogous definition of *decreasing* positive semi-orbit. Increasing and decreasing positive semi-orbits are at the heart of the examinations we make of monotone dynamical systems. To that end, suppose π admits an increasing positive semi-orbit $\gamma^+(u_1)$ and a decreasing positive semi-orbit $\gamma^+(u_2)$ and that $u_1 \leq u_2$. Then any positive semi-orbit $\gamma^+(u)$ with $u_1 \leq u \leq u_2$ must lie above the increasing positive semi-orbit $\gamma^+(u_1)$ but below the decreasing positive semi-orbit $\gamma^+(u_2)$. Moreover, if positive semi-orbits for π are precompact, an important result in the theory of monotone dynamical systems (see, e.g., Smith (1995), Theorem 2.1) asserts that $\omega(u_1)$ and $\omega(u_2)$ are equilibria for π. Since $\pi(u_1, t) \leq \pi(u_2, t)$ for all $t > 0$, $\omega(u_1) \leq \omega(u_2)$. So the omega limit set $\omega(u)$ for any u with $u_1 \leq u \leq u_2$ is contained in the set

$$\{v : \omega(u_1) \leq v \leq \omega(u_2)\}$$

which is called the *order interval* from $\omega(u_1)$ to $\omega(u_2)$ and denoted $[\omega(u_1), \omega(u_2)]$.

In the preceding scenario, the positive semi-orbit $\gamma^+(u_2)$ can be viewed as providing a "ceiling" for both the transient and asymptotic phases of the positive semi-orbit $\gamma^+(u)$, while the positive semi-orbit $\gamma^+(u_1)$ can be viewed as providing a "floor". We shall see that in many instances such semi-orbits can be interpreted as representing best and worst case scenarios for the dynamical or semi-dynamical system π. In the context of reaction-diffusion models for interacting biological species in isolated bounded habitats, positive semi-orbits that originate at configurations which are so-called *lower solutions* to the corresponding steady-state elliptic system are increasing, while positive semi-orbits that originate at configurations which are *upper solutions* to the corresponding elliptic systems are decreasing. We discuss upper and lower solutions in the context of ODEs, elliptic *and* parabolic PDEs and systems thereof in the next subsection.

The utility of the notions of monotonicity and comparison extends beyond systems which preserve a partial ordering. For example, in many systems of reaction-diffusion equations for interacting species in an isolated bounded habitat, the growth law for some species density may be such that for $t \geq t_0 \geq 0$ the density is a parabolic upper or lower solution to some single equation reaction-diffusion model. For specificity, assume that the density of the system component is given by u and that v denotes the density in the comparison single equation model. Then if u is an upper solution for the v equation and the density v is chosen so that $v(t_0) = u(t_0),\ u(t) \geq v(t)$ for all $t \geq t_0$. Likewise, if u is a lower solution, $u(t) \leq v(t)$. Consequently, $v(t)$ provides a "floor" for the density $u(t)$ in the first case and a "ceiling" in the second. Such information can be very useful in obtaining best and worst case scenarios for the density u. We explore this idea in Sections 5.3 and 5.4 and throughout Chapter 7.

Since reaction-diffusion models for interacting biological species in an isolated bounded habitat are continuous time models, the dynamical and semi-dynamical systems we consider in this volume are primarily continuous time dynamical or semi-dynamical systems. However, we do have occasion to employ discrete time systems and consequently we include a few remarks regarding discrete time dynamical and semi-dynamical systems. As in the case of continuous time dynamical or semi-dynamical systems, one would want the underlying state space Y to be a metric space. (For our purposes, Y is a closed subset of a Banach space and hence a complete metric space.) A *discrete time dynamical system* π on Y is a continuous function $\pi : Y \times \mathbb{Z} \to Y$, where $\mathbb{Z}$ denotes the integers, so that discrete time analogues to (1.69) and (1.70) hold. Namely, we require

$$\pi(u, 0) = u \quad \text{for all} \quad u \in Y \tag{1.83}$$

and

$$\pi(u, k + k') = \pi(\pi(u, k), k') \tag{1.84}$$

for all $k, k' \in \mathbb{Z}$ so that $\pi(u, k+k')$ and $\pi(u, k)$ are defined. If π is to be a semi-dynamical system, the integers $\mathbb{Z}$ in the preceding are replaced with the nonnegative integers $\mathbb{Z}^+ \cup \{0\}$.

Suppose now that $S : Y \to Y$ is given by

$$S(u) = \pi(u, 1).$$

Then S is continuous and for $k > 0$ it follows from (1.84) that

$$\pi(u, k) = S^k u$$

where S^k is the composition $S \circ S \circ \cdots \circ S$ (k times). Likewise, if $\pi(u, -1)$ is defined, $\pi(u, -1) = S^{-1}$ and

$$\pi(u, -k) = S^{-k}u.$$

Of course, the restriction of a continuous time dynamical or semi-dynamical system to the integers or nonnegative integers, respectively, is a discrete time dynamical or semi-dynamical system. In the case of an autonomous system of ordinary differential equations of the form (1.74) or reaction-diffusion equations, the associated discrete-time systems track the value along solution trajectories after every 1 unit of time.

An alternative way of viewing such trajectories in the ODE case (1.74), say, is to think of $\pi((y_1^0, \ldots, y_n^0), k+1)$ as the value at time 1 of the solution to the system (1.74) with initial configuration $\pi((y_1^0, \ldots, y_n^0), k)$. Such is always possible since the system is autonomous. Now suppose that (1.74) is replaced with

$$y_i' = f_i(t, y_1, \ldots, y_n) \tag{1.85}$$

$i = 1, \ldots, n$ where $f_i(t+1, y_1, \ldots, y_n) = f_i(t, y_1, \ldots, y_n)$ for all $t \in \mathbb{R}$, $i = 1, \ldots, n$ and all $(y_1, \ldots, y_n) \in \mathbb{R}^n$. Let $\phi((y_1^0, \ldots, y_n^0), t)$ denote the unique solution to (1.85) so that

$$\phi((y_1^0, \ldots, y_n^0), 0) = (y_1^0, \ldots, y_n^0).$$

Now define $\pi : \mathbb{R}^n \times \mathbb{Z} \to \mathbb{R}^n$ by

$$\pi((y_1^0, \ldots, y_n^0), k) = \phi((y_1^0, \ldots, y_n^0), k). \tag{1.86}$$

Since f_i is 1-periodic for all $i \in \{1, \ldots, n\}$, $\phi((y_1^0, \ldots, y_n^0), k+1)$ is the value after 1 time unit of the solution to (1.85) which has the value $\phi((y_1^0, \ldots, y_n^0), k)$. This fact makes π as given in (1.86) into a dynamical system, although $\phi : \mathbb{R}^n \times \mathbb{R} \to \mathbb{R}^n$ is not. To convert (1.85) into a continuous time dynamical system, we would need to employ a construction called a *skew product flow* which tracks the state of the system (1.85) as well as ϕ. We discuss this construction in detail in the periodic reaction-diffusion setting in Section 5.5.

Understanding the asymptotic behavior of discrete time dynamical and semi-dynamical systems involves the same concepts as in the continuous time case. One still has the notions of omega limit set, invariance and so forth. However, there are some subtleties that we should point out. First, if a discrete time dynamical or semi-dynamical system is associated to a system of ODEs or reaction-diffusion equations in the manner we have described, an equilibrium of the discrete dynamical system corresponds to a point on a periodic orbit of the system of differential equations, but need not be an equilibrium to the continuous time system. This observation will be employed when we analyze single species reaction-diffusion models with time-periodic coefficients in Section 3.6. Of course, there are discrete dynamical or semi-dynamical systems which arise in ways other than sampling the solution to a system of differential equations successively at times $0, \Delta t, 2\Delta t, 3\Delta t, \ldots$ for some prespecified length of time Δt. As an example, consider the so-called discrete logistic equation, which arises from discretizing a potential solution y to the logistic equation

$$y' = ry\left(1 - \frac{y}{K}\right) \tag{1.87}$$

by $y'_j = y(j\Delta t)$ and approximating $y'(j\Delta t)$ by the forward difference $y'(j\Delta t) = \frac{y_{j+1} - y_j}{\Delta t}$. So doing one arrives at the equation

$$y_{j+1} = \tilde{r} y_j \left(1 - \frac{y_j}{\tilde{K}}\right) \tag{1.88}$$

$j = 0, 1, 2, 3, \ldots$ where $\tilde{r} = 1 + r\Delta t$ and $\tilde{K} = K\left(\frac{1 + r\Delta t}{r\Delta t}\right)$. It is immediate that (1.88) defines a discrete semi-dynamical system. However, if for some value of j, it is the case that y_j exceeds $\tilde{K}$, then $y_{j+1} < 0$. Consequently, the invariance of positivity that solutions of (1.87) enjoy does not carry over to solutions of (1.88). The reason for this rather profound difference between the two systems is simple. Positive solutions to the differential equation would have to pass through 0 before they can take on negative values. However, 0 is an equilibrium solution to (1.87) and solutions to initial value problems for (1.87) are unique. Consequently, no solution to (1.87) which is positive at 0 can be negative at some later time. On the other hand, in the discrete model (1.88) solutions may jump across 0, and the only possibility for an invariant set with a meaningful ecological interpretation is $[0, \tilde{K}]$. Note that $[0, K]$ is invariant for (1.87) regardless of the value of r. In (1.88), however, it is not hard to verify that $[0, \tilde{K}]$ is invariant only when $\tilde{r} \leq 4$ (which is equivalent to $r < \frac{3}{\Delta t}$ in (1.87)). In (1.87), any solution with $y(0) \in (0, K)$ increases monotonically over time toward the equilibrium K, regardless of the value of r, whereas in (1.88), orbits can be very complicated, even chaotic, depending on the value of $\tilde{r}$. For more detail, see Murray (1993, Section 2.3.).

There are discrete analogues to (1.87) other than (1.88) whose solutions track those to (1.87) more closely. One possibility is just to sample solutions to (1.87) at discrete time intervals. The resulting model is known as the Beverton-Holt model (Beverton and Holt, 1957). Another is the model

$$y_{j+1} = y_j \exp\left(r\left(1 - \frac{y_j}{K}\right)\right) \tag{1.89}$$

which results from solving the initial value problem

$$\frac{dy}{dt} = r\left(1 - \frac{y_j}{K}\right) y$$
$$y(0) = y_j$$

and evaluating the solution at time 1. The model (1.89) is sometimes referred to as a Ricker model (Ricker, 1954, 1975), and is widely used in the study of fisheries (Quinn and Deriso, 1999). Both alternates to (1.88) leave $(0, \infty)$ invariant and are such that

$$y_j < y_{j+1} \quad \text{if} \quad 0 < y_j < K$$

while

$$y_j > y_{j+1} \quad \text{if} \quad y_j > K,$$

just as is the case with solutions to (1.87). However, only the Beverton-Holt model is such that $(0, K)$ and (K, ∞) are invariant, as is the case with solutions to (1.87). Indeed, solutions to (1.89) can be very complicated, even chaotic. For more details, see May (1975).

1.6.2 Basic Concepts in Partial Differential Equations: An Example

The reaction-diffusion models that are the subject of this book are partial differential equations which describe how population densities in space change over time. Since they describe the way that things change over time, it is natural to think of them as dynamical systems; however, as noted, the state space for a reaction-diffusion model will be a set of functions representing the possible spatial densities of a spatially distributed population. Thus, to formulate reaction-diffusion models as dynamical systems we need to define appropriate state spaces of functions and determine how the models act on them. In general we will not be able to solve reaction-diffusion models explicitly, but that is also the case with many nonlinear systems of ordinary differential equations. What we can do in many cases is determine when a model predicts persistence and when it predicts extinction, and perhaps describe some features of its dynamics, by using methods from the theory of dynamical systems. However, there are some new technical issues that arise in formulating reaction-diffusion models as dynamical systems. Many of those are related to the fact that the state spaces for reaction-diffusion models are infinite dimensional. Others have to do with problems such as verifying that the set of nonnegative densities is invariant. (Since negative population densities don't make sense, good models should predict that densities which are initially nonnegative remain so.) To illustrate some of the issues related to formulating reaction-diffusion models as dynamical systems and to introduce some ideas that will be important in their analysis, we briefly review the explicit solutions of some simple linear models and derive a few of their basic properties.

The discussion that follows is a quick review of some standard ideas in the theory of partial differential equations. A complete treatment of this material is given in many standard texts, for example, Strauss (1992). Consider the model

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + ru \quad \text{on} \quad (0,1)\times(0,\infty) \\ &u(0,t) = u(1,t) = 0 \text{ on} \quad (0,\infty), \end{aligned} \tag{1.90}$$

with initial condition $u(x,0) = f(x)$. Equation (1.90) can be interpreted as a linear growth model for a population that diffuses at rate d, increases in numbers locally at rate r, and inhabits a one-dimensional patch of unit length with an absorbing boundary (i.e. the boundary is lethal to the population). To solve (1.90) one typically looks for solutions in the form $u(x,t) = X(x)T(t)$ and then constructs a general solution as a series of such special solutions. (This is the method of separation of variables; it is discussed in many standard references, again, for example, Strauss (1992).) Substituting $u = X(x)T(t)$ into (1.90) and dividing through by $X(x)T(t)$ yields

$$\frac{T'(t)}{T(t)} = \frac{dX''(x) + rX(x)}{X(x)}. \tag{1.91}$$

The right side of (1.91) depends only on X; the left side only on t. Thus, the only way that (1.91) can hold is if both sides are constant. Suppose that both sides of (1.91) are equal to the constant σ. Then we have

$$dX'' + rX = \sigma X \tag{1.92}$$

and

$$T'(t) = \sigma T(t). \tag{1.93}$$

There are no further restrictions on T, but the boundary conditions $u(0,t) = u(1,t) = 0$ require that

$$X(1) = X(0) = 0. \tag{1.94}$$

It is possible to solve (1.92) explicitly for any given choice of σ, but it turns out that there are nonzero solutions satisfying (1.94) only if $\sigma = r - dn^2\pi^2$ for some positive integer n. In that case we have $X_n(x) = k_1 \sin(n\pi x)$ and $T_n(t) = k_2 e^{(r-dn^2\pi^2)t}$, where k_1 and k_2 are arbitrary constants, so $u_n(x,t) = e^{(r-n^2\pi^2)t} \sin(n\pi x)$ is a solution of (1.90).

Notice that (1.92) can be written as

$$\left[d\left(\frac{\partial^2}{\partial x^2}\right) + r \right] X = \sigma X. \tag{1.95}$$

The differential operator $L = d(\partial^2/\partial x^2) + r$ is linear, so that $L(c_1X_1 + x_2X_2) = c_1L(X_1) + c_2L(x_2)$ for any constants c_1 and c_2. Thus, (1.95) is analogous to an eigenvalue problem for a matrix, with σ as the eigenvalue and L playing the same role as the matrix, but with the eigenvector being replaced by the eigenfunction $X(x)$. The notion of eigenvalues for differential operators will play a central role in our analysis of reaction-diffusion models. To continue the process of solving (1.90), we write $u(x,t)$ as a Fourier series

$$u(x,t) = \sum_{n=1}^{\infty} b_n e^{(r-dn^2\pi^2)t} \sin(n\pi x). \tag{1.96}$$

To satisfy the initial condition $u(x,0) = f(x)$ we need to choose the constants b_n so that

$$f(x) = \sum_{n=1}^{\infty} b_n \sin(n\pi x). \tag{1.97}$$

It turns out that if it is possible to express $f(x)$ in the form (1.97) then we must have $b_n = 2\int_0^1 f(x)\sin(n\pi x)dx$ (see Strauss (1992)). At this point a new problem arises: (1.96) and (1.97) involve infinite series of functions which may fail to converge for some (perhaps all) values of x and t, depending on the coefficients b_n. In the case of (1.96) there is another problem: the series must converge to a function that can be differentiated once in t and twice in x if it is to satisfy (1.90). We can impose conditions on $f(x)$ (or equivalently on $\{b_n\}$) so that (1.97) converges, but there are a number of possible choices for what is meant by convergence. For example, if we require that $\int_0^1 [f(x)]^2 dx$ is finite, then it turns out that $(1/2)\sum_{n=1}^{\infty} b_n^2 = \int_0^1 [f(x)]^2 dx$ (this is a version of Parseval's equality), and the series in (1.97) converges in the sense that

$$\lim_{m\to\infty} \int_0^1 \left[f(x) - \sum_{n=1}^{m} b_n \sin(n\pi x) \right]^2 dx = 0. \tag{1.98}$$

However, we could have $\int_0^1 f(x)^2 dx < \infty$ even if $f(x)$ is not continuous, and (1.98) does not guarantee that $\lim_{m\to\infty} \sum_{n=1}^{m} b_n \sin(n\pi x) = f(x)$ for all x. On the other hand, suppose that $f(x)$ is continuous, $f(0) = f(1) = 0$, and $\int_0^1 f'(x)^2 dx < \infty$. Let $a_n = 2\int_0^1 f'(x)\cos(n\pi x)dx$. Parseval's relation applies to cosine series as well as sine series, so $(1/2)\sum_{n=1}^{\infty} a_n^2 = \int_0^1 f'(x)^2 dx < \infty$. On the other hand, integration by parts shows that $nb_n = a_n$ so $b_n = (1/n)a_n$. In that case, we have $|b_n| \le (1/2)[(1/n)^2 + a_n^2]$ so that $\sum_{n=1}^{\infty} |b_n| < \infty$ (because $\sum_{n=1}^{\infty} 1/n^2 < \infty$). If $\sum_{n=1}^{\infty} |b_n| < \infty$ then since $|b_n \sin(n\pi x)| \le |b_n|$, the series in (1.97) is majorized by the convergent series $\sum_{n=1}^{\infty} |b_n|$ so it converges uniformly, that is,

$$\lim_{m\to\infty} \sup_{x\in[0,1]} \left| f(x) - \sum_{m=1}^{m} b_n \sin(n\pi x) \right| = 0. \tag{1.99}$$

In general the condition $\sum_{n=1}^{\infty} |b_n| < \infty$ is stronger than the condition $\sum_{n=1}^{\infty} b_n^2 < \infty$; for example $\sum_{n=1}^{\infty} 1/n$ diverges even though $\sum_{n=1}^{\infty} 1/n^2$ converges. Similarly, the conditions $\int_0^1 f'(x)^2 dx < \infty$, $f(x)$ is continuous, $f(0) = f(1) = 0$ are stronger than the condition $\int_0^1 [f(x)]^2 dx < \infty$.

The point here is that to make sense out of (1.90) we need to define a state space for the initial data $f(x)$, and the way we choose a metric on the state space actually determines what the space is. We could interpret (1.97) as an expansion of $f(x)$ in terms of "basis vectors" $\sin(n\pi x)$, in analogy with expressing $\vec{v} \in \mathbb{R}^3$ as $\vec{v} = v_1\vec{i} + v_2\vec{j} + v_3\vec{k}$ where $\vec{i}$, $\vec{j}$, and $\vec{k}$ are the standard unit vectors in the x, y, and z directions. However, in $\mathbb{R}^3$ the only restriction on v_1, v_2 and v_3 is that they are finite, and $v_1^2 + v_2^2 + v_3^2 < \infty$ if and only if $|v_1|+|v_2|+|v_3| < \infty$, which is true if and only if v_1, v_2, and v_3 are finite. On the other hand, requiring that each b_n is finite, that $\sum_{n=1}^{\infty} b_n^2 < \infty$, and that $\sum_{n=1}^{\infty} |b_n| < \infty$ in (1.97) impose different conditions on $\{b_n\}$, and thus define different subsets of the set of infinite sequences. Thus, in formulating models such as (1.90) we need to choose a metric that allows us to measure the "distance" between functions (or alternatively between sequences $\{b_n\}$), and the way we measure distance actually determines what the space is. The standard metrics corresponding to the notions of convergence shown in (1.98) and (1.99), respectively, are

$d(f,g) = \left[\int_0^1 |f(x)-g(x)|^2 dx\right]^{1/2}$ and $d(f,g) = \sup_{x\in[0,1]} |f(x)-g(x)|$, respectively. The standard spaces of functions corresponding to those metrics are denoted by $L^2([0,1])$ and $C([0,1])$, respectively. The space $L^2([0,1])$ consists of all functions $f(x)$ on $[0,1]$ such that the Lebesgue integral of $[f(x)]^2$ over $[0,1]$ exists and is finite. The space $C([0,1])$ consists of all continuous functions on $[0,1]$. (The subspace of $C([0,1])$, consisting of continuous functions with $f(0) = f(1) = 0$ is denoted $C_0([0,1])$.) All of these are Banach spaces. In our analysis of reaction-diffusion models we will need to use those spaces (and various others) as state spaces. In many cases the choice of a state space will depend on technical aspects of the mathematics involved in dealing with whatever features are built into a particular model. For example, if a model has coefficients that depend on x, we might need to use different state spaces depending on whether the coefficients were continuous or not.

To verify that $L^2([0,1])$ and $C_0([0,1])$ might be legitimate state spaces for (1.90) we must consider (1.96). We could rewrite (1.96) as $u(x,t) = \sum_{n=1}^{\infty} u_n(t)\sin(n\pi x)$ where $u_n(t) = b_n e^{(r-dn^2\pi^2)t}$. Notice that for $n > \sqrt{r/d}/\pi$ we have $|u_n(t)| \le |b_n|$ for all $t \ge 0$, so that if $\sum_{n=1}^{\infty} b_n^2 < \infty$ then $\sum_{n=1}^{\infty} |u_n^2(t)| < \infty$ for all t. Thus, it is reasonable to use either $L^2([0,1])$ or the space of all functions $f(x)$ on $[0,1]$ whose Fourier coefficients $\{b_n\}$ satisfy $\sum_{n=1}^{\infty} |b_n| < \infty$ as state spaces for (1.90). Note also that for $n > \sqrt{r/d}/\pi$ we have $u_n(t) \to 0$ as $t \to \infty$. Thus, for large t, only the coefficients b_n with $n \le \sqrt{r/d}\pi$ are important. The model (1.90) in effect squeezes state space down toward the finite dimensional subspace spanned by $\{\sin(n\pi x) : n \le \sqrt{r/d}/\pi\}$.

If we want $u(x,t)$ to satisfy (1.90) we need to verify that $\partial u/\partial t$ and $\partial^2 u/\partial x^2$ make sense. Suppose that the coefficients b_n satisfy $|b_n| \le B_0$ for some finite B_0. (This will be true if $\sum_{n=1}^{\infty} b_n^2 < \infty$ or $\sum_{n=1}^{\infty} |b_n| < \infty$.) If we differentiate the series in (1.96) by x term by term we obtain the series $\sum_{n=1}^{\infty} b_n n\pi e^{(r-dn^2\pi^2)t}\cos(n\pi x)$. The series is majorized by the series $\sum_{n=1}^{\infty} B_n(t)$ where $B_n(t) = B_0 n\pi e^{(r-dn^2\pi^2)t}$. We have $\lim_{n\to\infty} |B_{n+1}/B_n| = \lim_{n\to\infty} \left(\left[(n+1)/n\right] e^{(n^2-(n+1)^2)d\pi^2 t}\right) = 0$ for any $t > 0$, since $n^2-(n+1)^2 < 0$, so $\sum_{n=1}^{\infty} B_n(t)$ converges for all $t > 0$ by the ratio test. Hence, the series $\sum_{n=1}^{\infty} b_n n\pi e^{(r-dn^2\pi^2)t}\cos(n\pi x)$ converges uniformly for any given $t > 0$. Similar analysis show that the series obtained by differentiating (1.96) term by term any number of times in x or t still converge uniformly. Thus, all of those series converge to continuous functions which are the derivatives of $u(x,t)$.

The key point here is that the model (1.90) has the effect of smoothing out solutions to (1.90). Even if $f(x)$ is discontinuous, $u(x,t)$ will be differentiable infinitely many

times in both x and t for $t > 0$. This smoothing property is a key feature of reaction-diffusion models. It often implies that the model maps bounded sets in state space into compact sets. To see how that works, let B_0 be a fixed constant and let F_0 be the subset of $L^2([0, 1])$ consisting of functions satisfying $\int_0^1 [f(x)]^2 dx \leq B_0^2$. Let F_t be the set of solutions $w(x, t)$ to (1.90), evaluated at time t, such that $w(x, 0) \in F_0$. Fix a value of $t > 0$ and suppose that $\{w_k\}$ is a sequence in F_t, so that $w_k(x, 0) = f_k(x) \in B_0$ for each k. If $f_k(x) \in B_0$ then we may write $f_k(x) = \sum_{k=1}^{\infty} b_{nk} \sin(n\pi x)$, with coefficients $\{b_{nk}\}$ satisfying $\sum_{k=1}^{\infty} b_{nk}^2 \leq B_0^2$. It follows that $|b_{nk}| \leq B_0$ for each coefficient b_{nk}. Furthermore, we can write

$$w_k(x, t) = \sum_{n=1}^{\infty} b_{nk} e^{(r-dn^2\pi^2)t} \sin(n\pi x) \quad \text{and} \quad \partial w_k/\partial x = \sum_{n=1}^{\infty} b_{nk} n\pi e^{(r-dn^2\pi^2)t} \cos(n\pi x),$$

provided those series converge. The series are majorized by the series $\sum_{n=1}^{\infty} B_0 e^{(r-dn^2\pi^2)t}$ and $\sum_{n=1}^{\infty} B_0 n\pi e^{(r-dn^2\pi^2)t}$, which are both convergent for any given $t > 0$; thus, $\{w_k\}$ and $\{\partial w_k/\partial x\}$ are bounded uniformly in k and x. Since $\{\partial w_k/\partial x\}$ is bounded uniformly in x and k, the set of functions $\{w_k\}$ is also equicontinuous by the mean value theorem. Ascoli's theorem (see Rudin (1976)) then implies that the sequence $\{w_k(x, t)\}$ has a subsequence $\{w_{k_i}(x, t)\}$ which converges uniformly on [0, 1] to some continuous function $w(x)$. Uniform convergence implies $\int_0^1 (w_{k_i}(x, t) - w(x))^2 dx \to 0$ as $i \to \infty$ so that $w_{k_i}(x, t)$ converges to $w(x)$ in $L^2([0, 1])$. This feature of always being able to extract a convergent subsequence is the essence of compactness. Thus, the set F_t of solutions to (1.90) at time t whose initial data belong to the bounded set F_0 is compact. Note that F_0 is not compact. The functions $f_k(x) = \sqrt{B_0} \sin(k\pi x)$ belong to F_0 (since $\int_0^1 [f_k(x)]^2 dx = B_0/2$), but no subsequence of $\{f_k\}$ converges in $L^2([0, 1])$ because $\int_0^1 |f_k(x) - f_\ell(x)|^2 dx = B_0$ for any $k \neq \ell$. The compactness of F_t arises from the smoothing property of (1.90).

The solution (1.96) to (1.90) predicts that all solutions to (1.90) will decay to zero if $r/d < \pi^2$, while at least some solutions will grow exponentially if $r/d > \pi^2$. Thus, the model gives a criterion for the growth rate r needed to balance the loss of individuals across the boundary if they disperse by diffusion at rate d. However, before drawing too many conclusions, we should check that solutions to (1.90) which correspond to positive initial densities at least remain nonnegative. Suppose that $w(x, t)$ satisfies (1.90) on $(0, 1) \times (0, T]$ and is continuous on $[0, 1] \times [0, T]$ with $w(x, 0) \geq 0$. Let $v(x, t) = e^{-at} w(x, t)$; then by (1.90) we have

$$\frac{\partial v}{\partial t} = -av + e^{-at} \frac{\partial w}{\partial t} = d \frac{\partial^2 v}{\partial x^2} + (r - a)v. \tag{1.100}$$

Choose a large enough so that $r - a < 0$. Suppose $w(x, t) < 0$ for some (x, t). Then $v(x, t) < 0$ at the same point, so the minimum of v is negative. (Since v is continuous on $[0, 1] \times [0, T]$, it must have a minimum.) Since $v \geq 0$ for $x = 0$ or 1 and for $t = 0$, the

minimum must occur at a point (x_0, t_0) in $(0, 1) \times (0, T]$ where (1.90) and hence (1.100) are satisfied. If $(x_0, t_0) \in (0, 1) \times (0, T)$ then $\partial v/\partial t = 0$ and $\partial^2 v/\partial x^2 \geq 0$ at $(x, t) = (x_0, t_0)$, so at this point (1.100) implies $0 \geq (r - a)v(x_0, t_0)$. Since $r - a < 0$ and $v(x_0, t_0) < 0$, this is a contradiction. If the minimum occurs on $(0, 1) \times \{T\}$, we have $\partial v/\partial t \leq 0$ at (x_0, t_0), but otherwise the analysis is the same. Thus, if $w(x, t) < 0$ somewhere, we obtain a contradiction, so we must have $w(x, t) \geq 0$ for all $(x, t) \in [0, 1] \times [0, T]$. This type of result is called a maximum principle, although in this case we applied it to a minimum. Suppose now w_1 and w_2 are solutions to (1.90) with $w_1(x, 0) \geq w_2(x, 0)$. Then $w = w_1 - w_2$ is also a solution to (1.90), and $w(x, 0) \geq 0$, so $w(x, t) \geq 0$ for all $t > 0$, and hence $w_1(x, t) \geq w_2(x, t)$ for all t. Thus, the model (1.90) is order preserving.

In the simple case described above we could solve the model (1.90) explicitly by using some calculus, and we could then analyze the solution by using some basic results from real analysis. In general it is not possible to give explicit solutions to reaction-diffusion equations. It *is* possible to show that they have solutions which depend continuously on initial conditions, and that those solutions are smooth (so that reaction-diffusion models send bounded sets of initial data into sets with compact closures). In models where the reaction term for the density u_i of the ith species has the form $f_i(x, t, u_1, \ldots, u_N)u_i$, it is possible to show that the set of $\vec{u} = (u_1, \ldots, u_N)$ with $u_i \geq 0$ for all i is positively invariant; that is, if $u_i(x, t_1) \geq 0$ for all i then $u_i(x, t) \geq 0$ for all i and all $t > t_1$. Thus, we will be able to formulate reaction-diffusion models as dynamical systems on state spaces analogous to $L^2([0, 1])$ or $C_0([0, 1])$. Once we have formulated the models properly, we can obtain criteria for persistence analogous to the criterion $r/d > \pi^2$ for persistence in (1.90). To prove that reaction-diffusion models have the properties described above requires many technicalities. In general we simply state the results we need, and refer the reader to other sources for the details. However, we will try to be precise and accurate in our statements of results about reaction-diffusion models, and in some cases we must use technical terms in definitions and the statements of theorems. One context where this is an issue is in the construction of appropriate state spaces. We have already seen that (1.90) could be formulated in $L^2([0, 1])$ or in $C_0([0, 1])$, and there are many more spaces like those that occur in reaction-diffusion theory. For the reader who is more interested in biological applications than mathematical precision, the good news is that it is often unnecessary to know all the details about the state space to understand the predictions of the model.

1.6.3 Modern Approaches to Partial Differential Equations: Analogies with Linear Algebra and Matrix Theory

The classical approach to partial differential equations is to attempt to find explicit solutions such as (1.96) and then to observe the properties of those solutions. This approach can be very useful but it is limited by the fact that many partial differential equations cannot be solved explicitly, at least in terms of standard functions such as sines and cosines or exponentials. The modern approach to partial differential equations is to prove that solutions exist without computing them explicitly and then to deduce their properties, often by using methods quite different than those used to show their existence. For reaction-diffusion models the basic existence theory can be understood by analogy with systems of ordinary differential equations. For the equilibria of reaction-diffusion equations the basic existence theory is somewhat analogous to the theory of algebraic equations; in particular, in the

linear case the theory closely resembles matrix theory. More specifically, recall that for any $n \times n$ matrix the dimension of the nullspace plus the rank of the matrix must equal n. The rank of the matrix is the dimension of the image of $\mathbb{R}^n$ under multiplication by the matrix, so if the dimension of the nullspace is zero (i.e. only the zero vector is mapped to zero by the matrix), then the matrix maps $\mathbb{R}^n$ onto $\mathbb{R}^n$. Also, if the dimension of the nullspace is zero, the mapping of $\mathbb{R}^n$ onto $\mathbb{R}^n$ is one-to-one. Thus, if M is an $n \times n$ matrix, I the identity matrix, and λ a real number, then the matrix $M - \lambda I$ is invertible unless $(M - \lambda I)\vec{v} = 0$ for some nonzero vector $\vec{v}$, i.e. $M - \lambda I$ is invertible unless λ is an eigenvalue of M. If it happens that M is symmetric and positive definite (that is, $M\vec{v} \cdot \vec{v} \geq m_0|\vec{v}|^2$ for all $\vec{v} \in \mathbb{R}^n$, where $m_0 > 0$ is a constant), then $M\vec{v} = \vec{0}$ implies $0 = M\vec{v} \cdot \vec{v} \geq m_0|\vec{v}|^2$, which is possible only if $\vec{v} = \vec{0}$. It follows that if M is symmetric and positive definite then M is invertible, and we can draw this conclusion without computing M^{-1}. Now consider the system of differential equations $d\vec{y}/dt = M\vec{y}$. We have $d|\vec{y}|^2/dt = 2\vec{y} \cdot d\vec{y}/dt = 2(\vec{y} \cdot M\vec{y}) \geq 2m_0|\vec{y}|^2$, so $|\vec{y}|^2 \geq e^{2m_0 t}|\vec{y}(0)|^2$. Hence $|\vec{y}|$ grows exponentially with rate m_0 unless $\vec{y}(0) = \vec{0}$. Again, we did not actually compute $\vec{y}(t)$, but we still could draw conclusions about how $\vec{y}(t)$ behaves. We could represent $\vec{y}(t)$ as $\vec{y}(t) = e^{tM}\vec{y}(0)$, where $e^{tM} = \sum_{j=0}^{\infty}(t^j/j!)M^j$ is the matrix exponential (see Brauer and Nohel (1969), for example.) To show that the related nonlinear system

$$d\vec{y}/dt = M\vec{y} + \vec{f}(\vec{y}) \tag{1.101}$$

has solutions, we might write it as

$$\vec{y}(t) = \vec{y}(0) + \int_0^t [M\vec{y}(s) + \vec{f}(\vec{y}(s))]ds \tag{1.102}$$

and use Picard iteration or a fixed point theorem (again, see Brauer and Nohel (1969)) to conclude that solutions exist. An alternate formulation would be to write the equation as

$$\begin{aligned} d(e^{-tM}\vec{y})/dt &= e^{-tM}(d\vec{y}/dt - M\vec{y}) \\ &= e^{-tM}\vec{f}(\vec{y}(t)) \end{aligned}$$

so that

$$e^{-tM}\vec{y} - \vec{y}(0) = \int_0^t e^{-sM}\vec{f}(\vec{y}(s))ds$$

and hence

$$\vec{y}(t) = e^{tM}\vec{y}(0) + \int_0^t e^{(t-s)M}\vec{f}(\vec{y}(s))ds. \tag{1.103}$$

It turns out that in the context of reaction-diffusion models the formulation analogous to (1.103) is preferable to (1.102). That is because the operator analogous to M will be a differential operator, while the operator analogous to e^{tM} will be the solution operator for a linear diffusion equation. For example, in (1.90), the operator analogous to M is $d\partial^2/\partial x^2 + r$, while the operator analogous to e^{tM} is the solution operator that maps

$u(x,0) = \sum_{n=1}^{\infty} b_n \sin(n\pi x)$ to $u(x,t) = \sum_{n=1}^{\infty} b_n e^{(r-dn^2\pi^2)t} \sin(n\pi x)$. As we noted in the discussion of (1.90), the solution operator makes sense if $\int_0^1 [u(x,0)]^2 dx < \infty$, and because of its smoothing properties it maps bounded sets into compact sets. The operator $d\partial^2/\partial x^2 + r$, however, may not even make sense when applied to an arbitrary function $u(x,0)$ with $\int_0^1 [u(x,0)]^2 dx < \infty$, and when it does make sense it can map bounded sets of functions into unbounded sets. (For example, the operator $d\partial^2/\partial x^2 + r$ maps the bounded sequence $\{\sin(n\pi x)\}$ to the unbounded sequence $\{(-dn^2\pi^2 + r)\sin(n\pi x)\}$.)

Reaction-diffusion models are a subclass of a more general class of equations known as quasilinear parabolic systems. All the models we consider will be second order. The most general type of single species models we study are of the form

$$\frac{\partial u}{\partial t} = \nabla \cdot [d(x,t,u)\nabla u - \vec{b}(x,t)u] + f(x,t,u), \tag{1.104}$$

the most general type of multispecies models we will study are of the form

$$\frac{\partial u_i}{\partial t} = \nabla \cdot [d_i(x,t)\nabla u_i - \vec{b}_i(x,t)u_i] + f_i(x,t,\vec{u}), \tag{1.105}$$

$i = 1 \ldots n$. In most cases of (1.104) we will have $d = d(x,t)$, so that the nonlinear terms in (1.104) will only involve u but not its derivatives, as in (1.105). Such models are called semilinear. In (1.105) the equations are coupled only in the undifferentiated terms; such systems are called weakly coupled. Most of the models we study will have coefficients that do not depend on t, and in those that do have time-dependent coefficients we usually assume that the coefficients are periodic in t. The analysis of systems such as (1.105) will often require rather detailed information about single equations involving the operators that occur in the system. In the subsections that follow we sketch out the modern theory for single equations, and then state some of the corresponding results for systems. The relevant theory for single equations is usually formulated in a setting which is slightly more general than that of diffusion models. Specifically, the theory is usually formulated for equations of the form

$$\frac{\partial u}{\partial t} = \sum_{i,j=1}^{n} a_{ij}(x)\frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{n} b_i(x)\frac{\partial u}{\partial x_i} + c(x)u \tag{1.106}$$

where the operator

$$L = \sum_{i,j=1}^{n} a_{ij}(x)\frac{\partial^2}{\partial x_i \partial x_j} + \sum_{i=1}^{n} b_i(x)\frac{\partial}{\partial x_i} + c(x) \tag{1.107}$$

is elliptic. We generally assume that the operator L is uniformly strongly elliptic, that is, there are constants $A_1 \geq A_0 > 0$ such that

$$A_0|\vec{\xi}|^2 \leq \sum_{i,j=1}^{n} a_{ij}(x)\xi_i\xi_j \leq A_1|\vec{\xi}|^2 \tag{1.108}$$

for any $\vec{\xi} \in \mathbb{R}^n$ and any x for which L is defined. In the case of a diffusion operator $Lu = \nabla \cdot [d(x)\nabla u - \vec{b}(x)u] + r(x)u$, the ellipticity condition (1.108) reduces to $0 < d_0 \leq d(x) \leq d_1$ for some constants d_0 and d_1. We also assume that $a_{ij} = a_{ji}$. This is reasonable because $\partial^2 u/\partial x_i \partial x_j = \partial^2 u/\partial x_j \partial x_i$ for any smooth function u. (In the case of diffusion operators we have $a_{ij} = 0$ for $i \neq j$.)

1.6.4 Elliptic Operators: Weak Solutions, State Spaces, and Mapping Properties

To understand the issues involved in analyzing elliptic operators it is instructive to consider the problem

$$\begin{aligned} &\frac{d^2u}{dx^2} = g(x) \quad 0 < x < 1 \\ &u(0) = u(1) = 0. \end{aligned} \tag{1.109}$$

If $g(x)$ is continuous, then taking

$$u(x) = ax + \int_0^x \int_0^y g(z)dzdy \tag{1.110}$$

with $a = -\int_0^1 \int_0^y g(z)dzdy$ yields a function $u(x)$ which is twice continuously differentiable on $(0, 1)$, continuous on $[0, 1]$, and which satisfies (1.109) on $(0, 1)$. On the other hand, if $g(x)$ is discontinuous, the situation becomes a bit more delicate. (Problems involving discontinuous terms arise in ecological models if the environment changes drastically across some interface and we will want to consider scenarios where that happens.) Suppose for example that $g(x) = 0$ for $0 \leq x < 1/2$ while $g(x) = 1$ for $1/2 \leq x \leq 1$. In that case (1.110) yields $u(x) = (-x/8)$ for $0 \leq x < 1/2$ and $u(x) = (x^2/2) - (5x/8) + 1/8$ for $1/2 \leq x \leq 1$. The derivative $u'(x)$ is given by $u'(x) = -1/8$ for $0 < x < 1/2$, $u'(x) = x - 5/8$ for $1/2 \leq x < 1$, so $u'(x)$ is well defined and continuous. However, if we try to compute $u''(x)$ for $x = 1/2$, we find that at $x = 1/2$ the limit from the right for the difference quotient $[u'(x+h) - u'(x)]/h$ is $\lim_{h \to 0+} [(1/2) + h) - 5/8) - (1/2 - 5/8)]/h = 1$, while the limit from the left is $\lim_{h \to 0-} [(-1/8) - (-1/8)]/h = 0$. Thus, $u''(1/2)$ does not exist so $u(x)$ cannot satisfy (1.109) at $x = 1/2$. However, $u''(x)$ exists and satisfies (1.109) everywhere else. The point is that $u(x)$ satisfies (1.110), which is the integrated version of (1.109), but fails to satisfy (1.109) everywhere because $u(x)$ is not smooth enough. However, $u''(x)$ exists and equals $g(x)$ everywhere except at a single point, so we have

$$\int_0^1 |u''(x) - g(x)|^2 dx = 0. \tag{1.111}$$

Thus, $u''(x) = g(x)$ in terms of the norm on $L^2([0, 1])$.

The preceding example brings us to the general notion of weak solutions. Roughly speaking, a weak solution to a differential equation is a solution to some integrated version of the equation which has the property that smooth solutions to the integrated equation are actual solutions to the original equation. A standard way of defining weak solutions is based on the fact that if $f(x)$ and $g(x)$ are continuous functions such that $\int_0^1 h(x) f(x) dx =$

$\int_0^1 h(x)g(x)dx$ for all smooth functions $h(x)$ on $[0, 1]$, then $f(x) = g(x)$ for all x. (To see that $f(x_0) = g(x_0)$ for any fixed x_0, one would choose a sequence of smooth functions $h_n(x)$ with $h_n(x) = 0$ outside the interval $x_0 - 1/n < x < x_0 + 1/n$, $h_n(x) \geq 0$, and $\int_0^1 h_n(x)dx = 1$. If $f(x)$ is continuous at x_0 then for any $\epsilon > 0$ there is a number N such that $f(x_0) - \epsilon < f(x) < f(x_0) + \epsilon$ for $x \in (x_0 - 1/N, x_0 + 1/N)$; then for $n > N$ we have $\int_0^1 h_n(x)f(x)dx = \int_{x_0-1/n}^{x_0+1/n} h_n(x)f(x)dx \geq \int_{x_0-1/n}^{x_0+1/n} h_n(x)(f(x_0) - \epsilon)dx = (f(x_0) - \epsilon)\int_{x_0-1/n}^{x_0+1/n} h_n(x)dx = f(x_0) - \epsilon$. Similarly, $\int_0^1 h_n(x)f(x)dx \leq f(x_0) + \epsilon$. Since $\epsilon > 0$ was arbitrary, we have $\int_0^1 h_n(x)f(x)dx \to f(x_0)$ as $n \to \infty$. Likewise, $\int_0^1 h_n(x)g(x)dx \to g(x_0)$ as $n \to \infty$, so $f(x_0) = g(x_0)$.) It is possible for the relation $\int_0^1 h(x)f(x)dx = \int_0^1 h(x)g(x)dx$ to hold for all smooth $h(x)$ even if $f(x)$ and $g(x)$ are discontinuous. However, if $f(x)$ or $g(x)$ is discontinuous, it is no longer necessarily the case that $f(x) = g(x)$ for all x. Indeed, the relation may still hold even if there are points where $f(x) \neq g(x)$, provided there are not too many such points. If $f(x) = 1$ for all x and $g(x) = 1$ for all x except, say, $x = 1/4, 1/2$, and $3/4$, where $g(x) = 0$, then $\int_0^1 h(x)f(x)dx = \int_0^1 h(x)g(x)dx$ for all $h(x)$.

We may now define weak derivatives, which provide one way of formulating weak solutions. If $f(x)$ is differentiable and $h(x)$ is a smooth function with $h(0) = h(1) = 0$, then

$$\begin{aligned} \int_0^1 f'(x)h(x)dx &= f(x)h(x)|_0^1 - \int_0^1 f(x)h'(x)dx \\ &= -\int_0^1 f(x)h'(x)dx \end{aligned} \tag{1.112}$$

via integration by parts. We can then define a weak derivative of $f(x)$ to be a function $g(x)$ with the property that for any $h(x)$

$$\int_0^1 g(x)h(x)dx = -\int_0^1 f(x)h'(x)dx. \tag{1.113}$$

If $f'(x)$ exists as a continuous function then (1.112) and (1.113) imply $g(x) = f'(x)$, but (1.113) makes sense in some cases where $f'(x)$ is not continuous. In the case of (1.109) with $g(x) = 0$ for $x < 1/2$ and $g(x) = 1$ for $x \geq 1/2$, a direct calculation shows that the function $u(x)$ defined in (1.110) has a weak second derivative $v(x)$ which is equal to $g(x)$ in the sense that for any smooth $h(x)$, $\int_0^1 h(x)v(x)dx = \int_0^1 h(x)g(x)dx$. The formulation (1.113) is the basis for the theory of distributions; see Strauss (1992). We present it here to illustrate how the notion of solving a differential equation can be extended to cases where some of the terms in the equation are not necessarily smooth. Models with discontinuous coefficients arise naturally in some spatial contexts; moreover, there are some aspects of

the mathematical theory of reaction-diffusion models that are facilitated by the use of state spaces such as $L^2([0, 1])$ that contain discontinuous functions.

The example (1.109), (1.110) illustrates some of the mapping properties of the operator d^2/dx^2 and its inverse subject to the given boundary conditions. We can now interpret d^2/dx^2 as an operator on suitable state spaces, that is, as a function between Banach spaces. To define an operator we need to specify its domain and tell how it acts on the elements of its domain. In the case of (1.109) there are a couple of natural choices. The simplest choice for the domain of d^2/dx^2 subject to the boundary conditions of (1.109) is the space of functions on [0, 1] whose first and second derivatives are continuous and which satisfy the boundary conditions. The space $C^2([0, 1])$ is defined to be the set of all functions on [0, 1] which are twice continuously differentiable. The norm on $C^2([0, 1])$ is

$$||u||_{C^2([0,1])} = \sup_{x\in[0,1]} (|u''(x)|) + \sup_{x\in[0,1]} (|u'(x)|) + \sup_{x\in[0,1]} (|u(x)|), \tag{1.114}$$

and under that norm $C^2([0, 1])$ is a Banach space. (We discuss that point in more detail in the next paragraph.) If we let $X = \{u \in C^2([0, 1]) : u(0) = u(1) = 0\}$, retain (1.114) as the norm on X, and let $A = d^2/dx^2$ with the domain of A taken to be X, then A maps X into $C([0, 1])$. Furthermore, if $u, v \in X$ then we have

$$\begin{aligned} ||Au - Av||_{C([0,1])} = ||A(u - v)||_{C([0,1])} &= \sup_{x\in[0,1]} |u''(x) - v''(x)| \\ &\le ||u - v||_{C^2([0,1])} \end{aligned}$$

so that A is continuous. The inverse operator A^{-1} for A is defined by (1.110), and it is easy to see that if $g \in C([0, 1])$ then $||A^{-1}g||_{C^2([0,1])} \le C||g||_{C([0,1])}$ for some constant C. Thus, A^{-1} is also continuous as a function from $C([0, 1])$ into X. Finally, A^{-1} maps bounded sets in $C([0, 1])$ into bounded sets in X, but $X \subseteq C([0, 1])$ and by Ascoli's theorem any set that is bounded in X has compact closure in $C([0, 1])$. Thus, if we define E as the operator from X into $C([0, 1])$ which acts as the identity operator on X, that is, $Eu = u$, and combine E with A^{-1} then the operator EA^{-1} maps $C([0, 1])$ into $C([0, 1])$ continuously, and does so in a way that maps bounded sets into sets whose closures are compact. This is exactly the type of mapping property that is required for the application of modern mathematical methods to equilibrium problems for reaction-diffusion models.

The choice of spaces $C([0, 1])$ and $X \subseteq C^2([0, 1])$ above is not the only possibility. We could also choose to work in the space Y of functions which are square integrable and which have weak first and second derivatives in the sense of (1.113) which are also square integrable, with norm

$$||u||_Y = \left[\int_0^1 (|u''(x)|^2 + |u'(x)|^2 + |u(x)|^2)dx\right]^{1/2}. \tag{1.115}$$

If we use Lebesgue integrals then Y turns out to be a Banach space. A problem now arises with the boundary conditions, because (1.115) might still make sense even if $u(0), u(1)$ were undefined or if $u(x)$ were discontinuous at 0 or 1 (or elsewhere). However, by using the Cauchy-Schwartz inequality for integrals (e.g., see Royden (1968)), we can see that

for $u \in Y$,

$$\begin{aligned} |u(x_1) - u(x_2)| &= \int_{x_1}^{x_2} u'(x)dx \\ &\leq \left(\int_{x_1}^{x_2} dx \right)^{1/2} \left(\int_{x_1}^{x_2} |u'(x)|^2 dx \right) \\ &\leq |x_2 - x_1|^{1/2} ||u||_Y . \end{aligned} \tag{1.116}$$

Thus, if $u \in Y$, then u is continuous, so it makes sense to talk about $u(0)$ and $u(1)$, and we may define the space $Y_0 = \{u \in Y : u(0) = u(1) = 0\}$. We can now define an operator B as $B = d^2/dx^2$ with domain Y_0. The operator B is different from A because it acts on a different space, although Au and Bu represent the same function for those choices of u where both make sense. It is clear from (1.115) that B maps Y_0 into $L^2([0, 1])$ continuously, and it is not too hard to show that (1.110) defines an inverse operator B^{-1} that maps $L^2([0, 1])$ continuously into Y_0. It is also true (but harder to show) that the embedding operator E_0 that maps Y_0 to $L^2([0, 1])$ by taking $E_0 u = u$ maps bounded sets in Y_0 to sets with compact closures in $L^2([0, 1])$. Thus, the mapping from $L^2([0, 1])$ into itself defined by $E_0 B^{-1}$ has the same type of mapping properties as the operator EA^{-1} on $C[0, 1])$. This means that we could use many of the same analytic methods while working in either $C([0, 1])$ or $L^2([0, 1])$. The reason for wanting to have both spaces available for use is that each has some advantages and disadvantages from the viewpoint of analysis. The functions in $C([0, 1])$ are continuous, so they will always attain maximum and minimum values, which is an observation that is sometimes useful. On the other hand, the norm in $L^2([0, 1])$ arises from an inner product (analogous to the dot product for vectors) given by $< u, v >= \int_0^1 u(x)v(x)dx$, and having an inner product is also sometimes useful. In what follows we use some state spaces which are generalizations of $C([0, 1])$ and $C^2([0, 1])$, and others that are generalizations of $L^2([0, 1])$ and the space Y whose norm is defined in (1.115).

To verify that $C([0, 1])$ is a Banach space requires only basic ideas from real analysis, as discussed by Rudin (1976), for example. The key idea is that any sequence which converges in the norm of $C([0, 1])$ is uniformly convergent, so taking the limit of a sequence of continuous functions with respect to the norm on $C([0, 1])$ yields another continuous function. To correctly define $L^2([0, 1])$ and verify that it is a Banach space we must interpret integrals in the sense of Lebesgue (see Royden (1968), for example.) The reason is that there are sequences of functions $f_n(x)$ which are integrable in sense of the usual Riemann integral defined in most calculus texts, and for which the sequence $\{f_n(x)\}$ is a Cauchy sequence with respect to the metric defined by $d(f_n, f_m) = ||f_n - f_m|| = \left(\int_0^1 |f_n(x) - f_m(x)|^2 dx \right)^{1/2}$, which do not converge to a Riemann integrable function. The problem is essentially that $\{f_n\}$ might converge pointwise to some function $f(x)$ which is so badly discontinuous that $f(x)$ and $[f(x)]^2$ are not integrable in the sense of Riemann. Lebesgue integrals can handle functions which are too badly discontinuous to be Riemann integrable; for example the function on [0, 1] which is zero for all rational numbers but one for all irrational numbers is not Riemann integrable, but it is Lebesgue integrable. The two notions of integral agree when both make sense. In what follows we will always interpret integrals as Lebesgue integrals. If we use Lebesgue integrals to define $L^2([0, 1])$ then the

completeness of $L^2([0,1])$ (and hence the fact that $L^2([0,1])$ is a Banach space) follows from the standard convergence theorems for Lebesgue integrals (see Royden (1968)).

When we try to formulate appropriate state spaces for reaction-diffusion models in more than one space dimension we encounter a few more technical issues. The boundary of an interval always consists of two points, but the boundary of a region in two or three dimensions could be very complicated, even fractal. We usually impose some conditions on the boundaries occurring in our models, typically requiring them to be smooth curves or surfaces. Another problem is that the elliptic operators which occur in our models do not have all the mapping properties we might want if we try to define them on $C^2(\overline{\Omega})$. (Here $\Omega \subseteq \mathbb{R}^n$ is a bounded domain and $\overline{\Omega}$ its closure). Finally, the formula (1.116) which implies that functions in Y must be continuous is not valid in exactly the same form in higher space dimensions. Since continuity is a desirable property we will sometimes want to work in spaces whose norms are defined by integrals but whose elements are continuous functions. To do that we must sometimes use spaces constructed from the space $L^p(\Omega)$, whose norm is $||u|| = \left(\int_\Omega |u(x)|^p dx\right)^{1/p}$, where $p \geq 1$ but p is not necessarily equal to 2.

The problem with treating elliptic operators of the form L shown in (1.107) in $C^2(\overline{\Omega})$ is that although L will be continuous as a map from $C^2(\Omega)$ into $C(\overline{\Omega})$, the inverse operator L^{-1} (i.e. the solution operator for the equation $Lu = f$ under suitable boundary conditions) will not in general be continuous as a map from $C(\overline{\Omega})$ to $C^2(\overline{\Omega})$. To define spaces on which L will have a continuous inverse we need a notion of continuity for functions which is stronger than simple continuity. The type of continuity we need is called *Hölder continuity*. Let x_0 be a point in $\mathbb{R}^n$ and let α be a real number with $0 < \alpha \leq 1$. The function $f(x)$ is said to be Hölder continuous with exponent α at x_0 if there exist a neighborhood of x_0 and a constant C such that $|f(x) - f(x_0)| < C|x - x_0|^\alpha$ for all x in the neighborhood of x_0. In the case $\alpha = 1$ the function $f(x)$ is said to be *Lipschitz continuous*. As an example, (1.116) shows that the function u is Hölder continuous with exponent $1/2$. Let $\Omega \subseteq \mathbb{R}^n$ be a bounded domain, and denote the closure of Ω by $\overline{\Omega}$. A function $f(x)$ is Hölder continuous with exponent α on $\overline{\Omega}$ if the quantity

$$[f]_\alpha = \sup_{\substack{x,y\in\overline{\Omega} \\ x\neq y}} \frac{|f(x) - f(y)|}{|x - y|^\alpha} \tag{1.117}$$

is finite. The space of functions that are Hölder continuous on $\overline{\Omega}$ with exponent α is denoted by $C^{0,\alpha}(\overline{\Omega})$ or simply $C^\alpha(\overline{\Omega})$. The norm on $C^\alpha(\overline{\Omega})$ is

$$\begin{aligned} ||u||_\alpha = ||u||_{0,\alpha} &= \sup_{x\in\overline{\Omega}} |u(x)| + \sup_{\substack{x,y\in\overline{\Omega} \\ x\neq y}} \frac{|u(x) - u(y)|}{|x - y|^\alpha} \\ &= ||u||_0 + [u]_\alpha, \end{aligned} \tag{1.118}$$

where $||u||_0 = \sup_{\overline{\Omega}} |u(x)|$ is the norm for $C(\overline{\Omega})$. To describe the partial derivatives of a function u defined on a subset of $\mathbb{R}^n$, it is common to use the multi-index notation $\beta = (\beta_1, \ldots, \beta_n)$ where $\beta_1, \ldots, \beta_n$ are integers, to define the order of β, denoted $|\beta|$, by $|\beta| = \beta_1 + \cdots + \beta_n$ and write $\partial^{|\beta|} u / \partial x_1^{\beta_1} \partial x_2^{\beta_2} \ldots \partial x_n^{\beta_n}$ as $\partial^\beta u$. The space of functions on $\overline{\Omega}$ which have spatial derivatives up to order k that are continuous on $\overline{\Omega}$, with the derivatives

of order k being Hölder continuous with exponent α, is denoted $C^{k,\alpha}(\overline{\Omega})$ or $C^{k+\alpha}(\overline{\Omega})$. The norm on $C^{k+\alpha}(\overline{\Omega})$ can be written as

$$||u||_{k+\alpha} = \sup_{x\in\overline{\Omega}}|u(x)| + \sum_{|\beta|\le k}\sup_{x\in\overline{\Omega}}|\partial^\beta u(x)| + \sum_{|\beta|=k}[\partial^\beta u]_\alpha \tag{1.119}$$

where the notation $[\ \ ]_\alpha$ is defined in (1.117). The spaces $C^{k+\alpha}(\overline{\Omega})$ are Banach spaces. See Gilbarg and Trudinger (1977) and Friedman (1976) for additional discussion. As noted at the beginning of this discussion, the reason for considering these spaces is that if an elliptic operator L has the form shown in (1.107) and there is a solution operator or inverse operator L^{-1} for L, the inverse operator will typically map $C^\alpha(\overline{\Omega})$ into $C^{2+\alpha}(\overline{\Omega})$, but will not necessarily map $C(\overline{\Omega})$ into $C^2(\overline{\Omega})$ as was the case in one space dimension. Thus, although L might make sense as a mapping form $C^2(\overline{\Omega})$ into $C(\overline{\Omega})$, if we want L to have a continuous inverse we will usually need to think of L as an operator from $C^{2+\alpha}(\overline{\Omega})$ into $C^\alpha(\overline{\Omega})$ instead. This point is discussed in some detail by Gilbarg and Trudinger (1977). To correctly state the mapping properties for elliptic operators on spaces of Hölder continuous functions we must put some restrictions on the boundary of the underlying domain Ω. To derive some of the mapping properties of elliptic operators it is necessary to do calculations that involve changes of coordinates which "flatten" parts of the boundary in the sense of mapping them to hyperplanes. When a differential operator is written in terms of the new coordinates derivatives of the functions defining the coordinate changes occur in the coefficients because of the chain rule. Thus, the theory requires that the changes of coordinates are smooth enough that the coefficients of the operator under consideration are well defined and sufficiently smooth in the new coordinate system. Recall that a change of coordinates is a function Φ which maps an open subset of $\mathbb{R}^n$ into another open subset of $\mathbb{R}^n$ in such a way that Φ has an inverse function Φ^{-1} and Φ and Φ^{-1} are at least continuous. We say that the boundary $\partial\Omega$ of a domain $\Omega \subseteq \mathbb{R}^n$ is of class $C^{k+\alpha}$ if for each point $x_0 \in \partial\Omega$ there is a neighborhood U containing x_0 and a change of coordinates Φ on U such that

(i) if $y = (y_1, \ldots, y_n) = \Phi(x)$, the image under Φ of $\partial\Omega \cap U$ lies in the hyperplane $\{y \in \mathbb{R}^n : y_n = 0\}$ while the image of $\Omega \cap U$ lies in the half-space $\{y \in \mathbb{R}^n : y_n > 0\}$, and

(ii) each of the coordinates functions $y_1(x), \ldots, y_n(x)$ defining Φ belongs to $C^{k+\alpha}(\overline{U})$ and each of the functions $x_1(y), \ldots, x_n(y)$ defining Φ^{-1} belongs to $C^{k+\alpha}(\Phi(\overline{U}))$, where $\Phi(\overline{U})$ is the image of $\overline{U}$ under Φ.

We can now describe the mapping properties of operators of the form L shown in (1.107), subject to the ellipticity condition (1.108), on spaces of Hölder continuous functions.

Theorem 1.1. Suppose that $\Omega \subseteq \mathbb{R}^n$ is a bounded domain with $\partial\Omega$ of class $C^{2+\alpha}$ for some $\alpha \in (0, 1)$. Suppose that the coefficients of the operator L shown in (1.107) belong to $C^\alpha(\overline{\Omega})$, satisfy (1.108), and also satisfy $c(x) \le 0$. If $f \in C^\alpha(\overline{\Omega})$ and $g \in C^{2+\alpha}(\overline{\Omega})$, the problem

$$\begin{aligned} Lu &= f(x) \text{ in } \quad \Omega \\ u &= g(x) \text{ on } \quad \partial\Omega \end{aligned} \tag{1.120}$$

has a unique solution $u \in C^{2+\alpha}(\overline{\Omega})$ which satisfies the inequality

$$||u||_{2+\alpha} \leq C(||f||_\alpha + ||g||_{2+\alpha}) \tag{1.121}$$

for a constant C independent of f and g where $||\cdot||_\alpha$ and $||\ \ ||_{2+\alpha}$ are the norms of $C^\alpha(\overline{\Omega})$ and $C^{2+\alpha}(\overline{\Omega})$ respectively, as defined in (1.119).

Remark: This result is a version of Theorem 6.14 of Gilbarg and Trudinger (1977) which incorporates some of the remarks given in the discussion of that theorem. A number of related results are derived in Chapter 6 of Gilbarg and Trudinger (1977). Note that the boundary condition is formulated in terms of the restriction of a function g that is defined on all of $\overline{\Omega}$ to the boundary $\partial\Omega$. If we started with a function $g_0 \in C^{2+\alpha}(\partial\Omega)$, then since we are assuming $\partial\Omega$ is of class $C^{2+\alpha}$ we could extend g_0 to a function $g \in C^{2+\alpha}(\overline{\Omega})$ in such a way that $||g||_{C^{2+\alpha}(\overline{\Omega})} \leq C||g_0||_{C^{2+\alpha}(\partial\Omega)}$. The following in a version of Theorem 6.31 of Gilbarg and Trudinger (1977) which treats another type of boundary condition:

Theorem 1.2. Suppose that Ω, L and f are as in Theorem 1.1. Suppose that $g(x), \gamma(x), \beta(x) \in C^{1+\alpha}(\partial\Omega)$ with $\beta(x) > 0$ and $\gamma(x) \geq 0$. Suppose that $c(x) \leq 0$ and either $c(x) \not\equiv 0$ or $\gamma(x) \not\equiv 0$. Let $\partial/\partial\vec{n}$ denote the outward normal derivative on $\partial\Omega$. The problem

$$\begin{aligned} &Lu = f(x) \quad \text{on} \quad \Omega \\ &\gamma(x)u + \beta(x)\frac{\partial u}{\partial \vec{n}} = g(x) \quad \text{on} \quad \partial\Omega \end{aligned} \tag{1.122}$$

has a unique solution $u \in C^{2+\alpha}(\overline{\Omega})$, and there is a constant C independent of f and g so that

$$||u||_{2+\alpha} \leq C(||f||_\alpha + ||g||_{1+\alpha}) \tag{1.123}$$

where $||g||_{1+\alpha}$ is the norm of $C^{1+\alpha}(\partial\Omega)$.

Remark: If $c = \gamma = 0$ then (1.22) may not be solvable for all choices of f. Something of this sort already occurs in the problem $d^2u/dx^2 = f(x),\ u'(0) = u'(1) = 0$. If we integrate the equation from 0 to 1 we obtain $\displaystyle\int_0^1 f(x)dx = \int_0^1 u''(x)dx = u'(1) - u'(0) = 0$ so the equation is not solvable unless $\displaystyle\int_0^1 f(x)dx = 0$. It is also the case that if $c = \gamma = 0$ in (1.122) then the homogeneous problem with $f = g = 0$ has the nontrivial solutions $u = k$ where k is any constant. This is no accident.

Theorem 1.3. Suppose that L, Ω, γ, and β are as in Theorems 1.1. and 1.2., but without the restrictions $c \leq 0$ or $\gamma \geq 0$. Then each of the problems (1.120), (1.122) satisfies one or the other of the following alternatives. Either

(i) the homogeneous problem (i.e. the problem with $f = 0$ and $g = 0$) has only the trivial solution $u = 0$ and the nonhomogeneous problem has a unique solution $u \in C^{2+\alpha}(\overline{\Omega})$ for each $f \in C^\alpha(\overline{\Omega})$ and (for 1.120) $g \in C^{2+\alpha}(\overline{\Omega})$ or (for 1.122) $g \in C^{1+\alpha}(\partial\Omega)$;

or

(ii) the homogeneous problem has nontrivial solutions; in that case the nullspace of L, i.e. the set of solutions to the homogeneous problem, is a finite dimensional subspace of $C^{2+\alpha}(\overline{\Omega})$.

Remark: Theorem 1.3 is a version of Theorem 6.15 of Gilbarg and Trudinger (1977). It is a special case of a more general result about operators known as the Fredholm Alternative which we discuss later in this section. A key point in establishing Theorem 1.3, which will also arise in the derivation of other results, is that an operator satisfying the hypotheses of Theorems 1.1 or 1.2 with homogeneous boundary conditions (i.e. $g = 0$) will have an inverse L^{-1} which is compact as a linear operator on $C^{\alpha}(\overline{\Omega})$; that is, L^{-1} maps bounded sets in $C^{\alpha}(\overline{\Omega})$ into sets with compact closures. More precisely, L^{-1} maps $C^{\alpha}(\overline{\Omega})$ continuously into $C^{2+\alpha}(\overline{\Omega})$, but $C^{2+\alpha}(\overline{\Omega})$ embeds compactly in $C^{2}(\overline{\Omega})$ by Arzela's theorem, and $C^{2}(\overline{\Omega})$ then embeds in $C^{\alpha}(\overline{\Omega})$ by the mean value theorem, so if $E : C^{2+\alpha}(\overline{\Omega}) \to C^{\alpha}(\overline{\Omega})$ is given by $Eu = u$ then the mapping $EL^{-1} : C^{\alpha}(\overline{\Omega}) \to C^{\alpha}(\overline{\Omega})$ is compact since L^{-1} is continuous and E is a compact operator.

The reason for the conditions $c \leq 0$ in Theorem 1.1 and $c \leq 0,\ \gamma \geq 0$, with $c \not\equiv 0$ or $\gamma \not\equiv 0$ in Theorem 1.2 is that those conditions imply uniqueness for the trivial solutions to (1.120) and (1.122), respectively, when $f = 0,\ g = 0$. Any other condition which guarantees uniqueness of the trivial solutions to those problems could be combined with Theorem 1.3 to yield an existence theorem for solution of the nonhomogeneous problem. The condition $c \leq 0$ implies that L satisfies a maximum principle, which means (among other things) that solutions to $Lu = 0$ cannot have a positive maximum or negative minimum inside Ω unless they are constant throughout Ω. The maximum principle can be used to show uniqueness for the homogeneous problem. We discuss maximum principles later in this section.

Theorems 1.1–1.3 provide a description of the mapping properties of elliptic operators on spaces of Hölder continuous functions which will be adequate for our purposes, but they do not address problems along the lines of (1.120) or (1.222) when f is continuous but not Hölder continuous or when f is discontinuous. Some of the situations we want to study are best described by models which have discontinuous terms. Moreover, even in models with no discontinuities built into them having the ability to work with functions that are merely continuous can facilitate our mathematical analysis. Thus, we consider problems such as (1.120) and (1.122) in cases where f is only assumed to belong to some space of integrable functions such as the space $L^2([0, 1])$ we considered in our simple one-dimensional example. To do that requires an appropriate notion of weak derivatives, which in turn is based on the notion of integration by parts in $\mathbb{R}^n$, so we shall digress briefly to discuss those topics and then return to the mapping properties of elliptic operators.

The result for functions on $\mathbb{R}^n$ which gives the closest analogue to the integration by parts formula is the divergence theorem. Recall that if $\Omega \subseteq \mathbb{R}^n$ is a bounded domain with a C^1 boundary and $\vec{F}$ is a C^1 vector field on Ω which is continuous on $\overline{\Omega}$ (i.e. $\vec{F} \in [C^1(\Omega)]^n \cap [C(\overline{\Omega})]^n$), then the divergence theorem states that

$$\int_{\Omega} \nabla \cdot \vec{F} dx = \int_{\partial\Omega} \vec{F} \cdot \vec{n} dS, \tag{1.124}$$

where $dx = dx_1 \ldots dx_n$ is the volume element on Ω, dS is the surface element on $\partial\Omega$, and $\vec{n}$ is the outward unit normal on $\partial\Omega$. Suppose that u and v are C^1 functions on Ω with

either $u = 0$ or $v = 0$ on $\partial\Omega$, and let $\vec{e}_k$ be the unit vector in the x_k direction. We have

$$0 = \int_{\partial\Omega} uv\vec{e}_k \cdot \vec{n} dS = \int_{\Omega} \nabla \cdot (uv\vec{e}_k) dx = \int_{\Omega} \left(\frac{\partial u}{\partial x_k} v + u \frac{\partial v}{\partial x_k} \right) dx$$

so that

$$\int_{\Omega} \frac{\partial u}{\partial x_k} v = -\int_{\Omega} u \frac{\partial v}{\partial x_k} dx. \tag{1.125}$$

The formula (1.125) is the basis for the definition of weak derivatives in $\mathbb{R}^n$. If the function $w(x)$ satisfies the relation

$$\int_{\Omega} wv dx = -\int_{\Omega} u \frac{\partial v}{\partial x_k} dx \tag{1.126}$$

for all functions v that are smooth and are equal to zero outside a compact subset of Ω, then w is said to be the *weak derivative of u with respect to x_k on* Ω. Higher weak derivatives are defined analogously; so $w = \partial^2 u / \partial x_k \partial x_j$ in the weak sense if

$$\int_{\Omega} wv dx = (-1)^2 \int_{\Omega} u \frac{\partial^2 v}{\partial x_k \partial x_j} dx = \int_{\Omega} u \frac{\partial^2 v}{\partial x_k \partial x_j} dx$$

for all smooth functions v that are zero outside some compact subset of Ω, and so on. Certain calculations based on the divergence theorem are widely used in partial differential equations. Some of these are known as Green's formulas. An example is the following. Suppose $u, v, \in C^2(\overline{\Omega})$. Then

$$\begin{aligned} \int_{\Omega} v(\nabla \cdot d(x) \nabla u) dx &= \int_{\Omega} (\nabla \cdot [v d(x) \nabla u] - d(x) \nabla u \cdot \nabla v) dx \\ &= \int_{\partial\Omega} v d(x) \nabla u \cdot \vec{n} dS - \int_{\Omega} d(x) \nabla u \cdot \nabla v dx \\ &= \int_{\partial\Omega} v d(x) \frac{\partial u}{\partial \vec{v}} dS - \int_{\Omega} d(x) \nabla u \cdot \nabla v dx. \end{aligned}$$

Because weak derivatives are defined by (1.126) to satisfy the formula (1.125), they will by definition also satisfy Green's formulas and other formulas based on the divergence theorem when all the derivatives exist and all the integrals make sense and are finite. Weak derivatives are discussed in some detail by Adams (1975), Friedman (1976), and Gilbarg and Trudinger (1977).

The state spaces we need to use to treat models with discontinuous terms can be constructed by using the idea of weak derivatives in the setting of the spaces $L^p(\Omega)$ of functions on Ω whose pth power is integrable in the sense of Lebesgue. The L^p spaces will be familiar to most of those readers who have had a course on real analysis which treats Lebesgue integration; they are discussed in detail, for example, by Royden (1968). For those readers unfamiliar with Lebesgue integrals, one of their essential features is that they agree with the ordinary Riemann integrals of elementary calculus when both types of integrals make sense, but Lebesgue integrals make sense for some functions for which Riemann integrals do not. As a consequence, it is possible to interchange integration with taking the limit of a sequence of functions more readily in the context of Lebesgue integrals than in the context of Riemann integrals. As an example, if the functions $f_n(x)$ are Lebesgue

integrable on a bounded domain Ω, are bounded by a Lebesgue integrable function $f_0(x)$ in the sense that $|f_n(x)| \leq f_0(x)$ for all n, and $f_n(x) \to f(x)$ for each $x \in \Omega$, then $f(x)$ is Lebesgue integrable on Ω and $\int_\Omega f_n dx \to \int_\Omega f dx$ as $n \to \infty$. (See Royden (1968)). This is not true in general for Riemann integrals, where convergence of the integrals $\int_\Omega f_n dx$ normally requires uniform convergence of the functions.

Lebesgue integrals are defined in terms of what is known as Lebesgue measure. Lebesgue measure is a generalization of the notion of length (in $\mathbb{R}$), area (in $\mathbb{R}^2$), volume (in $\mathbb{R}^3$), etc. The Lebesgue measure of an interval is simply its length, but Lebesgue measure makes sense for sets more complicated than intervals. For example, in one dimension, the set of all rational numbers in [0, 1] has measure 0 while the set of all irrational numbers in [0, 1] has measure 1. This reflects the fact that relatively few points (only countably many) in [0, 1] are rational. Any surface or hypersurface of dimension $n-1$ or lower in $\mathbb{R}^n$ will have Lebesgue measure zero, and any finite or even countable union of sets with Lebesgue measure zero will also have Lebesgue measure zero. Lebesgue integrals are actually defined on equivalence classes of functions which are equal outside of a set of measure zero, and if a function is Lebesgue integrable at all then its integral over any set of measure zero is equal to zero. The appropriate notion of convergence for a sequence of functions relative to Lebesgue integration is convergence almost everywhere, that is, pointwise convergence outside of a set of measure zero. If $\{f_n\}$ is a sequence of Lebesgue integrable functions with $|f_n|$ bounded by a Lebesgue integrable function $f_0(x)$ for all n and $f_n \to f$ almost everywhere in Ω, then f is Lebesgue integrable and $\int_\Omega f_n dx \to \int_\Omega f dx$ as $n \to \infty$. When $f_n \to f$ almost everywhere it is standard to write "$f_n \to f$ a.e.". The significance of the convergence properties of the Lebesgue integral is that they guarantee that spaces of Lebesgue integrable functions are complete as metric spaces, i.e. they are Banach spaces. To be specific, for $1 \leq p < \infty$ the space $L^p(\Omega)$ is the set of all functions f on Ω for which $|f|^p$ is integrable, with the norm

$$||f||_p = \left(\int_\Omega |f(x)|^p dx \right)^{1/p}. \tag{1.127}$$

(Once again, to be precise, the elements in $L^p(\Omega)$ are actually equivalence classes of functions, with each equivalence class consisting of functions which are equal outside a set of measure zero.) To be Lebesgue integrable a function must have the property of measurability, which means that if $S \subseteq \mathbb{R}$ is a set such that the Lebesgue measure of S is well defined in $\mathbb{R}$ then the Lebesgue measure of the set $\{x \in \Omega : f(x) \in S\}$ is well defined in $\mathbb{R}^n$. In addition to the spaces $L^p(\Omega)$, we may sometimes want to consider the space $L^\infty(\Omega)$ consisting of Lebesgue measurable functions which are bounded except perhaps on a set of measure zero. The norm on $L^\infty(\Omega)$ is given by

$$\begin{aligned} ||f||_\infty = \inf\{\sup_\Omega |g(x)| : g \quad &\text{is measurable on} \quad \Omega \quad \text{and} \\ &g = f \quad \text{almost everywhere}\}. \end{aligned} \tag{1.128}$$

If $f \in C(\overline{\Omega})$, then $||f||_\infty = \sup_{\overline{\Omega}} |f|$ so that $C(\overline{\Omega})$ is a closed subspace of $L^\infty(\Omega)$. (The space $C(\overline{\Omega})$ is a subspace of $L^p(\Omega)$ for any $p \geq 1$, but in general is not closed.)

We can now define state spaces based on L^p spaces. Denote by $W^{k,p}(\Omega)$ the space of functions whose weak derivatives of order up to k belong to $L^p(\Omega)$. The norm of f in $W^{k,p}(\Omega)$ is denoted by $||\ \ ||_{k,p}$. It is defined in terms of $L^p(\Omega)$ norms of the weak derivatives of f in much the same way that the norm of f in $C^{k+\alpha}(\overline{\Omega})$ is defined in terms of the norms in $C(\overline{\Omega})$ and $C^{\alpha}(\overline{\Omega})$ of derivatives of f in (1.119), namely

$$||f||_{k,p} = \sum_{|\beta| \leq k} ||\partial_\beta f||_p, \tag{1.129}$$

where once again $\beta = (\beta_1, \ldots, \beta_n)$, where $\beta_1, \ldots, \beta_n$ are nonnegative integers, $|\beta| = \beta_1 + \cdots + \beta_n$, and $\partial_\beta f$ denotes the derivative $\partial^{|\beta|} f / \partial x_1^{\beta_1} \ldots \partial x_n^{\beta_n}$, now taken in the weak sense as in (1.129). The spaces $W^{k,p}(\Omega)$ are called Sobolev spaces, and they are Banach spaces; see Gilbarg and Trudinger (1997) or Adams (1975). An alternative way to define them is to take the completion of $C^k(\overline{\Omega})$ (or $C^{k+\alpha}(\overline{\Omega})$, for that matter) with respect to the norm (1.129). A particular Sobolev space which we will use in our discussion of eigenvalues for elliptic operators is the space $W^{1,2}(\Omega)$. That space is of interest partly because its norm can be viewed as arising form the inner product

$$< u, v >= \int_\Omega [\nabla u \cdot \nabla v + uv] dx \tag{1.130}$$

(where again ∇u and ∇v are interpreted in the weak sense).

In some cases we will also want to work in the subspace $W_0^{1,2}(\Omega) \subseteq W^{1,2}(\Omega)$, which is obtained by taking the completion in Ω relative to (1.130) of the space of continuously differentiable functions that are zero outside a compact subset of Ω (which means that they are zero on $\partial\Omega$). The space $W_0^{1,2}(\Omega)$ can be viewed as being the subspace of $W^{1,2}(\Omega)$ consisting of functions which are zero on $\partial\Omega$, but some care is required in that interpretation since functions in $W^{1,2}(\Omega)$ are not necessarily continuous on $\overline{\Omega}$.

The fact that functions in Sobolev spaces need not be continuous on $\overline{\Omega}$ means that some care must be taken in formulating boundary conditions on them. For functions $f(x) \in C(\overline{\Omega})$ the mapping from f to the restriction of f to $\partial\Omega$ maps $C(\overline{\Omega})$ continuously to $C(\partial\Omega)$. In the case of Sobolev spaces we need to use the notion of trace. If Y is a space of functions on $\partial\Omega$, the function $u \in W^{m,p}(\Omega)$ has trace $y \in Y$ if for any sequence $\{u_n\}$ of smooth (i.e. infinitely differentiable) functions u_n on $\overline{\Omega}$ which converge to u in the norm of $W^{m,p}(\Omega)$, the functions obtained by restricting u_n to $\partial\Omega$ converge to y in the norm of Y, with $||y||_Y \leq C||u||_{m,p}$ for some constant C independent of u. We have the following (see Adams (1975, Theorems 5.22, 7.53, and 7.57)).

Lemma 1.4. Suppose $\Omega \subseteq I\!R^n$ is a bounded domain with $\partial\Omega$ of class $C^{2+\alpha}$. For $p \in (1, \infty)$ functions in $W^{2,p}(\Omega)$ have traces in $W^{1,p}(\partial\Omega)$. For $m = 1, 2$ and $p < n/m$, functions in $W^{m,p}(\Omega)$ have traces in $L^q(\partial\Omega)$ for $q \in [p, (n-1)p/(n-mp)]$. For $p \geq n/m$, functions in $W^{2,p}(\Omega)$ have traces in $L^q(\partial\Omega)$ for $q \in [p, \infty)$.

Remarks: The spaces $W^{1,p}(\Omega)$ actually have traces which belong to the fractional order Sobolev space $W^{1-1/p,p}(\partial\Omega)$, as defined in Agmon et al. (1959) or Adams (1975); see for example Adams (1975, Theorem 7.53). This is a relatively fine technical point but it is relevant to the formulation of boundary conditions in Sobolev spaces.

We can now state results in Sobolev spaces which are analogous to Theorems 1.1 and 1.2.

Theorem 1.5. Suppose that $\Omega \subseteq I\!R^n$ is a bounded domain with $\partial\Omega$ of class $C^{2+\alpha}$, and that L has the form (1.107), (1.108) holds, and the coefficients of L all belong to $C^\alpha(\overline{\Omega})$. Suppose further that $c \leq 0$. Let $p \in (1, \infty)$. If $f \in L^p(\Omega)$ and $g \in W^{2,p}(\Omega)$ then the problem (1.120) (with the condition $u = g$ on $\partial\Omega$ interpreted as meaning that the traces of u and g on $\partial\Omega$ are equal almost everywhere) has a unique solution $u \in W^{2,p}(\Omega)$ satisfying $||u||_{2,p} \leq C(||f||_{0,p} + ||g||_{2,p})$ for some constant C independent of f and g.

Remarks: Results of this type are discussed by Agmon et al. (1959). The key idea is that for any $u \in W^{2,p}(\Omega)$ with $u = 0$ on $\partial\Omega$ (i.e. trace of u on $\partial\Omega$ is 0), we have the estimate $||u||_{2,p} \leq C_1(||u||_{0,p} + ||Lu||_{0,p})$ for a constant C_1 independent of u; see (Agmon et al. 1959). Once this estimate is available we may take $v = u - g$ so that $v = 0$ on $\partial\Omega$, $Lv = f - Lg \in L^p(\Omega)$ in Ω, and then analyze the problem for v in much the same way as in the case considered in Theorem 1.1, which is discussed in detail in Gilbarg and Trudinger (1977, Chapter 6); see Agmon et al. (1959). A similar analysis can be applied in the case of mixed boundary conditions:

Theorem 1.6. Suppose that L and Ω satisfy the hypotheses of Theorem 1.5. Suppose that c, β and γ satisfy the hypotheses of Theorem 1.2, that $f \in L^p(\Omega)$ and $g \in W^{1,p}(\Omega)$. Then the problem (1.122) has a unique solution $u \in W^{2,p}(\Omega)$, which satisfies $||u||_{2,p} \leq C(||f||_{o,p} + ||g||_{1,p})$ for some constant C independent of g or f.

Remarks: The "g" in the boundary condition in (1.122) should be interpreted as the trace of $g \in W^{1,p}(\Omega)$ on $\partial\Omega$. The key estimates by Agmon et al. (1959) are cast in terms of a norm on g which is essentially the norm of the trace of $g \in W^{1,p}(\Omega)$ on $\partial\Omega$ in the space $W^{1-1/p,1/p}(\partial\Omega)$; see Agmon et al. (1959, Formula 14.2) and compare with the discussion by Adams (1975, Chapter 7). If $g_0 \in W^{1,p}(\partial\Omega)$ then g_0 can be extended to $g \in W^{1,p}(\Omega)$ in such a way that $||g||_{W^{1,p}(\Omega)} \leq C||g_0||_{W^{1,p}(\partial\Omega)}$. If we omit the condition $c \leq 0$ from Theorem 1.5 or the conditions on c, γ, and β from Theorem 1.6 we would still be able to obtain a result analogous to Theorem 1.3.

An important feature of the Sobolev spaces $W^{m,p}(\Omega)$ is that they embed in the spaces $C^{k,\alpha}(\overline{\Omega})$ and $W^{j,q}(\Omega)$ under suitable conditions on $\partial\Omega, m, p, k, \alpha, j$, and q. Some of the embeddings are compact. An appropriate condition on $\partial\Omega$ for bounded domains is the local Lipschitz property. That property holds if $\partial\Omega$ is of class $C^{2+\alpha}$ (or even just C^1), but it will also be true if in a neighborhood of each point $x_0 \in \partial\Omega$ the boundary of Ω can be expressed (possibly after rotating coordinates or interchanging the i and j coordinates for some choices of i and j) as the graph of a function $x_n = \Psi(x_1, \ldots, x_{n-1})$ where Ψ is Lipschitz; that is, there is a constant such that $|\Psi(x_1, \ldots, x_{n-1}) - \Psi(y_1, \ldots, y_{n-1})| < C|(x_1 - y_1, \ldots, x_{n-1} - y_{n-1})|$. These domains include domains whose boundaries consist of finitely many smooth surfaces which meet at corners, such as polygons and polyhedra. We have the following:

Theorem 1.7. Suppose that $\Omega \subseteq I\!R^n$ is a bounded domain with $\partial\Omega$ locally Lipschitz. Let m and k denote integers with $k \geq 0$ and $m \geq 1$, and let $p \in [0, \infty)$.

(i) If $mp < n$, then $W^{m+k,p}(\Omega)$ embeds compactly in $W^{k,q}(\Omega)$ for $q \in [1, np/(n-mp))$. (If $q = np/(n-mp)$, the embedding is continuous but will not be compact.)

(ii) If $mp = n$, then $W^{m+k,p}(\Omega)$ embeds compactly in $W^{k,q}(\Omega)$ for $q \in [1, \infty)$.

(iii) If $mp > n$, then $W^{m+k,p}(\Omega)$ embeds compactly in $C^k(\overline{\Omega})$. If $(m-1)p \leq n < mp$ and $\alpha \in (0, m - (n/p))$ then $W^{m+k,p}(\Omega)$ embeds compactly in $C^{k+\alpha}(\overline{\Omega})$.

Remarks: This theorem is essentially Theorem 6.2 of Adams (1975); it is known as the Rellich-Kondrachov Theorem. In particular, it implies that $W^{2,p}(\Omega)$ embeds compactly in $C^{1+\alpha}(\overline{\Omega})$ for $p > n$ and $\alpha \in (0, 1 - (n/p))$ by taking $m = k = 1$. Note that $C^k(\overline{\Omega})$ embeds in $W^{k,q}(\Omega)$ for any $q \geq 1$, so in case (iii) $W^{m+k,p}(\Omega)$ also embeds compactly in $W^{k,q}(\Omega)$ for $q \in [1, \infty)$. There are a number of possible refinements and generalizations of the embedding theorem. In particular, parts (i) and (ii) of Theorem 1.7 remain valid if we merely require $\partial\Omega$ to satisfy a *cone condition*. The boundary $\partial\Omega$ of a bounded domain $\Omega \subseteq \mathbb{R}^n$ satisfies a *cone condition* if there is a fixed cone in $\mathbb{R}^n$ which can be moved by rigid motions (rotations and translations) to a position where its vertex is at $x_o \in \partial\Omega$ and the cone itself lies inside Ω, where $x_0 \in \partial\Omega$ is an arbitrary point on $\partial\Omega$. The point of using this type of condition instead of requiring $\partial\Omega$ to be $C^{2+\alpha}$ is that we can treat domains with corners, etc.

The way that we will typically use Theorem 1.7 is to formulate the solution operator for L as a compact operator from $C(\overline{\Omega})$ into $C(\overline{\Omega})$, or from $C^{1+\alpha}(\overline{\Omega})$ into $C^{1+\alpha}(\overline{\Omega})$.

Theorem 1.8. Suppose L has the form (1.107), with (1.108) satisfied, with all the coefficients of L belonging to $C^{\alpha}(\overline{\Omega})$ and $c \leq 0$. Suppose that $\Omega \subseteq \mathbb{R}^n$ is bounded and that $\partial\Omega$ is of class $C^{2+\alpha}$. The solution operator L^{-1} for the problem $Lu = f$ in Ω, $u = 0$ on $\partial\Omega$ can be extended to $C(\overline{\Omega})$ from $C^{\alpha}(\overline{\Omega})$ (or restricted to $C(\overline{\Omega})$ from $L^p(\Omega)$) to define a compact operator from $C(\overline{\Omega})$ into $C(\overline{\Omega})$; similarly, L^{-1} can be restricted from $C^{\alpha}(\overline{\Omega})$ to $C^{1+\alpha}(\overline{\Omega})$.

Proof: Suppose $f \in C(\overline{\Omega})$. Then $f \in L^p(\Omega)$ for any p. Choose $p > n$. Then by Theorem 1.5, there is a solution operator L^{-1} for L such that $L^{-1} : L^p(\Omega) \to W^{2,p}(\Omega)$ is continuous, which is equivalent to the existence of a constant C such that $||L^{-1}f||_{2,p} \leq C||f||_{0,p}$ for all $f \in L^p(\Omega)$. Since $||f||_{0,p} \leq C_1||f||_0$ for some constant C_1, where $||\cdot||_0$ denotes the norm of $C(\overline{\Omega})$, L^{-1} restricted to $C(\overline{\Omega})$ maps $C(\overline{\Omega})$ continuously into $W^{2,p}(\Omega)$. However, the embedding E of $W^{2,p}(\Omega)$ into $C(\overline{\Omega})$ is compact, so the operator EL^{-1} is continuous and maps bounded subsets of $C(\overline{\Omega})$ into subsets of $C(\overline{\Omega})$ with compact closure. Thus EL^{-1} defines a solution operator which is compact as an operator from $C(\overline{\Omega})$ to $C(\overline{\Omega})$. The case of $C^{1+\alpha}(\overline{\Omega})$ is similar.

Remark: Analogous results hold under the boundary conditions of (1.122). In our treatment of the equilibria of reaction-diffusion models the compactness of solution operators will play an important (if technical) role in the analysis. An important feature of compact operators is that they have eigenvalues. We have the following.

Lemma 1.9. A compact linear operator A from Banach space into itself has a countable set of eigenvalues. The eigenvalues have no limit point other than zero. The multiplicity of each nonzero eigenvalue is finite; that is, the dimension of the nullspace of $A - \sigma I$ is finite for each eigenvalue σ.

Remarks: Lemma 1.9 is essentially Theorem 5.5 of Gilbarg and Trudinger (1977). It is a standard result in functional analysis. So far we have generally considered Banach spaces of real valued functions, but if we consider the analogous spaces of functions which may be complex valued and allow multiplication by complex numbers then Theorem 1.8 still applies. Thus, even if the operator A is originally defined only as a mapping from a space X of real valued functions into itself, A can be extended to the space $Z : \{x+iy : x, y \in X\}$. If viewed as an operator on Z, A may have complex eigenvalues. Such is precisely analogous

to the case of matrices with real entries, which may also have complex eigenvalues. If a linear operator is compact it must be continuous (another basic fact from functional analysis), and thus bounded in the sense that $||A|| = \sup\{||Ax||/||x|| : x \in X, x \neq 0\} < \infty$. If σ is an eigenvalue of A there must be $x \in X, \quad x \neq 0$, such that $Ax = \sigma x$, so $|\sigma| = ||Ax||/||x|| \leq ||A|| < \infty$. Thus, the set of eigenvalues of a compact operator is bounded. If L is an elliptic operator such that L^{-1} exists as a compact operator on a space X, then for each nonzero eigenvalue μ of L^{-1} we have $L^{-1}x = \mu x$ for some $x \in X, \ x \neq 0$, so that $Lx = (1/\mu)x$. Thus, the elliptic operator L will have eigenvalues corresponding to nonzero eigenvalues of EL^{-1}. If $L^{-1} : X \to Y$ is combined with an embedding $E : Y \to X$ so that EL^{-1} is compact then it turns out that it is still generally true that L will have eigenvalues corresponding to nonzero eigenvalues of EL^{-1}, but some care must be taken in the rigorous mathematical analysis because even if $EL^{-1} : X \to X$ the original operator L may only make sense on the subspace $Y \subseteq X$. This is not usually a problem because if $x \in X$ is an eigenvector for EL^{-1} corresponding to an eigenvalue $\mu \neq 0$ then $x = (1/\mu)EL^{-1}x = (1/\mu)L^{-1}x \in Y$ so Lx makes sense and $(1/\mu)x = Lx$.

In some of the applications we study we encounter the problem of solving equations of the form $Lu - \sigma u = f$ where σ is an eigenvalue of L. Since σ is an eigenvalue, the operator $L - \sigma I$ is not invertible, so we cannot expect to solve $Lu - \sigma u = f$ for arbitrary choices of f. On the other hand, the nullspace of $L - \sigma I$ is typically finite dimensional, so there will be many functions f for which $Lu - \sigma u = f$ has a solution. To address this problem we will need to use the notion of adjoint operators. Recall that if M is an $n \times n$ matrix of real numbers and $\vec{v}, \vec{w} \in I\!R^n$ we have $M\vec{v} \cdot \vec{w} = \vec{v} \cdot M^T \vec{w}$ where M^T is the transpose of M. In general, if H is a Hilbert space (that is, a Banach space whose norm $|| \cdot ||$ arises from the inner product $< \cdot, \cdot >$ as $||u|| = \sqrt{< u, u >}$) and $A : H \to H$ is a continuous (i.e. bounded) linear operator, then the adjoint of A is the operator A^* such that $< Au, v >=< u, A^*v >$ for any $u, v \in H$. In the case of differential operators there is an additional complication, which is that they generally cannot be formulated as continuous linear operators from a given Hilbert or Banach space into itself. For example, if we define the operator L as a differential operator of the form (1.107) acting on $C^{2+\alpha}(\overline{\Omega})$ then L does not map $C^{2+\alpha}(\overline{\Omega})$ into itself but rather into $C^{\alpha}(\overline{\Omega})$. If we attempt to define L on $C^{\alpha}(\overline{\Omega})$ we find that not all Hölder continuous functions have Hölder continuous partial derivatives, so we cannot define L as a map of all of $C^{\alpha}(\overline{\Omega})$ into $C^{\alpha}(\overline{\Omega})$, either. The problem of correctly formulating the adjoint operators of differential operators in a rigorous way as maps between Hilbert or Banach spaces can be resolved (see Kato (1966)), but we do not discuss it further here. In what follows we will sometimes need to use facts about adjoint operators in a technical way, but for many purposes it will suffice to consider the "formal" adjoints operators corresponding to differential operators. Roughly speaking, the formal adjoint of a differential operator is the representation that the actual adjoint operator relative to the Hilbert space $L^2(\Omega)$ would have on its domain of definition. We now introduce the notion of formal adjoint operators and discuss the relationship between solvability of $Lu - \sigma u = f$ when σ is an eigenvalue of L and the eigenfunctions of the formal adjoint operator. To do so we must also interpret the Sobolev space $W^{1,2}(\Omega)$ as a Hilbert space and formulate the problem $Lu = f$ in $W^{1,2}(\Omega)$.

The space $L^2(\Omega)$ is a Hilbert space with respect to the inner product

$$< u, v >_{0,2} = \int_{\Omega} uv dx \tag{1.131}$$

in the case where we require functions in $L^2(\Omega)$ to be real valued and use only real scalars,

or as

$$< u, v >_{0,2} = \int_\Omega u\overline{v}dx$$

where $\overline{v}$ denotes the complex conjugate of v in the case where functions in $L^2(\Omega)$ may be complex valued. The space $W^{1,2}(\Omega)$ is also a Hilbert space with respect to the inner product shown in (1.131) (or in the corresponding complex case, with v and ∇v replaced by $\overline{v}$ and $\nabla\overline{v}$) where ∇ is understood in the weak sense. The inner product in $W^{1,2}(\Omega)$ is sometimes denoted $< , >_{1,2}$. All Sobolev spaces built upon $L^2(\Omega)$, i.e. $W^{2,2}(\Omega)$, $W^{3,2}(\Omega)$, etc., can be viewed as Hilbert spaces in an analogous way. To compute the adjoint for an elliptic operator and to formulate an appropriate notion of a weak solution in $W^{1,2}(\Omega)$ we rewrite $< v, Lu >_{0,2}$ via the divergence theorem. For those purposes it is convenient to write the elliptic operator in the form

$$\begin{aligned} Lu = &\sum_{i,j=1}^{n} \frac{\partial}{\partial x_i}\left(a_{ij}(x)\frac{\partial u}{\partial x_j}\right) + \sum_{i=1}^{n}\frac{\partial}{\partial x_i}(B_i(x)u) \\ &+\sum_{i=1}^{n} b_i(x)\frac{\partial u}{\partial x_i} + c(x)u. \end{aligned} \tag{1.132}$$

We still assume $a_{ij} = a_{ji}$ and that (1.108) holds. If the coefficients a_{ij} and B_i are differentiable this form is equivalent to an operator of the form (1.107):

$$Lu = \sum_{i,j=1}^{n} a_{ij}\frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{n}\left(b_i + B_i + \sum_{j=1}^{n}\frac{\partial a_{ij}}{\partial x_j}\right)\frac{\partial u}{\partial x_i} + \left(c + \sum_{i=1}^{n}\frac{\partial B_i}{\partial x_i}\right)u. \tag{1.133}$$

Assuming for the moment that u and v are smooth, we have

$$\begin{aligned} \frac{\partial}{\partial x_i}\left(v\left[\sum_{j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j} + B_i u\right]\right) = \\ v\frac{\partial}{\partial x_i}\left(\sum_{j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j} + B_i u\right) + \frac{\partial v}{\partial x_i}\left(\sum_{j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j} + B_i u\right) \end{aligned}$$

so that by the divergence theorem

$$\begin{aligned} &\int_\Omega v\sum_{i=1}^{n}\frac{\partial}{\partial x_i}\left(\sum_{j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j} + B_i u\right)dx \\ &= \int_{\partial\Omega} v\sum_{i=1}^{n}\left[\left(\sum_{j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j}\right)\cdot n_i + B_i n_i u\right]dS \\ &\quad - \int_\Omega\left[\sum_{i,j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j}\frac{\partial v}{\partial x_i} + \sum_{i=1}^{n} B_i\frac{\partial v}{\partial x_i}u\right]dx \end{aligned} \tag{1.134}$$

where $\vec{n} = (n_1, \ldots, n_n)$ is the outward unit normal to $\partial\Omega$. If $(a_{ij}(x)) = d(x)I$ as in most of the problems we consider, then (1.134) becomes

$$\int_\Omega v\nabla \cdot \left[d(x)\nabla u + \vec{B}u\right] dx = \int_{\partial\Omega} v\left[d(x)\frac{\partial u}{\partial \vec{n}} + (\vec{B}\cdot\vec{n})u\right] dS - \int_\Omega [d(x)\nabla u \cdot \nabla v + (\vec{B}\cdot\nabla v)u]dx. \tag{1.135}$$

If we multiply Lu times v, integrate over Ω, and apply (1.134) to the first two terms we obtain the relation

$$\int_\Omega vLudx = \int_\Omega \left(-\sum_{i,j=1}^n a_{ij}\frac{\partial u}{\partial x_j}\frac{\partial v}{\partial x_i} - \sum_{i=1}^n B_i\frac{\partial v}{\partial x_i}u + \sum_{i=1}^n vb_i\frac{\partial u}{\partial x_i} + cuv\right)dx + \int_{\partial\Omega} v\sum_{i=1}^n\left[\left(\sum_{j=1}^n a_{ij}\frac{\partial u}{\partial x_j}\right)n_i + B_i n_i u\right]dS. \tag{1.136}$$

We can now define weak solutions of $Lu = f$ in $W^{1,2}(\Omega)$. We will need to use the space $W_0^{1,2}(\Omega)$. (Recall that $W_0^{1,2}(\Omega)$ is the closure in $W^{1,2}(\Omega)$ of the set $C_0^1(\Omega)$ of continuously differentiable functions on Ω which are zero except on some compact subset of Ω. Thus, functions in $W_0^{1,2}(\Omega)$ are zero on $\partial\Omega$ in a weak sense.) A function $u \in W^{1,2}(\Omega)$ is a weak solution of the problem (1.120), i.e. $Lu = f \in L^2(\Omega)$ and $u = g$ on $\partial\Omega$ in the sense that $g \in W^{1,2}(\Omega)$ and $u - g \in W_0^{1,2}(\Omega)$, provided

$$\int_\Omega \left[-\sum_{i,j=1}^n a_{ij}\frac{\partial u}{\partial x_j}\frac{\partial v}{\partial x_i} - \sum_{i=1}^n B_i\frac{\partial v}{\partial x_i}u + \sum_{i=1}^n b_i\frac{\partial u}{\partial x_i}v + cuv\right]dx = \int_\Omega vf dx \tag{1.137}$$

holds for all $v \in C_0^1(\Omega)$. The absence of a boundary term in (1.137) reflects the fact that functions in $C_0^1(\Omega)$ are zero in some neighborhood of $\partial\Omega$. Since $C_0^1(\Omega)$ is dense in $W_0^{1,2}(\Omega)$, the formula (1.137) extends to $v \in W_0^{1,2}(\Omega)$. It turns out that if $c + \sum_{i=1}^n \partial B_i/\partial x_i$ (the coefficient of the undifferentiated term in L as in (1.133)) is nonpositive in the weak sense then the problem $Lu = f$ in Ω, $u = g$ on $\partial\Omega$, will have a unique weak solution in $W^{1,2}(\Omega)$ with no additional conditions on $\partial\Omega$, but before stating a result to that effect we will give a weak formulation of another boundary value problem and define the formal adjoint L^* for L. We need to define L^* to state some of the results on the existence of solutions to $Lu = f$ and related problems.

The other boundary condition which is natural for an operator of the form L is

$$\sum_{i=1}^n\left(\sum_{j=1}^n a_{ij}\frac{\partial u}{\partial x_j}\right)n_i + (\vec{B}\cdot\vec{n})u + \gamma(x)u = g \quad \text{on} \quad \partial\Omega. \tag{1.138}$$

This condition may seem complicated but in the case $Lu = \nabla \cdot [d(x)\nabla u - \vec{V}(x)u]$ (which is most relevant to our models) the condition simply states that the flux $[-d(x)\nabla u + \vec{V}u]\cdot\vec{n}$ out of Ω across $\partial\Omega$ is given by a term γu proportional to the density together with an external source term g. Thus, if $\gamma = g = 0$ the boundary condition is a no-flux boundary condition while if $\gamma > 0$ but $g = 0$ the boundary condition says that the flux out of Ω across $\partial\Omega$ is proportional to the local density. Thus, (1.138) is a boundary condition which is relevant for our modeling purposes. The weak formulation for $Lu = f$ under the boundary condition (1.138) is

$$\begin{aligned}\int_{-\Omega}\left[-\sum_{i,j=1}^{n} a_{ij}\frac{\partial u}{\partial x_j}\frac{\partial v}{\partial x_i} - \sum_{i=1}^{n} B_i\frac{\partial v}{\partial x_i}u + \sum b_i\frac{\partial u}{\partial x_i}v + cuv\right]dx \\ = \int_{\Omega} vf\,dx + \int_{\partial\Omega} v[g-\gamma u]dS\end{aligned} \tag{1.139}$$

for any $v \in W^{1,2}(\Omega)$. (For the boundary condition (1.138) we require $\partial\Omega$ to be piecewise C^1 so that $\vec{n}$ is well defined almost everywhere on $\partial\Omega$. It is also possible to formulate boundary value problems where u is specified on part of $\partial\Omega$ and (1.138) holds on the remainder of $\partial\Omega$; see Gilbarg and Trudinger (1977).)

It is fairly easy to verify the form L^* should have, but it is less obvious what boundary conditions on v should be associated with L^* to ensure that $\int_{\Omega} uL^*v\,dx = \int vLu\,dx$ under a given set of boundary conditions on u. If we take

$$\begin{aligned}L^*v = \sum_{i,j=1}^{n}\frac{\partial}{\partial x_i}\left(a_{ij}\frac{\partial v}{\partial x_j}\right) - \sum_{i=1}^{n}\frac{\partial}{\partial x_i}(b_i v) \\ - \sum_{i=1}^{n} B_i\frac{\partial v}{\partial x_i} + cv\end{aligned} \tag{1.140}$$

we can calculate as in the derivation of (1.136) to obtain

$$\begin{aligned}\int_{\Omega} uL^*v\,dx = \int_{\Omega}\left(-\sum_{i,j=1}^{n} a_{ij}\frac{\partial u}{\partial x_i}\frac{\partial v}{\partial x_j} + \sum_{i=1}^{n} b_i\frac{\partial u}{\partial x_i}v - \sum_{i=1}^{n} uB_i\frac{\partial v}{\partial x_i} + cuv\right)dx \\ + \int_{\partial\Omega} u\sum_{i=1}^{n}\left[\left(\sum_{j=1}^{n} a_{ij}\frac{\partial v}{\partial x_i}\right)n_i - b_i n_i v\right]dS.\end{aligned} \tag{1.141}$$

Since $a_{ij} = a_{ji}$, the integrals over Ω on the right sides of (1.141) and (1.136) are the same. Thus we shall have $\int_{\Omega} uL^*v\,dx = \int_{\Omega} vLu\,dx$ if we can impose boundary conditions on v that correspond to those on u in such a way that the boundary integrals in (1.136) and (1.141) are the same. The simplest case is when Lu is augmented with the boundary condition $u = 0$. In that case we would simply restrict our attention to the subspace $W_0^{1,2}(\Omega)$ of $W^{1,2}(\Omega)$. Since functions in $W_0^{1,2}(\Omega)$ are zero on $\partial\Omega$ as far as integral formulas such as (1.136) and (1.141)

are concerned, the boundary integrals drop out so that $\int_\Omega vLudx = \int_\Omega uL^*vdx$ if L^* has the form (1.140). For boundary conditions of the form (1.138) (but in the homogeneous case where $g = 0$) the boundary integrals in (1.136) and (1.141) both reduce to $-\int_{\partial\Omega} \gamma uvdS$ if we impose the boundary condition

$$\sum_{i=1}^{n}\left[\left(\sum_{j=1}^{n} a_{ij}\frac{\partial v}{\partial x_j}\right)n_i\right] - \sum_{i=1}^{n} b_i n_i v + \gamma(x)v = 0. \tag{1.142}$$

In the case $Lu = \nabla\cdot[d(x)\nabla u - \vec{V}(x)u]$ with boundary conditions $[d(x)\nabla u - \vec{V}(x)u]\cdot\vec{n} + \gamma(x)u = 0$, the adjoint operator L^* will have boundary conditions $d(x)\partial v/\partial\vec{n} + \gamma(x)v = 0$ on $\partial\Omega$. In particular, no-flux boundary conditions on L lead to Neumann conditions on L^*. We can now state a result on solvability which embodies the eigenvalues of L. An eigenvalue of L is a number σ such that $L\sigma = \sigma\phi$ for some nonzero ϕ satisfying the boundary conditions of L. We will state the result in the case of homogeneous Dirichlet boundary conditions and then remark on how it should be modified for other boundary conditions.

Theorem 1.10. Suppose that $\Omega \subseteq I\!R^n$ is a bounded domain, that L has the form (1.132) with all coefficients bounded and measurable, and that (1.108) holds. The operator L has a countable discrete set $\Sigma \subseteq I\!R$ of real eigenvalues such that if $\sigma \notin \Sigma$, then the problems

$$Lu = \sigma u + f \quad \text{in} \quad \Omega, \quad u = 0 \quad \text{on} \quad \partial\Omega \tag{1.143}$$

and

$$L^*v = \sigma v + f \quad \text{in} \quad \Omega, \quad v = 0 \quad \text{on} \quad \partial\Omega \tag{1.144}$$

have unique solutions in $W^{1,2}(\Omega)$ for any $f \in L^2(\Omega)$. If $\sigma \in \Sigma$ then the operators $L - \sigma I$ and $L^* - \sigma I$ with homogeneous Dirichlet boundary conditions have finite dimensional nullspaces which contain nonzero elements. If $\sigma \in \Sigma$ the problem (1.143) is solvable if and only if

$$\int_\Omega f\phi^* dx = 0 \tag{1.145}$$

for all $\phi^* \in W_0^{1,2}(\Omega)$ with $L^*\phi^* = \sigma\phi^*$.

Remarks: Theorem 1.10 is a version of the Fredholm alternative. A similar version is given as Theorem 8.6 of Gilbarg and Trudinger (1977), but the notation used there is different. Note that Theorem 1.10 does not exclude the possibility of complex eigenvalues. In fact, operators satisfying the theorem may indeed have complex eigenvalues. Usually the condition of formal self-adjointness, i.e. $L = L^*$ in (1.136) and (1.141) and in their boundary conditions, implies that the eigenvalues are real.

As in the case of Theorems 1.2, 1.3, 1.5 and 1.6, if the coefficient of the undifferentiated term in Lu is nonpositive, then $\Sigma \subseteq (-\infty, 0)$ and in particular L is invertible. For operators

of the form (1.132) that coefficient is $c + \sum_{i=1}^{n} \partial B_i/\partial x_i$ (see (1.133)). If c or $\partial B_i/\partial x_i$ are not continuous on $\overline{\Omega}$ we may need to interpret nonpositivity in the weak sense; i.e. $\int_\Omega \left[cw - \sum_{i=1}^{n} B_i(\partial w/\partial x_i) \right] dx \leq 0$ for all $w \in C_0^1(\Omega)$ with $w \geq 0$.

If we want to determine the solvability of $Lu = \sigma u + f$ in Ω, $u = g$ on $\partial\Omega$, we would write $\tilde{u} = u - g$ and apply the Fredholm alternative to the problem $L\tilde{u} = \sigma\tilde{u} + f - Lg$ (formulated in the appropriate weak sense). A version of the Fredholm alternative including nonhomogeneous boundary conditions is given as part of Theorem 8.6 of Gilbarg and Trudinger (1977).

The homogeneous Dirichlet conditions on L and L^* may be replaced by homogeneous boundary conditions (1.138) for L and (1.142) for L^* and Theorem 1.10 will remain valid. In that case we would require $\partial\Omega$ to be piecewise C^1, and we would need to impose some additional conditions to conclude that $\Sigma \subseteq (-\infty, 0)$. If $c + \sum_{i=1}^{n} \partial B_i/\partial x_i \leq 0$ and either this last inequality is strict on an open subset of Ω or $\gamma(x) > 0$ on a relatively open subset of $\partial\Omega$ then we may conclude $\Sigma \subseteq (-\infty, 0)$.

The solutions whose existence is asserted in Theorem 1.10 may only be solutions in the weak sense if f and the coefficients of L are not continuous or if $\partial\Omega$ is not smooth. However, if L, f, and $\partial\Omega$ are smooth enough to apply the theory described in Theorems 1.2, 1.3, 1.5, and 1.6, then weak solutions are also classical solutions. Thus, if everything is smooth, the problem $Lu = \sigma u + f$ has a solution $u \in C^{2+\alpha}(\overline{\Omega})$ if and only if it has a solution in $W^{1,2}(\Omega)$. To see why this is so, note that if $u \in W^{1,2}(\Omega)$, then $u \in L^p(\Omega)$ for all $p < \infty$ if $n = 2$ or for $p < 2n/(n-2)$ if $n \geq 3$. (If $n = 1$, $u \in W^{1,2}([a, b])$ implies that $u \in C^{1/2}([a, b])$ by the calculation in (1.116).) If $u \in L^{p_0}(\Omega)$ then Theorem 1.5 (or 1.6) implies $u \in W^{2,p_0}(\Omega)$. Then by Theorem 1.7 we may conclude either $u \in L^{p_1}(\Omega)$ for some $p_1 > p_0$ or $u \in C^\alpha(\overline{\Omega})$ depending on n. If we can only conclude that $u \in L^{p_1}(\Omega)$ we still have $u \in W^{2,p_1}(\Omega)$ by Theorem 1.5 (or 1.6) so we have $u \in L^{p_2}(\Omega)$ for some $p_2 > p_1$ or $u \in C^\alpha(\overline{\Omega})$ by Theorem 1.7, again depending on n. If we repeat this argument enough times we eventually will get $u \in W^{2,p_k}(\Omega)$ where p_k is large enough that $W^{2,p_k}(\Omega)$ embeds in $C^\alpha(\overline{\Omega})$. Then by Theorem 1.1 (or 1.2) we have $u \in C^{2+\alpha}(\overline{\Omega})$.

Even if the coefficients of L are merely bounded and measurable and Ω merely satisfies a cone condition, the solution operator L^{-1} is a continuous map of $L^2(\Omega)$ into $W^{1,2}(\Omega)$, and $W^{1,2}(\Omega)$ embeds compactly in $L^2(\Omega)$ by Theorem 1.7, so we can view the solution operator as a compact operator on the Hilbert space $L^2(\Omega)$. Generally if L is formally self-adjoint we will have $< L^{-1}u, v > = < u, L^{-1}v >$ where $< , >$ is the inner product in $L^2(\Omega)$. In other words, L^{-1} is a symmetric compact operator on $L^2(\Omega)$. Such operators have many nice properties which we will sometimes exploit in our treatment of eigenvalues in Chapter 2.

For linear equations such as those defining eigenvalues for elliptic operators, the spaces $W^{1,2}(\Omega)$ and $L^2(\Omega)$ are adequate for most types of analysis. For nonlinear equations of the form $Lu = f(x, u)$ we generally want to work in either the Hölder spaces $C^\alpha(\overline{\Omega})$ or in $W^{2,p}(\Omega)$ for p large enough that $W^{2,p}(\Omega)$ embeds in $C^\alpha(\overline{\Omega})$. The reason is that nonlinear functions of $u \in L^2(\Omega)$ are not necessarily in $L^2(\Omega)$. (As an example consider $u(x) = x^{-1/3}$ on $(0, 1)$. We have $u \in L^2(\Omega)$ but $u^2 = x^{-2/3} \notin L^2(\Omega)$.) However, if $u \in C^\alpha(\overline{\Omega})$ then $f(x, u) \in C^\alpha(\overline{\Omega})$ if f is C^α in x and Lipschitz in u, and it follows that $f(x, u) \in L^p(\Omega)$ for all $p \in [1, \infty]$.

1.6.5 Reaction-Diffusion Models as Dynamical Systems

The models we want to study will usually have the form

$$\begin{aligned} &\frac{\partial u_i}{\partial t} = L_i u_i + f_i(x, u_1, \ldots, u_m) \text{ in } \quad \Omega \times (0, \infty) \\ &B_i u_i = 0 \qquad\qquad\qquad\quad \text{on} \quad \partial\Omega \times (0, \infty) \\ &u_i(x, 0) = w_i(x) \qquad\qquad \text{on} \quad \Omega, \end{aligned} \tag{1.146}$$

$i = 1, \ldots, m$ where for each i, L_i is elliptic and has the form (1.107), the operator B_i defines boundary conditions of the forms shown in (1.120) or (1.122), and L and Ω satisfy the hypotheses of Theorem 1.3. In some cases we will allow L_i and/or f_i to depend on t as well as x. Often we have $L_i u = \nabla \cdot [d_i(x)\nabla u - \vec{b}_i(x)u]$ or even simply $L_i u = d_i \nabla^2 u = d_i \Delta u$. Systems such as (1.146) are called parabolic in the terminology of partial differential equations. There are a number of ways to formulate the existence theory for systems such as (1.146). A classical approach based on *a priori* estimates analogous to those described in Theorems 1.1–1.3 is given by Friedman (1964). Treatments based on the theory of analytic semigroups of operators are given by Friedman (1976), Pazy (1983), and Henry (1981). A rather general version of existence theory has been developed by Amann (1988, 1989, 1990, and the references therein). For our purposes the key issue will be to verify that the system (1.146) generates a semiflow on an appropriate state space. Results to that effect are derived by Mora (1983). Here we just give a sketch of how such results are obtained, omitting the technical details, and state some of the most relevant results. A similar discussion is given in Cantrell et al. (1993a). In the context of systems such as (1.146) there is an important distinction between local and global solutions. A local solution is one that exists for some time interval $[0, T)$ where T is finite. A global solution exists for all $t > 0$. Generally, the way that a local solution can fail to be a global solution is by becoming infinite in a finite time. This occurs, for example, in the ordinary differential equation $du/dt = u^2$ if $u(0) > 0$. For the models we treat densities will generally remain bounded or at most grow exponentially, so the solutions will be global.

Before stating the results we will need about the system (1.146) and related models, we will briefly sketch the ideas behind the results. The usual setting for an abstract treatment of (1.146) is a situation in which we have a pair of Banach spaces X and Y with $X \subseteq Y$ and a linear operator $A : X \to Y$ with certain properties, including the continuity of A and of $(A - \lambda I)^{-1}$ for complex λ satisfying $Re\lambda \leq \Lambda_0$ for some Λ_0. For models such as (1.146) we would normally choose function spaces such as $Y = [L^p(\Omega)]^m$ and $X = \{u \in [W^{2,p}(\Omega)]^m : B_i u_i = 0 \text{ on } \partial\Omega \text{ for } i = 1, \ldots, m\}$, but allow the functions in X and Y to be complex. By subtracting a constant multiple cu_i of u_i from $L_i u_i$ and adding it to $f_i(x, \vec{u})$ we can rearrange (1.146) (if it is necessary) so that each of the operators L_i satisfies the hypotheses of Theorem 1.5 or 1.6. If we let A denote the $m \times m$ matrix of operators with the operators $-L_i$ on the diagonal and off diagonal entries all zero, it follows from Theorems 1.5 and/or 1.6 that A^{-1} exists as a bounded (i.e. continuous) operator from Y into X. Furthermore, the *a priori* estimates underlying Theorem 1.5 and 1.6, i.e. the inequalities $||u||_{2,p} \leq C(||u||_{0,p} + ||L_i y||_{0,p})$, imply that for $\lambda \in \mathbb{C}$ such that $|\lambda| \geq R_0$ for some fixed R_0 and for $-(\pi/2) - \delta < \arg\lambda < (\pi/2) + \delta$ for some $\delta > 0$, we have the estimate

$$||(A + \lambda I)^{-1} u||_Y \leq C||u||_Y/|\lambda|, \tag{1.147}$$

for some constant C independent of u (see Friedman (1976)). It follows from (1.147) that $-A$ generates an analytic semigroup of operators on Y, which is usually denoted e^{-tA}. (If we had a single equation with $L = \nabla^2 = \Delta$ we might write the semigroup as $e^{t\Delta}$.) By a semigroup of operators we mean a family $S(t)$ of operators defined for $t \geq 0$ and depending continuously on t such that for each $t \geq 0$, $S(t)$ is a continuous (i.e. bounded) linear operator from Y to Y, $S(0) = I$, and for $s, t \geq 0$, $S(s)S(t) = S(s+t)$. The operator $-A$ is called the infinitesimal generator of e^{-tA}. (The defining property of the infinitesimal generator B of a semigroup $S(t)$ is that $\lim_{h \to 0+} ([S(h)u - u]/h) = Bu$ for all u in the domain of B, where the limit is taken in the metric induced by the norm on Y.) Results asserting that elliptic operators generate analytic semigroups are discussed in detail by Friedman (1976) and Pazy (1983); see also Henry (1981). The key properties of e^{-tA} are that e^{-tA} defines a semigroup of operators which are continuous (i.e. bounded) on Y, and depend analytically on t for $t \in \mathbb{C}$ with $|\arg t| < \delta$, and for any such t the operators $d(e^{-tA})/dt$ and Ae^{-tA} are also continuous on Y with $d(e^{-tA}u)/dt = Ae^{-etA}u$ for any $u \in Y$. Furthermore, for $t \in \mathbb{C}$ with $|\arg t| < \delta$, we have

$$||Ae^{-tA}u||_Y \leq (C/|t|)||u||_Y \tag{1.148}$$

for $u \in Y$, for some constant C independent of u. (Again, see Friedman (1976), Pazy (1983), or Henry (1981).)

For the nonlinear case (1.146) it is natural to express the problem in an abstract form

$$\frac{du}{dt} = -Au + F(u), \quad u(0) = u_0 \in Y, \tag{1.149}$$

(where $F(u)$ is the matrix with terms $f_i(x, \vec{u})$ on the diagonal and with zeros everywhere else) and express the solution as

$$u(t) = e^{-tA}u_0 + \int_0^t e^{-(t-s)A}F(u(s))ds. \tag{1.150}$$

The problem with (1.150) is that it is not clear that solutions to (1.150) actually make sense in the context of (1.149). The difficulty is that if we apply A to both sides of (1.150) we obtain

$$Au = Ae^{-tA}u_0 + \int_0^t Ae^{-(t-s)A}F(u(s))ds, \tag{1.151}$$

and all we can say about the size of the term in the integral is that $||Ae^{-(t-s)A}F(u(s))|| \leq (c/|t-s|)||F(u(s))||_Y$. That creates a problem because $\int_0^t (1/|t-s|)ds$ does not converge. (If $u_0 \in X$ then $Ae^{-tA}u_0 = e^{-tA}(Au_0)$ is continuous as $t \to 0$, but the integral term remains a problem.) Fortunately, operators which generate analytic semigroups can be analyzed by methods taken from complex variable theory and the theory of Laplace transforms, and thus shown to have fractional powers which have some nice properties. Specifically, we have $||A^\gamma e^{-tA}u||_Y \leq (C/|t|^\gamma)||u||_Y$. Thus, if we apply A^γ to (1.150) we obtain

$$A^\gamma u = A^\gamma e^{-tA}u_0 + \int_0^t A^\gamma e^{-(t-s)A}F(u(s))ds, \tag{1.152}$$

and for $0 < \gamma < 1$ the integral term is well behaved if $F(u)$ is bounded in Y, because $\int_0^t [1/(t-s)^\gamma]ds$ converges if $0 < \gamma < 1$. Furthermore, we can define Banach spaces $X^\gamma \subseteq Y$ by taking X^γ to be the completion of X in Y with respect to the norm $||u||_\gamma = ||A^\gamma u||_Y$, and since A^{-1} is a compact operator on Y it follows that the embedding of X^{γ_1} into X^{γ_2} is compact if $\gamma_1 > \gamma_2$. Thus, we can use (1.150) to define a semiflow on X^γ for $\gamma \in (0, 1)$ provided $F(u(s))$ is smooth by using standard fixed point theorems, just as we might for a system of ordinary differential equations. Also, if we know that orbits which are bounded in X^{γ_2} are also bounded in X^{γ_1} for some $\gamma_1 > \gamma_2$ then we can conclude that bounded orbits in X^{γ_2} are precompact because of the compact embedding of X^{γ_1} into X^{γ_2}. (See Friedman (1976), Pazy (1983), and Henry (1981).) In fact, we can arrange (1.146) so that the operator e^{-tA} satisfies an estimate of the form $||e^{-tA}u||_y \leq Ce^{-\beta t}||u||_Y$ and $||A^\gamma e^{-tA}u||_Y \leq C(e^{-\beta t}/|t|^\gamma)||u||_Y$, so that if $F(u)$ is bounded in Y we have u bounded in X^γ via (1.151). In practice we will usually try to obtain bounds on $\vec{u}(t)$ in $[C(\overline{\Omega})]^m$, but such bounds imply bounds for $f_i(x, \vec{u})$ in $L^p(\Omega)$ for any $p \in [1, \infty]$ if the functions f_i are smooth, so it is generally sufficient to obtain bounds on $\vec{u}$ in $[C(\overline{\Omega})]^m$ to conclude that orbits for the system defined in (1.150) are bounded in X^γ for any $\gamma \in (0, 1)$ and hence are precompact in each space X^γ. Again, the details of this approach to parabolic equations and systems are discussed by Friedman (1976), Pazy (1983), and Henry (1981).

There are two remaining problems with this approach. First, it is not obvious what it means to have $\vec{u} \in X^\gamma$ in terms of the smoothness of $\vec{u}$; secondly, it is not obvious that solutions to (1.150) are classical solutions to (1.146). The first problem is relatively easy to resolve. If we start with $Y = [L^p(\Omega)]^m$ and $X \subseteq [W^{2,p}(\Omega)]^m$ then X^γ embeds in $[C^{1+\alpha}(\overline{\Omega})]^m$ if $0 < \alpha < 2\gamma - (n/p) - 1$. This fact and more precise results about the embeddings of X^γ into Hölder and Sobolev spaces follow from (Pazy, 1983, Theorem 4.3). To be sure that solutions to (1.150) are classical solutions to (1.146) we would need to assume that the functions $f_i(x, u)$ are Hölder continuous in x and at least Lipschitz in u, but in that case there are *à priori* estimates for parabolic equations analogous to the estimates underlying Theorems 1.1, 1.2, 1.5 and 1.6 for elliptic equations which show that solutions as defined by (1.150) are indeed classical solutions. Such estimates are discussed by Friedman (1964). The issue of smoothness is also discussed in Friedman (1976) and Pazy (1983). Thus, while the semiflows defined by (1.150) may need to be defined in X^γ, $C^{1+\alpha}(\overline{\Omega})$, or other subspaces of X^γ such as $C(\overline{\Omega})$ or $C^1(\overline{\Omega})$, the orbits $\vec{u}(t)$ will represent classical solutions of (1.146) if the functions f_i are smooth. All of the theoretical considerations discussed above can be extended in a natural way to the case where the operators L_i and the functions f_i depend on t, as long as all coefficients depending on t are uniformly Hölder continuous; see Friedman (1964, 1976). In that case the models will no longer generate semi-dynamical systems, because of the time dependence in the coefficients, but as we shall see in later chapters, there are ways to circumvent that problem in some cases.

We may now state some results on systems such as (1.146).

Theorem 1.11. Suppose that the domain Ω, operators L_i, and boundary conditions B_i in (1.146) satisfy the hypotheses of Theorem 1.3 for $i = 1, \ldots, m$. Suppose that for each $i = 1, \ldots, m$ the function $f_i(x, \vec{u})$ is measurable and is bounded uniformly in x if $\vec{u}$ is restricted to any bounded subset of $\mathbb{R}^m$, and $f_i(x, \vec{u})$ is Lipschitz continuous in $\vec{u}$, uniformly for $x \in \Omega$ and for $\vec{u}$ restricted to any bounded subset of $\mathbb{R}^m$. Let $Y = [L^p(\Omega)]^m$ for some $p > n$ and let $X = \{\vec{u} \in [W^{2,p}(\Omega)]^m : B_i u_i = 0 \text{ on } \partial\Omega \text{ for } i = 1, \ldots, m\}$. Let A be the matrix of operators with $-L_i$ as the ith diagonal element and with all off-diagonal

terms equal to zero. Let $X^\gamma \subseteq Y$ denote the space generated by A^γ for $\gamma \in (0, 1)$, so that $||u||_{X^\gamma} = ||A^\gamma u||_Y$. Then there exists a $\gamma_0 \in (0, 1)$ such that for $\gamma \in (\gamma_0, 1)$ the system (1.146) generates a local semiflow on X^γ. Bounded orbits in X^γ are precompact.

Remarks: This sort of result is discussed by Henry (1981, Ch. 3). The key points in the proof are as follows: the *a priori* estimates of Agmon et al. (1959), as used in Theorem 1.5 and 1.6, imply that $-A$ generates an analytic semigroup on $[W^{2,p}(\Omega)]^m$. The general theory of analytic semigroups allows us to formulate (1.146) as (1.150), and to define X^γ. Since $p > n$ we can choose γ_0 so that for $\gamma \in (\gamma_0, 1)$ we have $0 < 2\gamma - (n/p) - 1$ and hence X^γ embeds in $[C^{1+\alpha}(\overline{\Omega})]^m$ for some $\alpha > 0$ by Theorem 4.3 of Pazy (1983). The hypotheses on f_i imply that if $\vec{u} \in [C^{1+\alpha}(\overline{\Omega})]^m$ then $f_i \in L^p(\Omega)$ for all $p \geq 1$, so in particular $(f_1, \ldots, f_m) \in Y$. Thus, (1.152) makes sense and shows that (1.150) defines a semi-dynamical system on X^γ. Finally, since $(\lambda I - A)^{-1}$ exists as a linear compact operator on $[L^p(\Omega)]^n$ for λ real and sufficiently large (by Theorem 1.5 or 1.6), the embeddings $X^{\gamma_1} \hookrightarrow X^{\gamma_2}$ for $\gamma_> \gamma_2 > \gamma_0$ are compact, and the compactness of bounded orbits follows.

We may sometimes prefer to work in the more concrete spaces $C(\overline{\Omega})$ or $C^1(\overline{\Omega})$. We have the following.

Theorem 1.12. (Mora, 1983) Suppose that the hypotheses of Theorem 1.11 hold and that in addition the functions f_i are all C^2 in both x and $\vec{u}$, i.e. $f_i \in C^2(\overline{\Omega} \times \mathbb{R}^m)$ for each i. Then (1.146) generates a local semiflow on $[C(\overline{\Omega})]^m$ under Neumann boundary conditions. Under Dirichlet boundary conditions (1.146) generates a local semiflow on the subspaces of $[C(\overline{\Omega})]^m$ and of $[C^1(\overline{\Omega})]^m$ consisting of functions that are zero on $\partial\Omega$. Under Neumann or Robin conditions (1.146) generates a local semiflow on the subspace of $[C^1(\overline{\Omega})]^m$ consisting of functions satisfying the boundary conditions. In each case bounded orbits are precompact.

We usually work with semilinear models of the form (1.146), but we also consider logistic models with nonlinear diffusion of the form

$$\begin{aligned} &\frac{\partial u}{\partial t} = \nabla \cdot d(x, u)\nabla u + f(x, u) \text{ in } \quad \Omega \\ &u = 0 \qquad\qquad\qquad\qquad\qquad\quad \text{on } \quad \partial\Omega. \end{aligned} \tag{1.153}$$

It turns out that these models also generate local semiflows on fractional order Sobolev spaces $W^{s,p}(\Omega)$ where s is not necessarily an integer (see Adams, 1975), which have the property of embedding in $C^{1+\alpha}(\overline{\Omega})$, provided that $d(x, u)$ and $f(x, u)$ are C^2 in both x and u and that $d_0 \leq d(x, u)$ for some $d_0 > 0$. Such a result is derived by Amann (1986). Much more general results on quasilinear systems are given in more recent work by Amann (1988, 1989, 1990). Some other sources for discussions of reaction-diffusion models as dynamical systems are Hirsch (1988) and Smith (1995).

The results we have discussed so far on reaction-diffusion models as dynamical systems are local in time. In general, some additional information is required to conclude that a given orbit exists globally in time. For a semi-dynamical system on a Banach space Z in which bounded orbits are precompact it suffices to show that for each $T > 0$ there is a $B(T) < \infty$ so that $\sup\{||\vec{u}(t)||_Z : 0 \leq t < T\} \leq B(T)$ to conclude that the orbit $u(t)$ exists for all $t > 0$. In the models we consider it will suffice to show that $\sup\{|\vec{u}(x, t)| : x \in \overline{\Omega}, 0 \leq t < T\} < B(T)$ because the bound on $|\vec{u}|$ implies a bound in $[L^p(\Omega)]^m$ for any $p \in [1, \infty]$ and then (1.152) or analogous formulas imply boundedness in spaces X^γ which either play the role of state spaces for the semi-dynamical system or which

embed in $[C^{1+\alpha}(\overline{\Omega})]^m$, which in turn embeds in state spaces constructed from $[C(\overline{\Omega})]^m$ or $[C^1(\overline{\Omega})]^m$. For most of the models we consider it is relatively easy to get bounds on $|\vec{u}|$ via arguments based on the maximum principle or related comparison theorems, but in a few cases some work is required. Issues related to global existence are discussed by Henry (1981). See also Amann (1985, 1989), Fitzgibbon et al. (1992), Hollis and Morgan (1991), or Morgan (1990).

1.6.6 Classical Regularity Theory for Parabolic Equations

In some cases we may want to treat solutions to systems such as (1.146) from the viewpoint of classical partial differential equations. To that end we now discuss some results analogous to Theorems 1.1 and 1.2 for parabolic equations. Recall the definitions (1.117)–(1.119) for $C^{\alpha}(\overline{\Omega})$ and $C^{k+\alpha}(\overline{\Omega})$. For functions on $\overline{\Omega} \times [0, T]$ define

$$[f]_{\alpha,\alpha/2} = \sup_{\substack{(x,t),(y,s)\in\overline{\Omega}\times[0,T] \\ (x,t)\neq(y,s)}} \left(\frac{|f(x,t) - f(y,s)|}{|x-y|^{\alpha} + |t-s|^{\alpha/2}} \right). \tag{1.154}$$

Functions with $[\ ]_{\alpha,\alpha/2}$ finite form a Banach space $C^{\alpha,\alpha/2}(\overline{\Omega} \times [0, T])$ under the norm

$$||u||_{\alpha,\alpha/2} = \sup_{\overline{\Omega}\times[0,T]} |u(x,t)| + [u]_{\alpha,\alpha/2}. \tag{1.155}$$

Let ∂_x^{β} denote the derivative with respect to x corresponding to the multi-index $\beta = (\beta_1, \ldots, \beta_n)$, as in (1.119), and let ∂_t denote the derivative with respect to t. Define $C^{2+\alpha,1+\alpha/2}(\overline{\Omega} \times [0, T])$ to be the space of functions on $\overline{\Omega} \times [0, T]$ whose derivatives up to order two in x and order one in t are Hölder continuous, with norm

$$\begin{aligned} ||u||_{2+\alpha,1+\alpha/2} = \sup_{(x,t)\in\overline{\Omega}\times[0,T]} |u(x,t)| + \sum_{|\beta|\leq 2} \sup_{(x,t)\in\overline{\Omega}\times[0,1]} |\partial_x^{\beta} u(x,t)| \\ + \sup_{(x,t)\in\overline{\Omega}\times[0,T]} |\partial_t u(x,t)| + \sum_{|\beta|=2} [\partial_x^{\beta} u(x,t)]_{\alpha,\alpha/2} + [\partial_t u(x,t)]_{\alpha,\alpha/2}. \end{aligned} \tag{1.156}$$

The spaces $C^{\alpha,\alpha/2}(\overline{\Omega}\times[0, T])$ and $C^{2+\alpha,1+\alpha/2}(\overline{\Omega}\times[0, T])$ are Banach spaces; see Friedman (1964). We also will need to use the space $C^{1+\delta,\delta/2}(\overline{\Omega} \times [0, T])$ whose norm is given by

$$||u||_{1+\delta,\delta/2} = ||u||_{\delta,\delta/2} + \sum_{|\beta|=1} ||\partial_x^{\beta} u||_{\delta,\delta/2}. \tag{1.157}$$

We have:

Theorem 1.13. (Friedman, 1964) Suppose that $\partial\Omega$ is a bounded domain with $\partial\Omega$ of class $C^{2+\alpha}$ and that L is an elliptic operator of the form (1.107), satisfying (1.108), but with coefficients a_{ij}, b_i, and c which may depend on t as well as x. Suppose that a_{ij}, b_i, and $c \in C^{\alpha,\alpha/2}(\overline{\Omega}\times[0, T])$. If $f(x,t) \in C^{\alpha,\alpha/2}(\overline{\Omega}\times[0, T])$, $g(x,t) \in C^{2+\alpha,1+\alpha/2}(\overline{\Omega}\times[0, T])$, and $Lg = f$ for $t = 0$ and $x \in \partial\Omega$, then the problem

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu = f(x,t) \text{ in } \quad \Omega \times (0, T] \\ &u(x,t) = g(x,t) \qquad \text{on} \quad \partial\Omega \times [0, T] \cup (\Omega \times \{0\}) \end{aligned} \tag{1.158}$$

has a unique solution $u \in C^{2+\alpha,1+\alpha/2}(\overline{\Omega} \times [0,T])$ which satisfies

$$||u||_{2+\alpha,1+\alpha/2} \leq C(||f||_{\alpha,\alpha/2} + ||g||_{2+\alpha,1+\alpha/2}). \tag{1.159}$$

where C is a constant independent of f and g.

Remarks: Theorem 1.13 result is a version of Theorems 6 and 7 of Friedman (1964, Ch. 3.) See also Ladyzhenskaya et al. (1968). If the compatibility condition $Lg = f$ for $t = 0$ on $\partial\Omega$ is omitted the problem will still have a unique solution but it may not be smooth for $t = 0$. Ladyzhenskaya et al. (1968) also treat the case of boundary conditions analogous to (1.122). In that case we have the following result.

Theorem 1.14. Suppose that Ω, L, and f satisfy the hypotheses of Theorem 1.13. Suppose that $g(x) \in C^{2+\alpha}(\overline{\Omega})$ and $\gamma(x)$, $\beta(x)$, and $h(x) \in C^{1+\alpha}(\partial\Omega)$, with $\gamma \geq 0$ and $\beta > 0$ on $\partial\Omega$. Suppose also that $\gamma(x)g(x) + \beta(x)\partial g/\partial\vec{n} = h(x)$ on $\partial\Omega$. Then the problem

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu = f(x,t) && \text{in} \quad \Omega \times (0,T] \\ &u(x,0) = g(x) && \text{in} \quad \overline{\Omega} \\ &\gamma(x)u(x,t) + \beta(x)\frac{\partial u}{\partial \vec{n}}(x,t) = h(x) && \text{on} \quad \partial\Omega \times [0,T] \end{aligned} \tag{1.160}$$

has a unique solution in $C^{2+\alpha,1+\alpha/2}(\overline{\Omega} \times [0,T])$ which satisfies

$$||u||_{2+\alpha,1+\alpha/2} \leq C(||f||_{\alpha,\alpha/2} + ||g||_{2+\alpha} + ||h||_{1+\alpha}) \tag{1.161}$$

where the norm on h is taken $C^{1+\alpha}(\partial\Omega)$ and the norm of g is taken in $C^{2+\alpha}(\overline{\Omega})$, and the constant C independent of f, g, and h.

For certain convergence arguments an additional *a priori* estimate called a $1+\delta$ estimate (Friedman, 1964, Theorem 4 of Ch. 7) is also needed. A version of this result is:

Lemma 1.15. (Friedman, 1964) Suppose that Ω and L satisfy the hypotheses of Theorem 1.13 with the additional condition that the coefficients a_{ij} are uniformly Lipschitz in $\overline{\Omega} \times [0,T]$. Suppose that $f(x,t)$ is continuous on $\overline{\Omega} \times [0,T]$ with $f(x,0) = 0$ on $\partial\Omega$. Then for any $\delta < 1$ there is a constant C independent of $f(x,t)$ such that any solution of

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu = f(x,t) \text{ in} \quad \Omega \times (0,T] \\ &u(x,t) = 0 \qquad\quad \text{on} \quad (\partial\Omega \times (0,T]) \cup (\overline{\Omega} \times \{0\}) \end{aligned} \tag{1.162}$$

satisfies

$$||u||_{1+\delta,\delta/2} \leq C \sup_{(x,t)\in\overline{\Omega}\times[0,T]} |f(x,t)|. \tag{1.163}$$

Remarks: The analogous result is valid if the boundary condition $u = 0$ on $\partial\Omega \times (0,T]$ is replaced with the boundary condition $\gamma(x)u + \beta(x)\partial u/\partial\vec{n} = 0$ on $\partial\Omega \times (0,T]$ with γ and β as in Theorem 1.14. See Friedman (1964, Ch. 7).

Theorem 1.13 and Lemma 1.15 and the corresponding results for Robin boundary conditions imply that the trajectories of the semi-dynamical systems whose existence is asserted in Theorem 1.11 actually correspond to classical solutions of (1.146) if $\partial\Omega$, f_i,

and the coefficients of L_i and B_i are sufficiently smooth. (Theorem 1.13 and Lemma 1.15 are stated for a single parabolic equation but can be applied to (1.146) componentwise because in the system (1.146) there is no coupling between equations in the terms involving derivatives.)

1.6.7 Maximum Principles and Monotonicity

Methods based on comparisons between different solutions of a reaction-diffusion model or between solutions of different models play an important role in the mathematical theory of reaction-diffusion models. Comparisons between solutions are made possible by maximum principles, which typically place restrictions on the nature and location of maximum and minimum points of solutions to partial differential equations. Maximum principles for classical solutions are treated in detail by Protter and Weinberger (1967) and Walter (1970). Extensions to weak solutions are discussed by Gilbarg and Trudinger (1977). Maximum principles are the basis of theoretical approaches to reaction-diffusion models based on monotone iteration (Leung, 1989, Pao, 1992) or monotone semi-dynamical systems (Hirsch, 1988b; Hess, 1991; Smith, 1995).

A version of the maximum principle for elliptic equations is as follows (see Protter and Weinberger (1967)).

Theorem 1.16. Suppose that the operator L has the form (1.107) and satisfies (1.108), with $c(x) \leq 0$. Suppose that $\Omega \subseteq I\!R^n$ is a bounded domain and the coefficients of L are uniformly bounded on Ω.

(i) Suppose that $u \in C^2(\Omega)$ and $Lu \geq 0$ in Ω. If u attains a maximum $M \geq 0$ at any point in the interior of Ω then $u(x) \equiv M$ in Ω.

(ii) Suppose further that $u \in C^2(\Omega) \cap C(\overline{\Omega})$ and that each point on $\partial\Omega$ lies on the boundary of some ball contained in Ω. If $u(x) = M$ at some point $x_0 \in \partial\Omega$ for which $\partial u/\partial \vec{n}$ exists, then either $\partial u/\partial \vec{n} > 0$ at x_0 or $u(x) \equiv M$ in Ω.

Remark: The geometric condition on $\partial\Omega$ in (ii) will hold if $\partial\Omega$ is of class $C^{2+\alpha}$. If $u \in C^{2+\alpha}(\overline{\Omega})$ then $u \in C^2(\Omega) \cap C(\overline{\Omega})$. The corresponding results hold in the case of a minimum $M \leq 0$. In that case if $u(x) = M \leq 0$ at a point $x_0 \in \partial\Omega$ then either $\partial u/\partial \vec{n} < 0$ at x_0 or $u(x) \equiv M$ in Ω. In some cases the condition $c \leq 0$ can be weakened but counter-examples show that some restrictions on c are necessary; see Protter and Weinberger (1967).

The maximum principle has various implications. Suppose $u_1, u_2 \in C^2(\Omega) \cap C(\overline{\Omega})$ are solutions of $Lu = f(x)$ in Ω and $u_1 - u_2 = 0$ on $\partial\Omega$. If L satisfies the hypotheses of Theorem 1.16 then $u_1 - u_2$ cannot have a positive maximum M inside Ω, because then we would have $u_1 - u_2 \equiv M > 0$ in Ω so that $u_1 - u_2 \equiv M > 0$ on $\partial\Omega$. Hence $u_1 - u_2 \leq 0$ in Ω. Similarly, $u_1 - u_2$ cannot have a negative minimum inside Ω, so that $u_1 - u_2 \geq 0$ in Ω. It follows that $u_1 = u_2$, so that the solution to $Lu = f$ is unique. A similar analysis using part (ii) of Theorem 1.16 applies to the case of boundary conditions of the form $\gamma(x)u + \beta(x)\partial u/\partial \vec{n} = g$ on $\partial\Omega$ if $\gamma \geq 0$ and $\beta > 0$ on $\partial\Omega$. These observations explain the condition $c(x) \leq 0$ in Theorems 1.1 and 1.3. If $c(x) \leq 0$ then the maximum principle implies that the solution $u \equiv 0$ to the homogeneous problem $Lu = 0$ in Ω, $u = 0$ (or $\gamma u + \beta \partial u/\partial \vec{n} = 0$) on $\partial\Omega$ is unique, so in that case Theorems 1.1 and 1.2 follow from Theorem 1.3. If $-Lu \geq 0$ in Ω then since $Lu \leq 0$ in Ω the maximum principle implies that u cannot have a nonpositive minimum M inside Ω unless $u \equiv M$. If $u \geq 0$ on $\partial\Omega$

then we must have $u \geq 0$ on Ω, with $u > 0$ on Ω unless $u \equiv 0$. If $Lu_1 \leq Lu_2$ in Ω and $u_1 \geq u_2$ on $\partial\Omega$, then $-L(u_1 - u_2) \geq 0$ in Ω and $u_1 - u_2 \geq 0$ on $\partial\Omega$, so $u_1 \geq u_2$ on Ω. These applications of the maximum principle are representative but far from exhaustive. In some cases it is convenient to use the ideas behind Theorem 1.16 rather than the theorem itself. For example, suppose that u is an equilibrium of a diffusive logistic equation, so that $0 = \nabla \cdot d(x)\nabla u + r[1 - (u/K)]u$ in Ω, and that $u = 0$ on $\partial\Omega$. If u is continuous on $\overline{\Omega}$ then u must attain a maximum somewhere in $\overline{\Omega}$. If u has a maximum $M > K$ at some point $x^* \in \Omega$ then for $x = x^*$ we must have $\partial u/\partial x_i = 0$ and $\partial^2 u/\partial x_i^2 \leq 0$ for $i = 1, \ldots, n$; but then for $x = x^*$ we have $0 \leq -\nabla \cdot d(x)\nabla u = r[1 - (M/K)]M < 0$, which is a contradiction. Thus, since $u = 0 < K$ on $\partial\Omega$, we must have $u \leq K$ for $x \in \Omega$.

The maximum principle extends to parabolic equations. In fact, some results based on the maximum principle for parabolic equations are valid without the hypothesis $c \leq 0$ required for the elliptic case.

Theorem 1.17. Suppose that L has the form (1.107) but with coefficients that may depend on t. Suppose that (1.108) holds and $c(x, t) \leq 0$. Let $\Omega \subseteq \mathbb{R}$ be a bounded domain and suppose that the coefficients of L are uniformly bounded on $\Omega \times (0, T]$.

(i) Suppose that $u \in C^{2,1}(\Omega \times (0, T])$, that is, the first derivative of u with respect to t and the derivatives of u of order 2 or less in the space variables are continuous on $\Omega \times (0, T]$. Suppose that $\partial u/\partial t - Lu \leq 0$ in $\Omega \times (0, T]$. If u attains a maximum $M \geq 0$ at a point $(x_0, t_0) \in \Omega \times (0, T]$, then $u(x, t) \equiv M$ on $\Omega \times (0, t_0]$.

(ii) Suppose further that $u \in C^{2,1}(\Omega \times (0, T]) \cap C(\overline{\Omega} \times (0, T])$, and that each point of $\partial\Omega$ lies on the boundary of some ball lying inside Ω. If $u(x_0, t_0) = M$ at some point of $\partial\Omega \times (0, T]$ for which $\partial u/\partial\vec{n}$ exists, then either $\partial u/\partial\vec{n} > 0$ at (x_0, t_0) or $u \equiv M$ on $\overline{\Omega} \times (0, t_0]$.

Remarks: Clearly if $u \in C(\Omega \times [0, T])$ then the conclusion $u \equiv M$ extends to $\Omega \times [0, t_0]$ in (i) and (ii). Results of this type are discussed by Protter and Weinberger (1967); see also Friedman (1964) and Leung (1989). As in the elliptic case, if $u_t - Lu \geq 0$ then u cannot attain a minimum $M \leq 0$ at a point $(x_0, t_0) \in \Omega \times (0, T]$ unless $u \equiv M$ on $\Omega \times (0, t_0]$, and similarly if $u(x_0, t_0) = M$ at a point $(x_0, t_0) \in \partial\Omega \times (0, T]$ then either $\partial u/\partial\vec{n} < 0$ at (x_0, t_0) or $u(x, t) \equiv M$ in $\Omega \times (0, t_0]$.

Corollary 1.18. Suppose that L and $\Omega \times (0, T]$ satisfy the hypotheses of Theorem 1.17 except for the requirement $c(x, t) \leq 0$. Suppose that $\gamma(x)$ and $\beta(x)$ are bounded functions on $\partial\Omega$ with $\gamma(x) \geq 0$ and $\beta(x) > 0$. If $u(x, t) \in C^{2,1}(\Omega \times (0, T]) \cap C(\overline{\Omega} \times [0, T])$ with $u_t - Lu \geq 0$ on $\Omega \times (0, T]$ and $\gamma(x)u(x, t) + \beta(x)\partial u(x, t)/\partial\vec{n} \geq 0$ on $\partial\Omega \times (0, T]$ or $u \geq 0$ on $\partial\Omega \times (0, T]$, then either $u(x, t) > 0$ on $\Omega \times (0, T]$ or $u(x, t) \equiv 0$ on $\overline{\Omega} \times [0, t_0]$ for some $t_0 > 0$. If $u(x, 0) > 0$ for some $x \in \Omega$, or if there is a $t_1 > 0$ such that for each $t \in (0, t_1)$ either $u(x, t) > 0$ or $\gamma u(x, t) + \beta\partial u(x, t)/\partial\vec{n} > 0$ for some $x \in \partial\Omega$, then $u(x, t) > 0$ in $\Omega \times (0, T]$.

Remarks: To eliminate the requirement $c \leq 0$ introduce the new variable $w = e^{-kt}u$. Then w satisfies $w_t - (Lw - kw) = e^{-kt}(u_t - Lu) \geq 0$. If we choose k large enough then $c - k \leq 0$ so that Theorem 1.17 applies to w. If $w < 0$ then w must have a negative minimum M on $\overline{\Omega} \times (0, T]$, but then $w \equiv M < 0$ on $[0, t_0] \times \overline{\Omega}$ for some $t_0 > 0$, contradicting the hypothesis $w(x, 0) = u(x, 0) \geq 0$. Hence $w \geq 0$, and thus $u \geq 0$. If $w = 0$ at any point $(x, t) \in \Omega \times (0, T]$ then Theorem 1.17 implies $w \equiv 0$ on $\overline{\Omega} \times [0, t_0]$, which implies $u \equiv 0$

on $\overline{\Omega} \times [0, t_0]$. If $u(x, 0) > 0$ for some $x \in \Omega$ or either $u(x, t) > 0$ or $\gamma u + \beta \partial u/\partial \vec{n} > 0$ for some $x \in \partial\Omega$ for $t \in [0, t_1]$ then $u \not\equiv 0$ on $\overline{\Omega} \times [0, t_0]$ so we must have $w > 0$ and hence $u > 0$ on $\Omega \times (0, T]$.

An important feature of maximum principles is that they permit comparisons between solutions.

Theorem 1.19. Suppose that L and Ω satisfy the hypotheses of Theorem 1.17 with $c(x, t) \equiv 0$. Suppose that $f(x, t, u), \quad \partial f(x, t, u)/\partial u \in C(\overline{\Omega} \times [0, T] \times I\!R)$. If $\overline{u}, \underline{u} \in C^{2,1}(\overline{\Omega} \times (0, T]) \cap C(\overline{\Omega} \times [0, T]$ with

$$\frac{\partial \overline{u}}{\partial t} - L\overline{u} \geq f(x, t, \overline{u}) \quad \text{in} \quad \Omega \times (0, T], \tag{1.164}$$

$$\frac{\partial \underline{u}}{\partial t} - L\underline{u} \leq f(x, t, \underline{u}) \quad \text{in} \quad \Omega \times (0, T], \tag{1.165}$$

$\overline{u}(x, 0) \geq \underline{u}(x, 0)$ on Ω, and either $\overline{u}(x, t) \geq \underline{u}(x, t)$ or

$$\gamma(x)\overline{u} + \beta(x)\frac{\partial \overline{u}}{\partial \vec{n}} \geq \gamma(x)\underline{u} + \beta(x)\frac{\partial \underline{u}}{\partial \vec{n}} \quad (\gamma \geq 0, \beta > 0)$$

on $\partial\Omega \times (0, T]$, then either $\overline{u} \equiv \underline{u}$ or $\overline{u} > \underline{u}$ on $\Omega \times (0, T]$.

Remarks: Theorem 1.19 follows from Corollary 1.18 by setting $u = \overline{u} - \underline{u}$ so that $\partial u/\partial t - Lu - c(x, t)u \geq 0$, where $c(x, t) = [f(x, t, \overline{u}) - f(x, t, \underline{u})]/(\overline{u} - \underline{u})$ is bounded because $\partial f/\partial u$ is continuous. Results of this type are discussed by Protter and Weinberger (1967), Walter (1970), Fife (1979), Smoller (1982), Leung (1989) and Pao (1992). Comparison theorems such as Theorem 1.19 provide the technical basis for applying the theory of monotone dynamical systems to reaction-diffusion models, as in the work of Hirsch (1988), Smith (1995) and others. Similar results can be obtained for elliptic equations but in that case the condition $c(x) \leq 0$ cannot be completely eliminated, so some additional condition on f is needed. It suffices to assume that $\partial f/\partial u \leq 0$ since $f(x, \overline{u}) - f(x, \underline{u}) = [\partial f(x, \xi)/\partial u](\overline{u} - \underline{u})$ by the mean value theorem. (In general ξ depends on x.) Analogous results hold for systems of reaction-diffusion equations.

Theorem 1.20. Suppose that Ω and the operators $L_i, \ i = 1, \ldots, m$ satisfy the hypotheses of Theorem 1.17, with the coefficient c_i of the undifferentiated term in L_i equal to zero for each i. Suppose that for each i the functions $f_i(x, t, \vec{u})$ and $\partial f_i(x, t, \vec{u})/\partial u_j, \ j = 1, \ldots, m$, belong to $C(\overline{\Omega} \times [0, T] \times I\!R)$, and that

$$\partial f_i/\partial u_j \geq 0 \quad \text{for} \quad i \neq j. \tag{1.166}$$

If $\vec{w} = (w_1, \ldots, w_m)$ and $\vec{v} = (v_1, \ldots v_m)$ satisfy

$$\frac{\partial w_i}{\partial t} - L_i w_i \geq f_i(x, t, \vec{w}) \quad \text{in} \quad \Omega \times (0, T], \tag{1.167}$$

$$\frac{\partial v_i}{\partial t} - L_i v_i \leq f_i(x, t, \vec{v}) \quad \text{in} \quad \Omega \times (0, T], \tag{1.168}$$

with

$$w_i(x, 0) \geq v_i(x, 0) \quad \text{on} \quad \Omega,$$

and either

$$w_i \geq v_i \quad \text{on} \quad \partial\Omega \times (0, T]$$

or

$$\gamma_i(x) w_i + \beta_i(x) \frac{\partial w_i}{\partial \vec{n}} \geq \gamma_i(x) v_i + \beta_i(x) \frac{\partial v_i}{\partial \vec{n}} \ (\gamma_i \geq 0, \beta_i > 0) \quad \text{on} \quad \partial\Omega \times (0, T]$$

for $i = 1, \ldots, m$, then $w_i \geq v_i$ in $\Omega \times (0, T]$ for $i = 1, \ldots, m$.

Remarks: Condition (1.166) is sometimes called a Kamke condition or quasimonotone condition. Systems satisfying (1.166) are called cooperative. Condition (1.166) is used in the theory of systems of ordinary differential equations in results analogous to Theorem 1.20; see Hirsch (1982) or Smith (1995). In Theorem 1.20 it is possible to have $w_i > v_i$ for some components but $w_j \equiv v_j$ for others. Results analogous to Theorem 1.20 can be derived for elliptic systems but require some additional hypotheses on the functions f_i; see Protter and Weinberger (1967). Other references include Walter (1970), Fife (1979), Smoller (1982), and Smith (1995).

Certain systems which do not satisfy (1.166) still admit comparison principles. Those include many models for two competing species. Suppose that u_1 and u_2 satisfy

$$\partial u_i / \partial t - L_i u_i = f_i(x, t, u_1, u_2) \quad \text{for} \quad i = 1, 2, \tag{1.169}$$

with $\partial f_1 / \partial u_2 \leq 0$ and $\partial f_2 / \partial u_1 \leq 0$ and with the operators L_i as in Theorem 1.20. If we let $\tilde{u}_2 = k - u_2$ for some constant k then we have

$$\begin{aligned} \partial u_1 / \partial t - L_1 u_1 &= \tilde{f}_1(x, t, u_1, \tilde{u}_2) = f_1(x, t, u_1, k - \tilde{u}_2) \\ \partial \tilde{u}_2 / \partial t - L_2 \tilde{u}_2 &= \tilde{f}_2(x, t, u_1, \tilde{u}_2) = -f_2(x, t, u_1, k - \tilde{u}_2) \end{aligned} \tag{1.170}$$

so that $\partial \tilde{f}_1 / \partial \tilde{u}_2 = -\partial f_1 / \partial u_2 \geq 0$ and $\partial \tilde{f}_2 / \partial u_1 = -\partial f_2 / \partial u_1 \geq 0$. Thus the system (1.169) can be converted to a system (1.170) which satisfies Theorem 1.20. Thus, if (w_1, w_2) and (v_1, v_2) are solutions of (1.169) satisfying homogeneous boundary conditions and $w_1 \geq v_1$, $w_2 \leq v_2$ for $t = 0$ then $w_1 \geq v_1$ and $w_2 \leq v_2$ for all $t > 0$. Models for more than two competitors and predator-prey models usually cannot be converted into forms satisfying Theorem 1.20.

If the functions $\underline{u}, \overline{u}$ satisfy the hypotheses of Theorem 1.19, or if the vector valued functions $\vec{v}, \vec{w}$ satisfy the hypotheses of Theorem 1.20, we say that $\underline{u}$ and $\vec{v}$ are subsolutions (or lower solutions) and $\overline{u}$ and $\vec{w}$ are supersolutions (or upper solutions) for their respective models. Sub- and supersolutions can be used in various ways to show the existence of solutions to reaction-diffusion equations and systems and the elliptic equations and systems describing their equilibria. Some versions of the existence theory for systems do not require the condition (1.166). Existence theory via sub- and supersolutions is treated in detail by Leung (1989) and Pao (1992). In the case of equations or systems satisfying comparison principles such as Theorems 1.19 and 1.20, sub- and supersolutions can be used to construct iteration schemes consisting of sequences of linear problems whose solutions converge monotonically to solutions of the original nonlinear problem; see Leung (1989) and Pao (1992). If each of the functions f_i is either monotone increasing or monotone decreasing in u_j for $j \neq i$ then it may still be possible to construct monotone iteration schemes from

sub- and supersolutions but such schemes may be more complicated. (Systems in which each function f_i is monotone increasing or monotone decreasing in u_j for $j \neq i$ can be embedded in larger systems for which (1.166) is satisfied; see for example Cosner (1997).) Finally, existence of solutions can be deduced from the existence of sub- and supersolutions without any monotonicity assumptions on f_i by methods based on the Schauder fixed point theorem. (Applications of the Schauder fixed point theorem typically require that the solution operators $(\partial/\partial t - L)^{-1}$ or L^{-1} be compact, but that follows from the regularity properties of elliptic and parabolic operators.) All of these ideas and more are discussed by Leung (1989) and Pao (1992). A simple result on existence via sub- and supersolutions is the following.

Proposition 1.21. Suppose that L, Ω, and f satisfy the hypotheses of Theorem 1.19. Suppose that L and Ω also satisfy the hypotheses of Theorem 1.13 and that $f(x,t,u)$ is Hölder continuous with exponent α with respect to x and exponent $\alpha/2$ with respect to t. Suppose that $h(x) \in C^{2+\alpha}(\overline{\Omega})$ with $Lh = f(x,0,0)$ on $\partial\Omega$, and that $\overline{u}$ and $\underline{u}$ satisfy (1.164), (1.165) respectively with

$$\underline{u}(x,0) \leq h(x) \leq \overline{u}(x,0) \quad \text{on} \quad \overline{\Omega} \times \{0\}$$

and

$$\underline{u}(x,t) \leq 0 \leq \overline{u}(x,t) \quad \text{on} \quad \partial\Omega \times [0,T].$$

Then the problem

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu = f(x,t,u) \text{ in} \quad \Omega \times (0,T] \\ &u = 0 \qquad\qquad\qquad\quad \partial\Omega \times (0,T] \\ &u(x,0) = h(x) \qquad\quad \text{on} \quad \overline{\Omega} \times \{0\} \end{aligned} \tag{1.171}$$

has a solution $u^* \in C^{2+\alpha,1+\alpha/2}(\overline{\Omega} \times [0,T])$ with $\underline{u}(x,t) \leq u^*(x,t) \leq \overline{u}(x,t)$.

Remarks: If the compatibility condition $Lh = f(x,0,0)$ on $\partial\Omega$ is omitted then u^* still will exist but may not be smooth for $t = 0$. Analogous results hold for boundary conditions $\gamma u + \beta \partial u/\vec{n} = 0$. Theorem 1.19 implies that $\underline{u} \leq \overline{u}$ on $\overline{\Omega} \times [0,T]$ and that u^* is unique. Results similar to Proposition 1.21 hold for the corresponding elliptic problems $-Lu = f(x,u)$ in Ω, $u = g(x)$ on $\partial\Omega$ (or $\gamma(x)u + \beta(x)\partial u/\partial\vec{n} = g(x) \quad$ on $\quad \partial\Omega$) but in the elliptic case we must require $\overline{u}(x) \leq \overline{u}(x)$ as an additional hypothesis, and u^* is not necessarily unique.

Sketch of Proof: Choose a constant C large enough that $\partial f/\partial u + C \geq 0$ on $\overline{\Omega} \times [0,T]$ for $\underline{u} \leq u \leq \overline{u}$. To construct the iteration let $\underline{u}^0 = \underline{u}$, $\overline{u}^0 = \overline{u}$, and define $\underline{u}^k$ and $\overline{u}^k$ recursively as the solutions of

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu + Cu = f(x,t,\underline{u}^{k-1}) + C\underline{u}^{k-1} \text{ in} \quad \Omega \times (0,T] \\ &u = 0 \qquad\qquad\qquad\qquad\qquad\quad \text{on} \quad \partial\Omega \times (0,T] \\ &u(x,0) = h(x) \qquad\qquad\qquad\quad \text{in} \quad \overline{\Omega} \times \{0\} \end{aligned}$$

and

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu + Cu = f(x,t,\overline{u}^{k-1}) + C\overline{u}^{k-1} \text{ in } \quad \Omega \times (0,T] \\ &u = 0 \qquad\qquad\qquad\qquad\qquad\qquad\quad \text{on } \quad \partial\Omega \times (0,T] \\ &u(x,0) = h(x) \qquad\qquad\qquad\qquad\quad \text{in } \quad \overline{\Omega} \times \{0\} \end{aligned}$$

respectively. If we let $v^k = \underline{u}^k - \underline{u}^{k-1}$ then we have

$$\begin{aligned} &\frac{\partial v^1}{\partial t} - Lv^1 + Cv^1 \geq 0 \quad \text{in } \quad \Omega \times (0,T] \\ &v^1 \geq 0 \qquad\qquad\qquad\quad \text{on } \quad (\partial\Omega \times (0,T]) \cup (\overline{\Omega} \times \{0\}) \end{aligned}$$

so $v^1 \geq 0$ in $\Omega \times (0,T]$ by Theorem 1.19. If $v^k \geq 0$ then $\underline{u}^k \geq \underline{u}^{k-1}$ so

$$\begin{aligned} &\frac{\partial v^{k+1}}{\partial t} - Lv^{k+1} + Cv^{k+1} = f(x,t,\underline{u}^k) - f(x,t,\underline{u}^{k-1}) + C(\underline{u}^k - \underline{u}^{k-1}) \\ &\geq 0 \quad \text{in } \quad \Omega \times (0,T] \end{aligned}$$

and $v^{k+1} = 0$ on $(\partial\Omega \times (0,T]) \cup (\overline{\Omega} \times \{0\})$ so $v^{k+1} \geq 0$ by Theorem 1.19. Hence by induction $v^k \geq 0$ for all $k \geq 1$, so that $\underline{u}^k \geq \underline{u}^{k-1}$. Similarly, since $\bar{u}^k$ is the solution of

$$\begin{aligned} &\frac{\partial u}{\partial t} - Lu + Cu = f(x,t,\overline{u}^{k-1}) + C\overline{u}^{k-1} \text{ in } \quad \Omega \times (0,T] \\ &u = 0 \qquad\qquad\qquad\qquad\qquad\qquad\quad \text{on } \quad \partial\Omega \times (0,T] \\ &u(x,0) = h(x) \qquad\qquad\qquad\qquad\quad \text{on } \quad \overline{\Omega} \times \{0\}, \end{aligned}$$

arguments similar to those shown above imply via induction that $\overline{u}^{k+1} \leq \overline{u}^k$ and that for each k $\underline{u}^k \leq \overline{u}^k$. Since $\{\underline{u}^k\}$ is increasing and bounded above, $\{\underline{u}^k\}$ converges pointwise. The convergence of $\{\underline{u}^k\}$ in $C^{2+\alpha,1+\alpha/2}(\overline{\Omega} \times [0,T])$ follows via parabolic regularity, i.e. by Lemma 1.17 and Theorem 1.13. Hence $\{\underline{u}^k\}$ converges to a solution of (1.171). (The sequence $\{\overline{u}^k\}$ also converges to a solution of (1.171).)

Remarks: In the elliptic case we would require $\underline{u} \leq \overline{u}$ on Ω, and the inequalities (1.164) and (1.165) would be replaced by $-L\overline{u} \geq f(x,\overline{u})$ on Ω, $-L\underline{u} \leq f(x,\underline{u})$ on Ω. The iterations will still be monotone because even in the elliptic case the operator $-L + CI$ will satisfy a comparison principle if $C > 0$. Analogous results hold for systems satisfying (1.166), with sub- and supersolutions defined by (1.168) and (1.167) respectively. Again, the case of elliptic systems is quite similar to the parabolic case, except that we must require $w_i \geq v_i$ on Ω as a hypothesis and solutions to elliptic systems of the form $-Lu_i = f(x,\vec{u})$ are not necessarily unique, even under the condition (1.166). Another approach to obtaining solutions of elliptic problems via monotonicity can be developed by explicitly considering the solutions of elliptic problems as equilibria of parabolic models. Such an approach was introduced by Aronson and Weinberger (1975, 1978) and has been applied and extended by many others.

Theorem 1.22. Suppose that L has the form (1.107) and satisfies (1.108), and that L and Ω satisfy the hypotheses of Theorem 1.1, but without the restriction $c \leq 0$. Suppose that

the coefficients a_{ij} of L are uniformly Lipschitz in $\overline{\Omega}$, and that $f(x,u)$ and $\partial f(x,u)/\partial u$ are Hölder continuous in x and continuous in u on $\overline{\Omega} \times I\!R$. Finally, suppose that $\overline{u}$ and $\underline{u}$ are super- and subsolutions to the problem

$$\begin{aligned} Lu + f(x,u) &= 0 \text{ in } \quad \Omega \\ u &= 0 \qquad\qquad \text{on } \quad \partial\Omega; \end{aligned} \tag{1.172}$$

that is, $-L\overline{u} \geq f(x,\overline{u})$ and $-L\underline{u} \leq f(x,\underline{u})$ on Ω with $\underline{u} \leq 0 \leq \overline{u}$ on $\partial\Omega$ and $\underline{u} \leq \overline{u}$ on Ω. Let v be the solution to

$$\begin{aligned} \frac{\partial v}{\partial t} &= Lv + f(x,v) \text{ on } \quad \Omega \times (0,\infty) \\ v &= 0 \qquad\qquad\qquad\quad \text{on } \quad \partial\Omega \times (0,\infty) \\ v(x,0) &= \underline{u}(x). \end{aligned} \tag{1.173}$$

Then $v(x,t)$ is monotonically increasing with respect to t, and as $t \to \infty$ $v(x,t)$ converges to an equilibrium u^* of (1.173) which is the minimal equilibrium that satisfies $\underline{u}(x) \leq u^*(x) \leq \overline{u}(x)$. If w satisfies (1.173) but with $w(x,0) = \overline{u}(x)$ then $w(x)$ is monotonically decreasing with respect to t and converges to $u^{**}(x)$, the maximal equilibrium for (1.173) which satisfies $\underline{u}^*(x) \leq u^{**}(x) \leq \overline{u}(x)$.

Proof: If $\underline{u}(x)$ is a solution to (1.172) then $v(x,t) = \underline{u}(x)$ so we have $u^*(x) = \underline{u}(x)$. If $\underline{u}(x)$ is not a solution to (1.172) then we cannot have $v = \underline{u}$ we so must have $v(x,t) > \underline{u}(x) = v(x,0)$ for any $t > 0$ by Theorem 1.19. Thus, $v(x,\epsilon) > v(x,0)$ for any $\epsilon > 0$. However, $v_\epsilon(x,t) = v(x,t+\epsilon)$ satisfies (1.173) but with $v_\epsilon(x,0) = v(x,\epsilon) > v(x,0)$. Thus, $v_\epsilon(x,t) > v(x,t)$ for all $t > 0$ by Theorem 1.19, so $v(x,t+\epsilon) > v(x,t)$, i.e. $v(x,t)$ is increasing in t. (Since $v(x,0) \leq \overline{u}(x)$ it follows by Theorem 1.19 that $v(x,t)$ is bounded, so that $v(x,t)$ exists for all $t > 0$.) Since $v(x,t)$ is bounded above and increasing with t, we must have $v(x,t) \to u^*(x)$ for each $x \in \Omega$, where $u^*(x) \leq \overline{u}(x)$. It remains to verify that $u^*(x)$ is indeed a solution of (1.172). Let $u_n(x,t) = v(x,t+n-1)$. Then $u_n(x,1) = v(x,n)$. Also, $\partial u_n/\partial t = Lu_n + f(x,u_n)$ on $\Omega \times [0,1]$. Let $\rho_1(t)$ be a smooth function with $\rho_1(t) = 0$ for $t \leq 1/4$ and $\rho_1(t) = 1$ for $t \geq 1/2$. (Such functions are used in the construction of partitions of unity and mollifiers; see Friedman (1976) and Gilbarg and Trudinger (1977).) We have $\partial(\rho_1 u_n)/\partial t - L(\rho_1 u_n) = \rho_1 f(x,u_n) - u_n \partial\rho_1/\partial t$ in $\overline{\Omega} \times [0,1]$. Moreover, $\rho_1 f - u_n \partial\rho_1/\partial t$ is bounded uniformly in $C(\overline{\Omega} \times [0,1])$ since $\underline{u} \leq u_n \leq \overline{u}$ for all n and is zero for $t < 1/4$. So Lemma 1.15 applies to $\rho_1 u_n$, and thus the sequence $\{\rho_1 u_n\}$ is uniformly bounded in $C^{1+\delta,\delta/2}(\overline{\Omega} \times [0,1])$ for some $\delta > 0$. It follows that the sequence $\{u_n\}$ is uniformly bounded in $C^{1+\delta,\delta/2}(\overline{\Omega} \times [1/2,1])$. Let $\rho_2(t)$ be a smooth function with $\rho_2(t) = 0$ for $t \leq 1/2$ and $\rho_2(t) = 1$ for $t \geq 3/4$. Then $\partial(\rho_2 u_n)/\partial t - L(\rho_2 u_n) = \rho_2 f(x,u_n) - u_n \partial\rho_2/\partial t$ in $\overline{\Omega} \times [1/2,1]$ and $\rho_2 u_n = 0$ for $t = 1/2$. Since $\{u_n\}$ is uniformly bounded in $C^{1+\delta,\delta/2}(\overline{\Omega} \times [1/2,1])$, so is the expression $\rho_2 f(x,u_n) - u_n \partial\rho_2/\partial t$. Thus it follows from Theorem 1.13 that $\{\rho_2 u_n\}$ is uniformly bounded in $C^{2+\delta,1+\delta/2}(\overline{\Omega} \times [1/2,1])$ so that $\{u_n\}$ is uniformly bounded in $C^{2+\delta,1+\delta/2}(\overline{\Omega} \times [3/4,1])$. Hence, u_n, $\partial u_n/\partial t$, and the derivatives of u_n of order two or less in the space variables are uniformly bounded and equicontinuous on $\overline{\Omega} \times [3/4,1]$. The Arzela-Ascoli Theorem implies that $\{u_n\}$ must have a subsequence which converges uniformly along with its first derivative in t and derivatives of order up to two in the space variables on $\overline{\Omega} \times [3/4,1]$. Passing to the subsequence, we have $u_n \to \tilde{u}$ in

$\overline{\Omega} \times [3/4, 1]$ where $\tilde{u}$ satisfies $\partial\tilde{u}/\partial t - L\tilde{u} = f(x, \tilde{u})$ in $\overline{\Omega} \times [3/4, 1]$ because of the convergence of the derivatives of u_n and the fact that $\partial u_n/\partial t - Lu_n = f(x, u_n)$ for each n. However, $u_n(x, t) = v(x, t + n - 1) \to u^*(x)$ as $n \to \infty$ for any fixed $(x, t) \in \overline{\Omega} \times [3/4, 1]$ so we must have $\tilde{u} = u^*$. Thus, $u^*(x)$ satisfies the equation $\partial u/\partial t - Lu = f(x, u)$, but since $\partial u^*/\partial t = 0$ we have that u^* satisfies (1.172). If $z(x)$ is any equilibrium for (1.173) with $z(x) \geq \underline{u}(x)$ then $z(x) \geq v(x, t)$ by Theorem 1.19, but since $v(x, t) \to u^*(x)$ as $t \to \infty$ we must have $z(x) \geq u^*(x)$. The proof that $w(x, t) \to u^{**}(x)$ is analogous.

Remarks: Theorem 1.22 can be extended to systems which have the appropriate monotonicity properties. Such systems include those that satisfy the cooperativity condition (Kamke condition) (1.166), and those which can be converted into systems satisfying (1.166). An important class of examples are models for two competing species such as (1.169). Suppose that $\partial f_1/\partial u_2 < 0$ and $\partial f_2/\partial u_1 < 0$ in (1.169) and that f_1, f_2 do not depend on t. It follows from (1.170) and the related discussion that if (v_1, v_2) and (w_1, w_2) satisfy

$$\begin{aligned}
\frac{\partial v_1}{\partial t} - L_1 v_1 &\leq f_1(x, v_1, v_2) \\
\frac{\partial v_2}{\partial t} - L_2 v_2 &\geq f_2(x, v_1, v_2) \\
\frac{\partial w_1}{\partial t} - L_1 w_1 &\geq f_1(x, w_1, w_2) \\
\frac{\partial w_2}{\partial t} - L_2 w_2 &\leq f_2(x, w_1, w_2)
\end{aligned}$$

in $\Omega \times (0, T]$ with $v_1 \leq w_1$, $v_2 \geq w_2$ on $(\partial\Omega \times (0, T]) \cup (\overline{\Omega} \times \{0\})$ then $v_1 \leq w_1$ and $v_2 \geq w_2$ on $\overline{\Omega} \times [0, T]$. Suppose that $(\underline{u}_1, \overline{u}_2)$ and $(\overline{u}_1, \underline{u}_2)$ depend only on x, with $\underline{u}_i \leq \overline{u}_i$ for $i = 1, 2$, and

$$\begin{aligned}
-L_1 \underline{u}_1 &\leq f_1(x, \underline{u}_1, \overline{u}_2) \\
-L_2 \overline{u}_2 &\geq f_2(x, \underline{u}_1, \overline{u}_2) \\
-L_1 \overline{u}_1 &\geq f_1(x, \overline{u}_1, \underline{u}_2) \\
-L_2 \underline{u}_2 &\leq f_2(x, \overline{u}_1, \underline{u}_2) \text{ on } \quad \Omega
\end{aligned}$$

with $\underline{u}_i = 0$ on $\partial\Omega$, $\overline{u}_i \geq 0$ on $\partial\Omega$. Let (v_1, v_2) and (w_1, w_2) be solutions to (1.169) which are zero on $\partial\Omega \times (0, \infty)$ with $v_1(x, 0) = \underline{u}_1(x)$, $v_2(x, 0) = \overline{u}_2(x)$, and $w_1(x, 0) = \overline{u}_1(x)$, $w_2(x, 0) = \underline{u}_2(x)$. Then as $t \to \infty$, we have $v_1(x, t) \uparrow v_1^*(x)$, $v_2(x, t) \downarrow v_2^*(x)$; $w_1(x, t) \downarrow w_1^*(x)$, and $w_2(x, t) \uparrow w_2^*(x)$ where (v_1^*, v_2^*) and (w_1^*, w_2^*) are equilibria for (1.169) with $v_1^* \leq w_1^*$ and $v_2^* \geq w_2^*$. The same result would hold under Robin or Neumann boundary conditions. We return to this point later in our discussion of competition models.

Sometimes we consider models where the reaction term is not continuous with respect to x, so that we must work with weak solutions in $W^{2,p}(\Omega)$ or even $W^{1,2}(\Omega)$. There are versions of the maximum principle that apply in that situation. The following is a version of Theorems 8.1 and 8.19 of Gilbarg and Trudinger (1977):

Theorem 1.23. Suppose that L has the form (1.132) and that L and Ω satisfy the hypotheses of Theorem 1.10. Suppose further that the coefficient $c + \sum_{i=1}^{n} \partial B_i / \partial x_i$ of the undifferentiated term in L is nonpositive in the sense that

$$\int_\Omega \left[cw - \sum_{i=1}^{n} B_i \frac{\partial w}{\partial x_i} \right] dx \leq 0$$

for all $w \in C_0^1(\Omega)$ with $w \geq 0$. If $u \in W^{1,2}(\Omega)$ and $Lu \geq 0$ on Ω (in the weak sense) then $\sup_\Omega u \leq \sup_{\partial\Omega} u^+$, where u^+ denotes the positive part of u on $\partial\Omega$, i.e. $u^+ = (1/2)(|u| + u)$. If there is an open ball B with $\overline{B} \subseteq \Omega$ such that $\sup_B u = \sup_\Omega u \geq 0$ then u is constant on Ω.

Remarks: Analogous results can be obtained in the parabolic case. Evidently this has been done by Liang et al. (1983), but we have not read that paper. This type of maximum principle can be used to extend the method of super-and subsolutions to models where the reaction terms are not smooth. The following result can be obtained by the methods used by Berestycki and Lions (1980).

Theorem 1.24. Suppose that L and Ω satisfy the hypotheses of Theorem 1.5, and that $f(x, u)$ is measurable in x for all u, continuous in u for almost all $x \in \Omega$, and bounded on bounded subsets of $\Omega \times I\!R$. Suppose that for any finite interval $I \subseteq I\!R$ there is a constant C such that $f(x, u) + Cu$ is increasing in u on $\Omega \times I$. If $\underline{u}, \overline{u} \in W^{2,p}(\Omega)$ for some $p > n$ and $\underline{u}, \overline{u}$ satisfy

$$-L\underline{u} \leq f(x, \underline{u}) \quad \text{on} \quad \Omega, \quad \underline{u} \leq 0 \quad \text{on} \quad \partial\Omega$$

and

$$-L\overline{u} \geq f(x, \overline{u}) \quad \text{on} \quad \Omega, \quad \overline{u} \geq 0 \quad \text{on} \quad \partial\Omega$$

in the weak sense, then there exists a solution $u^* \in W^{2,p}(\Omega)$ to the problem $Lu = f(x, u)$ in Ω, $u = 0$ on $\partial\Omega$, with $\underline{u} \leq u^* \leq \overline{u}$.

Remarks: This result and various related results can be derived by using the methods of Berestycki and Lions (1980). Several examples are treated in that paper. An advantage of working in Sobolev space is that neither f nor $\underline{u}$ and $\overline{u}$ need to be as smooth as would be necessary if we were working in spaces of Hölder continuous functions. In particular, this fact makes it possible to use sub- and supersolutions which are constructed by piecing together sub- and supersolutions defined on subdomains of Ω. We have the following result.

Theorem 1.25. (Berestycki and Lions, 1980) Suppose that L and Ω satisfy the hypotheses of Theorem 1.5 and that Ω_1 is a subdomain of Ω with $\overline{\Omega_1} \subseteq \Omega$ and $\partial\Omega_1$ of class $C^{2+\alpha}$. Let $\Omega_2 = \Omega \backslash \Omega_1$ and let $\vec{n} = (\nu_1, \ldots, \nu_n)$ be the outward normal to Ω_1. If $\underline{u}_i \in W^{2,2}(\Omega_i)$ and $f_i(x) \in L^1(\Omega_i)$ satisfy $-L\underline{u}_i \leq f_i$ on Ω_i for $i = 1, 2$, with $\underline{u}_1 = \underline{u}_2$ and $\sum_{i,j=1}^{n} a_{ij} \nu_j (\partial \underline{u}_1 / \partial x_i) \leq \sum_{i,j=1}^{n} a_{ij} \nu_j (\partial \underline{u}_2 / \partial x_i)$ on $\partial\Omega_1$ then the function u defined by $\underline{u}(x) \equiv \underline{u}_i(x)$ for $x \in \Omega_i, i = 1, 2$, belongs to $W^{1,2}(\Omega)$ and satisfies $-L\underline{u} \leq f$ in Ω,

where $f(x) = f_i(x)$ on Ω_i. Similarly, if $\overline{u}_i \in W^{2,2}(\Omega_i)$ and $-L\overline{u}_i \geq f_i$ on Ω_i for $i = 1, 2$ with $\overline{u}_1 = \overline{u}_2$ and $\sum_{i,j=1}^{n} a_{ij}\nu_j(\partial\overline{u}_1/\partial x_i) \geq \sum_{i,j=1}^{n} a_{ij}\nu_j(\partial\overline{u}_2/\partial x_i)$ on $\partial\Omega_1$ then the function $\overline{u}(x) \equiv \overline{u}_i(x)$ on Ω_i, $i = 1, 2$, belongs to $W^{1,2}(\Omega)$ and satisfies $-L\overline{u} \geq f$ on Ω.

Remarks: The inequalities are to be interpreted in the weak sense. The point of the result is that it provides a way to link together local sub- and supersolutions to form global ones. In solving problems like $-Lu = f(x, u)$ we would choose $f_i(x) = f(x, \underline{u}_i)$ when defining $\underline{u}$ and $f_i(x) = f(x, \overline{u}_i)$ when defining $\overline{u}$.

There are many possible variations and extensions of the maximum principle, comparison theorems, and the method of sub- and supersolutions, but those we have discussed are adequate for the purposes of this book. There are also a number of alternative ways to obtain results on positivity of solutions, comparison principles, etc. An elliptic or parabolic operator will satisfy a maximum principle if and only if it has a positive Green's function. Green's functions sometimes can be formulated in terms of integral kernels, which may make sense even when applied to functions that are not continuous. Green's functions for parabolic problems are treated in detail by Friedman (1964). Alternatively, if L is an elliptic operator of the form (1.107) then for Ω sufficiently large the resolvent operator $(\lambda I - L)^{-1}$ will exist and be positive, in the sense of mapping positive functions to positive functions. The semigroup e^{tL} corresponding to L, which gives the solution to $\partial u/\partial t = Lu$, can be expressed as a limit of a series of powers of the resolvent of L which all have positive coefficients. See Friedman (1976, Part 2, Section 1). Thus, the semigroup inherits some of the positivity properties of the resolvent $(\lambda I - L)^{-1}$. Finally, there are some types of models other than reaction-diffusion systems which satisfy results analogous to maximum principles. In later chapters, we discuss how some of them can be treated by methods similar to those used to study reaction-diffusion models.