
Contents

Preface	xiii
PART 1. MODELING	1
Chapter 1. Introduction	3
1.1 Why Individual-based Modeling and Ecology?	3
1.2 Linking Individual Traits and System Complexity: Three Examples	5
1.3 Individual-based Ecology	9
1.4 Early IBMs and their Research Programs	10
1.5 What Makes a Model an IBM?	13
1.6 Status and Challenges of the Individual-based Approach	15
1.7 Conclusions and Outlook	18
Chapter 2. A Primer to Modeling	21
2.1 Introduction	21
2.2 Heuristics for Modeling	23
2.3 The Modeling Cycle	25
2.3.1 Task 1: Formulate the Question	26
2.3.2 Task 2: Assemble Hypotheses for Essential Processes and Structures	26
2.3.3 Task 3: Choose Scales, State Variables, Processes, and Parameters	27
2.3.4 Task 4: Implement the Model	31
2.3.5 Task 5: Analyze, Test, and Revise the Model	32
2.3.6 Task 6: Communicate the Model and its Results	33
2.4 Summary and Discussion	34
Chapter 3. Pattern-oriented Modeling	36
3.1 Introduction	36
3.2 Why Patterns, and What are Patterns?	38
3.3 The Tasks of Pattern-oriented Modeling	39
3.3.1 Identify Multiple Patterns	40
3.3.2 Use Patterns to Design an IBM	42
3.3.3 Use Patterns in Model Analysis and Testing	44
3.3.4 Use Patterns for Parameterization	45
3.4 Discussion	46

PART 2. INDIVIDUAL-BASED ECOLOGY	49
Chapter 4. Theory in Individual-based Ecology	51
4.1 Introduction	51
4.2 Basis for Theory in IBE	52
4.3 Goals of IBE Theory	53
4.4 Theory Structure	56
4.4.1 Fundamental Axiom	56
4.4.2 Theories	56
4.4.3 Testing	57
4.5 Theory Development Cycle	57
4.6 Example: Development of Habitat Selection Theory for Trout	60
4.7 Summary and Discussion	65
Chapter 5. A Conceptual Framework for Designing Individual-based Models	68
5.1 Introduction	68
5.2 Emergence	70
5.2.1 Emergent and Imposed System Behaviors	71
5.2.2 Comparison of Emergent vs. Imposed Behaviors	74
5.2.3 Design Guidance for Emergence	75
5.3 Adaptive Traits and Behavior	76
5.3.1 What Adaptive Traits Are	76
5.3.2 Advantages of Adaptive Traits to Model Behavior	78
5.3.3 Directly and Indirectly Adaptive Traits	79
5.3.4 Design Guidance for Adaptive Traits and Behavior	80
5.4 Fitness	81
5.4.1 Fitness Concepts for Modeling Adaptive Traits	81
5.4.2 The Completeness and Directness of Fitness Measures	82
5.4.3 Examples of Fitness Measures	84
5.4.4 Design Guidance for Fitness Measures	85
5.5 Prediction	87
5.5.1 The Importance of Modeling Prediction	88
5.5.2 Approaches for Modeling Prediction	89
5.5.3 Design Guidance for Prediction	90
5.6 Interaction	91
5.6.1 Approaches for Modeling Interaction	92
5.6.2 Design Guidance for Interaction	93
5.7 Sensing	94
5.7.1 Modeling How Individuals Sense	94
5.7.2 Design Guidance for Sensing	96
5.8 Stochasticity	97
5.8.1 Stochasticity and Ignorance	97
5.8.2 Uses of Stochasticity in IBMs	98
5.8.3 Design Issues and Guidance for Stochasticity	100
5.9 Collectives	100
5.9.1 Representing Collectives	101
5.9.2 Design Guidance for Collectives	103
5.10 Scheduling	104
5.10.1 Scheduling: Designing a Model of Time	104

CONTENTS	vii
5.10. Alternative Ways of Modeling Time and Concurrency	106
5.10. Design Guidance for Scheduling	109
5.11 Observation	110
5.12 Summary, Conclusions, and Conceptual Design Checklist	112
5.12. Conceptual design checklist	113
Chapter 6. Examples	117
6.1 Introduction	117
6.2 Group and Social Behavior	118
6.2.1 Reynold's Boids	119
6.2.2 The Huth-Wissel Model of Fish Schools	121
6.2.3 The CluBoids Model of Huse Et Al.	125
6.2.4 Hemelrijk's DomWorld Model	128
6.2.5 Summary and Lessons: Group and Social Behavior	132
6.3 Population Dynamics of Social Animals	137
6.3.1 The Woodhoopoe Model of Neuert Et Al.	138
6.3.2 The Marmot Model of Dorndorf Et Al.	142
6.3.3 The Canid Model of Pitt Et Al.	146
6.3.4 Summary and Lessons: Population Dynamics of Social Species	148
6.4 Movement: Dispersal and Habitat Selection	155
6.4.1 The Lynx Dispersal Model of Schadt Et Al.	156
6.4.2 Habitat Selection Theory in the Trout Model of Railsback Et Al.	161
6.4.3 Dispersal Success in Spatially Explicit Population Models	164
6.4.4 Summary and Lessons: Dispersal and Habitat Selection	166
6.5 Regulation of Hypothetical Populations	168
6.5.1 The Lomnicki Model of Unequal Resource Partitioning	169
6.5.2 Uchmański's Models of Regulation and Individual Variability	170
6.5.3 The Social Spider Model of Ulbrich Et Al.	175
6.5.4 Summary and Lessons: Regulation of Hypothetical Popu- lations	175
6.6 Comparison to Classical Models	177
6.6.1 The Predator-Prey Models of Donalson and Nisbet	178
6.6.2 The Logistic Equation Analysis of Law Et Al.	182
6.6.3 Separation of Time Scales in the Model of Fahse Et Al.	183
6.6.4 Summary and Lessons: Classical Models vs. IBMs	187
6.7 Dynamics of Plant Populations and Communities	189
6.7.1 Fixed-radius Neighborhood Models	190
6.7.2 Zone of Influence Models	191
6.7.3 The Field-of-Neighborhood (FON) Approach of Berger and Hildenbrandt	192
6.7.3.1 FON Example 1: Cyclic population dynamics of plants.	195
6.7.3.2 FON Example 2: Self-thinning in Monocultures.	197
6.7.4 Grid-based plant IBMs	199
6.7.4.1 Example: The Winkler and Stöcklin model	200
6.7.5 Individual-based Forest Models	202
6.7.5.1 Gap Models	203
6.7.5.2 Growth-yield models	204

viii	CONTENTS
6.7.6	Summary and Lessons: Plant IBMs 204
6.8	Structure of Communities and Ecosystems 207
6.8.1	Adaptive Traits in the Community IBM of Schmitz 208
6.8.2	The Plant Community IBM of Pachepsky Et Al. 213
6.8.3	The Beech Forest Model BEFORE 215
6.8.4	Summary and Lessons: IBMs of Communities and Ecosystems 220
6.9	Artificially Evolved Traits 221
6.9.1	The Huse and Giske Model of Horizontal Movement in Marine Fish 224
6.9.2	The Model of Strand Et Al.: Vertical Movement, Energy Allocation, and Spawning 225
6.9.3	Giske Et Al.'s "Hedonic" Model of Vertical Movement 227
6.9.4	Summary and Lessons: Artificial Evolution of Adaptive Traits 228
6.10	Summary and Conclusions 229
PART 3.	THE ENGINE ROOM 231
Chapter 7.	Formulating Individual-based Models 233
7.1	Introduction 233
7.2	Contents of an IBM Formulation 234
7.3	Formulating an IBM's Spatial Elements 235
7.3.1	Discrete Space 236
7.3.2	Continuous Space 237
7.3.3	Hybrid Approaches 238
7.4	Formulating Logical and Probabilistic Rules 239
7.5	Formulating Adaptive Traits 241
7.5.1	A Framework for Modeling Decisions 241
7.5.2	Probabilistic and Logical Rules 242
7.5.3	Direct Fitness-seeking 242
7.5.4	Artificially Evolved Traits 243
7.5.5	Decision Heuristics 244
7.6	Controlling Uncertainty 245
7.6.1	Keep Submodels Simple 246
7.6.2	Consider Borrowing Existing Submodels 246
7.6.3	Design Submodels Carefully and Thoroughly 247
7.7	Using Object-oriented Design and Description 248
7.8	Using Mechanistic and Discrete Mathematics 250
7.9	Designing Super-individuals 252
7.10	Summary and Conclusions 254
Chapter 8.	Software for Individual-based Models 256
8.1	Introduction 256
8.2	The Importance of Software Design for IBMs 259
8.3	Software Terminology and Concepts 260
8.3.1	Discrete-event Simulation 261
8.3.2	Software Platforms 261
8.3.3	Observability 261
8.3.4	Object-oriented Programming 261

CONTENTS	ix
8.3.5 Causality	264
8.3.6 Software Evolution and Maintenance	264
8.4 Software Platforms	265
8.4.1 Criteria for Selecting a Platform	265
8.4.2 Types of Platforms	267
8.4.3 Swarm and Related Frameworks	270
8.4.4 Summary for Software Platforms	271
8.5 Software Testing	273
8.5.1 Testing Methods	274
8.5.2 Automation and Documentation of Testing	278
8.6 Moving Software Development Forward	279
8.6.1 Keep Model Formulation and Software Development Separate	279
8.6.2 Collaborate with Software Professionals	280
8.6.3 Design Software to Resemble the System Being Modeled	282
8.6.4 Make Multiple Representations of the Model and its Software	282
8.6.5 Implement Observability and Analysis Tools Early	284
8.7 Important Implementation Techniques	286
8.7.1 Obtain Critical Reviews of the Code	286
8.7.2 Use Defensive Programming Practices	286
8.7.3 Select a Good Pseudo-random Number Generator	288
8.7.4 Reduce Execution Time—if Necessary	288
8.7.5 Accommodate Software Evolution and Maintenance	290
8.8 Some Favorite Software Myths	291
8.9 Summary and Conclusions	293
 Chapter 9. Analyzing Individual-based Models	 296
9.1 Introduction	296
9.2 Steps in Analyzing an IBM	297
9.3 General Strategies for Analyzing IBMs	299
9.3.1 The Main Strategy: Simulation Experiments	299
9.3.2 Analyzing From the Bottom Up	301
9.3.3 Analyzing Model Structure Separately	302
9.4 Techniques for Analyzing IBMs	303
9.4.1 Currencies for Contrasting Model Versions	303
9.4.1.1 Observed patterns	304
9.4.1.2 Census Data	305
9.4.1.3 Variability in Results	306
9.4.1.4 Stability Properties and Diversity	306
9.4.2 Independent Analysis of Submodels	307
9.4.3 Early Analysis of Extremely Simple Patterns	307
9.4.4 Model Simplification	308
9.4.5 Unrealistic Scenarios	308
9.4.6 Multiple Observation Perspectives	310
9.5 Statistical Analysis	311
9.5.1 Summarizing Simulation Results	311
9.5.2 Contrast of Treatments	312
9.5.3 Quantifying Relationships	314
9.5.4 Comparing Results to Observed Patterns	315
9.5.5 Inferring Causality?	317

x	CONTENTS
9.6 Sensitivity and Uncertainty Analysis	317
9.7 Robustness Analysis	319
9.7.1 Examples	319
9.7.2 The Questions of Robustness Analysis	320
9.7.3 Robustness of Highly Variable and Sensitive Systems	323
9.8 Parameterization	323
9.9 Independent Predictions	327
9.10 Summary and Conclusions	328
 Chapter 10. Communicating Individual-based Models and Research	 331
10.1 Introduction	331
10.2 Types of IBE Work to Communicate	332
10.3 Complete and Efficient Model Description	333
10.4 Common Review Comments	335
10.4.1 Comparison of IBM Results to Classical Model Results	336
10.4.2 Generality and Robustness of Results	337
10.4.3 Readability	337
10.5 Visual Communication of Executable Models	338
10.6 Communicating Software	340
10.7 Summary and Conclusions	341
 PART 4. CONCLUSIONS AND OUTLOOK	 345
 Chapter 11. Using Analytical Models in Individual-based Ecology	 347
11.1 Introduction	347
11.2 Classifications of Ecological Models	348
11.3 Benefits of Analytical Models	350
11.4 Analytical Approximation of IBMs	351
11.5 Using Analytical Models to Understand and Analyze IBMs	354
11.5.1 Adopting System-level Concepts	354
11.5.2 Using Analytical Models as a Framework for Simplifying IBMs	355
11.5.3 Using Analytical Constructs to Analyze IBMs	357
11.6 Summary and Discussion	359
 Chapter 12. Conclusions and Outlook for Individual-based Ecology	 362
12.1 Introduction	362
12.2 Why Do We Need IBE?	363
12.3 How is IBE Different From Traditional Ecology?	364
12.3.1 How We Address Complexity	365
12.3.2 We Develop General Understanding by Studying Specific Systems	366
12.3.3 Behavior and Population Ecology are Tightly Linked: Evolution Underlies All	367
12.3.4 Modeling and Empirical Research are Closely Linked	367
12.3.5 Environmental Processes are Integral to Models and thus Explicit	367
12.3.6 "Theory" is not Separate from Real-world Problem-solving	368

CONTENTS	xi
12.3. Testing and Analysis are Integral to Modeling	368
12.3. Research is Inherently Interdisciplinary	368
12.4 What Can Ecology Contribute to the Science of Complex Systems?	369
12.5 A Visit to the Individual-based Ecology Laboratory	370
References	373
Appendix Glossary	409