doi:10.1111/j.1558-5646.2009.00878.x

THERMAL GAMES: PUTTING TEMPERATURE BACK ON THE EVOLUTIONARY AGENDA

Richard John Walters[1,2] and David Berger[1]

[1]Zoological Museum, University of Zurich-Irchel, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[2]E-mail: richard.john.walters@googlemail.com

Received September 25, 2009
Accepted September 25, 2009

Review of: *Thermal Adaptation—A Theoretical and Empirical Synthesis*. Edited by Michael J. Angilletta Jr. 2009. Oxford University Press, Oxford, U.K. ISBN 978-0-19-857088-2 $65.00.

Temperature is so fundamental to life itself that it will no doubt come as a surprise to some that our current understanding of thermal adaptation is as incomplete and fragmented as it is. A long history of empirical work on responses of organisms to temperature stems from ecological physiology, and has largely accumulated without a conceptual framework necessary to interpret its adaptive significance. Angilletta's attempt to synthesize this traditionally data-rich theory-poor field is therefore both worthy and long overdue; but to do so in the rousing and pithy manner that he has taken in *Thermal Adaptation* is arguably an admirable feat.

Angilletta accredits his motivation for writing the book to Richard Levins' vision of a unified theoretical and empirical approach to biological research. The author has devoted his keen naturalist's interest in herps to this aim from the start of his scientific career in the early 1990s. Thus, Angilletta arguably is the youngster amongst those bringing the field of thermal adaptation forward in recent years, by adamantly attending and organizing symposia on the topic, publishing, and proselytizing, culminating in the publication of this book.

Thermal biology is said to have largely lagged behind other related fields in realizing an integrated vision despite a vast and venerable literature. A quick search of the ISI web of science database[3] suggests that the number of articles published since 1990 containing the words "evolution AND temperature" are comparable to topics as fundamental to evolution as speciation, natural or sexual selection, and are well ahead of more avant-garde topics such as developmental biology and meta-population theory. It is clear that the evolutionary consequences of temperature appear to have gained precedence in recent years, making this synthesis a timely endeavor.

The reaction norm takes the center stage as the conceptual framework to bridge current theoretical and empirical aspects of thermal biology and to provide a means to apply modeling approaches developed within other fields. The opening chapter is dedicated to providing young researchers with an overview of the methodologies required to ask the why questions. A comparative outlook details the advantages and disadvantages of applying optimality theory, quantitative genetics, and allelic simulations, while details of experimental designs for artificial selection and methodology for analyzing phylogenetic independent contrasts

[3] A search of the ISI Web of Science database for papers containing the words "evolution AND temperature," published in biological journals for the years 1990–2008 inclusive, yielded a total of 4504. This amount compares well with repeated searches on other key topics (papers containing the words "evolution AND..."): "natural selection," 6849; "speciation," 5639; "sexual selection," 5124; "competition," 4929; "dispersal," 3957; "predation," 2503; "niche," 1100; "developmental biology," 768; "metapopulation," 428.

are helpfully provided in boxes. The second chapter is devoted to spelling out the enormous temporal and spatial thermal complexity of environments. From mathematical and physical models used to describe body temperatures at the local scale to statistical models and artificial neural networks used to map them at the global scale, Angilletta skillfully traverses the details of potentially dull topics by engaging the reader with great pace and clarity. Together these introductory chapters successfully set the tone and focus for the rest of the book, providing common ground for theoreticians and empiricists to join forces on.

"Anyone familiar with physics and chemistry should be unimpressed by the discovery that life depends on temperature." And with that opening motivational sentence we start getting down to serious business. In his flagship chapter three, Angilletta explains the concept of thermal sensitivity from a multilevel perspective, encompassing physiological properties of cell size, membrane structure, oxidative circulation, and the temperature dependence of enzymes, to full organismal performance in growth, development, and reproduction. The mathematical models of Gilchrist (1995) and Lynch and Gabriel (1987), which serve as the main theoretical framework throughout the book, are introduced. It is with astounding ease that the focal points of these models are explained, but what makes this chapter particularly rewarding is the subsequent section on the observed incongruence between theoretical predictions and empirical data. Combining physiological and evolutionary constraint explanations, nicely integrating the earlier parts of the chapter, this section evaluates the general assumptions of models on thermal adaptation and the usefulness of different empirical methods to describe thermal reaction norms and partitioning their genetic and phenotypic components. The chapter concludes by pinpointing issues that might contribute to the mismatch, nicely setting the stage for the more intricate evolutionary explanations that follow in later chapters. In spite of the considerable number of empirical and theoretical studies cited, some fields of thermal adaptation do feel neglected at this point, notably the role of heat shock proteins in *Drosophila*, allelic diversity in yeast and bacteria, or work on metabolic theory. However, these shortcomings seem a strategic decision rather than a failure to recognize essential literature, because these aspects are picked up elsewhere in the book. In fact, this style of writing manifests throughout this small volume and appears to have been necessary to achieve the effective transfer of key points pertinent to this and other chapters.

Theoretical predictions of optimal reaction norms will undoubtedly flounder when organisms are capable of buffering temperature fluctuations through behavior. The importance of thermoregulation has been long recognized although poorly understood given the practical difficulties of accurately observing and quantifying its consequences in the field. The resurgence of interest in this topic reflects both recent technical advancements and the rather successful application of optimality models. Chapter four stresses the evolutionary significance of thermoregulation, and by integrating recent perspectives such as the "hotter is better" hypothesis (e.g., Frazier et al. 2006; Kingsolver and Huey 2008), Angilletta succeeds in demonstrating how the incorporation of behavior might explain some of the discrepancies underscored in the previous chapter. Useful boxes detailing contemporary methods to measure and model thermoregulatory behavior are once again combined with theoretical models and carefully chosen case studies to nail home the message that integrated approaches are needed if we are to advance our current state of understanding. This time the cost-benefit model of Huey and Slatkin (1976) is the center of attention, providing the basis for exploring direct and indirect costs of thermoregulation in a spatially complex environment under competition and predation. We end up convinced that the adaptive significance of physiological responses can only be understood in light of behavior. Fittingly the chapter ends with an exploratory discussion on hypotheses pertaining to the evolution of endothermy.

It is a common trait that organisms acclimate to extreme thermal conditions by shifting a part or all of their reaction norms. The ideal strategy would be to instantly respond to environmental change in an infinitely plastic way, which is in effect the basis of the long espoused beneficial acclimation hypothesis. However, interpreting acclimation ability with respect to life history and environmental variance requires that we take a cost-benefit approach. This is the subject of chapter five. Angilletta elegantly walks the reader through the various testable predictions from the Gabriel and Lynch (1992) and Gabriel (2005) optimality models. Unfortunately, much of the empirical evidence appears at odds with the conditions predicted to promote reversible versus developmental acclimation and plasticity of the thermal optimum versus plasticity of thermal breadth. There are plenty of incongruous findings in this section for both modelers and empiricists to investigate further. Better, more realistic experimental designs may help explain some of the disparate results, although many indications point to genetic or other constraints. A poor understanding of these constraints and the costs associated with plasticity is manifested in the slight nature of this chapter.

Up to this point all discussion has referred to the evolution of performance. The goal of chapter six is to translate performance into fitness and describe the impact of temperature on life history. The temperature-size rule (Atkinson 1994), the observation that 80+% of ectotherm species mature at a larger body size when reared at colder temperatures, forms the basis of discussion. Numerous recent studies have since validated the phenomenon originally observed by Ray in 1960, although its generality and applicability appear to vary among taxonomic groups. Establishing the rule, however, has proved far easier than explaining it. Angilletta uses the energetic and allocation models of Berrigan and Koella

(1994) and Kozłowski et al. (2004) to explore the adaptive significance of this pattern, only to ascertain that it should only occur under a very restricted set of assumptions. Surprisingly, discussion on this topic ends somewhat abruptly, concluding that the unhealthy state of the field stems from a search for simple universal explanation. Yet surprisingly, neither is there any mention of the critique associated with the Bertalanffy's growth equation used for modeling age and size at maturity (e.g., Day and Taylor 1997) nor any attempt to understand the adaptive significance of exceptions of the rule through the lenses proposed in previous chapters (Walters and Hassall 2006; Kingsolver and Huey 2008). Few would disagree with the view that any explanation is likely to be complex. But without a framework to provide a null hypothesis, or the means to understand the adaptive significance of such a rule given its apparent environmental dependency (Diamond and Kingsolver in press), the reader is left wanting.

Chapter seven aims to synthesize the empirical and theoretical background laid out in chapters three to six. Incongruence between theoretical models and empirical data is to be expected in a complex world where selection on thermoregulation, acclimation, and life-history traits are interrelated. Evidence suggests that most traits have different thermal optima and breadth, even at the individual level, and that preferred temperatures may not reflect thermal optima. Thermal coadaptation is advanced as a conceptual framework to understand the myriad of adaptive solutions. Building upon the latest models of Gabriel, Gilchrist, himself, and colleagues, together with the latest empirical analyses of thermal reaction norms presented by Martin and Huey (2008), Angilletta attempts to disentangle these influences by presenting a novel hypothesis. Although this chapter draws heavily on theory to develop a synthesis, its conclusions will likely be of most interest to empiricists attempting to identify genetic or physiological constraints that can shape the thermal reaction norm and the response of correlated traits to selection.

Having made the case for more complex modeling, Angilletta introduces the reader to the idea of "Thermal Games" in chapter eight. The realization that optimal phenotypes are not selected in isolation but are affected by the dynamics of their competitors, prey, predators, parasites, and mutualists requires that we reassess optimal strategies in light of frequency-dependent selection and coevolution. The aim of this chapter is to promote the exciting potential of game theory to the field of thermal biology rather than review the benefits and limitations of its application. Using a simple model of the ideal free distribution, Angilletta starts off by exploring the thermoregulatory behavior of individuals under competition, and the nonintuitive behavioral cascades that are predicted to occur once both competition and predation at various trophic levels are incorporated. The second half of the chapter is largely dedicated to the models of Kopp and Gavrilets (2006) on the evolution of performance curves. Drawing upon both analytical and allelic simulation models, Angilletta illustrates how qualitatively different conclusions can emerge once biotic interactions and their interactions with density-dependent processes and gene flow are taken into account. Although short, the chapter makes patent the point that ecological complexity is crucial to our understanding of thermal adaptation. Critically, it provides the reader with concrete examples to demonstrate just how such complexity can be distilled and managed using models that are capable of capturing, at the very least, the essence of key processes.

As could be expected, the final chapter addresses the contemporary topic of adaptation to anthropogenic climate change. As one comes to expect from Angilletta at this point, the chapter provides far more than a simple rehash of chapters past. It starts by tapping into concurrent debates in the field of macroecology on the role of correlative versus mechanistic models of species distributions, identifying the need to capture both behavioral complexity and evolutionary processes to improve forecasts. Discussion of adaptive responses to environmental change appropriately starts with the generic analytical model of Lynch and Gabriel before touring the reader through subsequent advancements, notably the establishment of a quantitative genetic basis for the thermal optima necessary to assess critical rates of adaptation. The model has since been extended to address the role of performance breadth, demographic stochasticity, coevolution, and gene flow on extinction risk under directional selection. At each stage critical changes to the underlying assumptions of the model are introduced in such a way as to facilitate the reader's immediate understanding of the model's advantages and limitations without getting bogged down in unnecessary detail. Consistent with the other chapters, this review is elegantly concise and yet has sufficient depth and breadth to provide a solid basis for future research work for both the ecologist and evolutionary biologist. The only topic that seems to have escaped attention is the role of temperature on dispersal itself. According to our search of the ISI database, papers on this topic are as prevalent as those associated with biotic interactions and which have figured so prominently throughout the book.[4]

This compact but nonetheless dense and thorough book will be an inspiration and reference for the specialist and the newcomer

[4] A search within the set of papers containing the words "evolution AND temperature" for associations with other specific topics was conducted. More than 89% of papers could be assigned to at least one of the following five subject areas: life history, 1992 ("growth or development or reproduction or size"); physiology, 914 ("physiology or metabolic or kinetic or chemical or enzyme"); distribution, 563 ("distribution or latitude or altitude"); biotic interactions, 274 ("competition or predation or mutualism or parasitism or pathogen"); dispersal, 268 ("dispersal or migration or flight or movement"). Topics are not mutually exclusive but did show little overlap.

alike. Angilletta's enthusiasm is infectious and justified—without a doubt, thermal adaptation is back on the evolutionary agenda.

LITERATURE CITED

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms. Adv. Ecol. Res. 25:1–58.

Berrigan, D., and J. C. Koella. 1994. The evolution of reaction norms: simple models for age and size at maturity. J. Evol. Biol. 7:549–566.

Day, T., and P. D. Taylor. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. Am. Nat. 149:381–393.

Diamond, S., and J. Kingsolver. 2010. Environmental dependence of thermal reaction norms: host plant quality can reverse the temperature-size rule". Am. Nat. *In press.*

Frazier, M., R. B. Huey, and D. Berrigan. 2006. Thermodynamics constrains the evolution of insect population growth rate: "warmer is better". Am. Nat. 168:512–520.

Gabriel, W. 2005. How stress selects for reversible phenotypic plasticity. J. Evol. Biol. 18:873–883.

Gabriel, W., and M. Lynch. 1992. The selective advantage of reaction norms for environmental tolerance. J. Evol. Biol. 5:41–59.

Gilchrist, G. W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. Am. Nat. 146:252–270.

Huey, R. B., and M. Slatkin. 1976. Cost and benefits of lizard thermoregulation. Q. Rev. Biol. 51:363–384.

Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: three rules. Evol. Ecol. Res. 10:251–268.

Kopp, M., and S. Gavrilets. 2006. Multilocus genetics and the coevolution of quantitative traits. Evolution 60:1321–1336.

Kozłowski, J., M. Czarnołeski, and M. Dańko. 2004. Can optimal resource allocation models explain why ectotherms grow larger in cold? Integr. Comp. Biol. 44:480–493.

Lynch, M., and W. Gabriel. 1987. Environmental tolerance. Am. Nat. 129:283–303.

Martin, T. L., and R. B. Huey. 2008. Why "suboptimal" is optimal: Jensen's inequality and ectotherms thermal preferences. Am. Nat. 171:E102–E118.

Walters, R. J., and M. Hassall. 2006. The temperature-size rule: does a general explanation exist after-all? Am. Nat. 167:510–523.

Book Review Editor: J. Thompson