

# Contents

Preface	xi
Mathematical Symbols	xv

## PART I THEORY

1. Introduction	3
1.1 At the Sources	3
1.1.1 <i>The Puzzle of Population Cycles</i>	3
1.1.2 <i>Modeling Nature</i>	4
1.1.3 <i>The Balance of Nature</i>	5
1.2 General Philosophy of the Approach	6
1.2.1 <i>Defining the Phenomenon to Be Explained</i>	8
1.2.2 <i>Formalizing Hypotheses as Mathematical Models</i>	11
1.2.3 <i>Contrasting Models with Data</i>	14
2. Population Dynamics from First Principles	17
2.1 Introduction	17
2.2 Exponential Growth	19
2.2.1 <i>Derivation of the Exponential Model</i>	20
2.2.2 <i>Comparison with the Law of Inertia</i>	22
2.2.3 <i>“Laws”: Postulates, Theorems, Empirical Generalizations?</i>	25
2.3 Self-Limitation	26
2.3.1 <i>Upper and Lower Density Bounds</i>	26
2.3.2 <i>Formalizing the Notion of Self-Limitation</i>	27
2.3.3 <i>The Logistic Model</i>	29
2.4 Consumer-Resource Oscillations	30
2.4.1 <i>Three More Postulates</i>	31
2.4.2 <i>The Lotka-Volterra Predation Model</i>	33

2.5	Process Order	36
2.6	Synthesis	44
3.	Single-Species Populations	47
3.1	Models without Population Structure	47
3.1.1	<i>Continuous-Time Models</i>	48
3.1.2	<i>Discrete-Time Models</i>	52
3.1.3	<i>Delayed Differential Models</i>	56
3.2	Exogenous Drivers	58
3.2.1	<i>Stochastic Variation</i>	60
3.2.2	<i>Deterministic Exogenous Factors</i>	61
3.3	Age- and Stage-Structured Models	64
3.3.1	<i>Mathematical Frameworks</i>	65
3.3.2	<i>An Example: Flour Beetle Dynamics</i>	68
3.4	Second-Order Models	70
3.4.1	<i>Maternal Effect Hypothesis</i>	70
3.4.2	<i>Kin Favoritism Model</i>	72
3.5	Synthesis	76
4.	Trophic Interactions	78
4.1	Responses of Predators to Fluctuations in Prey Density	79
4.1.1	<i>Functional Response</i>	79
4.1.2	<i>Aggregative Response</i>	88
4.1.3	<i>Numerical Response</i>	90
4.2	Continuous-Time Models	93
4.2.1	<i>Generalized Lotka-Volterra Models</i>	94
4.2.2	<i>Models Not Conforming to the LV Framework</i>	99
4.2.3	<i>Anatomy of a Predator-Prey Cycle</i>	102
4.2.4	<i>Generalist Predators</i>	104
4.3	Discrete-Time Models: Parasitoids	108
4.3.1	<i>Functional and Numerical Responses</i>	109
4.3.2	<i>Dynamical Models</i>	111
4.4	Grazing Systems	112
4.4.1	<i>Grazer's Functional Response</i>	113
4.4.2	<i>Dynamics of Vegetation Regrowth</i>	117
4.4.3	<i>Dynamics of Grazer-Vegetation Interactions</i>	120
4.4.4	<i>Plant Quality</i>	123
4.5	Pathogens and Parasites	127
4.5.1	<i>Transmission Rate</i>	127

4.5.2	<i>Microparasitism Models</i>	128
4.5.3	<i>Macroparasitism Models</i>	131
4.6	Tritrophic Models	133
4.7	Synthesis	136
5.	Connecting Mathematical Theory to Empirical Dynamics	137
5.1	Introduction	137
5.2	Qualitative Types of Deterministic Dynamics	139
5.2.1	<i>Attractors</i>	139
5.2.2	<i>Sensitive Dependence on Initial Conditions</i>	140
5.3	Population Dynamics in the Presence of Noise	146
5.3.1	<i>Simple Population Dynamics</i>	146
5.3.2	<i>Stable Periodic Oscillations</i>	147
5.3.3	<i>Chaotic Oscillations</i>	148
5.3.4	<i>Quasi-Chaotic Oscillations</i>	151
5.3.5	<i>Regular Exogenous Forcing</i>	153
5.3.6	<i>Synthesis</i>	153
5.4	Population Regulation	154
5.4.1	<i>Definition of Density Dependence</i>	155
5.4.2	<i>Regulation: Evolution of the Concept</i>	156
5.4.3	<i>The Stationarity Definition of Regulation</i>	156
5.4.4	<i>Beyond Stationarity: Stochastic Boundedness</i>	157
5.4.5	<i>Synthesis</i>	158

## PART II DATA

6.	Empirical Approaches: An Overview	163
6.1	Introduction	163
6.2	Analysis of Population Fluctuations	164
6.2.1	<i>The Structure of Density Dependence</i>	164
6.2.2	<i>Probes: Quantitative Measures of Time-Series Patterns</i>	165
6.2.3	<i>Phenomenological versus Mechanistic Approaches</i>	167
6.3	Experimental Approaches	168
7.	Phenomenological Time-Series Analysis	173
7.1	Basics	173
7.1.1	<i>Variance Decomposition</i>	173
7.1.2	<i>Data Manipulations Prior to Analysis</i>	175
7.1.3	<i>Diagnostic Tools</i>	178

7.2	Fitting Models to Data	183
7.2.1	<i>General Framework</i>	183
7.2.2	<i>Choosing the Base Lag</i>	186
7.2.3	<i>Functional Forms</i>	188
7.2.4	<i>Model Selection by Cross-Validation</i>	191
7.3	Synthesis	195
8.	Fitting Mechanistic Models	197
8.1	Model Selection	198
8.2	Analysis of Ancillary Data	200
8.3	One-Step-Ahead Prediction	201
8.4	Trajectory Matching	203
8.5	Fitting by Nonlinear Forecasting	205

PART III  
CASE STUDIES

9.	Larch Budmoth	213
9.1	Introduction	213
9.2	Analysis of Time-Series Data	217
9.3	Hypotheses and Models	220
9.3.1	<i>Plant Quality</i>	220
9.3.2	<i>Parasitism</i>	229
9.3.3	<i>Putting It All Together: A Parasitism-Plant Quality Model</i>	235
9.4	Synthesis	237
10.	Southern Pine Beetle	239
10.1	Introduction	239
10.2	Analysis of Time-Series Data	240
10.3	Hypotheses and Models	243
10.3.1	<i>General Review of Hypotheses</i>	243
10.3.2	<i>Interaction with Hosts</i>	247
10.3.3	<i>Interaction with Parasitoids</i>	253
10.3.4	<i>The Predation Hypothesis</i>	255
10.4	An Experimental Test of the Predation Hypothesis	259
10.4.1	<i>Rationale</i>	259
10.4.2	<i>Results</i>	264
10.5	Synthesis	271

11.	Red Grouse	272
11.1	Numerical Patterns	273
11.2	Hypotheses and Models	281
	<i>11.2.1 Overview</i>	281
	<i>11.2.2 Parasite-Grouse Hypothesis</i>	282
	<i>11.2.3 Kin Favoritism Hypothesis</i>	285
11.3	Experiments	289
	<i>11.3.1 Density Manipulation</i>	289
	<i>11.3.2 Parasite Manipulation</i>	291
11.4	Synthesis	294
12.	Voles and Other Rodents	296
12.1	Introduction	296
12.2	Analysis of Time-Series Data	297
	<i>12.2.1 Methodological Issues</i>	297
	<i>12.2.2 Numerical Patterns</i>	301
12.3	Hypotheses and Models	310
	<i>12.3.1 Maternal Effect Hypothesis</i>	311
	<i>12.3.2 Interaction with Food</i>	316
	<i>12.3.3 Predation</i>	317
12.4	Fitting the Predation Model by NLF	321
12.5	Lemmings	325
	<i>12.5.1 Numerical Patterns</i>	326
	<i>12.5.2 Testing Alternative Trophic Hypotheses</i>	328
	<i>12.5.3 Lemming-Vegetation Dynamics at Barrow</i>	331
12.6	Synthesis	335
	<i>12.6.1 Summary of Findings</i>	335
	<i>12.6.2 Toward a General Trophic Theory     of Rodent Dynamics</i>	339
13.	Snowshoe Hare	344
13.1	Introduction	344
13.2	Numerical Patterns	345
13.3	Models	349
13.4	Experiments	356
13.5	Synthesis	362
14.	Ungulates	365
14.1	Introduction	365

14.2	Interaction with Food	368
14.3	Interaction with Predators	371
14.4	Numerical Dynamics	376
14.5	Synthesis	381
15.	General Conclusions	383
15.1	What Mechanisms Drive Oscillations in Nature?	383
15.2	Structure of Density Dependence	386
15.3	What about Chaos?	390
15.4	Population Ecology: A Mature Science	392
	Glossary	397
	References	405
	Index	437