

# Contents

<b>1</b>	<b>Cryptic Female Choice and Other Types of Post-copulatory Sexual Selection</b> . . . . .	1
	William G. Eberhard	
1.1	Introduction . . . . .	2
1.2	Cryptic Female Choice and Alternative Theories Regarding Post-copulatory Selection . . . . .	2
1.2.1	Sexual Selection . . . . .	2
1.2.2	Natural Selection Favoring Species Isolation (SI) . . . . .	6
1.3	How to Distinguish Between CFC and the Other Hypotheses. . . . .	7
1.3.1	CFC and SC . . . . .	7
1.3.2	CFC and SI . . . . .	9
1.3.3	CFC and SAC . . . . .	10
1.4	The Current State of Affairs . . . . .	18
1.5	Peering into the Future . . . . .	19
	References . . . . .	23
<b>2</b>	<b>Potential for CFC in Black Widows (Genus <i>Latrodectus</i>): Mechanisms and Social Context</b> . . . . .	27
	Maydianne C.B. Andrade and Emily C. MacLeod	
2.1	Introduction . . . . .	28
2.2	Natural History and Biology of <i>Latrodectus</i> Spiders in the Context of CFC . . . . .	31
2.2.1	Comparative Context and Variation . . . . .	31
2.2.2	Ecology and Phenology: CFC May Be More Likely that Mate Choice . . . . .	32
2.2.3	Reproductive Biology and Possible Mechanisms of CFC . . . . .	35
2.3	CFC in <i>Latrodectus</i> : Potential Mechanisms and Evidence . . . . .	42
2.3.1	CFC and Control of Copulation Frequency . . . . .	42

2.3.2	CFC and Control of Copulation Duration . . . . .	44
2.3.3	CFC and the Mechanics of Ejaculation and Plug Placement . . . . .	46
2.4	Conclusions . . . . .	47
	References . . . . .	48
<b>3</b>	<b>Cryptic Female Choice Within the Genus <i>Argiope</i>: A Comparative Approach . . . . .</b>	<b>55</b>
	Jutta Schneider, Gabriele Uhl and Marie E. Herberstein	
3.1	The Genus <i>Argiope</i> —an Excellent Model for Cryptic Female Choice . . . . .	56
3.2	Mating System and the Potential for Cryptic Female Choice . . .	58
3.3	Male Mating Rates: Monogyny and Bigyny . . . . .	58
3.4	It Takes Two to Tango: Male Mate Choice . . . . .	60
3.5	Limits to Female Mating Rate: One-Shot Genitalia and Mating Plugs . . . . .	61
3.6	Programmed Death of Males . . . . .	65
3.7	Copulation Mechanism . . . . .	66
3.8	Female Sexual Selection Strategies . . . . .	68
	3.8.1 Female Choice . . . . .	68
	3.8.2 Cryptic Female Choice . . . . .	69
	3.8.3 Female Aggression and Sexual Cannibalism . . . . .	70
	3.8.4 Controlling Copulation Duration . . . . .	72
	3.8.5 Control of the Transfer and Storage of Sperm . . . . .	72
3.9	Conclusions and Outlook . . . . .	74
	References . . . . .	75
<b>4</b>	<b>Post-copulatory Sexual Selection in Two Tropical Orb-weaving <i>Leucauge</i> Spiders . . . . .</b>	<b>79</b>
	Anita Aisenberg, Gilbert Barrantes and William G. Eberhard	
4.1	Introduction . . . . .	80
4.2	Background on <i>Leucauge</i> Sexual Biology . . . . .	81
4.3	Pre-copulatory Behavior . . . . .	83
4.4	Copulation . . . . .	85
	4.4.1 Movements of the Female and Male's Body and Legs . . .	85
	4.4.2 Cheliceral Claspings . . . . .	86
	4.4.3 <i>L. mariana</i> : Movements of Male Genitalia When the Female Lacked a Plug . . . . .	88
	4.4.4 <i>L. argyra</i> : Movements of Male Genitalia When the Female Lacked a Plug . . . . .	91
	4.4.5 Movements of Male Genitalia When the Female Has a Plug . . . . .	92
	4.4.6 Female Participation During Copulation . . . . .	95
4.5	Factors Affecting the Outcomes of Copulation . . . . .	98
	4.5.1 Correlations with Courtship Behavior . . . . .	98
	4.5.2 Evidence from Experimental Manipulations . . . . .	99

4.6	Discussion . . . . .	100
4.6.1	The Non-passive Females of <i>Leucauge</i> . . . . .	100
4.6.2	Why Do Females Influence Copulation Outcomes? Functions of Male and Female Traits . . . . .	101
4.6.3	Why Do Female <i>Leucauge</i> Make Mating Plugs? . . . . .	104
4.7	Directions for Future Research . . . . .	105
	References . . . . .	106
<b>5</b>	<b>Copulatory and Post-copulatory Sexual Selection in Haplogyne Spiders, with Emphasis on Pholcidae and Oonopidae.</b> . . . . .	<b>109</b>
	Lucía Calbacho-Rosa and Alfredo V. Peretti	
5.1	Introduction . . . . .	109
5.1.1	Overview on Post-copulatory Sexual Selection. . . . .	109
5.1.2	The Need for Fine-Scaled Studies on Cryptic Female Choice in Different Organisms . . . . .	111
5.2	Haplogyne and Entelegyne Spiders . . . . .	111
5.2.1	Haplogyne Spiders: Reproductive Sexual Morphology and Sexual Behavior . . . . .	113
5.2.2	The Value of Haplogyne Spiders to Evaluate CFC . . . . .	119
5.3	Evaluating CFC and Other Alternatives Step by Step . . . . .	120
5.3.1	Genitalic and Non-genitalic Male Copulatory Courtship. . . . .	120
5.3.2	Female Copulatory Behavior: Resistance Versus Copulatory Dialogues with the Male . . . . .	125
5.3.3	Pholcid Genitalia and Post-copulatory Sexual Selection. . . . .	127
5.3.4	Sperm Dumping and Its Role to Bias Paternity. . . . .	131
5.4	Conclusions and Prospects. . . . .	136
	References . . . . .	137
<b>6</b>	<b>Cryptic Female Choice and Nuptial Prey Gifts in a Spider Model</b> . . . . .	<b>145</b>
	Luiz Ernesto Costa-Schmidt	
6.1	Introduction . . . . .	146
6.2	What Is This Chapter About?. . . . .	147
6.3	Nuptial Gifts and CFC: Beyond the Males' World . . . . .	148
6.4	A Sexual Strategy Shaped in Concert . . . . .	149
6.5	Nuptial Gifts and CFC in Spiders . . . . .	150
6.5.1	Conditions for CFC Occurrence via Nuptial Gifts Within Spiders. . . . .	150
6.5.2	Classes of Nuptial Gifts in Spiders . . . . .	152
6.5.3	Spiders' Prey Gifts: Structure and Multimodal Communication Issues. . . . .	153

6.6	The Integrate Role of Reproductive Stages Defining CFC Opportunity . . . . .	156
6.6.1	Prey Gift and Mate Choice . . . . .	157
6.6.2	Copulatory Courtship. . . . .	159
6.6.3	Post-copulatory CFC . . . . .	162
6.7	Concluding Remarks . . . . .	163
	References. . . . .	164
<b>7</b>	<b>Male and Female Mate Choice in Harvestmen: General Patterns and Inferences on the Underlying Processes . . . . .</b>	<b>169</b>
	Glauco Machado, Gustavo S. Requena, Carlos Toscano Gadea, Estefanía Stanley and Rogelio Macías-Ordóñez	
7.1	Introduction . . . . .	170
7.2	Mating Systems . . . . .	173
7.2.1	General Characterization . . . . .	173
7.2.2	Potential for Female Mate Choice . . . . .	175
7.3	Pre-copulatory Interactions . . . . .	177
7.3.1	General Characterization . . . . .	177
7.3.2	Tactile Courtship and Nuptial Gifts . . . . .	178
7.4	Copulatory Interactions . . . . .	182
7.4.1	General Characterization . . . . .	182
7.4.2	Genital Morphology. . . . .	183
7.4.3	Genital Interaction . . . . .	185
7.5	Post-copulatory Interactions. . . . .	187
7.5.1	General Characterization . . . . .	187
7.5.2	Mate Guarding . . . . .	188
7.5.3	Cryptic Female Choice . . . . .	190
7.5.4	Direct Benefits . . . . .	192
7.6	Male Mate Choice . . . . .	192
7.6.1	Males Repelling Females. . . . .	193
7.6.2	Female Courtship and Aggressive Behaviors . . . . .	194
7.7	Concluding Remarks . . . . .	195
	References. . . . .	197
<b>8</b>	<b>Cryptic Female Choice in Crustaceans . . . . .</b>	<b>203</b>
	Stefan Dennenmoser and Martin Thiel	
8.1	Introduction . . . . .	204
8.2	A Brief Introduction to Crustacean Mating Patterns . . . . .	205
8.2.1	Mating Systems . . . . .	205
8.2.2	Reproductive Biology . . . . .	206
8.3	Cryptic Female Choice in Crustaceans . . . . .	207
8.3.1	Multiple Matings: Behavioral and Molecular Evidence . . . . .	207
8.3.2	Indicators and Mechanisms of CFC in Crustaceans . . . . .	208
8.3.3	Selected Case Studies . . . . .	224

8.4	Crustaceans Compared to Other Invertebrates . . . . .	227
8.5	Conclusions . . . . .	229
	References . . . . .	229
<b>9</b>	<b>Female Choice in Damselflies and Dragonflies . . . . .</b>	<b>239</b>
	Alex Córdoba-Aguilar, Daniel González-Tokman, Ángela Nava-Bolaños, Karina Cuevas-Yáñez, Miguel Rivas and Adriana Nava-Sánchez	
9.1	Introduction . . . . .	240
9.2	Precopulatory Female Choice . . . . .	240
	9.2.1 Wing Pigmentation . . . . .	240
	9.2.2 Defending and Showing Oviposition Sites . . . . .	242
	9.2.3 Male Body Color . . . . .	242
	9.2.4 Male Body Temperature . . . . .	243
9.3	Post-copulatory Female Choice . . . . .	244
	9.3.1 Copulation Duration . . . . .	244
	9.3.2 Sperm Ejection. . . . .	245
	9.3.3 Oviposition Duration . . . . .	245
9.4	What Do Odonate Females Choose? . . . . .	247
9.5	Female Choice Despite Male Coercion? . . . . .	247
9.6	Concluding Remarks . . . . .	250
	References . . . . .	251
<b>10</b>	<b>What Is Indirect Cryptic Female Choice? Theoretical Considerations and an Example from a Promiscuous Earwig . . . . .</b>	<b>255</b>
	Yoshitaka Kamimura	
10.1	Introduction: Direct and Indirect Mechanisms for Collecting Good/Sexy Sperm. . . . .	256
10.2	Possible Mechanisms of Indirect CFC. . . . .	257
	10.2.1 Remating with Another Male. . . . .	257
	10.2.2 Discarding of Sperm and Failure to Transport Sperm to Storage Organs or Fertilization Sites . . . . .	260
	10.2.3 Prevention of Complete Intromission and Ejaculation or Forceful Termination of Mating Before Sperm are Transferred . . . . .	262
	10.2.4 Reduction in the Rate or Number of Offspring Produced, Failure to Ovulate, or Failure of Eggs to Mature . . . . .	262
10.3	Why Females Do not Allow Complete Sperm Displacement: A CFC Hypothesis . . . . .	263
	10.3.1 Model. . . . .	264
	10.3.2 Interpretation of Model Predictions. . . . .	265
10.4	A Case Study of a Promiscuous Earwig . . . . .	267
	10.4.1 Study Species and Problems . . . . .	267
	10.4.2 Staged Mating Experiment . . . . .	270
	10.4.3 Simulation Study . . . . .	273

10.5 Discussion . . . . . 275

10.5.1 Interrelationships Between CFC and FMM. . . . . 275

10.5.2 Alternative Hypotheses for the Function of Elongated Spermatheca in *E. plebeja* . . . . . 276

10.5.3 Other Possible Indirect CFC in *E. plebeja* and Related Species . . . . . 277

10.5.4 Alternative Hypotheses for FMM in *E. plebeja*. . . . . 277

10.5.5 Ecological Conditions for the Evolution of Indirect CFC . . . . . 278

10.6 Interrelationships Between Pre- and Postcopulatory Sexual Selection. . . . . 279

10.7 Conclusions . . . . . 280

References. . . . . 280

**11 Cryptic Female Choice in Crickets and Relatives**

**(Orthoptera: Ensifera)** . . . . . 285

Karim Vahed

11.1 Introduction . . . . . 285

11.1.1 Distinguishing Cryptic Female Choice from Other Processes . . . . . 287

11.1.2 Reproduction in Crickets and Relatives. . . . . 288

11.2 Mechanisms of Cryptic Female Choice in Crickets. . . . . 290

11.2.1 Manipulation of the Duration of Spermatophore Attachment . . . . . 290

11.2.2 Control of Sperm Uptake/Storage in the Spermatheca (Beyond Control of Spermatophore Attachment) . . . . . 299

11.2.3 Repeated Mating with the Same Male/Choosing to Mate Subsequently with a Different Male. . . . . 303

11.2.4 Resistance During Copulation . . . . . 304

11.2.5 The Rate of Oviposition Following Mating and/or Differential Allocation of Resources to Offspring . . . . . 305

11.3 Evidence for Ultimate Benefits of Cryptic Female Choice to the Female . . . . . 306

11.4 Male–Female Interactions During and After Copulation: From Courtship to Coercion. . . . . 308

11.4.1 “Courtship” that Occurs Between Repeated Copulations . . . . . 309

11.4.2 Nuptial Gifts and Cryptic Female Choice . . . . . 310

11.4.3 Prolonged Copulation During Ejaculate Transfer: Copulatory Structures and Coercion? . . . . . 312

11.4.4 “Titillators”: Copulatory Structures and Courtship? . . . 313

11.4.5	Ejection/Removal of Sperm from the Spermatheca . . .	314
11.4.6	All hormones in the Ejaculate and Mating Plugs . . . . .	315
11.5	Conclusions . . . . .	316
	References . . . . .	317
<b>12</b>	<b>Sexual Selection Within the Female Genitalia in Lepidoptera . . . . .</b>	<b>325</b>
	Carlos Cordero and Joaquín Baixeras	
12.1	Introduction . . . . .	325
12.2	Complexity and Diversity of Male and Female Genitalia: Form and Function . . . . .	329
12.2.1	Male Genitalia Structure . . . . .	330
12.2.2	Female Genitalia Structure . . . . .	333
12.2.3	The Function: Mating . . . . .	334
12.3	Selection on Genitalia in Lepidoptera: Some Illustrative Hypotheses . . . . .	338
12.4	Sexual Coevolution of Signa and Spermatophore Envelopes . . .	341
12.5	Conclusions . . . . .	345
	References . . . . .	346
<b>13</b>	<b>Who's Zooming Who? Seminal Fluids and Cryptic Female Choice in Diptera . . . . .</b>	<b>351</b>
	Laura K. Sirot and Mariana F. Wolfner	
13.1	Introduction . . . . .	352
13.2	Female Mechanisms to Influence MPCRS . . . . .	353
13.2.1	Sperm Storage, Maintenance, and Release . . . . .	353
13.2.2	Nutrition, Egg Production, and Release . . . . .	356
13.2.3	Remating Patterns . . . . .	357
13.3	Seminal Fluid Proteins: Male-Derived Modulators of MPCRS . . . . .	358
13.3.1	Sperm Storage, Maintenance, and Release . . . . .	359
13.3.2	Nutrition, Egg Production, and Release . . . . .	360
13.3.3	Remating Patterns . . . . .	361
13.4	Female Use of Sfps for Exerting CFC . . . . .	361
13.4.1	Regulating Duration and Rate of Sfp Effects . . . . .	361
13.4.2	Modulating Sensitivity to Sfps . . . . .	364
13.5	Molecular Signatures of a Battle for Control . . . . .	364
13.5.1	Ability of Sfps to Enter the Female Circulatory System . . . . .	365
13.5.2	Redundancy of Sfp Function . . . . .	365
13.5.3	Interspecific Divergence in Sfp Sequences . . . . .	366
13.5.4	Mimicry of Female Messenger Molecules . . . . .	367
13.6	CFC on Sfps . . . . .	368
13.6.1	Sexual Selection on Sfp Quantity . . . . .	368
13.6.2	Sexual Selection on Sfp Quality . . . . .	370

13.6.3	Predicted Evolutionary Patterns of CFC on Sfps . . . . .	371
13.6.4	Differentiating CFC on Sfps from Other Forms of Selection . . . . .	372
13.7	Conclusions and Future Directions . . . . .	373
	References . . . . .	375
<b>14</b>	<b>An Integrative View of Postcopulatory Sexual Selection in a Soldier Fly: Interplay Between Cryptic Mate Choice and Sperm Competition . . . . .</b>	<b>385</b>
	Flavia Barbosa	
14.1	Introduction . . . . .	385
14.2	The Soldier Fly: Natural History and Mating Behavior . . . . .	387
14.3	Cryptic Female Choice by Female Control of Oviposition Timing in a Soldier Fly . . . . .	389
14.4	Sperm Competition (SC) and Cryptic Male Choice (CMC) in the Soldier Fly . . . . .	391
14.5	Copulation Duration, Sperm Competition Cues, and Fertilization Success . . . . .	395
14.6	Conclusions and Future Directions . . . . .	397
	References . . . . .	399
<b>15</b>	<b>Species-Specific Behavioral Differences in Tsetse Fly Genital Morphology and Probable Cryptic Female Choice . . . . .</b>	<b>403</b>
	R.D. Briceño and W.G. Eberhard	
15.1	Introduction . . . . .	404
15.2	Background: The Natural History of <i>Glossina</i> . . . . .	405
15.3	Copulatory Courtship Behavior . . . . .	406
15.4	Clasping Male Genitalia . . . . .	406
	15.4.1 Morphology of Male Clasping Genitalia . . . . .	406
	15.4.2 Behavior of Male Grasping Genitalia. Observations of the Behavior of Cerci and Associated Structures . . . . .	411
15.5	Deducing the Functions of Clasping Genitalia from Morphology and Behavior . . . . .	414
15.6	Experimental Tests of the Functions of Male Genital Structures . . . . .	414
15.7	Intromittent Male Genitalia . . . . .	416
	15.7.1 Morphology of Intromittent Male Genitalia . . . . .	416
	15.7.2 Behavior of Intromittent Male Genitalia . . . . .	416
	15.7.3 Pneumopophyses . . . . .	417
	15.7.4 Distal Triangular Sclerite of Phallobase . . . . .	417
	15.7.5 Phallobase as a Unit . . . . .	418



- 15.8 Discussion . . . . . 420
  - 15.8.1 Stimulation of the Female: Implications  
from Morphological Designs and Behavior. . . . . 420
  - 15.8.2 Female Responses to Male Stimuli . . . . . 422
  - 15.8.3 Species Specificity and Evolutionary Transitions . . . . . 422
  - 15.8.4 Alternative Explanations for the Evolution  
of Genital Morphology and Behavior in *Glossina*. . . . . 423
  - 15.8.5 Limits of the Techniques Used . . . . . 427
- References. . . . . 428
  
- 16 Evaluating Cryptic Female Choice in Highly Promiscuous  
*Tribolium* Beetles. . . . . 431**
  - Tatyana Y. Fedina and Sara M. Lewis
  - 16.1 Conditions Favoring Extreme Female Promiscuity . . . . . 432
    - 16.1.1 Habitat, Food, Life History, and Population Cycles . . . 432
    - 16.1.2 Benefits and Costs of Female Polyandry. . . . . 433
    - 16.1.3 Evidence for Pre-mating Female Assessment  
of Long-Range Male Pheromones. . . . . 435
    - 16.1.4 Lack of Pre-mating Interactions . . . . . 436
    - 16.1.5 Effect of Extreme Promiscuity on Sexual Selection . . . 438
  - 16.2 Cryptic Female Choice During Copulation . . . . . 439
    - 16.2.1 Female Reproductive Anatomy  
and Male Spermatophore. . . . . 439
    - 16.2.2 Male Copulatory Courtship and Female  
Quiescence Behavior . . . . . 441
    - 16.2.3 Female Control Over Spermatophore Transfer . . . . . 443
    - 16.2.4 Female Influence Over Sperm Quantity Transferred. . . 444
  - 16.3 Postcopulatory Cryptic Female Choice . . . . . 445
    - 16.3.1 Inferring CFC from MxF Statistical Interactions . . . . . 445
    - 16.3.2 Sperm Movement into Storage . . . . . 446
    - 16.3.3 Spermatophore Ejection After Mating. . . . . 448
    - 16.3.4 Potential for CFC During Sperm Storage and Use . . . . . 449
    - 16.3.5 Cryptic Female Choice via Re-mating . . . . . 449
    - 16.3.6 Comparative Study of CFC Evolution  
and Mechanisms . . . . . 451
  - 16.4 Latest Developments and Future Directions . . . . . 452
  - 16.5 Conclusions . . . . . 453
  - References. . . . . 454
  
- 17 Female Choice in Social Insects. . . . . 461**
  - Boris Baer
  - 17.1 Introduction . . . . . 461
  - 17.2 Social Insects . . . . . 463
  - 17.3 The Reproductive Biology of Social Insect Queens . . . . . 464

17.4 Why Social Insect Queens Should Be Choosy . . . . . 466

17.5 Evidence for Cryptic Queen Choice . . . . . 468

    17.5.1 Morphologically Based Cryptic Female Choice . . . . . 469

    17.5.2 Molecular Based Cryptic Female Choice . . . . . 472

    17.5.3 Ultimate Consequences of Cryptic Queen Choice . . . . . 473

17.6 Conclusions . . . . . 474

References . . . . . 474

**18 Mating Is a Give-and-Take of Influence and Communication**

**Between the Sexes . . . . . 479**

Rafael L. Rodríguez

18.1 Introduction . . . . . 479

18.2 Examples of Back-and-Forth Interactions Leading  
to Pair Formation . . . . . 481

    18.2.1 Females Advise Males on How to Court Them . . . . . 481

    18.2.2 Male–Female Signal Exchanges Lead  
to Pair Formation . . . . . 481

    18.2.3 Females Reassure Males About Their Receptivity . . . . . 483

    18.2.4 When Males Succeeded in Attracting  
a Mate but Did not Realize It . . . . . 483

18.3 Examples of Back-and-Forth Interactions that  
Take Place During Copulation . . . . . 484

    18.3.1 Females Advise Males on How to Court Them:  
Copulatory Dialogues . . . . . 485

    18.3.2 Females Warn Males of Likely Failure . . . . . 486

    18.3.3 Females Help the Males to Achieve Intromission . . . . . 486

    18.3.4 Females Stimulate the Male’s Genitalia . . . . . 487

    18.3.5 Females Let the Male Know When They Are  
Ready to Lay Eggs . . . . . 487

18.4 Examples of Male–Female Interactions that I Have  
not Considered to Be Reciprocal . . . . . 488

    18.4.1 Females Signal to Attract More Potential Mates  
and Broaden Their Prospects for Choice . . . . . 488

    18.4.2 Females Push or Kick the Male, Rather Than  
Gently Tap Him . . . . . 489

    18.4.3 Females Cooperate with the Male to Form  
a Copulatory Plug . . . . . 489

18.5 Discussion . . . . . 490

    18.5.1 The Evolution of Female Feedback and Male  
Attentiveness . . . . . 490

    18.5.2 Evolutionary Consequences of Female Feedback  
and Male Attentiveness . . . . . 492

References . . . . . 493

**Index . . . . . 497**



<http://www.springer.com/978-3-319-17893-6>

Cryptic Female Choice in Arthropods  
Patterns, Mechanisms and Prospects

Peretti, A.V.; Aisenberg, A. (Eds.)

2015, XXV, 509 p. 82 illus., 25 illus. in color., Hardcover

ISBN: 978-3-319-17893-6