Contents

List of Contributors xiii
Preface xv
About the Companion Website xix

Part I INTRODUCTION AND THEORETICAL CONCEPTS 1

1 Genotype-by-Environment Interactions and Sexual Selection: Female Choice in a Complex World 3
Michael J. Wade

1.1 Introduction 3
1.2 Classical female choice 4
1.3 The instability of “good genes” when male quality is a complex trait 6
1.3.1 Additive effects of genes on genotypic value 8
1.3.2 Genotype-by-environment interaction 9
1.3.3 Gene-by-gene interaction 12
1.3.4 Indirect genetic effects sensu quantitative genetics 13
1.4 Discussion 16
Acknowledgments 17
References 17

2 GEIs when Information Transfer is Uncertain or Incomplete 19
Thomas Getty

2.1 Introduction 19
2.2 Lewontin’s “very annoying conclusions” 21
2.3 Ignorance, uncertainty, and information 21
2.4 Information and fitness 22
Contents

2.5 Bayesian Statistical Decision Theory
2.6 Discrimination and selection: the signal detection perspective
2.7 Search, discrimination, and mate choice by female pied flycatchers
2.8 Optimal search and the marginal value of additional information
2.9 Biological signaling theory
2.10 GEIs in condition, signals, and preferences
2.11 Conclusions

References

3 Local Adaptation and the Evolution of Female Choice
Luke Holman and Hanna Kokko
3.1 Introduction
3.2 The Jekyll and Hyde nature of GEIs
3.3 The model
  3.3.1 Overview
  3.3.2 Initialization phase
  3.3.3 Dispersal
  3.3.4 Determination of condition and viability selection
  3.3.5 Breeding
  3.3.6 Mutation
3.4 Less local adaptation, more female choice!
3.5 Can we generalize?
3.6 GEIs often maintain costly choice in a suitably variable world
3.7 Insights from the model
3.8 Prospects for empirical work
3.9 Prospects for theoretical work
3.10 Conclusions

References

4 Genotype-by-Environment Interactions when the Social Environment Contains Genes
Jason B. Wolf, Nick J. Royle, and John Hunt
4.1 Introduction
4.2 Modeling genotype-by-social environment interactions
  4.2.1 A simple GEI model when the environment is abiotic
  4.2.2 A simple model for gene interactions
  4.2.3 A simple GSEI model
  4.2.4 Summary
4.3 Measuring genotype by social environment interactions
4.4 Empirical evidence for genotype by social environment interactions
4.5 Future directions
Contents

Acknowledgments 94
References 94

Part II PRACTICAL ISSUES FOR MEASURING GEIs 99

5 Quantifying Genotype-by-Environment Interactions in Laboratory Systems 101
Derek A. Roff and Alastair J. Wilson

5.1 Introduction 101
5.2 Two perspectives on phenotypic plasticity 102
5.2.1 The character state approach 102
5.2.2 Norm of reaction approach 103
5.3 Breeding designs to detect and estimate G × E 105
5.3.1 Common garden 105
5.3.2 Clones 106
5.3.3 Inbred lines 107
5.3.4 Isofemale lines 108
5.3.5 Conventional breeding designs 108
5.3.6 “Unconventional” pedigree designs 109
5.3.7 Selection experiments 109
5.4 Statistical methodologies 109
5.4.1 Mixed-model analysis of variance 110
5.4.2 Linear mixed effect model 111
5.4.3 The animal model 113
5.4.4 Individually fitted functions 115
5.4.5 Random regression models 119
5.4.6 Random regression models as covariance functions 120
5.4.7 Multivariate models 121
5.5 Worked examples 122
5.5.1 Example 1 122
5.5.2 Example 2 126
5.5.3 Example 3 130
5.6 Recommendations 133
Acknowledgments 134
References 134

6 Influence of the Environment on the Genetic Architecture of Traits Involved in Sexual Selection within Wild Populations 137
Matthew R. Robinson and Anna Qvarnström

6.1 Introduction 137
6.2 Application of sexual selection theory to wild populations 139
6.2.1 Identifying the key parameters 139
6.2.2 Acquisition and allocation determine the form of GEI 140
6.2.3 The genetic basis of female mate choice may show GEI 143
6.2.4 Fitness associations may be environmentally dependent 144
6.2.5 Covariance between the sexes 146
6.3 Methods for examining GEI in wild populations 146
6.3.1 Identifying the relevant environmental variables 147
6.3.2 The “animal” model 148
6.3.3 Character-state approach 148
6.3.4 Factor analytic models 150
6.3.5 Autoregressive functions 151
6.3.6 Reaction norm models: random regressions 151
6.3.7 Estimating environmental sensitivity as an alternative 155
6.3.8 Estimating genetic covariance across environments 156
6.3.9 Estimating covariance with fitness across environments 157
6.4 Worked examples of the analysis methods 158
6.5 Summary 164
References 165

7 From Genotype × Environment to Transcriptome × Environment: Identifying and Understanding Environmental Influences in the Gene Expression Underlying Sexually Selected Traits 169
Jennifer C. Perry and Judith E. Mank
7.1 Introduction 169
7.2 Gene expression variation allows a static genome to respond to varying environments 170
7.3 From GEIs to TEIs in sexually selected traits 172
7.4 Can we safely ignore the genomic basis of phenotypes? 174
7.5 The first step is identifying the transcriptomic basis of sexually selected traits 175
7.6 A note on gene expression and sexually selected behavior 178
7.7 The next step is to understand how gene expression responds to environmental influences 179
7.8 A few notes on technology and experimental design 180
7.9 Conclusion 182
Acknowledgments 183
References 183
Contents

Part III    EMPIRICAL STUDIES ON GEIs AND SEXUAL SELECTION 189

8    Phenotypic Plasticity and Genotype × Environment Interactions in Animal Communication 191
Michael D. Greenfield

8.1   Introduction 191
8.1.1   GEI and the lek paradox 193
8.1.2   GEI and signal (un)reliability 194
8.1.3   Achroia grisella: a model species for sexual selection studies 195
8.2   Natural history and acoustic communication 196
8.3   Quantitative genetics of song and preference 199
8.3.1   Do genetic tradeoffs maintain $V_A$ for song traits? 199
8.3.2   GEI, ecological crossover, and the maintenance of $V_A$ 200
8.4   On the role of GEI in natural populations 203
8.4.1   Indirect genetic effects (IGEs) 203
8.4.2   Reaction norm diversity and ecological crossover 203
8.4.3   Does environmental heterogeneity help to sustain $V_A$? 204
8.4.4   Synopsis 205
8.5   Are male songs reliable signals? 206
8.6   Prognosis 207
Acknowledgments 208
References 208

9    The Use of Inbreeding to Assess the Genetic Component of Condition Underlying GEIs in Sexual Traits 213
Lawrence Bellamy, Kevin Fowler, and Andrew Pomiankowski

9.1   Introduction 213
9.2   Sexual traits and genetic condition 214
9.3   Studies of environmental variation 215
9.4   Studies of genetic variation 216
9.5   The use of inbreeding to infer the genetics of condition-dependent traits 217
9.6   Designing inbreeding experiments 218
9.6.1   Choice of control traits 218
9.6.2   Controlling for body size covariation 220
9.6.3   Outbred controls 220
9.6.4   Experimental scale 221
9.6.5   GEI 221
Contents

9.7 Methods 222
9.8 Results 223
  9.8.1 Fish 223
  9.8.2 Birds 229
  9.8.3 Arthropods 230
9.9 Discussion 232
  9.9.1 Do secondary sexual traits suffer from inbreeding depression? 232
  9.9.2 Does inbreeding depression in sexual traits persist after controlling for body size? 233
  9.9.3 Do sexual traits suffer greater inbreeding depression than non-sexual traits? 233
  9.9.4 Does inbreeding reveal condition-dependent GEIs? 234
9.10 Concluding remarks 235
Acknowledgments 236
References 236

10 Genotype-by-Environment Interactions and Reliable Signaling of Male Quality in Bank Voles 241
Suzanne C. Mills, Mikael Mokkonen, Esa Koskela, and Tapio Mappes

10.1 Introduction 241
10.2 The bank vole 242
  10.2.1 Environmental heterogeneity 244
  10.2.2 Female reproductive success 244
  10.2.3 Male signals, heritability, and reliability 245
  10.2.4 Intralocus sexual conflict 247
10.3 GEIs on male dominance in the bank vole 249
10.4 Suggestions to reconcile the disruption of the signal-preference covariance 251
  10.4.1 Parallel norms of reaction for male signal and female mate preference 251
  10.4.2 Alternative strategies for male signal and female preferences 256
  10.4.3 GEI on female reproductive success and sexual conflict 257
10.5 Summary 258
References 259

11 Sexual Selection and Genotype-by-Environment Interactions in Drosophila Cuticular Hydrocarbons 265
Fiona C. Ingleby, David J. Hosken, and John Hunt

11.1 Introduction 265
11.2 Abiotic environments 267
  11.2.1 Temperature and desiccation stress 267
  11.2.2 Dietary effects and condition dependence 270
## Contents

11.3 Biotic environments  
11.3.1 IGEs on *D. serrata* CHC expression  271  
11.3.2 Circadian clocks and the social environment in *D. melanogaster* CHC expression  274

11.4 Consequences of GEI and environmental variation in *Drosophila* CHCs and directions for future research  275

Acknowledgments  278

References  278

12 Genotype-by-Environment Interactions and Sexual Selection in Guppies  282

**Gita R. Kolluru**

12.1 Introduction  282  
12.1.1 Overview  282  
12.1.2 Phenotypic responses to environmental variation  283  
12.1.3 GEI and sexual selection  285

12.2 Plasticity, GEI, and the guppy system  286  
12.2.1 The guppy mating system  286  
12.2.2 Sexually selected traits in guppies  287  
12.2.3 Environmental influences on sexually selected guppy traits  289  
12.2.4 Environmental heterogeneity in guppy populations  297

12.3 Summary and future directions  300  
12.3.1 Guppies and the positive and negative effects of GEI on sexually selected traits  300  
12.3.2 Behavioral syndromes as an emerging focus  302  
12.3.3 The challenge of human-induced environmental changes  303

Acknowledgments  304

References  304

13 Signal Reliability, Sex-Specific Genotype-by-Environment Interactions in Cuticular Hydrocarbon Expression, and the Maintenance of Polyandry through Chemosensory Self-Referencing in Decorated Crickets, *Gryllodes sigillatus*  312

**Scott K. Sakaluk, Carie Weddle, and John Hunt**

13.1 Introduction  312  
13.2 Sexual selection and polyandry in *Gryllodes sigillatus*  314  
13.3 Cuticular hydrocarbons in *G. sigillatus*  317  
13.4 Chemosensory self-referencing and the preference for novel males  318
## Contents

13.5 Sex-specific GEIs and the reliability of chemosensory self-referencing 323
13.6 Conclusion 325
  Acknowledgments 326
  References 326

*Conclusions and Final Thoughts* 331
*Index* 335