
Evolution and Diversity of Sex Ratio

in Insects and Mites

Dana L. Wrens
Department of Entomology
The Ohio State University, Columbus

and

Mercedes A. Ebbert
Department of Entomology
The Ohio State University, Wooster

Editors

Foreword by Eric L. Charnov



CHAPMAN & HALL
NEW YORK AND LONDON

Contents

Contributors	v
Foreword	xiii
<i>Eric L. Charnov</i>	
Preface	xvii
<i>Dana L. Wrensch and Mercedes A. Ebbert</i>	
Introduction	1
<i>Dana L. Wrensch and Mercedes A. Ebbert</i>	
1. Phylogenetic Perspectives on Genetic Systems and Reproductive Modes of Mites	8
<i>Roy A. Norton, John B. Kethley, Donald E. Johnston, and Barry M. OConnor</i>	
Introduction	8
Phylogeny and genetic systems of Parasitiformes	14
Phylogeny and genetic systems of Acariformes	21
Phylogenetic patterns in the distribution of thelytoky	38
Patterns and ecological correlates of genetic systems in mites	58
Patterns and ecological correlates of thelytoky in mites	70
Summary and conclusions	76
2. Patterns of Reproduction in Insects	100
<i>Esko Suomalainen and Anssi Saura</i>	
Introduction	100
The normal reproduction of insects	100
Patterns of reproduction out of the ordinary	101

3.	Evolutionary Flexibility Through Haploid Males or How Chance Favors the Prepared Genome	118
	<i>Dana L. Wrensch</i>	
	A restrictive elaboration of Hamilton's extreme biofacies	119
	"Restricted biofacies" of adaptive sex ratio regulation by haploid males	121
	Sex ratio control: the fertilization strategy that maximizes daughters	127
	An alternative model for the evolution of sex ratio regulation	129
	Haven't we underrated the haploid male?	137
	Summary of the New ESS _{NET} hypotheses: The $r_m * S_m$ model	141
4.	Endosymbiotic Sex Ratio Distorters in Insects and Mites	150
	<i>Mercedes A. Ebbert</i>	
	Introduction	150
	Definition and documentation of endosymbiotic sex ratio distorters	150
	Male-lethal infections	152
	Incompatibility infections	162
	Conversion infections	169
	Bimodal transmission of distorter infections	170
	Coevolutionary selection on endosymbiont-driven sex ratio	172
	Conclusion	180
5.	Evolution of Sex Determination and Sex Ratio within the Mite Cohort Tarsonemina (Acari: Heterostigmata)	192
	<i>Marek Kaliszewski and Dana L. Wrensch</i>	
	Evolution of mode of reproduction	198
	Evolution of sex ratio	206
6.	Sex Allocation Ratio Selection in Thysanoptera	214
	<i>Bernard J. Crespi</i>	
	Introduction	214
	Measuring sex ratio and sex allocation in Thysanoptera	214
	Four biofacies of thrips sex allocation	216
	Ecology, social behavior, and sex allocation in thrips	228
7.	Ecology and Evolution of Biased Sex Ratios in Bark and Ambrosia Beetles	235
	<i>Lawrence R. Kirkendall</i>	
	Introduction	235

The natural history of inbreeding in Scolytidae	236
Biogeographic patterns of inbreeding Scolytidae	249
The evolution of close inbreeding in Scolytidae	260
Sex ratios of inbreeding Scolytidae	274
Other biased sex ratios	310
Summary	316
8. Evolution of Sex Ratio Variation in Aphids	346
<i>Nancy A. Moran</i>	
Introduction	346
Sex, non sex, and sex allocation in aphid life cycles	347
Sex determination and the development of the sex ratio phenotype	349
Selection on the sex ratio in aphids	353
Fisherian Systems	355
Systems with variation in local conditions	356
Systems with population subdivision	359
Potential for sex allocation investigations in aphids	362
9. Sex Allocation in Social Insects: Problems in Prediction and Estimation	369
<i>Ross H. Crozier and Pekka Pamilo</i>	
The central place of social insects in sex allocation studies	369
Estimation	370
Inclusive fitness	373
Population interactions	375
Intercolony variation	376
Where to from here? How to evaluate the relative importance of the various factors affecting sex allocation?	379
10. Male Parentage and Sexual Deception in the Social Hymenoptera	384
<i>Peter Nonacs</i>	
Inclusive fitness and colony social systems	386
Sexual deception with monogyny and monandry	392
Evidence and conclusions	395
Summary	399

11.	Sex Ratio and Virginity in Haplodiploid Insects	402
	<i>H. Charles J. Godfray and Ian C. W. Hardy</i>	
	Introduction	402
	Will virgin females reproduce?	403
	Evidence for unmated oviposition	407
	Some ramifications	412
12.	Sex Ratio Manipulation by Parasitoid Wasps	418
	<i>Bethia H. King</i>	
	Introduction	418
	Sex ratio manipulation models	420
	Empirical support	422
	Limitations on sex ratio manipulation	430
	Summary	432
13.	Sex Determination and Sex Ratio Patterns in Parasitic Hymenoptera	442
	<i>Robert F. Luck, Richard Stouthamer and Leonard P. Nunney</i>	
	Modes of reproduction	442
	Sex determination	443
	Causes and consequences of thelytoky	448
	Sex-ratio-distorting factors	451
	Sex allocation	452
	Sex allocation in structured mating systems	453
	Genetic variation for sex ratio	458
	Sex allocation and variation in fitness	460
	Conclusion	463
14.	Sex Ratio Evolution in Parasitic Wasps	477
	<i>Steven H. Orzack</i>	
	Conclusions	504
15.	Sex Allocation and Pseudoarrhenotoky in Phytoseiid Mites	512
	<i>Maurice W. Sabelis and Kees Nagelkerke</i>	
	Introduction	512
	Paternal genome loss in males: evidence and phylogenetic distribution systems	512
	Selective advantages of uniparental male	515
	Sex allocation in phytoseiid mites	516
	Discussion	531

16. Alteration of Sex Ratios of Parasitoids for Use in Biological Control	542
<i>Richard W. Hall</i>	
Classical biological control	543
Augmentative biological control	544
Applications	545
17. Quantitative Genetics Applied to Haplodiploid Insects and Mites	548
<i>David C. Margolies and Thomas S. Cox</i>	
Basic concepts	549
Genetic similarity between relatives	550
Estimating heritability	551
Response to selection	555
Conclusion	556
Glossary	561
Author Index	573
Taxonomic Index	587
Subject Index	611