

Contents

Part I	Two-Species Competition	8
1.1	Introduction of Species in Competition	10
1.2	Harvesting of Predator-Prey Systems	12
1.3	Intermittent Harvesting	19
1.4	Some Economic Aspects of Harvesting	22
1.5	Optimization of Harvesting Frequency	24
1.6	Justification of the Optimal Harvesting Rule	26
1.7	A Nonlinear Optimization Problem	28
1.8	Economic Interpretation of the Optimal Harvesting Rule	30
1.9	Project: A Harvesting Model for Case Study 1	32
1.10	Project: Harvesting Models for Case Studies 2–4	34
Part II	Structured Population Models	36
2.1	A Nonlinear Pair-Formation Model	38

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 Models with Delays	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	
4 Introduction and Mathematical Preliminaries	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 2×2 Matrices	156
4.7 Project: A Model for Giving Up Smoking	158
4.8 Project: A Model for Retraining of Workers by their Peers	159
4.9 Project: A Continuous Two-Sex Population Model	160
5 Continuous Models for Two Interacting Populations	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

6 Harvesting in Two-species Models	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	
7 Models for Populations with Age Structure	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
8 Models for Populations with Spatial Structure	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

9	Epidemic Models	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
10	Models for Endemic Diseases	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

population growth with six billion people, the question, "How many people can the Earth support?" has what is best described as a checkered history. It was first asked at the end of the eighteenth century by Thomas Malthus (1798).

Malthus's theory of population growth, which remains dominant within existing economic systems and within much of the public discourse on society throughout the world, is that the Earth *Supports* as a decent bond by J.P. Cohen (2005). Cohen notes that both historical and scientific perspectives provide several "theoretical 'solutions'" to the question of overpopulation. First, he observes that underlying assumptions about slow, steady population growth (a population increases exponentially, that is, it grows at a constant rate) is reserved; second, that resource limitations necessarily limit population growth, and third, that the magnitude of such an expansion. The usefulness and validity of these assumptions are naturally limited since the environment, often called the "carrying capacity," is not a constant (see, for example, Cohen 2005). Per capita rates of population growth are not constant over time or across regions of changing environments. A limiting factor in the development of a more useful, practical and theoretical terms theory of population growth is the difficulty for scholars to provide models and frameworks that are both parsimonious and yet able to account for the complexity. The environmental landscape in which we live is dynamic and constantly experiences dramatic shifts due to technological innovation (such as the industrial revolution), climate, carbon emissions, and war) and periodically shifts our understanding of what we think is possible. Cohen observes that population patterns and growth rates depend on our scale of observation in both time and space. At one scale, they are definitely not constant. For example, Cohen notes that in the thirteenth-century repeated waves of Black Death, a form of bubonic plague, killed one-third of Europe, and that the population of India fell by perhaps 80 or 90 percent during the sixteenth century [pp. 38–41]. However, in spite of such sharp short-term decreases, world population size has actually grown steadily since prehistoric times, although not at a constant rate.