

Contents

| | | |
|----------|---|-----------|
| 1 | The History and Scope of Insect Behavior | 1 |
| 1.1 | Introduction | 1 |
| 1.1.1 | What Is Insect Behavior? | 1 |
| 1.1.2 | Insect Behavior's Biological Context | 3 |
| 1.1.3 | Historical Foundations | 6 |
| 1.1.4 | The Watershed Years | 9 |
| 1.1.5 | The Rise of Ethology | 13 |
| 1.2 | Conceptual Frameworks | 15 |
| 1.2.1 | Evolution by Natural Selection | 15 |
| 1.2.2 | Genetics and Behavior | 17 |
| 1.2.3 | The Comparative Approach | 24 |
| 1.2.4 | Conceptual Pitfalls | 25 |
| 1.3 | Phylogeny's Role | 28 |
| 1.3.1 | Microevolution and Macroevolution | 28 |
| 1.3.2 | Phylogenetic Systematics and Cladistics | 33 |
| 1.3.3 | Behavior and Speciation | 36 |
| 1.4 | Questions and Perspectives | 38 |
| 1.4.1 | Proximate and Ultimate Analyses | 40 |
| 1.4.2 | Types of Approach | 41 |
| 2 | Programming and Integrating Behavior | 45 |
| 2.1 | Introduction | 45 |
| 2.2 | Nerve-Based Coordination | 46 |
| 2.2.1 | The Insect Nervous System | 47 |
| 2.2.2 | Simple Reflexes and Repeated Motor Patterns | 50 |
| 2.2.3 | Ethological Explanations | 56 |
| 2.3 | Life in a Stimulus-Rich World | 59 |
| 2.3.1 | Sensory Tuning and Filtering | 60 |
| 2.3.2 | Memory and Learning | 68 |
| 2.3.3 | Insect Intelligence | 81 |
| 2.4 | Hormone-Based Coordination | 83 |
| 2.4.1 | Clocks and Reiterative Rhythms | 86 |
| 2.4.2 | Gated Rhythms | 88 |

| | |
|---|-----|
| 3 Spatial Adjustment | 93 |
| 3.1 Introduction | 93 |
| 3.2 Locomotion | 94 |
| 3.2.1 Terrestrial and Aquatic Locomotion | 96 |
| 3.2.2 Aerial Locomotion | 98 |
| 3.3 Orientation | 100 |
| 3.3.1 Locomotory Responses | 101 |
| 3.3.2 Posture and Position | 103 |
| 3.3.3 Orientation to Radiant Energy | 105 |
| 3.3.4 Magnetic Field Orientation | 108 |
| 3.3.5 Orientation to the Evidence of Others' Presence | 109 |
| 3.4 Thermoregulation | 110 |
| 3.4.1 Dormancy and Thermotolerance | 110 |
| 3.4.2 Regulation of Heat Gain | 113 |
| 3.4.3 Heat Production | 114 |
| 3.5 Migration | 116 |
| 3.5.1 Seasonal Migration | 117 |
| 3.5.2 Migration Under Ephemeral Conditions | 122 |
| 3.5.3 Dispersal and Navigation | 124 |
| 4 Foraging and Feeding | 131 |
| 4.1 Introduction | 131 |
| 4.1.1 Food Recognition and Acceptance | 134 |
| 4.1.2 Regulation of Feeding | 137 |
| 4.2 Foraging Strategies | 140 |
| 4.2.1 Herbivory | 141 |
| 4.2.2 Active Search | 141 |
| 4.2.3 Trapping and Ambush | 146 |
| 4.2.4 Parasites and Parasitoids | 148 |
| 4.2.5 Theft and Kleptoparasitism | 152 |
| 4.2.6 Insect Agriculture | 154 |
| 4.2.7 Nest Symbionts: Becoming a House Pet | 157 |
| 4.3 Coevolution and the Arms Race | 164 |
| 4.3.1 Attack, Defense, and Counterattack | 165 |
| 4.3.2 Employing Mercenaries for Protection | 170 |
| 4.3.3 The Tommy Tucker Syndrome: Food in Return for Services | 173 |
| 4.4 Feeding as a Communal Activity | 177 |
| 4.4.1 Simple Groups and Feeding Aggregations | 177 |
| 4.4.2 Social Feeding Behaviors | 181 |
| 5 Defense: A Survival Catalogue | 185 |
| 5.1 Introduction | 185 |
| 5.2 Defense Messages | 186 |
| 5.3 Passive Messages | 187 |
| 5.3.1 Crypsis: 'I'm Not Here!' | 187 |

| | | |
|----------|---|------------|
| 5.3.2 | Systemic Defenses: 'I'm Noxious!' | 194 |
| 5.3.3 | Mimicry: 'I'm Someone Else!' | 197 |
| 5.3.4 | Aposematic Defenses: 'I'm Dangerous!' | 202 |
| 5.4 | Active Messages | 204 |
| 5.4.1 | Attack: 'I'm Turning the Tables!' | 204 |
| 5.4.2 | Startle: 'I'm Not What You Thought!' | 209 |
| 5.4.3 | Group Actions: 'We're in This Together!' | 213 |
| 6 | Chemical Communication | 217 |
| 6.1 | Introduction | 217 |
| 6.2 | Mechanisms of Chemical Communication | 217 |
| 6.2.1 | Odor Creation and Reception | 218 |
| 6.2.2 | Communication Through Chemistry | 223 |
| 6.3 | The Functions of Chemical Communication | 227 |
| 6.3.1 | Finding and Choosing Mates | 228 |
| 6.3.2 | Assembly, Aggregation, and Recruitment | 231 |
| 6.3.3 | Alarm and Alert | 240 |
| 6.3.4 | Host-Marking | 242 |
| 6.3.5 | Recognition | 246 |
| 6.4 | The Information Content of Pheromones | 249 |
| 6.4.1 | Physiological Adjustments: The <i>Q/K</i> Ratio | 249 |
| 6.4.2 | Pheromones as Language: Syntax and Lexicon | 251 |
| 6.4.3 | Exploitation and Code-Breaking | 255 |
| 6.4.4 | The Chemical Channel and Other Signal Modes | 256 |
| 6.5 | Chemical Communication and Insect Control | 258 |
| 7 | Visual Communication | 261 |
| 7.1 | Introduction | 261 |
| 7.2 | Bioluminescence | 262 |
| 7.2.1 | The Physiology of Insect Light Production | 263 |
| 7.2.2 | Bioluminescence as a Communication Method | 264 |
| 7.3 | Light Reception | 268 |
| 7.3.1 | Receptors and Form Perception | 268 |
| 7.3.2 | Visual Acuity and Flicker Vision | 272 |
| 7.3.3 | Polarized Light Perception | 275 |
| 7.3.4 | Color Vision | 277 |
| 7.4 | Functions of Visual Communication | 279 |
| 7.4.1 | Aggregation and Dispersion | 281 |
| 7.4.2 | Alarm | 283 |
| 7.4.3 | Sexual Signals | 284 |
| 7.4.4 | Multimodal Signaling | 288 |
| 8 | Mechanocommunication | 291 |
| 8.1 | Introduction | 291 |
| 8.2 | Producing and Sending Signals | 292 |
| 8.2.1 | Sound Creation | 293 |

| | | |
|-----------|---|------------|
| 8.2.2 | Distance and Substrate | 295 |
| 8.3 | Receiving Signals | 296 |
| 8.3.1 | Vibration | 298 |
| 8.3.2 | Hearing | 303 |
| 8.3.3 | Communication by Touch | 305 |
| 8.4 | The Acoustic Channel | 307 |
| 8.4.1 | Parameters of Insect Song | 307 |
| 8.4.2 | Song Synchronies | 308 |
| 8.4.3 | Active Acoustics | 311 |
| 8.4.4 | Sound as a Communication Method | 313 |
| 8.5 | Functions of Insect Communicative Sounds | 314 |
| 8.5.1 | Protest, Alarm, and Aggression | 314 |
| 8.5.2 | Aposematic Sounds and Acoustic Mimicry | 319 |
| 8.5.3 | Sexual Signals | 321 |
| 8.5.4 | Social Sounds | 327 |
| 9 | Reproductive Behavior | 341 |
| 9.1 | Introduction | 341 |
| 9.2 | Courtship and Mating | 342 |
| 9.2.1 | The Physiology of Mating Behavior | 344 |
| 9.2.2 | Reproduction Modes | 346 |
| 9.2.3 | Complexity and Plasticity | 349 |
| 9.2.4 | Pollination and Male Reproductive Behavior | 354 |
| 9.3 | Courtship and Conflict | 359 |
| 9.3.1 | Dimorphism, Sexual Selection, and Mate Choice | 361 |
| 9.3.2 | Intrasexual Competition | 369 |
| 9.3.3 | Territoriality and Dominance | 371 |
| 9.3.4 | Nuptial Gifts | 372 |
| 9.4 | Mating Systems and Parental Investment | 380 |
| 9.5 | Oviposition Behavior | 382 |
| 9.5.1 | Selecting a Site or Host | 383 |
| 9.5.2 | Reproductive Rates and Energy Allocation | 387 |
| 10 | Parental Behaviors and Social Life | 389 |
| 10.1 | Introduction | 389 |
| 10.2 | Social Organization | 390 |
| 10.2.1 | Aggregations and Simple Groups | 390 |
| 10.2.2 | Parent-Offspring Interactions | 394 |
| 10.2.3 | Solitary and Communal Nesters | 400 |
| 10.3 | The Insect Social Register | 407 |
| 10.3.1 | The Ants | 410 |
| 10.3.2 | The Eusocial Wasps | 416 |
| 10.3.3 | The Bees | 420 |
| 10.3.4 | The Termites | 423 |
| 10.3.5 | Lesser Known Candidates | 427 |
| 10.4 | Implications and Correlates of Social Life | 428 |

| | | |
|----------------|---|------------|
| 10.4.1 | The Ecology of Parental Care | 430 |
| 10.4.2 | Paradoxes of Insect Sociality | 434 |
| 10.4.3 | Interspecific Social Interactions | 440 |
| Credits | | 445 |
| Plates | | 463 |
| Index | | 503 |