

Book Review

***Thermal Adaptation: a Theoretical and Empirical Analysis.* Michael J. Angilletta Jr.**

New York: Oxford University Press, 2009. 320 pp. ISBN 9780198570875 (hardback), \$135.00 and ISBN 0198570872 (paperback), \$65.00

The field of thermal biology has a long history and a key position in environmental studies and in organismal biology. Presently, its relevance is rising in the context of ongoing efforts to develop an understanding of the impacts of global warming on terrestrial and aquatic ecosystems. However, it seems that the level of firm knowledge in this field is still limited. A wealth of data has been, and is still being, collected. A large number of individual analyses of phenomena have led to several apparently disjunct ways of explanation and analysis. Accordingly, our current understanding still appears patchy; a widely accepted picture of thermal impact and adaptation does not (yet) exist or, phrased differently, if such an understanding exists it has not (yet) been widely accepted. Rapid progress is thus needed to develop a comprehensive and unifying view and understanding of thermal effects on organisms and ecosystems.

Michael Angilletta has undertaken the admirable effort to bring light into this complexity by reviewing the field with emphases on conceptual, empirical, and mathematical analyses of thermal patterns as well as on existing modelling efforts in evolutionary biology. He includes a wide range of examples from various aquatic and terrestrial environments, covering a wide range of organisms. As a result, this monograph clearly is a milestone among those written in the field of thermal biology and must be considered essential reading for specialists in the area and for those with a general interest in the role of temperature in evolution and environmental adaptation.

The preface to this monograph illustrates how the author intends to address the questions associated with thermal biology from the point of view of the whole organism. He emphasizes the need for quantitative models of thermal adaptation and introduces some that build on the concept of a thermal performance curve. The first chapter considers the historical developments in evolutionary thermal biology and lays out the relevant concepts and modelling

approaches as well as the tools of study. The theoretical basis includes optimality models, quantitative genetic models and analyses of selection, and evolution as well as the statistical tools required for such analyses. The monograph continues with a treatment of environmental temperature and its variability depending on radiation, air temperatures and wind, and how these become effective in natural environments. Analyses of thermal sensitivities follow with a treatment of reaction norms. This chapter also addresses various approaches to identify “proximate” biochemical and physiological mechanisms characterizing sensitivities and then investigates the relationships between performance and fitness. It reports ways of carrying out experiments and ways of testing available models for their applicability and limitations and also addresses the parameters investigated when quantifying thermal limitation. These are traditionally those characterizing the ultimate limits of passive tolerance to temperature extremes and measured as survivorship on various time scales. Relevant indicators of performance include fecundity, development and locomotion as well as trade-offs among them, and how they change during life history. Separate chapters focus on the treatment of thermoregulation and thermal acclimation as well as on associated costs and benefits to ectotherms and endotherms.

The volume essentially contrasts two major models (those of Lynn and Gabriel and of Gilchrist) and their predictive power for fitness as well as their suitability and support by experimental findings. This analysis should stimulate a lot of thinking and thereby further conceptual and experimental work. Interestingly, the analysis in subsequent chapters shows that looking at beneficial acclimation in terms of performance maximization is too simplistic. Thermal cues elicit seasonal adjustments, dormancy, growth, reproduction, and thermoregulation, and so drawing a simple picture for all of these performances is not possible. Trade-offs between performances may exist. The width of the thermal window may affect the level of performance and vice versa. Furthermore, acclimation may be most relevant in terms of shifting tolerance limits but less so for compensating performance optima.

Here, shifts in passive tolerance would also be involved. Acclimation capacity is likely limiting and acclimation may also involve a cost, which needs to be considered in a comprehensive picture. Such cost is not just energetic but may involve other constraints affecting function, e.g. a time lag of crucial function or a too-slow or too-fast velocity of reversible acclimation under variable environmental conditions.

Naturally, the diversity of the field means that not all aspects of thermal biology can be comprehensively addressed in one volume. In this context, I would like to include my personal view that knowledge of physiological mechanisms should serve as a link between empirical analysis and successful modelling of performance. This view in fact stems from recent evidence that such mechanisms respond to climate-associated temperature extremes and are responsible for eliciting ecosystem-level impact. Mechanism-based approaches will thus largely support the quantification of phenomena and the predictive power of models. While, clearly, the author acknowledges the need for a strong theoretical foundation for the field and for efforts to develop associated mathematical formulae and models, his personal background and interest as well as the patchiness of empirical phenomena may have prevented him from attempting to establish stronger links between the mechanistic background and his conceptual treatment of thermal biology. Also, in many of the examples reported, mechanistic causalities are largely lacking. However, a mechanism-oriented point of view may be needed to further understand thermal reaction norms, thermal adaptation, limitation, and the role of temperature in evolution. It may also be needed for an integration of molecular and whole-organism aspects into a comprehensive picture. For example, such an approach would allow addressing the questions of how passive resistance and performance capacity may be linked or how climate shapes performance capacity of organisms in various climatic zones.

The focus on temperature is well justified when examining the effects of anthropogenic climatic change on organisms and ecosystems. However, and beyond the scope of this book, it needs to be considered that temperature is a pervasive factor whose effects integrate with those of any other factor (e.g. desiccation in terrestrial habitats and salinity, hypoxia or CO₂ in aquatic environments). Elevated water temperatures cause enhanced stratification thereby supporting the development of hypoxia and hypercapnia and effects of these factors

will interact with those of temperature. Furthermore, one needs to be aware that this integration may influence or specify temperature effects. For example, oxygen solubility in aquatic media varies with temperature, a phenomenon that adds to the direct effect of temperature on aquatic organisms. In general, thermal biology appears as a good foundation from which to address these other factors.

In the future, the wealth of information compiled in this book will need to be complemented by the use of an integrative physiological concept that, apparently, does not yet exist. This would likely allow one to complement and to justify (or not) the various alternate theoretical approaches elaborated in this volume. Such analyses would deepen even further the insight into the constraints, trade-offs, and driving forces of adaptation as well as a deeper understanding of observed evolutionary processes. Finally, the challenge of linking genomic, molecular, and cellular aspects to whole-organism and ecosystem levels of analysis will have to be met and for many, this book will be an important stepping stone on the way to accomplishing such a vision and goal.

Overall, I recommend this fascinating book without hesitation to anyone with an interest in thermal biology. Michael Angilletta's book is a delightful read and provides an interesting and detailed account of current knowledge in thermal biology. The approach is consistent throughout. Chapters have successfully been compiled in a way that the development of current knowledge can be followed, thereby supporting a more profound understanding and easier access to the complexity of the questions that are currently being addressed in this field. The book also helps to develop a vision of where we need to push our conceptual, experimental, and modelling work further to come to a more comprehensive understanding. Accordingly, students and researchers alike will find the volume useful and interesting and it should be an important, if not indispensable, introductory volume and reference for years to come.

Hans O. Pörtner
Integrative Ecophysiology
Alfred Wegener Institute for Polar and
Marine Research
Bremerhaven, Germany
E-mail: hans.poertner@awi.de

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