

# CONTENTS

Preface, scope, and acknowledgments xiii

## 1 Definitions and predator recognition

- 1.1 Introduction 1
- 1.2 The predatory sequence 3
- 1.3 Definitions 7
  - 1.3.a *Adaptation and evolution* 7
  - 1.3.b *Antipredator terminology* 9
- 1.4 Ability of prey to recognize predators 13
- 1.5 Recognition by young animals 15
  - 1.5.a *Innate recognition* 15
  - 1.5.b *Learning to recognize predators* 18
- 1.6 Relaxed selection 24
- 1.7 Observer bias 28
- 1.8 Summary 30

## 2 Morphological traits to avoid detection

- 2.1 Introduction 33
- 2.2 Background matching 35
  - 2.2.a *Color resemblance in mammals* 35
  - 2.2.b *Color resemblance in birds* 38
  - 2.2.c *Color resemblance in birds' eggs* 42
  - 2.2.d *Special resemblance in birds' nests* 45
  - 2.2.e *Melanism* 47
  - 2.2.f *Changes in coloration with changing environments* 49
  - 2.2.g *Masquerade* 53

- 2.3 Concealing shadow 55
- 2.4 Disruptive coloration 59
- 2.5 Apostatic selection 61
- 2.6 Summary 64

### 3 Behavioral mechanisms to avoid detection

- 3.1 Introduction 67
- 3.2 Nest site selection in birds 68
  - 3.2.a *Habitat type* 71
  - 3.2.b *Distance from edges* 71
  - 3.2.c *Habitat patch size* 74
  - 3.2.d *Vegetation around the nest site* 75
  - 3.2.e *Nest height* 77
  - 3.2.f *Proximity to nests* 78
  - 3.2.g *Distribution of nests* 81
  - 3.2.h *Proximity to social insects* 83
- 3.3 Behavior reducing the probability of predators detecting nests 84
- 3.4 Refuges 87
  - 3.4.a *Physical structures* 88
  - 3.4.b *Habitat shifts in rodents* 89
  - 3.4.c *Habitat shifts in ungulates* 91
- 3.5 Reduced activity 94
  - 3.5.a *Hiding in ungulates* 99
- 3.6 Changes in foraging under risk of predation 100
  - 3.6.a *When to eat* 102
  - 3.6.b *Where to eat* 104
  - 3.6.c *What to eat* 107
  - 3.6.d *How much to eat* 108
  - 3.6.e *Effects of age and reproductive condition on risk-sensitive foraging* 108
- 3.7 Changes in reproduction under risk of predation 110
- 3.8 Summary 112

### 4 Vigilance and group size

- 4.1 Introduction 115
- 4.2 Measures of vigilance 116
- 4.3 Benefits of individual vigilance 118
- 4.4 Costs of individual vigilance 122
- 4.5 Effects of group size on vigilance 123
  - 4.5.a *Increased probability of predator detection* 124
  - 4.5.b *Reduced individual vigilance* 126

- 4.5.c *Increased foraging* 136
- 4.6 Why don't individuals cheat? 136
  - 4.6.a *Predator detection is not collective* 139
  - 4.6.b *Vigilant nondetectors are at an advantage* 141
  - 4.6.c *Predators select low-vigilance individuals* 141
  - 4.6.d *Individuals maintain vigilance so as not to lose group members* 142
  - 4.6.e *Multiple attacks are possible* 142
- 4.7 Vigilance in mixed-species groups 143
- 4.8 Summary 149

## 5 Factors affecting vigilance

- 5.1 Introduction 151
- 5.2 Distance from conspecifics and perceived group size 152
- 5.3 Position in the group 156
- 5.4 Sentinels 159
- 5.5 The influence of cover 162
- 5.6 Age and parity 166
- 5.7 Sex differences and dominance 170
- 5.8 Miscellaneous factors 172
- 5.9 Predator abundance 174
- 5.10 Interspecific differences in vigilance 176
- 5.11 Summary 178

## 6 Conspecific warning signals

- 6.1 Introduction 181
- 6.2 Acoustic constraints on alarm calls 183
  - 6.2.a *Localizability* 183
  - 6.2.b *Detectability* 184
- 6.3 Costs of warning signals 187
- 6.4 Benefits of warning signals 190
  - 6.4.a *Apparently selfish alarm calls* 190
  - 6.4.b *Mutually beneficial alarm calls* 192
  - 6.4.c *Altruistic and kin-selected alarm calls* 194
- 6.5 Alarm calls between species 201
- 6.6 Variation in alarm calls 205
  - 6.6.a *Sciurids* 205
  - 6.6.b *Birds* 210
  - 6.6.c *Primates* 212
- 6.7 Development of conspecific warning signals 215
  - 6.7.a *Ontogeny of response* 215

6.7.b *Ontogeny of alarm calls* 217

6.8 Use of warning signals in deception 219

6.9 Summary 221

## **7** Signals of unprofitability

7.1 Introduction 225

7.2 The evolution of aposematism 227

7.2.a *Individual selection* 227

7.2.b *Kin selection* 227

7.2.c *Synergistic selection* 229

7.3 Mechanisms by which predators select prey 230

7.3.a *Single prey* 230

7.3.b *Aggregated prey* 233

7.4 Aposematism in birds 235

7.4.a *Mimicry in birds* 241

7.5 Aposematism in mammals 242

7.6 Pursuit deterrence 244

7.6.a *Low-cost perception advertisement signals* 249

7.6.b *Auditory signals of perception advertisement* 250

7.6.c *Inspection as perception advertisement* 251

7.6.d *Foot drumming as advertising predator monitoring* 254

7.6.e *Stotting as perception and quality advertisement* 255

7.6.f *Leaping as quality advertisement* 258

7.6.g *Song as quality advertisement* 258

7.6.h *Quality advertisement in poikilotherms* 259

7.7 Summary 261

## **8** Antipredator benefits of grouping

8.1 Introduction 265

8.1.a *Definition of groups* 266

8.2 The dilution effect 267

8.2.a *Rates of encounter* 269

8.2.b *Reduced risk of capture* 271

8.3 The Trafalgar effect 274

8.4 The confusion effect 275

8.4.a *Oddity and confusion* 278

8.5 Predator "swamping" 280

8.5.a *Reproductive synchrony* 282

8.6 Miscellaneous mechanisms 285

8.7 Position in the group 285

8.7.a *Colonially nesting birds* 288

8.7.b *Flocks and herds* 291

8.8 Primate groups 293

8.9 Ecocorrelates of antipredator grouping in homeotherms 299

8.10 Summary 301

## 9 Morphological and physiological defenses

9.1 Introduction 305

9.2 Body size 306

9.2.a *Body size and locomotor performance* 309

9.3 Forms of locomotion 312

9.4 Spines and quills 314

9.5 Dermal plates and thickened skin 317

9.6 Weapons used for feeding 319

9.7 Sexually selected weaponry 319

9.8 Malodor and unpalatability 324

9.9 Venom resistance 327

9.10 Life history characteristics 329

9.11 Summary 332

## 10 Nest defense

10.1 Introduction 335

10.2 Scope of nest defense activities 337

10.2.a *The study of nest defense* 340

10.3 Distraction displays 343

10.4 Costs of nest defense 346

10.5 Benefits of nest defense 347

10.5.a *Driving predators away* 347

10.5.b *Silencing offspring* 349

10.6 Effects of predation risk on nest defense 350

10.7 Parent's renesting potential 354

10.7.a *Renesting potential within breeding seasons* 354

10.7.b *Renesting potential over lifetimes* 359

10.8 Parental sex 360

10.9 Parental interactions 363

10.10 Offspring age 364

10.10.a *Past and future parental investment* 366

10.10.b *Changes in offspring vulnerability* 366

10.10.c *Revisitation hypothesis* 367

10.11 Offspring number 368

- 10.12 Offspring condition 371
  - 10.12.a Harm-to-offspring hypothesis 372
- 10.13 Parental defense in mammals 375
- 10.14 Summary 377

## 11 Mobbing and group defense

- 11.1 Introduction 381
- 11.2 Definition of mobbing 383
- 11.3 Variation in mobbing behavior 384
- 11.4 Costs of mobbing 386
- 11.5 Benefits of mobbing 387
  - 11.5.a Direct benefits: lethal counterattack 387
  - 11.5.b Direct benefits: the move-on hypothesis 388
  - 11.5.c Direct benefits: perception advertisement 391
  - 11.5.d Direct benefits: selfish-herd effect and confusion effect 391
  - 11.5.e Direct benefits: attract the mightier 391
  - 11.5.f Indirect benefits: alerting others 392
  - 11.5.g Indirect benefits: silencing offspring 392
  - 11.5.h Benefits unclear: cultural transmission 393
  - 11.5.i Other hypotheses 395
- 11.6 Mobbing and group size 395
- 11.7 Mobbing and mixed-species associations in birds 398
- 11.8 Group defense in mammals 404
  - 11.8.a Snake-directed behavior in sciurids 404
  - 11.8.b Protective behavior in ungulates 405
  - 11.8.c Group attacks in primates 408
- 11.9 Summary 411

## 12 Flight and behaviors of last resort

- 12.1 Introduction 413
- 12.2 Freezing and immobility 414
- 12.3 Defense calls and flash coloration 415
- 12.4 Counterattack 417
- 12.5 Methods of escape 418
  - 12.5.a Birds 419
  - 12.5.b Mammals 422
- 12.6 Flight distance 423
- 12.7 Flight and weight gain in birds 426
- 12.8 Autotomy and deflection of attack 431
- 12.9 Fear screams 434

12.10 Death feigning 438

12.11 Summary 440

## 13 Framing questions about antipredator defenses

13.1 Introduction 443

13.2 Synergism between morphology and behavior 445

13.3 Defenses shown by different prey to different predators 447

13.4 Prey employ different defenses against different predators 447

13.5 Different prey use different defenses against the same predator 450

13.6 Prey summon several defenses against the same predator 453

13.6.a Repeated use of the same defense 453

13.6.b Different defenses 453

13.7 Predator-prey coevolution 456

13.8 Ten pressing questions 458

13.8.a How important is coloration in antipredator defense? 458

13.8.b How can we explain patterns of morphological and physiological defenses across taxa? 458

13.8.c How do antipredator morphology and behavior interact? 459

13.8.d Do prey recognize individual predators? 459

13.8.e How common are multifunctional defenses? 460

13.8.f How do predators respond to interactions with prey over time? 460

13.8.g How common are multiple attacks on grouped prey? 461

13.8.h Do predators select prey on the basis of condition? 461

13.8.i Do individual predators vary in hunting style? 462

13.8.j How do predator learning mechanisms affect antipredator defenses? 462

13.9 Why are defenses imperfect? 463

13.10 Summary 464

Appendix: Scientific names of vertebrates mentioned in the text 467

References 487

Prey species index 577

Subject index 587