

Contents

Preface	xv
---------	----

Acknowledgments	xix
-----------------	-----

1 The Theory of Sexual Selection	3
----------------------------------	---

1.1 Sexual Selection	3
----------------------	---

*Anisogamy; Competition over Mates;
Forms of Mating Competition*

1.2 Sex Traits and Sexual Dimorphism	13
--------------------------------------	----

1.3 Criticism of Darwin's Theory of Sexual Selection	17
--	----

1.4 Selection of Secondary Sex Signals	19
--	----

*Pleiotropic Gene Effects; Selection of
Ecological Sex Differences; Males Are
Unprofitable Prey; Male Contest
Competition; Female Choice and Mating
Preferences*

1.5 Evolution of Female Preferences for Male Traits	24
---	----

*The Fisher Process; Indicator Mechanisms;
Species Recognition; Direct Phenotypic
Benefits; Sensory Bias and the Origins of
Preferences; Mating Synchronization and
Stimulation*

1.6 Summary	31
-------------	----

2 Genetic Models of Fisherian Self-Reinforcing Sexual Selection	32
---	----

2.1 Introduction	32
------------------	----

2.2 Two-Locus Models	33
----------------------	----

2.3 Polygenic Models	37
----------------------	----

2.4 Direct Selection of Preferences, and Deleterious Mutations in the Preferred Trait	42
---	----

*Costs of Mate Choice; Direct Benefits of
Mate Choice*

2.5 The Evolution of Sexual Dimorphism by Fisherian Sexual Selection	45
--	----

2.6 Speciation by Sexual Selection?	46
-------------------------------------	----

2.7 Empirical Tests	47
---------------------	----

*Natural Selection Opposing Sexually
Selected Traits; Heritability of Trait and*

	<i>Preference; Covariance between Trait and Preference</i>	
2.8	Summary	52
3	Genetic Models of Indicator Mechanisms	53
3.1	Introduction	53
3.2	Three-Locus Models	54
	<i>Pure Epistatic Indicators; Condition-dependent Indicators; Revealing Indicators; Comparison of 3-Locus Models</i>	
3.3	Polygenic Models	60
3.4	Indicators and Direct Phenotypic Benefits	62
3.5	The Heritability of Fitness	64
	<i>Theory; Empirical Results</i>	
3.6	Condition Dependence of Secondary Sex Traits	68
	<i>Phenotypic Condition; Age Dependence; Fluctuating Asymmetry</i>	
3.7	Tests of Indicator Mechanisms	72
	<i>Parasite-mediated Sexual Selection</i>	
3.8	Summary	78
4	Empirical Methods	80
4.1	Introduction	80
4.2	Observations and Experiments	81
4.3	Trends among Species: Comparative Approaches	83
	<i>Qualitative Traits; Quantitative Traits</i>	
4.4	Measures of Sexual Selection	89
4.5	Selection of Quantitative, Correlated Traits	91
	<i>Theory; Example: Sexual Selection in Darwin Finches</i>	
4.6	Summary	98
5	Some Case Studies	100
5.1	Causes of Sexual Selection in Male and Female Katydid	100
5.2	Male Coloration and Female Choice in the Guppy	103
	<i>Natural Selection of Male Color Patterns; Sexual Selection of Male Color Patterns; Genetic Correlation between Female Preference and Male Ornaments</i>	
5.3	Advertisement Calls in the Tungara Frog	109
5.4	Plumage Ornaments in the Red-winged Blackbird and Long-tailed Widowbird	112
	<i>Wing Epaulet; Long Tail</i>	

5.5	Sexual Size Dimorphism in Elephant Seals	117
5.6	Secondary Sex Differences in Red Deer	119
5.7	Summary	123
6	Empirical Studies of Sexually Selected Traits: Patterns	124
6.1	Introduction	124
6.2	Patterns <i>Types of Study; Selection Mechanisms; Selected Traits; Open Questions</i>	126
6.3	Summary	131
7	Sexual Selection in Relation to Mating System and Parental Roles	143
7.1	Mating Systems	143
7.2	Sexual Selection, Parental Investment, Sex Ratio, and Reproductive Rate <i>Male and Female Parental Investment; Mate Control and the Operational Sex Ratio; Potential Reproductive Rates of Males and Females</i>	146
7.3	Monogamy and Sexual Selection <i>Variation in Mate Quality; Skewed Sex Ratios</i>	157
7.4	Sexual Monomorphism	161
7.5	Leks and Sexual Selection <i>An Australian Frog; Tetraonids; Birds of Paradise; Bowerbirds; Cotingids and Manakins; Other Birds; Fallow Deer</i>	163
7.6	Sex Role Reversal <i>Giant Waterbugs; Pipefishes; Spotted Sandpipers</i>	177
7.7	Summary	182
8	Benefits of Mate Choice	184
8.1	Fertilization Ability and Fecundity <i>Female Choice; Multiple Matings by Females; Male Choice of Females</i>	184
8.2	Nutrition Provided by the Male <i>Prey Gifts; Nutrients Synthesized by the Male; Mating Cannibalism; Food Gifts: Male Mating or Parental Effort?</i>	187
8.3	Parental Ability of the Mate	192
8.4	Territories and Other Defended Resources <i>The Polygyny Threshold Model</i>	193
8.5	Risk Reduction	198

8.6	Mate Complementarity	199
8.7	Mate Choice and Offspring Quality <i>Flies; Grasshoppers; Sulfur Butterflies; Frogs</i>	200
8.8	Direct Benefits Indicated by Male Traits	203
8.9	Summary	205
9	Species Recognition, Sexual Selection, and Speciation	207
9.1	Introduction <i>Divergence of Species Recognition Traits; Sexual Selection</i>	207
9.2	Selection for Species Recognition <i>Insects; Anurans; Lizards; Birds; Plants</i>	211
9.3	Sexual Selection, Species Divergence, and Speciation	223
9.4	Summary	226
10	Constraints	227
10.1	Predation <i>Male Bias in the Prey of Predators; Visual Signals; Acoustic Signals; Pheromones; Other Sexually Selected Behavior; Evolutionary Consequences of Predation on Males</i>	227
10.2	Other Mortality in Sexually Competing Males	235
10.3	Other Costs of Sexually Selected Traits	237
10.4	Physiological Constraints	238
10.5	Sexual Selection in Relation to Life History <i>Reproductive Effort; Sexual Bimaturism</i>	241
10.6	Genetic Constraints	244
10.7	Sensory Bias and Constraints	245
10.8	Summary	246
11	Sexual Size Dimorphism	247
11.1	Introduction	247
11.2	The Direction and Degree of Sexual Size Dimorphism <i>Female Advantages of Large Size; Female Advantages of Small Size; Male Advantages of Large Size; Male Advantages of Small Size; Dwarf Males</i>	251
11.3	Taxonomic Review	259

11.4	Arthropods and Other Invertebrates	260
11.5	Fishes	262
11.6	Amphibia	264
11.7	Reptiles <i>Lizards; Snakes; Turtles</i>	267
11.8	Birds <i>Waders; Birds of Prey</i>	269
11.9	Mammals <i>Large Herbivores; Marine Mammals; Primates</i>	282
11.10	Why Does Sexual Size Dimorphism Increase with Body Size?	290
11.11	Summary	292

12 Weapons 295

12.1	Introduction	295
12.2	Mammals <i>Weapons for Defense against Predators; Weapons Used against Rivals; Display of Strength and Vigor to Other Males; Female Choice in Relation to Male Weapons; The Evolution of Horns in Ungulates; Large Male Weapons in Pleistocene Mammals; Allometric Relationships</i>	295
12.3	Avian Spurs	308
12.4	Beetle Horns and Other Arthropod Weapons	309
12.5	Summary	314

13 Coloration and Other Visual Signals 315

13.1	Introduction	315
13.2	Invertebrates	316
13.3	Fishes	320
13.4	Amphibia	324
13.5	Reptiles <i>Conspicuous Male Colors; Conspicuous Female Colors</i>	326
13.6	Birds <i>Sex and Species Recognition; Mate Choice; Long Tails; Contests; Unprofitable Prey; Delayed Plumage Maturation</i>	329
13.7	Mammals	344
13.8	Parasites, Mate Choice, and Conspicuous Colors: Comparative Evidence	346
13.9	Summary	348

14	Acoustic Signals	349
14.1	Introduction	349
14.2	Male Contest Competition and Song <i>Insects; Anurans; Birds; Mammals</i>	351
14.3	Song and Mate Choice <i>Insects; Anurans; Birds; Mammals; Female Incitation of Male Competition?</i>	354
14.4	Selection of Responses to Song	365
14.5	Some Aspects of Method	366
14.6	Summary	367
15	Chemical Signals	369
15.1	Insects	369
15.2	Fishes, Amphibians, and Reptiles	374
15.3	Mammals <i>Male Contest Competition; Attraction and Priming of Mates</i>	375
15.4	Summary	378
16	Alternative Mating Tactics	379
16.1	Individual Differences and Mating Tactics <i>Age- and Size-dependent Differences; Responses to Changes in the Environment</i>	379
16.2	Dimorphism in Male Morphology and Behavior <i>Male Weapons; Genetic Variation in Cricket Mating Tactics; Male Trimorphism in an Isopod; Alternative Mating Tactics in Salmon and Sunfish; Plumage and Behavior Polymorphism in the Ruff</i>	383
16.3	Sex Allocation, Sex Change, and Sexual Selection <i>Theory; Sex Change in Fishes</i>	390
16.4	Some Empirical Problems	394
16.5	Summary	395
17	Sexual Selection in Plants	396
17.1	Introduction	396
17.2	What is Sexual Selection in Plants?	399
17.3	Sex Roles	401
17.4	Secondary Sex Differences	402
17.5	Pollen Production	405
17.6	Pollinator Attraction <i>Sexual Selection of Flowers; Scent; Nectar; Flower Phenology</i>	406

17.7	Male Scrambles and Female Choice in the Style? <i>Male Scrambles; Female Choice?</i>	418
17.8	Sexual Advertisement in Plants Compared with Animals	422
17.9	Allocation to Male and Female Function in Cosexual Organisms <i>Cosexuality versus Separate Sexes; Allocation to Pollinator Attraction; Sex Change in Plants</i>	426
17.10	Summary	432

18	Sexual Selection: Conclusions and Open Questions	433
18.1	Mechanisms of Sexual Selection	434
18.2	Traits Favored by Sexual Selection	436
18.3	Sexual Selection in Plants	439
18.4	Constraints	440
18.5	Relations with Some Adjacent Fields	440
	References	445
	Author Index	561
	Subject Index	581
	Taxonomic Index	588