

## Contents

	<i>Foreword by Nick Davies</i>	<i>page</i> xiii
	<i>Preface</i>	xv
<b>1</b>	<b>Introduction</b>	1
	1.1 A Historical Perspective	3
	1.2 Dealing with Competition	6
	1.2.1 Competition for Food	8
	1.2.2 Competition for Shelter	8
	1.2.3 Competition for Mates and Social Partners	10
	1.2.4 Competition for Multiple Resources	12
	1.3 The Tension between Conflict and Cooperation	13
	1.4 Conceptual and Semantic Confusions	13
	Box 1.1 The Meaning of Terms and a Glossary for the Concepts of Social Behaviour, Conflict and Cooperation	15
	1.5 The Focus of this Book	20
	CASE STUDY A: SEYCHELLES WARBLER	25
<b>2</b>	<b>Non-interference Rivalry</b>	35
	2.1 Competition: The Engine of Natural Selection	35
	2.2 Ecological Influences on the Nature of Competition	36
	2.2.1 Resource Availability and Renewal	37
	2.2.2 Clumping in Space and Time	38
	2.2.3 Predictability in Space and Time	39
	2.2.4 Divisibility	41
	2.2.5 Predation and Other Ecological Features	41
	2.3 Scramble Strategies and Animal Distributions	42
	2.3.1 Evolving Scramble Effort	44
	2.4 Competition and Collective Movement	46
	2.5 Competition for Information	48
	2.5.1 Social Learning and Recruitment of Others	48
	2.5.2 Producers, Scroungers and Deception	50
	2.6 Social Influences on Competition	52
	2.6.1 Population Density and Competition	53
	2.6.2 Sexual Conflict	55

2.6.3	Alternative Reproductive Tactics	55
2.6.4	Conditional Strategies	58
2.7	Conclusions	59
	CASE STUDY B: BANDED MONGOOSE	61
<b>3</b>	<b>Conflict</b>	67
3.1	Conflict and Cooperation	67
3.2	Sources of Conflict in Social Groups	72
3.2.1	Conflict over Group Membership	72
3.2.2	Conflict over Rank	77
3.2.2.1	Dominance–Submission	80
3.2.3	Conflict over Reproduction	82
3.2.3.1	Reproductive Skew	82
3.2.3.2	Mating Skew	87
3.2.3.3	Parental Care	88
3.2.3.4	Conflict over Helping	90
3.3	Social Conflict: Theoretical Approaches	92
3.3.1	Structured Population Models	92
3.3.2	Sealed Bid Models: Battleground and Resolution	97
3.3.2.1	Battleground Models	97
3.3.2.2	Resolution Models	99
Box 3.1	Contest Success Functions	101
3.3.2.3	Evolving Peace	105
3.3.3	Behavioural Conflict: Threats, Negotiation and Assessment	106
3.3.3.1	Threats and Coercion: Sequential Models	107
3.3.3.2	Negotiation Models	112
3.3.3.3	Assessment Models	113
3.4	Evolutionary Routes to Conflict Reduction	117
3.4.1	Kin Selection	117
3.4.2	Repression of Competition	118
3.4.2.1	Reproductive Dictatorship	118
3.4.2.2	Reproductive Levelling	118
3.4.2.3	Life History Segregation	119
3.4.2.4	Outgroup Threat	120
3.5	Intergroup Conflict and Cooperation	121
3.5.1	Consequences of Intergroup Conflict: Empirical Patterns	124
3.5.2	Intergroup Cooperation and the Major Transitions	126
3.6	Conclusions	128
	CASE STUDY C: PAPER WASP	130
<b>4</b>	<b>Cooperation</b>	136
4.1	Cooperation for Fitness Benefits	137
4.1.1	By-product Benefits or Mutualism	139
Box 4.1	Mutual Fitness Benefits by Group Augmentation	140

Box 4.2 Mutualism, By-product Mutualism and ‘Pseudoreciprocity’: What is the Difference?	142
4.1.2 Correlated Pay-offs	144
4.1.2.1 Reciprocity	145
4.1.2.1.1 Three Types of Information; Three Types of Reciprocity	145
4.1.2.1.2 Generalized Reciprocity	146
Box 4.3 Conditions and Mechanisms for the Evolution of Generalized Reciprocity	146
4.1.2.1.3 Direct Reciprocity	149
4.1.2.1.4 Indirect Reciprocity	149
4.1.2.1.5 The Importance of Information	149
4.1.2.1.6 Cooperation on Networks and Graphs	151
4.1.2.1.7 When Should We Expect Reciprocity?	160
4.1.2.1.8 Which Type of Reciprocity Should We Expect?	166
Box 4.4 Reciprocal Cooperation in Norway Rats	167
Box 4.5 Biological Markets and Cooperation	175
4.1.2.1.9 Negotiations and Trading	177
4.1.2.2 Kin Selection	180
4.1.2.2.1 Evidence for Kin-directed Care in Social Systems	184
4.1.2.2.2 Mechanisms to Promote Kin-directed Helping	186
4.1.2.2.3 Inadvertent Kin-directed Care	187
4.1.2.2.3.1 Longevity as a Driver for Inadvertent Kin-directed Cooperation	189
4.1.2.2.3.2 Limited Natal Dispersal	192
4.1.2.2.3.3 High Breeding Site Fidelity	195
4.1.2.2.3.4 Lekking and Mate Sharing	196
Box 4.6 Nepotistic Cooperation in Alarm-calling and Vigilance	197
4.1.2.2.3.5 Dispersal in Kin Coalitions	202
4.1.2.2.4 Kin Discrimination Involving Kin Recognition	202
Box 4.7 Fitness Benefits of Dispersing in Coalitions of Relatives	203
4.1.2.2.5 Mechanisms Underlying Active Kin Discrimination	209
4.1.2.2.6 Ecological Determinants of Kin-clustering and Cooperation	213
4.1.2.2.7 Kin Selection and Sexual Conflict Resolution	216

x	<b>Contents</b>	
	4.1.2.2.8 Kin Associations Do Not Always Lead to Cooperation	221
	4.1.2.2.9 Inbreeding and Kin-selected Benefits	226
	Box 4.8 Selective Paternal Care and Cannibalism in Fish Males	230
	4.1.2.2.10 Absence of Adjustment of Social Behaviour to Kinship	233
	4.2 Forced Cooperation	237
	4.2.1 Coercion	238
	4.2.1.1 Power Symmetry	238
	Box 4.9 When Does Punishment Create Cooperation, and How Common is it in Nature?	239
	4.2.1.2 Power Asymmetry	243
	4.2.2 Surreptitious Exploitation	246
	4.3 Conclusions	247
	CASE STUDY D: SOCIAL CICHLID	251
<b>5</b>	<b>Interspecific Relations</b>	263
	5.1 Types of Interspecific Interactions	266
	5.2 Non-interference Rivalry	266
	5.2.1 Character Displacement	266
	5.2.2 Specialists versus Generalists	268
	5.3 Conflict	271
	5.3.1 Interspecific Resource Monopolization	271
	5.3.2 How to Deal with Predators: Interspecific Associations	274
	Box 5.1 Interspecific Brood Mixing in Cichlids Through Passive or Active Processes	277
	5.3.3 Host–Parasite Relations	280
	5.4 Cooperation	284
	5.4.1 Commensalism	285
	5.4.2 Mutualism	286
	5.4.3 Reciprocity	288
	5.4.4 Manipulation	294
	5.5 Conclusions	294
	CASE STUDY E: AMBROSIA BEETLE	297
<b>6</b>	<b>Synopsis</b>	309
	6.1 Race	309
	6.2 Fight	310
	6.3 Share	312
	6.4 Interspecific Interactions	315
	6.5 General Conclusions	317
	6.5.1 Optimal Responses to Competition	317
	6.5.2 Future Directions	318

---

**Contents** xi

6.5.3	Less Encouraged	319
6.5.4	Final Inference	320
	CASE STUDY F: <i>HOMO SAPIENS</i>	321
	<i>References</i>	327
	<i>Subject Index</i>	398
	<i>Taxonomic Index</i>	404

*Colour plates can be found between pages 174 and 175.*