

Contents

<i>Preface</i>	page xi
<i>Introduction for game theorists</i>	xiv
<i>Introduction for biologists</i>	xx
<i>About this book</i>	xxvi
Part one: Dynamical Systems and Lotka–Volterra Equations	1
1 Logistic growth	3
1.1 Population dynamics and density dependence	3
1.2 Exponential growth	4
1.3 Logistic growth	5
1.4 The recurrence relation $x' = Rx(1 - x)$	5
1.5 Stable and unstable fixed points	6
1.6 Bifurcations	7
1.7 Chaotic motion	9
1.8 Notes	10
2 Lotka–Volterra equations for predator–prey systems	11
2.1 A predator–prey equation	11
2.2 Solutions of differential equations	12
2.3 Analysis of the Lotka–Volterra predator–prey equation	13
2.4 Volterra’s principle	15
2.5 The predator–prey equation with intraspecific competition	16
2.6 On ω -limits and Lyapunov functions	18
2.7 Coexistence of predators and prey	19
2.8 Notes	21
3 The Lotka–Volterra equations for two competing species	22
3.1 Linear differential equations	22
3.2 Linearization	24

3.3	A competition equation	26
3.4	Cooperative systems	28
3.5	Notes	30
4	Ecological equations for two species	31
4.1	The Poincaré–Bendixson theorem	31
4.2	Periodic orbits for two-dimensional Lotka–Volterra equations	33
4.3	Limit cycles and the predator–prey model of Gause	34
4.4	Saturated response	37
4.5	Hopf bifurcations	38
4.6	Notes	40
5	Lotka–Volterra equations for more than two populations	42
5.1	The general Lotka–Volterra equation	42
5.2	Interior rest points	43
5.3	The Lotka–Volterra equations for food chains	45
5.4	The exclusion principle	47
5.5	A model for cyclic competition	48
5.6	Notes	53
	Part two: Game Dynamics and Replicator Equations	55
6	Evolutionarily stable strategies	57
6.1	Hawks and doves	57
6.2	Evolutionary stability	59
6.3	Normal form games	61
6.4	Evolutionarily stable strategies	62
6.5	Population games	65
6.6	Notes	66
7	Replicator dynamics	67
7.1	The replicator equation	67
7.2	Nash equilibria and evolutionarily stable states	69
7.3	Strong stability	72
7.4	Examples of replicator dynamics	74
7.5	Replicator dynamics and the Lotka–Volterra equation	77
7.6	Time averages and an exclusion principle	78
7.7	The rock–scissors–paper game	79
7.8	Partnership games and gradients	82
7.9	Notes	85
8	Other game dynamics	86
8.1	Imitation dynamics	86

8.2	Monotone selection dynamics	88
8.3	Selection against iteratively dominated strategies	90
8.4	Best-response dynamics	93
8.5	Adjustment dynamics	97
8.6	A universally cycling game	98
8.7	Notes	100
9	Adaptive dynamics	101
9.1	The repeated Prisoner's Dilemma	101
9.2	Stochastic strategies for the Prisoner's Dilemma	103
9.3	Adaptive Dynamics for the Prisoner's Dilemma	104
9.4	An ESS may be unattainable	107
9.5	A closer look at adaptive dynamics	108
9.6	Adaptive dynamics and gradients	109
9.7	Notes	112
10	Asymmetric games	113
10.1	Bimatrix games	113
10.2	The Battle of the Sexes	114
10.3	A differential equation for asymmetric games	116
10.4	The case of two players and two strategies	119
10.5	Role games	122
10.6	Notes	125
11	More on bimatrix games	126
11.1	Dynamics for bimatrix games	126
11.2	Partnership games and zero-sum games	127
11.3	Conservation of volume	132
11.4	Nash–Pareto pairs	135
11.5	Game dynamics and Nash–Pareto pairs	137
11.6	Notes	139
	Part three: Permanence and Stability	141
12	Catalytic hypercycles	143
12.1	The hypercycle equation	143
12.2	Permanence	145
12.3	The permanence of the hypercycle	149
12.4	The competition of disjoint hypercycles	151
12.5	Notes	152
13	Criteria for permanence	153
13.1	Permanence and persistence for replicator equations	153

13.2	Brouwer's degree and Poincaré's index	155
13.3	An index theorem for permanent systems	158
13.4	Saturated rest points and a general index theorem	159
13.5	Necessary conditions for permanence	162
13.6	Sufficient conditions for permanence	166
13.7	Notes	170
14	Replicator networks	171
14.1	A periodic attractor for $n = 4$	171
14.2	Cyclic symmetry	173
14.3	Permanence and irreducibility	175
14.4	Permanence of catalytic networks	176
14.5	Essentially hypercyclic networks	177
14.6	Notes	180
15	Stability of n-species communities	181
15.1	Mutualism and M -matrices	181
15.2	Boundedness and B -matrices	185
15.3	VL-stability and global stability	191
15.4	P -matrices	193
15.5	Communities with a special structure	196
15.6	D -stability and total stability	199
15.7	Notes	201
16	Some low-dimensional ecological systems	203
16.1	Heteroclinic cycles	203
16.2	Permanence for three-dimensional Lotka–Volterra systems	206
16.3	General three-species systems	211
16.4	A two-prey two-predator system	213
16.5	An epidemiological model	216
16.6	Notes	219
17	Heteroclinic cycles: Poincaré maps and characteristic matrices	220
17.1	Cross-sections and Poincaré maps for periodic orbits	220
17.2	Poincaré maps for heteroclinic cycles	221
17.3	Heteroclinic cycles on the boundary of S_n	224
17.4	The characteristic matrix of a heteroclinic cycle	227
17.5	Stability conditions for heteroclinic cycles	230
17.6	Notes	232

Part four: Population Genetics and Game Dynamics	233
18 Discrete dynamical systems in population genetics	235
18.1 Genotypes	235
18.2 The Hardy–Weinberg law	236
18.3 The selection model	237
18.4 The increase in average fitness	238
18.5 The case of two alleles	240
18.6 The mutation–selection equation	241
18.7 The selection–recombination equation	243
18.8 Linkage	245
18.9 Fitness under recombination	247
18.10 Notes	248
19 Continuous selection dynamics	249
19.1 The selection equation	249
19.2 Convergence to a rest point	251
19.3 The location of stable rest points	254
19.4 Density dependent fitness	256
19.5 The Shahshahani gradient	257
19.6 Mixed strategists and gradient systems	261
19.7 Notes	264
20 Mutation and recombination	265
20.1 The selection–mutation model	265
20.2 Mutation and additive selection	266
20.3 Special mutation rates	268
20.4 Limit cycles for the selection–mutation equation	270
20.5 Selection at two loci	273
20.6 Notes	277
21 Fertility selection	278
21.1 The fertility equation	278
21.2 Two alleles	280
21.3 Multiplicative fertility	282
21.4 Additive fertility	285
21.5 The fertility–mortality equation	286
21.6 Notes	288
22 Game dynamics for Mendelian populations	289
22.1 Strategy and genetics	289
22.2 The discrete model for two strategies	292
22.3 Genetics and ESS	295

22.4	ESS and long-term evolution	298
22.5	Notes	300
	References	301
	Index	321
	Genetics and ESS	323
	The discrete model for two strategies	325
	Strategy and genetic characteristics of a Mendelian population	327
	Game dynamics for Mendelian populations	329
	Notes	336
	The fertility-normality equation and Poincaré maps	338
	ADDITIVE FERTILITY	339
	ADDITIONAL FERTILITY	340
	Multiplicative fertility	343
	Two alleles	343
	The fertility equation	344
	Fertility selection	345
	Notes	346
	Selection at two loci	347
	Limit cycles for the selection-mutation equation	349
	Special mutation rates	353
	Mutation and additive selection	353
	The selection-mutation model	354
	Notes	356
	Mutation and total stability	357
	Communities with a special structure	358
	Notes	361
	Mixed strategists and gradient systems	362
	The Shubshaban gradient	363
	Density dependent fitness	364
	The location of stable rest points	365
	Convergence to a rest point	366
	The selection equation	367
	Continuous selection dynamics	368
	Notes	369
	Essentially hypercyclic networks	370
	Permanence of catalytic networks	371
	Permanence and irreducibility	372
	Linkage	373
	The selection-recombination equation	374
	A periodic attractor for $n = 2$	375
	Replicator networks	376
	Notes	377
	The increase in average fitness	378
	The selection model	379
	The Hardy-Weinberg law	380
	Genotypes	381
	Discrete dynamical systems in population genetics	382
	Part four: Population Genetics	383