

Contents

Preface	ix
<i>Thomas Flatt and Andreas Heyland</i>	
List of contributors	xxiv
Part 1: Integrating mechanisms into life history evolution	1
1 Integrating mechanistic and evolutionary analysis of life history variation	3
<i>Christian Braendle, Andreas Heyland, and Thomas Flatt</i>	
1.1 Introduction	3
1.2 The life history framework	3
1.2.1 What is a life history?	3
1.2.2 Life history traits and fitness	4
1.2.3 Trade-offs and constraints	4
1.2.4 Empirical approaches in life history research	5
1.3 The study of causal mechanisms linking genotype to phenotype	5
1.4 How can mechanistic insights contribute to understanding life history evolution?	6
1.4.1 Why understanding mechanisms is important for answering evolutionary questions	7
1.4.2 The molecular identity and function of genes that affect life history	7
1.4.3 Are candidate life history genes ecologically and evolutionarily relevant?	8
1.4.4 How do trade-offs work?	9
1.5 Conclusions	10
2 Genomic insights into life history evolution	11
<i>Derek A. Roff</i>	
2.1 Introduction	11
2.2 Genomic analysis of trade-offs	12
2.2.1 Case Study 1: A transgenic analysis of the cost of resistance in <i>Arabidopsis thaliana</i>	12
2.2.2 Case Study 2: A QTL analysis of the cost of resistance to parasite infection in <i>Tribolium</i>	13
2.2.3 Case Study 3: A microarray analysis implicating a single gene in the cost of resistance to DDT in <i>Drosophila melanogaster</i>	15
2.2.4 Case Study 4: A microarray analysis of antagonistic pleiotropy and gene expression in <i>Drosophila melanogaster</i>	15
2.3 To what extent is the phenotype determined by different molecular/developmental mechanisms?	17
2.3.1 Comparisons among species	20
2.3.2 Comparisons among natural populations of the same species	20
2.3.3 Artificial selection experiments	21
2.3.4 A proposed experiment and predictions	23

2.4	Summary	24
2.5	Acknowledgments	25
Part 2: Growth, development, and maturation		27
3	Emerging patterns in the regulation and evolution of marine invertebrate settlement and metamorphosis	29
	<i>Andreas Heyland, Sandie Degnan, and Adam M. Reitzel</i>	
3.1	Background	29
3.2	Introduction to marine invertebrate life histories	30
3.3	Regulation of larval development and the evolution of feeding modes in echinoids: Energy allocation trade-offs during larval development	32
3.3.1	Hormonal regulation of juvenile development	34
3.3.2	Hormonal signaling and the evolution of alternative life history modes	34
3.4	Mechanisms underlying larval settlement and the evolution of alternative settlement strategies: Signal detection and modulation during settlement	36
3.4.1	The sensory system: Cues, receptors, and signal transduction mechanisms	37
3.4.2	The competence system	38
3.5	Settlement strategies: Evolution of sensory structures and signaling networks	40
3.6	Future directions	41
3.7	Summary	41
3.8	Acknowledgments	42
4	Evolution and the regulation of growth and body size	43
	<i>Alexander W. Shingleton</i>	
4.1	Introduction	43
4.2	The regulation of body size in insects	43
4.2.1	The regulation of critical size	45
4.2.2	The regulation of TGP	46
4.3	The regulation of growth rate	46
4.4	Environmental variation in body size: The functional interaction between critical size, TGP, and growth rate in insect size regulation	48
4.5	Trade-offs between body size and other traits	50
4.6	The evolution of body size	51
4.6.1	Evolutionary trends	51
4.6.2	Artificial selection	52
4.6.3	The developmental mechanisms underlying the evolution of body size	52
4.6.4	The relationship between evolutionary and environmental variation in body size	53
4.6.5	Can we predict which size-regulatory mechanisms are the target for selection on body size?	54
4.7	Summary	55
4.8	Acknowledgments	55
5	The genetic and endocrine basis for the evolution of metamorphosis in insects	56
	<i>Deniz F. Erezylmaz</i>	
5.1	Introduction	56
5.2	Endocrine regulation of metamorphosis	58
5.3	Comparative endocrinology across insect life history strategies	60

5.4	Endocrine titers and cuticle progression during embryonic development	60
5.5	Comparison of hemi- and holometabolous endocrine events during postembryonic development	62
5.6	The "status-quo" action of juvenile hormone and its signal transduction	64
5.7	The <i>broad</i> gene and specification of the pupal stage	65
5.7.1	Molecular aspects of Broad action	68
5.7.2	A <i>broad</i> -based view of the pronymph hypothesis	68
5.7.3	The appearance of <i>broad</i> in the arthropods	69
5.8	Summary	70
5.9	Acknowledgments	71
6	Thyroidal regulation of life history transitions in fish	72
	<i>Richard G. Manzon</i>	
6.1	Introduction	72
6.2	Fish ontogeny and life history transitions	74
6.3	Overview of the hypothalamic–pituitary–thyroid axis	74
6.4	The hypothalamic–pituitary axis	74
6.5	Thyroid tissue and hormone synthesis	75
6.5.1	Serum thyroid hormone distributor proteins, cellular uptake, and cytosolic transport	75
6.5.2	Thyroid hormone deiodinases	76
6.5.3	Thyroid hormone nuclear receptors	77
6.6	Thyroidal regulation of fish ontogeny and life history transitions	79
6.6.1	Embryogenesis and embryo to larval transitions	79
6.6.2	Larval to juvenile transitions	80
6.6.3	First or "true" metamorphoses in ray-finned fish	81
6.6.4	First or "true" metamorphosis in lampreys (Agnatha)	82
6.6.5	Smoltification: A juvenile transition in salmonids	84
6.7	Summary	85
6.8	Acknowledgments	86
7	Hormone regulation and the evolution of frog metamorphic diversity	87
	<i>Daniel R. Buchholz, Christine L. Moskalik, Saurabh S. Kulkarni, Amy R. Hollar, and Allison Ng</i>	
7.1	Introduction	87
7.2	Ecological context of metamorphic life history evolution	87
7.2.1	Escape from the growth versus development trade-off	88
7.3	Key concepts in the endocrinology of metamorphosis	88
7.3.1	Overview of the endocrinology of metamorphosis	88
7.3.2	Tissue sensitivity and tissue-specific responses to thyroid hormones	89
7.3.3	Tissue developmental asynchrony	90
7.4	Endocrine basis of amphibian life history evolution	90
7.4.1	Larval period duration	90
7.4.2	Size at metamorphosis	91
7.4.3	Direct development	91
7.4.4	Neoteny	92
7.5	Molecular mechanisms of peripheral control: Potential evolutionary targets underlying diversity in larval period diversity	92
7.5.1	Thyroid hormone transporters	92
7.5.2	Thyroid hormone metabolizing enzymes	93

7.5.3	Cytosolic thyroid hormone binding proteins	93
7.5.4	Thyroid hormone receptors	94
7.5.5	Modulation of thyroid hormone responsiveness by corticosterone and prolactin	95
7.6	Conclusions	96
7.7	Summary	97
Part 3: Reproduction		99
8 Asexual reproduction in Cnidaria: Comparative developmental processes and candidate mechanisms		101
<i>Adam M. Reitzel, Derek Stefanik, and John R. Finnerty</i>		
8.1	Introduction	101
8.2	Diversification of clonal reproduction in cnidarians	102
8.2.1	Diversity of clonal reproduction modes in cnidarian polyps	103
8.2.2	The role of developmental modularity in life history diversification	103
8.2.3	Evidence of modularity in cnidarian developmental programs	105
8.2.4	Elucidating the genetic architecture of cnidarian modules	106
8.3	Trade-offs and environmental signaling in asexual reproduction	109
8.4	Trade-offs between methods of asexual reproduction	110
8.5	Environmental signals and reception in cnidarian asexual reproduction	111
8.6	Looking ahead: Combining signaling with developmental mechanisms	112
8.7	Summary	113
8.8	Acknowledgments	113
9 The genetics and evolution of flowering time variation in plants: Identifying genes that control a key life history transition		114
<i>Joshua A. Banta and Michael D. Purugganan</i>		
9.1	Introduction	114
9.2	The natural and laboratory history of <i>Arabidopsis</i>	115
9.3	The molecular genetics of flowering time	116
9.3.1	Getting at the mechanistic basis: Genes controlling flowering time variation and what they do	117
9.3.2	<i>CRY2</i>	118
9.3.3	<i>PHYC</i>	120
9.3.4	<i>FRI</i>	120
9.3.5	<i>FLC</i>	121
9.4	Epistatic effects among <i>FRI</i> and <i>FLC</i>	121
9.5	Pleiotropic effects of genes controlling flowering time variation	122
9.6	Comparative functional genomics: The genetics of flowering time in other species	124
9.7	Synthesis and prospectus	125
9.8	Summary	126
9.9	Acknowledgments	126
10 Mechanisms of nutrient-dependent reproduction in dipteran insects		127
<i>Alan O. Bergland</i>		
10.1	Introduction	127
10.2	Larval nutrition and reproduction	128

10.2.1	Ovary size	128
10.2.2	Meal size	129
10.2.3	The effects of mate size	129
10.2.4	Larval nutrition and teneral reserves	130
10.3	Adult-acquired resources	131
10.3.1	Hunger	131
10.3.2	Finding nutrition	132
10.3.3	Oogenesis and ovulation	133
10.4	The evolutionary genetics of reproduction: Future prospects	135
10.5	Summary	135
10.6	Acknowledgments	136
11	Mechanisms underlying reproductive trade-offs: Costs of reproduction	137
	<i>Dominic A. Edward and Tracey Chapman</i>	
11.1	Introduction	137
11.2	Key life history traits and costs of reproduction	137
11.3	Intrinsic costs of reproduction: Trade-offs between reproductive activity and survival or future reproductive rate	138
11.3.1	Physiological costs of reproduction	140
11.3.2	Evolutionary costs of reproduction	141
11.3.3	Mechanisms underlying reproductive costs	141
11.3.4	Nutrients, nutrient sensing, and costs of reproduction between reproductive rate and lifespan	142
11.3.5	The presence of a germ line and costs of reproduction between reproductive rate and lifespan	144
11.4	Reproductive hormones as mediators of trade-offs between reproductive rate and lifespan	144
11.5	Male seminal fluid proteins as mediators of trade-offs between reproduction and lifespan in females	145
11.6	The immune system as a mediator of costs between current reproductive rate and survival	145
11.7	Damage as a mediator of trade-offs between current reproductive rate and survival	146
11.8	Resource allocation: Allocation versus adaptive signaling	147
11.9	Costs of reproduction in a fitness-based framework	148
11.10	New directions	150
11.10.1	Mechanistic data are incomplete	150
11.10.2	The evolution and conditional economics of reproductive costs	150
11.10.3	Integration of life history data from social species	151
11.11	Summary	151
11.12	Acknowledgments	152
12	Patterns and processes of human life history evolution	153
	<i>Michael P. Muehlenbein and Mark V. Flinn</i>	
12.1	The evolution of human life histories	153
12.1.1	Ecological dominance: Lowered mortality, better food and tools, and increased sociality	154

12.1.2	Human cognitive evolution	154
12.1.3	Prolonged development	156
12.1.4	High fertility, biparental and alloparental care	157
12.2	Proximate mechanisms of human life history patterns	159
12.2.1	Reproductive development	160
12.2.2	Ovarian and testicular functions	161
12.2.3	Reproductive behaviors	164
12.2.4	Reproductive senescence	166
12.3	Summary	167
Part 4: Lifespan, aging, and somatic maintenance		169
13 Parallels in understanding the endocrine control of lifespan with the firebug <i>Pyrhocoris apterus</i> and the fruit fly <i>Drosophila melanogaster</i>		171
<i>Magdalena Hodkova and Marc Tatar</i>		
13.1	Introduction	171
13.2	Reproductive diapause	172
13.3	Reproduction and its trade-offs	174
13.4	Endocrine regulation	176
13.5	Conclusion	178
13.6	Summary	179
13.7	Acknowledgments	179
14 The genetics of dietary modulation of lifespan		180
<i>Johannes H. Bauer and Stephen L. Helfand</i>		
14.1	Introduction	180
14.2	Calorie restriction as a modulator of life history traits	180
14.2.1	Is lifespan extension due to calorie restriction universal?	180
14.2.2	The difficulty of defining what constitutes calorie restriction	181
14.3	The evolution of dietary restriction and its lifespan-extending effect	182
14.4	Dietary restriction in lower organisms	183
14.4.1	<i>C. elegans</i>	183
14.4.2	<i>D. melanogaster</i>	185
14.5	Dietary restriction in higher organisms	188
14.5.1	Rodents	188
14.5.2	Primates	189
14.6	Concluding remarks	190
14.7	Summary	192
14.8	Acknowledgments	192
15 Molecular stress pathways and the evolution of life histories in reptiles		193
<i>Tonia S. Schwartz and Anne M. Bronikowski</i>		
15.1	Reptiles possess remarkable variation and plasticity in life history	193
15.2	The molecular stress networks: What is known in reptiles?	195
15.2.1	Metabolic pathways	195
15.2.2	Molecular mechanisms to regulate the production of reactive oxygen species	199
15.2.3	Molecular mechanisms to neutralize reactive oxygen species	200

15.2.4	Tolerance and resistance to reactive oxygen species	201
15.2.5	Molecular pathways for repair	202
15.2.6	Insulin/insulin-like growth factor signaling pathway	202
15.3	Environmental stress and evolving molecular pathways: Evidence in reptiles	203
15.3.1	Temperature (heat) stress	203
15.3.2	Hibernation: Supercooling, freeze tolerance, and anoxia tolerance	204
15.3.3	Dietary stress: Availability and type of food	206
15.3.4	Type of food	207
15.4	Perspective	207
15.5	Summary	208
15.6	Acknowledgments	209
16	Mechanisms of aging in human populations	210
	<i>Maris Kuningas and Rudi G.J. Westendorp</i>	
16.1	Introduction	210
16.2	Mechanisms of aging	211
16.2.1	Insulin/IGF-1 signaling	211
16.2.2	Lipid metabolism	212
16.2.3	Antioxidant enzymes	212
16.2.4	Macromolecule repair mechanisms	213
16.2.5	Cellular responses to damage	214
16.3	Convergence of longevity signals	214
16.3.1	Dietary restriction	215
16.4	Integration of genetic pathways and the environment	216
16.5	Summary	217
16.6	Acknowledgments	217
Part 5:	Life history plasticity	219
17	Mechanisms underlying feeding-structure plasticity in echinoderm larvae	221
	<i>Benjamin G. Miner</i>	
17.1	Introduction	221
17.2	Plasticity of feeding structures	221
17.3	Evidence for adaptive plasticity	222
17.4	Developmental regulation	224
17.5	Mechanisms of perception	224
17.6	Mechanisms of morphological response	225
17.7	Integrative response	227
17.8	Future directions	228
17.9	Summary	228
17.10	Acknowledgments	229
18	Evolution and mechanisms of insect reproductive diapause: A plastic and pleiotropic life history syndrome	230
	<i>Paul S. Schmidt</i>	
18.1	Introduction	230
18.2	Advances and methods	231

18.2.1	Clines	231
18.2.2	Temporal variation and seasonality	233
18.3	Diapause as a model system for life history evolution	233
18.4	Identifying genes for seasonality	235
18.4.1	Dormancy in <i>D. melanogaster</i>	236
18.4.2	Genes for diapause in <i>Drosophila</i>	238
18.5	Pathway and genomic analyses	239
18.5.1	Diapause and insulin signaling	239
18.5.2	Expression analyses	240
18.6	Summary	242
18.7	Acknowledgments	242
19	Seasonal polyphenisms and environmentally induced plasticity in the Lepidoptera: The coordinated evolution of many traits on multiple levels	243
	<i>Paul M. Brakefield and Bas J. Zwaan</i>	
19.1	Introduction	243
19.2	Frameworks for dissecting the evolution of polyphenisms	243
19.3	Case studies on the adaptive nature of seasonal polyphenisms	245
19.4	Environmental cues and the physiological regulation of plasticity	246
19.5	Genetics of the evolution of the seasonal polyphenism in wing pattern	247
19.6	Life history evolution in polyphenic butterflies	248
19.7	Perspectives: Suites of adaptive traits in combination with an ability to acclimate	251
19.8	Summary	252
19.9	Acknowledgments	252
20	Honey bee life history plasticity: Development, behavior, and aging	253
	<i>Brenda Rascón, Navdeep S. Mutti, Christina Tolfsen, and Gro V. Amdam</i>	
20.1	Introduction	253
20.2	Development	253
20.2.1	Female caste morphology: Physiology, function, and reproduction	253
20.2.2	An integrative molecular model for caste development: Differential nutrition during larval development triggers caste differentiation	254
20.3	Behavioral maturation and specialization	255
20.3.1	Specialization of foraging behavior	257
20.3.2	Central nervous system changes during behavioral maturation	258
20.3.3	Metabolic changes during behavioral maturation	259
20.4	Worker aging	260
20.4.1	Plasticity of aging	260
20.4.2	Oxidative stress	261
20.4.3	Metabolic patterns of senescence	262
20.4.4	Cognitive senescence	263
20.4.5	Impact of nutrition sensing pathways on lifespan	264
20.5	Concluding remarks	265
20.6	Summary	265
20.7	Acknowledgments	266

Part 6: Life history integration and trade-offs	267
21 Molecular mechanisms of life history trade-offs and the evolution of multicellular complexity in volvocalean green algae	271
<i>Aurora M. Nedelcu and Richard E. Michod</i>	
21.1 Introduction	271
21.2 The volvocalean green algal group	273
21.2.1 Overview	273
21.2.2 Life history trade-offs and the evolution of multicellularity in volvocalean algae	275
21.3 Mechanisms of life history trade-offs and the evolution of multicellularity in volvocalean algae	277
21.3.1 Overview	277
21.3.2 Acclimation and life history trade-offs in <i>Chlamydomonas</i>	278
21.3.3 The genetic basis for cell differentiation in <i>Volvox carteri</i>	279
21.4 Co-opting mechanisms underlying environmentally induced life history trade-offs for cell differentiation	280
21.5 Conclusion	282
21.6 Summary	282
21.7 Acknowledgments	283
22 Molecular basis of life history regulation in <i>C. elegans</i> and other organisms	284
<i>Birgit Gerisch and Adam Antebi</i>	
22.1 Introduction	284
22.2 <i>C. elegans</i> life history	285
22.3 Genetics of dauer formation	285
22.4 Dauer pheromone	285
22.5 Neurosensory signaling and processing	286
22.6 Sensory signal transduction and longevity	287
22.6.1 Insulin/IGF-1 signal transduction	287
22.6.2 TGF-beta signaling	288
22.6.3 Biogenic amine signaling	289
22.6.4 Neuropeptide-Y-like signaling	289
22.6.5 Steroid hormone signaling	289
22.7 Developmental timing and life history specification	291
22.8 Reproduction and longevity	293
22.9 Dietary restriction	294
22.10 Diapause in other nematode strains	294
22.11 <i>D. melanogaster</i> reproductive diapause	295
22.12 Torpor/hibernation of mammals	296
22.13 Prospectus	297
22.14 Summary	297
22.15 Acknowledgments	298
23 The costs of immunity and the evolution of immunological defense mechanisms	299
<i>Kurt A. McKean and Brian P. Lazzaro</i>	
23.1 Introduction	299
23.2 Innate immune defense in <i>Drosophila</i>	301

23.3	Trade-offs between reproduction and immunity	302
23.4	Deployment costs, tolerance, and the evolution of immune regulation	304
23.5	Multiple-fronts costs of immunity	307
23.6	Future directions	308
23.7	Summary	310

24 Intermediary metabolism and the biochemical-molecular basis of life history variation and trade-offs in two insect models **311**

Anthony J. Zera and Lawrence G. Harshman

24.1	Introduction	311
24.2	<i>Gryllus firmus</i> : Biochemical and molecular studies of trade-offs in lipid metabolism and life histories	312
24.2.1	Background on life history variation in <i>Gryllus</i> and methodological perspective	312
24.2.2	Lipid reserves: The physiological context of biochemical studies of life history trade-offs	313
24.2.3	Morph-specific differences in flux through pathways of lipid biosynthesis and oxidation	315
24.2.4	Enzymatic basis of flux trade-offs: Digging deeper into the functional hierarchy of life history trade-offs	316
24.2.5	Enzymological and molecular causes of differences in enzyme activities between morphs	319
24.2.6	Amino acid metabolism and life history trade-offs in <i>Gryllus</i>	320
24.3	<i>Drosophila melanogaster</i>	321
24.3.1	Laboratory selection on life history	322
24.3.2	Clinal variation in intermediary metabolism and life history traits in the field	323
24.4	Other studies and issues relevant to <i>Drosophila</i>	326
24.4.1	Additional biochemical and molecular studies	326
24.4.2	Influence of changes in allocation versus nutrient input on life history evolution	326
24.4.3	Quantitative-genetic variative in enzyme activities and fitness	327
24.5	Summary	327
24.6	Acknowledgments	328

25 Epistatic social and endocrine networks and the evolution of life history trade-offs and plasticity **329**

Lesley T. Lancaster and Barry Sinervo

25.1	Introduction	329
25.2	Endocrine networks and life history trade-offs	331
25.3	An example of a gated switch in developmental life history trade-offs	333
25.4	Social networks and life history trade-offs	333
25.5	Social dimensions to trade-offs: Endocrine mediation and fitness consequences	339
25.6	Corticosterone, egg size, and the trade-off between aspects of offspring quality in a lizard	339
25.7	Juvenile hormone, vitellogenin, and reproductive trade-offs in eusocial honeybees	341
25.8	Testosterone, growth hormone, social dominance, and smolting in Atlantic salmon	343
25.9	Gibberellins, auxin, ethylene, and reproductive allocation in monoecious plants	344
25.10	Conclusions and future directions	347
25.11	Summary	347

26	Hormonally-regulated trade-offs: Evolutionary variability and phenotypic plasticity in testosterone signaling pathways	349
	<i>Michaela Hau and John C. Wingfield</i>	
26.1	Introduction	349
26.2	Testosterone and trade-offs	350
26.3	Conservation versus variation in testosterone-regulated traits on an interspecific level	354
26.4	Signal production pathway	354
26.5	Signal transduction pathway	356
26.6	Plasticity of testosterone-regulated trade-offs on an individual level	356
26.7	Costs	357
26.8	Phenotypic plasticity and reaction norms	357
26.9	Development	359
26.10	Future directions of evolutionary endocrinology	360
26.11	Summary	361
26.12	Acknowledgments	361
	Part 7: Concluding remarks	363
27	Does impressive progress on understanding mechanisms advance life history theory?	365
	<i>Stephen C. Stearns</i>	
27.1	Introduction	365
27.2	How research on mechanisms is changing views on life history evolution	366
27.2.1	The nature of trade-offs: Signals, allocation, or both?	366
27.2.2	Ancient, conserved, broadly shared mechanisms?	367
27.2.3	Decoupling functions by duplicating modules	369
27.3	Is work on mechanisms changing theory?	369
27.3.1	Are these data forcing the theory to change?	369
27.3.2	Are we identifying general features of intermediate structure in the genotype-phenotype map?	370
27.3.3	Are the empirical problems with the theory being addressed?	371
27.4	Conclusion	373
27.5	Summary	373
28	What mechanistic insights can or cannot contribute to life history evolution: An exchange between Stearns, Heyland, and Flatt	375
	<i>Thomas Flatt, Andreas Heyland, and Stephen C. Stearns</i>	
28.1	Why mechanisms are important for life history theory: A response by Flatt and Heyland	375
28.2	Reply by Stearns: Mechanisms do not yet force the theory to change	379
	References	380
	Index	469