

# Contents

**Prologue** ..... xvii

**Part I Simple Single Species Models**

**1 Continuous Population Models** ..... 3

1.1 Exponential Growth ..... 3

1.2 The Logistic Population Model ..... 8

1.3 The Logistic Equation in Epidemiology ..... 13

1.4 Qualitative Analysis ..... 17

1.5 Harvesting in Population Models ..... 26

1.5.1 Constant-Yield Harvesting ..... 26

1.5.2 Constant-Effort Harvesting ..... 28

1.6 Eutrophication of a Lake: A Case Study ..... 31

1.7 Appendix: Parameters in Biological Systems ..... 38

1.8 Project: The Spruce Budworm ..... 42

1.9 Project: Estimating the Population of the United States..... 45

**2 Discrete Population Models** ..... 49

2.1 Introduction: Linear Models..... 49

2.2 Graphical Solution of Difference Equations ..... 53

2.3 Equilibrium Analysis ..... 56

2.4 Period-Doubling and Chaotic Behavior ..... 61

2.5 Discrete-Time Metered Models..... 67

2.6 A Two-Age Group Model and Delayed Recruitment ..... 70

2.7 Systems of Two Difference Equations ..... 76

2.8 Oscillation in Flour Beetle Populations: A Case Study ..... 80

2.9 Project: A Discrete *SIS* Epidemic Model ..... 86

2.10 Project: A Discrete-Time Two-Sex Pair-Formation Model ..... 88

**3 Continuous Single-Species Population**

|                                                        |     |
|--------------------------------------------------------|-----|
| <b>Models with Delays</b> .....                        | 91  |
| 3.1 Introduction .....                                 | 91  |
| 3.2 Models with Delay in Per Capita Growth Rates ..... | 93  |
| 3.3 Delayed-Recruitment Models .....                   | 98  |
| 3.4 Models with Distributed Delay .....                | 104 |
| 3.5 Harvesting in Delayed Recruitment Models .....     | 108 |
| 3.5.1 Constant-Effort Harvesting .....                 | 108 |
| 3.5.2 Constant-Yield Harvesting .....                  | 109 |
| 3.6 Nicholson's Blowflies: A Case Study .....          | 112 |
| 3.7 Project: A Model for Blood Cell Populations .....  | 116 |
| 3.8 Project: Some Epidemic Models .....                | 119 |
| 3.9 Project: A Neuron Interaction Model .....          | 119 |

**Part II Models for Interacting Species**

|                                                                        |     |
|------------------------------------------------------------------------|-----|
| <b>4 Introduction and Mathematical Preliminaries</b> .....             | 123 |
| 4.1 The Lotka–Volterra Equations .....                                 | 123 |
| 4.2 The Chemostat .....                                                | 126 |
| 4.3 Equilibria and Linearization .....                                 | 128 |
| 4.4 Qualitative Behavior of Solutions of Linear Systems .....          | 135 |
| 4.5 Periodic Solutions and Limit Cycles .....                          | 148 |
| 4.6 Appendix: Canonical Forms of $2 \times 2$ Matrices .....           | 156 |
| 4.7 Project: A Model for Giving Up Smoking .....                       | 158 |
| 4.8 Project: A Model for Retraining of<br>Workers by their Peers ..... | 159 |
| 4.9 Project: A Continuous Two-Sex Population Model .....               | 160 |
| <b>5 Continuous Models for Two Interacting Populations</b> .....       | 165 |
| 5.1 Species in Competition .....                                       | 165 |
| 5.2 Predator–Prey Systems .....                                        | 173 |
| 5.3 Laboratory Populations: Two Case Studies .....                     | 185 |
| 5.4 Kolmogorov Models .....                                            | 190 |
| 5.5 Mutualism .....                                                    | 191 |
| 5.6 The Spruce Budworm: A Case Study .....                             | 199 |
| 5.7 The Community Matrix .....                                         | 206 |
| 5.8 The Nature of Interactions Between Species .....                   | 209 |
| 5.9 Invading Species and Coexistence .....                             | 212 |
| 5.10 Example: A Predator and Two Competing Prey .....                  | 214 |
| 5.11 Example: Two Predators Competing for Prey .....                   | 217 |
| 5.12 Project: A Simple Neuron Model .....                              | 218 |
| 5.13 Project: A Plant–Herbivore Model .....                            | 221 |

|          |                                                  |     |
|----------|--------------------------------------------------|-----|
| <b>6</b> | <b>Harvesting in Two-species Models</b>          | 223 |
| 6.1      | Harvesting of Species in Competition             | 223 |
| 6.2      | Harvesting of Predator–Prey Systems              | 229 |
| 6.3      | Intermittent Harvesting of Predator–Prey Systems | 237 |
| 6.4      | Some Economic Aspects of Harvesting              | 242 |
| 6.5      | Optimization of Harvesting Returns               | 247 |
| 6.6      | Justification of the Optimization Result         | 251 |
| 6.7      | A Nonlinear Optimization Problem                 | 254 |
| 6.8      | Economic Interpretation of the Maximum Principle | 260 |
| 6.9      | Project: A Harvesting Model                      | 263 |
| 6.10     | Project: Harvesting of Two Species               | 264 |

### Part III Structured Population Models

|          |                                                             |     |
|----------|-------------------------------------------------------------|-----|
| <b>7</b> | <b>Models for Populations with Age Structure</b>            | 267 |
| 7.1      | Linear Discrete Models                                      | 267 |
| 7.2      | Linear Continuous Models                                    | 273 |
| 7.3      | The Method of Characteristics                               | 275 |
| 7.4      | Nonlinear Continuous Models                                 | 281 |
| 7.5      | Models with Discrete Age Groups                             | 288 |
| 7.6      | Project: Ordinary Differential Equations with Age Structure | 290 |
| 7.7      | Project: Nonlinear Age Structured Population Growth         | 290 |
| 7.8      | Project: A Size Structured Population Model                 | 291 |
| <b>8</b> | <b>Models for Populations with Spatial Structure</b>        | 293 |
| 8.1      | Introduction                                                | 293 |
| 8.2      | Some Simple Examples of Metapopulation Models               | 294 |
| 8.3      | A General Metapopulation Model                              | 297 |
| 8.4      | A Metapopulation Model with Residence and Travel            | 299 |
| 8.5      | The Diffusion Equation                                      | 301 |
| 8.6      | Solution by Separation of Variables                         | 304 |
| 8.7      | Solutions in Unbounded Regions                              | 314 |
| 8.8      | Linear Reaction–Diffusion Equations                         | 321 |
| 8.9      | Nonlinear Reaction–Diffusion Equations                      | 323 |
| 8.9.1    | Two-Species Interactions                                    | 326 |
| 8.10     | Diffusion in Two Dimensions                                 | 330 |
| 8.11     | Project: Cats and Birds in Space                            | 332 |
| 8.12     | Project: The Cable Equation                                 | 333 |
| 8.13     | Project: Some Equations of Diffusion Type                   | 335 |

## Part IV Disease Transmission Models

|           |                                                            |     |
|-----------|------------------------------------------------------------|-----|
| <b>9</b>  | <b>Epidemic Models</b>                                     | 345 |
| 9.1       | Introduction to Epidemic Models                            | 345 |
| 9.2       | The Simple Kermack–McKendrick Epidemic Model               | 350 |
| 9.3       | A Branching-Process Disease-Outbreak Model                 | 361 |
| 9.3.1     | Transmissibility                                           | 367 |
| 9.4       | Network and Compartmental Epidemic Models                  | 369 |
| 9.5       | More Complicated Epidemic Models                           | 373 |
| 9.5.1     | Exposed Periods                                            | 373 |
| 9.5.2     | Treatment Models                                           | 375 |
| 9.5.3     | An Influenza Model                                         | 376 |
| 9.5.4     | A Quarantine-Isolation Model                               | 377 |
| 9.6       | An SIR Model with a General Infectious Period Distribution | 382 |
| 9.7       | The Age of Infection Epidemic Model                        | 384 |
| 9.8       | Models with Disease Deaths                                 | 388 |
| 9.9       | A Vaccination Model                                        | 391 |
| 9.10      | The Next Generation Matrix                                 | 393 |
| 9.10.1    | A Global Asymptotic Stability Result                       | 403 |
| 9.11      | Directions for Generalization                              | 404 |
| 9.12      | Some Warnings                                              | 404 |
| 9.13      | Project: Discrete Epidemic Models                          | 405 |
| 9.14      | Project: Fitting Data for an Influenza Model               | 407 |
| 9.15      | Project: Social Interactions                               | 407 |
| <b>10</b> | <b>Models for Endemic Diseases</b>                         | 411 |
| 10.1      | A Model for Diseases with No Immunity                      | 411 |
| 10.2      | The SIR Model with Births and Deaths                       | 414 |
| 10.3      | Some Applications                                          | 420 |
| 10.3.1    | Herd Immunity                                              | 420 |
| 10.3.2    | Age at Infection                                           | 421 |
| 10.3.3    | The Interepidemic Period                                   | 422 |
| 10.3.4    | “Epidemic” Approach to Endemic Equilibrium                 | 424 |
| 10.3.5    | The SIS Model with Births and Deaths                       | 425 |
| 10.4      | Temporary Immunity                                         | 427 |
| 10.5      | Diseases as Population Control                             | 431 |
| 10.6      | Parameter Estimation: Ordinary Least Squares               | 434 |
| 10.6.1    | Connecting Models to Data                                  | 434 |
| 10.6.2    | Ordinary Least Squares (OLS) Estimation                    | 436 |
| 10.7      | Possible Extensions                                        | 441 |
| 10.8      | Project: Pulse Vaccination                                 | 443 |
| 10.9      | Project: A Model with Competing Disease Strains            | 445 |

10.10 Project: An Epidemic Model in Two Patches ..... 447

10.11 Project: Population Growth and Epidemics ..... 448

10.12 Project: Estimating Parameters for Leishmaniasis ..... 453

10.13 Project: Invasive Pneumococcal Disease Surveillance Data ..... 457

**Epilogue** ..... 465

**References** ..... 483

**Index** ..... 501