Differential Equations and Applications in Ecology, Epidemics, and Population Problems

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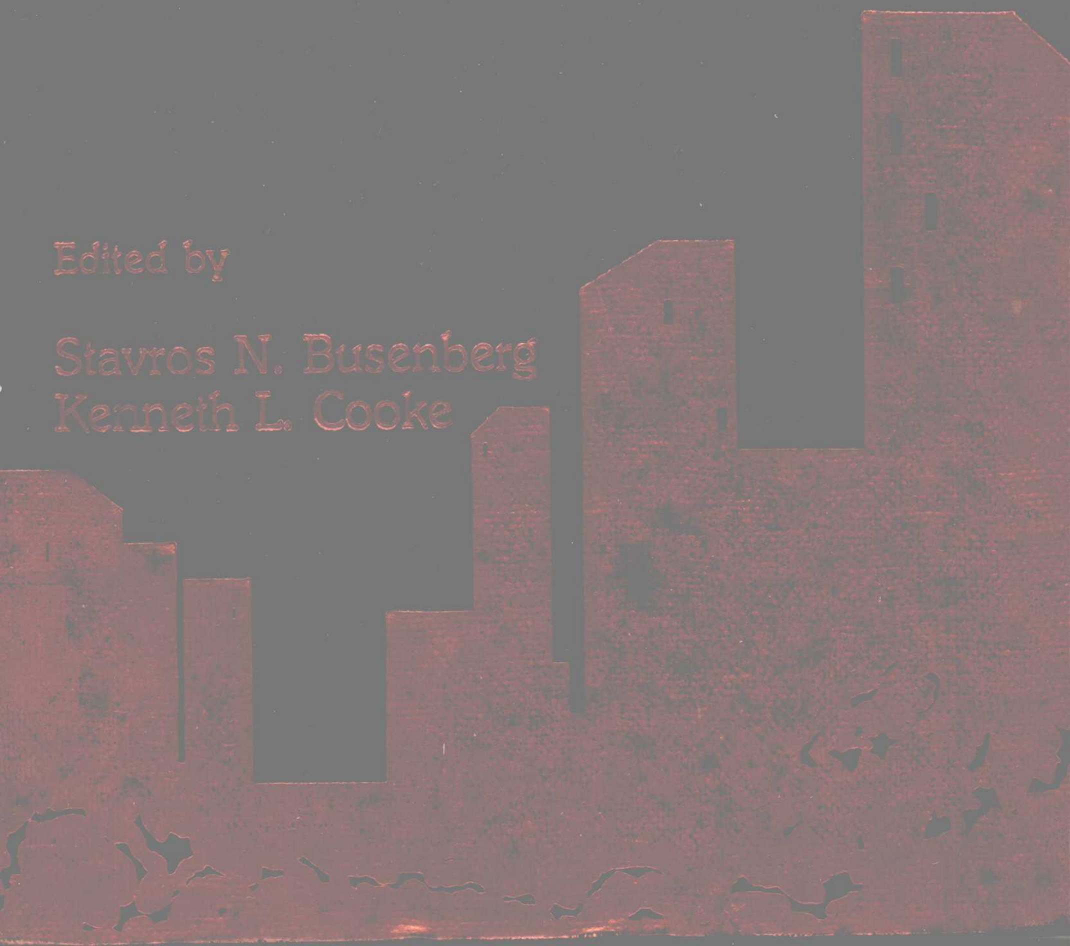

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Preface

In recent years there has been a rapid growth in the use of differential equations and of the methods of nonlinear dynamical systems in analyzing problems of population biology. The need for such applications has also motivated the consideration of a number of mathematical problems and the development of new techniques for their solution. This work involves vigorous cross-disciplinary interactions, and the papers and reports that describe it appear in a variety of mathematics, biomathematics, and science journals. The large number of these primary sources, and the usual delays in publication, present difficulties to the individual research worker who is attempting to keep abreast of the latest developments. It is, hence, useful to have periodic occasions that allow workers in this area the opportunity to interact with each other and to have their current work published in a timely fashion.

This volume contains papers and abstracts of talks presented at the research conference on Differential Equations and Applications to Ecology, Epidemics, and Population Problems that was held at Harvey Mudd College on January 10 and 11, 1981. This conference was followed by a week-long CBMS Regional Conference on Global Topological Methods in Applied Mathematics with James A. Yorke as principal lecturer, which was held at Pomona College. The two conferences were jointly organized with the intent of providing a forum for the exchange of ideas among workers in these fields.

The contents of this volume are collected in four groups. The first of these deals with aspects of population dynamics that involve the interaction between spatial and temporal effects. The second group treats other questions in population dynamics and some other areas of biomathematics. The third group deals with a number of topics in differential and functional differential equations that are continuing to find important applications in mathematical biology. The last group contains the abstracts of papers that were presented at the research conference but that do not appear in this volume. This book will be useful to students and researchers in theoretical biology and biomathematics as well as those interested in modern applications of differential equations. It should also have value for others with an interest in recent developments in these specific areas or in mathematical modeling in general.

The research reported herein covers a variety of areas but is tied together by a common thread. It consists of mathematics that is either a direct outgrowth from questions in population biology and biomathematics or else is applicable to such questions.

A central problem in ecology is the attempt to understand the interplay between spatial and temporal changes in the environment, the movements of individuals, and the dispersal of seed, pollen, and infections. The papers in the first group in this volume have this apsect of population biology as their common theme. Simon Levin leads off with a review of mathematical approaches to these problems. This is an area of intensive current work, and the paper reviews the recent literature on such questions as the formation of wave or pulse solutions and the existence and stability of spatially nonuniform steady states. In addition, this review provides a synopsis of current work and research trends. Levin dedicates this paper to the memory of Sol Rubinow, who would have enhanced the conference by his participation had it not been for the illness that led to his untimely death. David Green and Harlan Stech consider a single-species logistic population model with diffusion and hereditary terms and analyze the effects of one-dimensional spatial diffusion on the stability characteristics of this model. Next, Glenn Webb formulates a general model of an age-structured population of three genotypes experiencing spatial diffusion in a two-dimensional domain. Techniques from the theory of semigroups of continuous operators are used to obtain results on the existence and uniqueness of generalized solutions representing the genotype densities. J.P.E. Hodgson follows with a treatment of a two-species system with one-dimensional diffusion and with interaction terms that depend on the spatial variable. Michael Gilpin and Ted Case examine a sequence of invasions of an initially vacant region by different species. Since the species may arrive in many different orders, one seeks to find what stable communities will result. The questions addressed in this paper are related to some aspects discussed later by Brauer and Soudack; and Post, Travis, and DeAngelis.

One issue in the study of diseases is to determine conditions under which the disease or pestilence can establish itself over a long period of time. Herbert Hethcote, Harlan Stech, and Pauline van den Driessche introduce the next group of papers with a survey of work concerning the existence of thresholds of endemicity, the stability of constant solutions, the existence and stability of oscillatory solutions, and the effects of delays introduced via incubation periods or temporary immunities to a disease. The authors do not cover some areas of epidemic modeling such as those that include spatial spread (see the review paper by Simon Levin for some discussion of such models) or stochastic models. The bibliography that accompanies this paper points out the extent of the activity in this area of epidemic modeling and the usefulness of such an up-to-date survey of the area.

John Kemper provides an analysis and formulation of open questions concerning epidemics that can be modeled by separating the population into three classes: susceptibles, infected, and removed individuals (the so-called S-I-R models). Two distinct infected classes are used in this model and the paper addresses the question of whether or not the existence of the separate classes can be deduced from observable data. In the next paper, Mark Kramer and Gladys Reynolds address one of the major questions of epidemic modeling, namely, how to choose an effective strategy for combating the spread of an infection. They describe a computer simulation of gonorrhea transmission and control strategies and use actual data on this disease to compare three such strategies.

The two papers that follow deal with the stocking and harvesting of a population of plants or animals. Morton Gurtin and Lea Murphy consider the problem of finding an optimal harvesting strategy for an age-structured population. The concepts employed in this model have points in common with techniques used in mathematical economics. The inclusion of age-structure in the population allows the analysis of realistic problems but also adds to the mathematical complexity of the modeling equations. Fred Brauer and A. C. Soudack provide an overview of recent results concerning the qualitative behavior of a predator-prey (two species) model with harvesting and stocking. Questions concerning coexistence and extinction of species are analyzed, and some counterintuitive phenomena are uncovered. For example, it is possible to have a system that collapses when predators are not harvested, but in which coexistence occurs if predators are either stocked or harvested at a constant rate. This paper points out that genuinely nonlinear phenomena concerning domains of attraction are involved in these models which cannot be totally analyzed via consideration of linearized equations.

The next two papers address questions connected with age-structure of a population. Daniel Levine and Morton Gurtin study the consequences of predation that is selective on the basis of the age of the prey, including the case where one age group of a species acts as a predator on another age group of the same species (cannibalism). This situation occurs with several fish species, and the question raised is whether this behavior is an instrument for population control or primarily simply a source of food. J. M. Cushing provides an analysis of a single-species population model that utilizes a resource population. The model incorporates a maturation period through age dependence of the fecundity. The analysis shows that the delays that are due to such maturation periods can provide a stabilizing influence on the population. This is contrasted with a population model where delays commonly lead to instabilities. The questions of stability that are addressed here have points in common with those in the paper by Hethcote, Stech and van den Driessche where a comparison is made between the effects on stability of different types of delays.

Another ecological problem is explored by W. M. Post, Curtis Travis, and D. L. DeAngelis. This paper considers the Lotka-Volterra equations under coefficient conditions that describe species that are mutualistic (that is, mutually enhancing) rather than competitive or exploitative. The results of the analysis of these models are used to suggest feasible paths of evolution of mutualistic species. The effect of the introduction into an ecosystem of an evolved mutualistic genotype is considered, a situation that has analogies to the work reported in the paper by Gilpin and Case.

The next two papers deal with the analysis of problems that are motivated by population dynamics in variable environments. George Seifert considers the logistic equation with hereditary terms and with almost periodic coefficients. Results concerning the existence, uniqueness, and stability of almost periodic solutions to these equations are obtained. This paper provides useful tools for the analysis of the logistic equation with almost periodic coefficients. G. S. Ladde gives computable stability criteria for a generalization of the Lotka–Volterra equations in which there are time-delayed interactions and stochastic influences.

The next two papers are concerned with the analysis of biomathematical problems arising from problems in physiology. Jerome Eisenfeld derives conditions for systems of differential equations arising in compartmental models to have all their solutions tend to constant steady states. Examples are given of cases where this type of behavior does not occur and the question of extinction (washout) of a component is addressed. Robert Miura and Richard Plant consider a reaction diffusion equation in an annular region or a disk as a model of the ionic potentials that are involved in the phenomenon of spreading cortical depression. Numerical experiments are employed, using conditions that can be experimentally attained, in order to study the phenomenon of rotating waves of high ionic concentration; and a variety of such rotating wave patterns are examined.

The last group of papers consists of work on a variety of aspects of differential equations and dynamical systems, not necessarily motivated by biological applications. The usefulness of these results in analyzing equations arising in biomathematical models ties them closely to the preceding papers. M. Golubitsky and Hal Smith consider the bifurcations that can occur when a parametrized autonomous differential equation is perturbed by a periodic term. The methods of this paper are likely to be useful in the analysis of population models that incorporate seasonal fluctuations and in the comparison of such models to ones where average values of seasonally varying coefficients are employed. Steve Bernfeld gives methods of generalizing to n-dimensional systems a number of techniques that can be used to analyze the bifurcation of periodic solutions and the estimation of the number of such bifurcating solutions for autonomous differential systems. The widespread use of Hopf-type bifurcation analysis in population and physiological models underlines the applicability of such results. Mario Martelli provides an exposition of a class of nonlinear fixed point theorems obtained through the use of Brouwer's fixed point theorem and a continuation argument. Both bifurcations from the zero solution and from infinity are considered. F. A. Howes provides a clear and detailed exposition of boundary and interior layer phenomena in singularly perturbed higher order differential equations. George Pimbley considers the possibility of extending the Crandall–Liggett nonlinear semigroup generation theorem to systems of evolution equations. These types of systems have found applications in population models with age-structure and spatial diffusion as seen by the treatment in the paper by Webb. In the final paper, V. Sree Hari Rao gives an extension of the classical variation of constants formula to a generalized vector differential equation.

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These proceedings would not have been possible without the help of a number of individuals. Jim Yorke served on the organizing committee for the conference and contributed many ideas as well as active help. The help of Robert Borrelli with planning and with the local arrangements was invaluable. Pat Kelly and Sue Swanlund took care of all the secretarial work and many of the arrangements needed by the conference. Kevin Carosso helped with the creation of the index to this volume. A number of staff members and students of the Claremont Colleges provided much help with the local arrangements. The production of these proceedings was enhanced by the constant support provided by the editorial and production staff of Academic Press. We wish to extend our sincere thanks to all these individuals.

Our special gratitude goes to Sue Swanlund who prepared the camera-ready copy of the papers in this volume. She has contributed with admirable competence to both the arrangements for the conference and the production of this volume.

Contents

MODELS OF POPULATION DISPERSAL

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I. INTRODUCTION

The spatiotemporal structure of environment, and its effect upon the movement patterns of individuals, are central issues in ecological theory. A knowledge of plant and animal dispersal patterns is fundamental to an understanding of the outbreaks of pest populations, of the recovery of disturbed areas after periods of stress, and of the optimal spatial design of agricultural systems to minimize herbivore effects. Similarly, seed and pollen dispersal, together with the germination of dormant seeds and the released growth of understory plants, can play important roles in the secondary successional patterns of forest communities following disturbance. Mathematics has an important role to play in the description of movement patterns, and in an understanding of their evolution.

There are several distinct approaches to modelling populations in heterogeneous environments; the appropriate choice depends upon the system under investigation, upon the types

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of questions being asked, and upon the scales of interest. The most general development, and that most familiar to mathematicians, is built upon the theory of diffusion equations.

II. DIFFUSION MODELS

Random walk models have had a rich history in population biology. Okubo,(1980), [59], who has written the state-of-the-art text on the subject, traces their origin back to early work of Pearson and Blakeman, (1906), [63], in evolutionary theory and Brownlee's, (1911), [4], work on epidemics. In population genetics, the theory of the wave of advance of an advantageous allele prompted a number of fundamental theoretical papers (e.g. Fisher, (1937), [19], Kolmogorov et al. 1937, [36]), and important early experiments by Dobzhansky and Wright, (1943), [15], began to quantify the dispersal capabilities of *Drosophila*.

The basic equation of diffusion and growth utilized in those early papers was of the form

$$\frac{\partial n(\underset{\sim}{x}, t)}{\partial t} = D\nabla^2 n(\underset{\sim}{x}, t) + f(n(\underset{\sim}{x}, t)), \tag{1}$$

in which $n(\underset{\sim}{x},t)$ is the population density at position $\underset{\sim}{x}$ at time t. Equation (1) was advanced in an ecological context by Skellam, (1951), [70], and by Kierstead and Slobodkin, (1953), [34]; those papers have been cornerstones in the later development of the subject. Since their appearance, diffusion equations have been widely applied to describe movement, and they have formed the basis of most mathematical investigations. However, comparatively few experiments have been carried out which would allow an evaluation of the validity of such models.

Kareiva, (1981a,b), [28],[29], in studying the movement of flea beetles among collard plants, designed experiments to critically evaluate the applicability of diffusion models by means of mark and recapture experiments. In homogeneous environments, he found remarkable agreement between observation and the predictions of diffusion models (see discussion in Levin, (1981), [45]). A comprehensive survey of the literature concerning the foraging movements of phytophagous insects (Kareiva (1981a),[28]) showed that seven of the eleven cases examined were compatible with constant coefficient diffusion models.

With one exception, the deviations from the simplest model showed distributions in point-release mark-recapture experiments which were leptokurtic rather than normal (Kareiva, (1981a),[28]). Normality would be predicted on the basis of (1) with $f \equiv 0$; leptokurtic distributions are more peaked. Dobzhansky and Wright,(1943),[15], also found leptokursis in their experiments and suggested heterogeneity of either population or habitat as being responsible. The probable importance of population heterogeneity in these earlier experiments was borne out by later work (Dobzhansky and Powell, (1974), [14]) with more homogeneous populations; in those studies, leptokursis did not arise.

The problem of habitat heterogeneity is of profound importance in understanding the movements of individuals under natural circumstances. In deriving the appropriate modification of (1), it is critical to understand the mechanisms and the factors that control movement. The most familiar model for incorporating heterogeneity simply allows the diffusion coefficient to depend on spatial position, and (with $f \equiv 0$) takes the form

$$\frac{\partial n}{\partial t} = \nabla \cdot (D \nabla n), \tag{2}$$

where D depends on position. Under homogeneous boundary conditions, the steady states of such models are spatially uniform, and this is a hint that something may be wrong with (2) as a description of population movements. In general, in heterogeneous environments one expects to see accumulations of individuals in more favorable environments, and this implies non-uniform distributions; this is what is observed under natural conditions (Kareiva,(1981c),[30], Kareiva,(1981 b,c, [29] [30]). If one passes to the continuous limit from a random walk model in which emigration is locally determined, then in place of (2) one obtains (Patlak,(1943),[62], Dobzhansky et al. (1979),[14], Okubo,(1980),[59])

$$\frac{\partial n}{\partial t} = \nabla^2 (Dn), \tag{3}$$

which supports steady states in which n is inversely related to D. This is in better agreement with data in experimental situations, as has been reemphasized by Lapidus and Levandowsky,(1981),[38], with regard to models of chemotaxis. Lapidus and Levandowsky discuss the parallels between the dis-