

# Contents

	Preface and Acknowledgments	xi
<b>1</b>	<b>Kin Selection</b>	<b>3</b>
	1.1 Introduction	3
	1.2 Natural Selection as Gene Selection	5
	1.3 The Problem of Altruism	10
	1.4 Kin Selection and Hamilton's Rule	12
	1.5 Inclusive Fitness	24
	1.6 Kin Selection Works at All Gene Frequencies	27
	1.7 Gene Expression in Kin Selection Theory	31
	1.8 The Gene for Altruism and the Interests of the Rest of the Genome	32
	1.9 Parental Manipulation Theory	35
	1.10 Conclusion	36
	1.11 Summary	37
<b>2</b>	<b>Levels-of-selection Theory, Gene Selectionism, and Insect Societies</b>	<b>39</b>
	2.1 Introduction	39
	2.2 Colony-level, Group, Kin, and Gene Selection	39
	2.3 Two Examples of Colony-level Selection	50
	2.4 Levels-of-selection Theory	53
	2.5 Gene Selectionism, Levels-of-selection Theory, the Evolution of Individuality, and Suppression of Within-unit Conflict	56
	2.6 The Superorganism	64
	2.7 Conclusion	66
	2.8 Summary	67
<b>3</b>	<b>Kin Selection, Haplodiploidy, and the Evolution of Eusociality in Ants</b>	<b>69</b>
	3.1 Introduction	69
	3.2 Concepts in the Origin and Evolution of Eusociality	70
	3.3 The Origin of Eusociality in Ants	73
	3.4 The Epigenetic Theory of Insect Sociality	74
	3.5 The Haplodiploidy Hypothesis	77

3.6	A Critique of the Haplodiploidy Hypothesis (I)	82
3.7	A Critique of the Haplodiploidy Hypothesis (II)	93
3.8	Factors Promoting Worker Evolution via Relatedness and Sex Ratio Effects in Haplodiploid Populations	97
3.9	Factors Promoting Worker Evolution in Diploid and Haplodiploid Populations	101
3.10	Conclusion	104
3.11	Summary	104
<b>4</b>	<b>Sex Ratio Theory for the Social Hymenoptera</b>	<b>107</b>
4.1	Introduction	107
4.2	Fisher's Sex Ratio Theory	108
4.3	Sex Ratios in Social Haplodiploids: Basic Theory	113
4.4	Sex Ratios in Slave-making Ants	118
4.5	Sex Ratios under Multiple Mating	119
4.6	Sex Ratios under Worker Reproduction	126
4.7	Sex Ratios under Polygyny	136
4.8	Sex Ratios when there is Colony Fission, Colony Budding, or Polydomy	141
4.9	Sex Ratio with Local Mate Competition	145
4.10	Sex Ratio with Local Resource Competition and Local Resource Enhancement	151
4.11	Conclusion	152
4.12	Summary	152
<b>5</b>	<b>Tests of Sex Ratio Theory in Ants</b>	<b>156</b>
5.1	Introduction	156
5.2	Tests of the Trivers–Hare Model for Monogynous Species	156
5.3	Sex Ratio Data in Slave-making Ants	167
5.4	Sex Ratio Data in Multiply Mating Species	170
5.5	Sex Ratio Data in Species with Worker Reproduction	174
5.6	Sex Ratio Data in Polygynous Species	175
5.7	Sex Ratio Data in Species with Colony Fission, Colony Budding, or Polydomy	185
5.8	Sex Ratio Data in Species with Local Mate Competition	190
5.9	Sex Ratio Data in Species with Local Resource Competition	195
5.10	Conclusion	195
5.11	Summary	196

<b>6</b>	<b>Kin Conflict over Sex Allocation</b>	<b>200</b>
6.1	Introduction	200
6.2	Why do Colonies Vary in their Sex Ratios?	200
6.3	Do Queens and Workers Share Control of Sex Allocation?	208
6.4	What are the Mechanisms for Controlling Sex Allocation?	212
6.5	What Tactics could Queens and Workers use in the Sex Ratio Conflict?	214
6.6	What Factors Affect the Outcome of Queen–Worker Sex Ratio Conflict?	216
6.7	Conclusion	217
6.8	Summary	218
<b>7</b>	<b>Kin Conflict over Reproduction</b>	<b>220</b>
7.1	Introduction	220
7.2	Basic Theory of Kin Conflict	221
7.3	Factors Affecting Kin Conflict in Social Hymenoptera	223
7.4	Kin Conflict over Male Production	227
7.5	Kin Conflict in Multiple-queen Societies	244
7.6	Other Kinds of Kin Conflict in Ants	247
7.7	Conclusion	254
7.8	Summary	255
<b>8</b>	<b>Evolution and Ecology of Multiple-queen Societies</b>	<b>258</b>
8.1	Introduction	258
8.2	Types of Polygynous Society and their Features	259
8.3	Evolution of Foundress Associations	267
8.4	Evolution of Multicolonial, Secondary Polygyny	271
8.5	Evolution of Unicolonial Polygyny	282
8.6	Evolution of Functional Monogyny, Queen Aggression, and a Stable Reproductive Skew	285
8.7	Conclusion	296
8.8	Summary	296
<b>9</b>	<b>Life History Theory in Ants</b>	<b>299</b>
9.1	Introduction	299
9.2	Life History Theory in General and in Social Insects	301

9.3	The Evolution of a Perennial Life Cycle in Ants	303
9.4	Dispersal in Stable Habitats	309
9.5	Trade-offs, Propagule Size, and Modes of Colony Foundation	310
9.6	Modular Growth	315
9.7	Reaction Norms	318
9.8	Lineage-specific Effects and the Concept of <i>r</i> and <i>K</i> Selection	319
9.9	Special Issues in Social Insect Life History Evolution	322
9.10	Conclusion	325
9.11	Summary	326
<b>10</b>	<b>The Diversity of Life Histories in Ants</b>	<b>328</b>
10.1	Introduction	328
10.2	The Imported Fire Ant, <i>Solenopsis invicta</i>	328
10.3	The Red Ants, <i>Myrmica</i>	334
10.4	The Leptothoracines	341
10.5	The Wood Ants, <i>Formica</i>	351
10.6	The Argentine Ant, <i>Linepithema humile</i>	354
10.7	The Obligately Thelytokous Ant, <i>Pristomyrmex pungens</i>	357
10.8	The Army Ants, <i>Eciton</i>	358
10.9	Conclusion	363
10.10	Summary	363
<b>11</b>	<b>Mating Biology</b>	<b>365</b>
11.1	Introduction	365
11.2	Sexual Selection and Ant Sexual Behavior	365
11.3	Sperm Use and Sperm Competition in Ants	376
11.4	The Evolution of Multiple Mating in Ant Queens	380
11.5	The Location of Mating: Causes and Consequences	387
11.6	Conclusion	397
11.7	Summary	398
<b>12</b>	<b>The Division of Labor</b>	<b>400</b>
12.1	Introduction	400
12.2	The General Significance of a Division of Labor	401

12.3	Temporal Polyethism and a Confusion of Cause and Effect	404
12.4	An Algorithmic Approach to the Division of Labor	408
12.5	The Division of Labor: Empirical Studies	421
12.6	New Approaches: Spatial Patterns and the Division of Labor	432
12.7	Ant Colonies, Adaptive Redundancy, Complexity, and Organizations	439
12.8	Conclusion	441
12.9	Summary	442
	References	445
	Author Index	511
	Subject Index	519
	Taxonomic Index	526

