Contents

Preface

1	Evolutionary Thermal Biology			1
	1.1	The cha	llenge of evolutionary thermal biology	1
	1.2	2 Thermal reaction norms		3
	1.3	The role	e of theory	5
	1.4	Theoret	Theoretical approaches to evolutionary thermal biology	
		1.4.1	Optimality models	6
		1.4.2	Quantitative genetic models	8
		1.4.3	Allelic models	10
		1.4.4	The complementarity of theory	13
	1.5	Empirio	cal tools of the evolutionary thermal biologist	13
		1.5.1	Quantifying selection	14
		1.5.2	Experimental evolution	14
		1.5.3	Comparative analysis	15
	1.6	Conclus	sions	18
2	Ther	Thermal Heterogeneity		
	2.1	Operati	ve environmental temperature	20
	2.2	Global	patterns of operative temperature	23
		2.2.1	Latitudinal clines	23
		2.2.2	Altitudinal clines	27
	2.3	Quantif	fying local variation in operative temperatures	29
		2.3.1	Mathematical models	29
		2.3.2	Physical models	31
		2.3.3	Statistical models	32
	2.4	Conclus	sions	33
3	Thermal Sensitivity			35
	3.1	Pattern:	s of thermal sensitivity	35
	3.2	3.2 Proximate mechanisms and tradeoffs		41
		3.2.1	Thermal effects on enzymes (and other proteins)	41
		3.2.2	Membrane structure	43
		3.2.3	Oxygen limitation	44
		3.2.4	Conclusions from considering proximate mechanisms	45
	3.3	Optima	l performance curves	47
		3.3.1	Optimal performance curves: survivorship and related performances	47
		3.3.2	Optimal performance curves: fecundity and related performances	51
		3.3.3	Contrasting the two models	53

vii

	3.4 Using models to understand natural patterns		54	
		3.4.1 Survivorship	56	
		3.4.2 Locomotion	62	
		3.4.3 Development	66	
		3.4.4 Growth	66	
		3.4.5 Reproduction	68	
		3.4.6 Why do certain patterns differ from predicted ones?	69	
	3.5	Have we mischaracterized thermal clines?		
		3.5.1 Reciprocal transplant experiments	70	
		3.5.2 Laboratory selection experiments	71	
		3.5.3 Conclusions from reciprocal transplant and laboratory selection experiments	74	
	3.6	Have phenotypic constraints been correctly identified?	75	
		3.6.1 A jack of all temperatures can be a master of all	75	
		3.6.2 The proximate basis of performance determines tradeoffs	75	
	3.7	Do all performances affect fitness?	76	
	3.8	Does genetic variation constrain thermal adaptation?	79	
		3.8.1 A quantitative genetic model based on multivariate selection theory	81	
		3.8.2 A genetic model for survivorship and related performances	81	
		3.8.3 A genetic model for fecundity and related performances	83	
		3.8.4 Predictions of quantitative genetic models depend on genetic parameters	84	
	3.9	Does gene flow constrain thermal adaptation?	85	
	3.10	Conclusions	87	
4	Ther	oregulation	88	
	4.1	Quantifying patterns of thermoregulation	88	
	4.2	Benefits and costs of thermoregulation	91	
		4.2.1 Benefits of thermoregulation	91	
		4.2.2 Costs of thermoregulation	96	
4.3		An optimality model of thermoregulation		
	4.4	Do organisms thermoregulate more precisely when the benefits are greater?		
	4.5	Nonenergetic benefits of thermoregulation	105	
		4.5.1 Thermoregulation during infection	105	
		4.5.2 Thermoregulation during pregnancy	106 107	
	4.6	Do organisms thermoregulate less precisely when the costs are greater?		
	4.7 Nonenergetic costs of thermoregulation		111	
		4.7.1 Aggressive interactions with competitors	111	
		4.7.2 Risk of predation or parasitism	113	
		4.7.3 Risk of desiccation	116	
		4.7.4 Missed opportunities for feeding or reproduction	116	
		4.7.5 Interactions between different costs	118	
	4.8	Endothermic thermoregulation	119	
		4.8.1 The evolutionary origins of endothermy	119	
		4.8.2 Optimal thermoregulation by endotherms	122	
	4.9	Conclusions	125	
5		nal Acclimation	126	
	5.1	Patterns of thermal acclimation	126	
	5.2	The beneficial acclimation hypothesis	127	
		5.2.1 Developmental acclimation	127	
		5.2.2 Reversible acclimation	131	

Beyond the beneficial acclimation hypothesis

135

5.2.3

	5.3	Costs of thermal acclimation	135	
		5.3.1 Costs of energetic demands	136	
		5.3.2 Costs of time lags	139	
		5.3.3 Interaction between costs	139	
	5.4	Optimal acclimation of performance curves	140	
		5.4.1 Optimal developmental acclimation	141	
		5.4.2 Optimal reversible acclimation	143	
		5.4.3 Relaxing assumptions about fitness	145	
	5.5	Evidence of optimal acclimation	146	
		5.5.1 Does the thermal optimum acclimate more than the performance breadth?	146	
		5.5.2 Do organisms from variable environments acclimate more than		
		organisms from stable environments?	146	
	5.6	Constraints on the evolution of acclimation	149	
		5.6.1 Genetic variance and covariance	149	
		5.6.2 Gene flow	152	
	5.7	Toward ecological relevance	154	
	5.8	Conclusions	155	
. 4			157	
6		emperature and the Life History		
	6.1	The link between performance and the life history	157	
	6.2	General patterns of age and size at maturity	158	
		6.2.1 Thermal plasticity of age and size at maturity	158	
		6.2.2 Thermal clines in age and size at maturity	159	
	2.21	6.2.3 Experimental evolution of age and size at maturity	161	
	6.3	Optimal reaction norms for age and size at maturity	162	
		6.3.1 A comparison of two modeling approaches	163	
		6.3.2 Thermal effects on juvenile mortality	164	
		6.3.3 Thermal constraints on maximal body size	166	
		6.3.4 Thermal effects on population growth	169	
		6.3.5 A synergy of evolutionary mechanisms	170	
	6.4	General patterns of reproductive allocation	171	
		6.4.1 Thermal plasticity of offspring size	171	
		6.4.2 Thermal clines in offspring size	171	
		6.4.3 Experimental evolution of offspring size	172	
	6.5	Optimal size and number of offspring	174	
		6.5.1 Direct effect of temperature on the optimal offspring size	174	
		6.5.2 Indirect effects of temperature on the optimal offspring size	176	
		6.5.3 Teasing apart direct and indirect effects on reproductive allocation	177	
	6.6	Optimal variation in offspring size	178	
	6.7	Conclusions	179	
7	Ther	mal Coadaptation	181	
*	7.1	Traits interact to determine fitness	181	
	7.2	Coadaptation of thermal sensitivity and thermal acclimation	182	
	7.3	Coadaptation of thermal physiology and thermoregulatory behavior	186	
	7.0	7.3.1 Mechanisms favoring a mismatch between preferred temperatures and	100	
		thermal optima	189	
		7.3.2 Predicting coadapted phenotypes	193	
	7.4	Coadaptation of thermoregulatory behavior, thermal physiology, and life history	195	
	7.5	Constraints on coadaptation	195	
	7.6	Conclusions	196	
	1.0	Conclusions	190	

8 1	Thermal Games					
8	8.1 Filling the ecological vacuum		199			
8	8.2 Approaches to the study of frequency-dependent selection		200			
8	8.3	Optimal thermoregulation in an evolutionary game	200			
		8.3.1 Competition during thermoregulation	201			
		8.3.2 Predation during thermoregulation	203			
		8.3.3 Relaxing assumptions of simple models	205			
8	8.4	Optimal performance curves in an evolutionary game	207			
		8.4.1 The coevolution of thermal optima between species	207			
		8.4.2 The coevolution of thermal breadths between species	210			
		8.4.3 Gene flow and the coevolution of thermal optima	211			
8	8.5	Life-history evolution in a thermal game	212			
8	8.6	Conclusions	213			
9	Adap	ptation to Anthropogenic Climate Change	214			
(9.1	Recent patterns of climate change	214			
		9.1.1 Global change	214			
		9.1.2 Regional change	215			
		9.1.3 Local change	216			
(9.2	Observed responses to recent thermal change	216			
		9.2.1 Shifts in phenology	216			
		9.2.2 Shifts in geographic ranges	217			
		9.2.3 Disruption of ecological interactions	217			
		9.2.4 Changes in primary productivity	218 218			
•	9.3	Predicting ecological responses to global warming				
		9.3.1 Correlative versus mechanistic models	219			
		9.3.2 Mechanistic models of responses to environmental warming	220			
		9.3.3 Predicting differential responses of populations and species	223 224			
	9.4	Adaptation to directional thermal change				
		9.4.1 Adaptation of thermoregulation	227			
		9.4.2 Adaptation of the thermal optimum	229			
		9.4.3 Adaptation of the performance breadth	231			
	9.5	Thermal games in a warming world	232			
	9.6	Evolutionary consequences of gene flow in a warming world	233			
		9.6.1 Spatially heterogeneous warming can reduce the flow of	222			
		maladapted genotypes	233			
		9.6.2 Spatially heterogeneous warming can increase the flow of	225			
7)	9.7	preadapted genotypes Conclusions	235 236			
			238			
Refe	References					
Auth	hor I	Index	277			
Species Index						
Subj	Subject Index					