Preface

The first book that I read as a graduate student was *Foraging Theory* (Stephens, D. W., and J. R. Krebs. 1986, Foraging Theory. Princeton, Princeton University Press). At the time, I was planning to study the evolution of foraging behavior in snakes, and thus wanted to acquire a conceptual background for this work. As fate would have it, my subsequent research did not focus on foraging behavior (or snakes), but the book made a lasting impression on me anyway. The authors laid out a comprehensive and insightful theory, moving from simple models to complex ones, while drawing on relevant empirical data. The book culminated in a rigorous appraisal of the field's accomplishments, driven by the match between theoretical predictions and empirical observations. Had I pursued my interest in foraging biology, the book would surely have become my academic bible. Instead, I soon developed a greater interest in thermal biology, only to discover that no analogous resource existed for this discipline.

I don't want to give you the impression that little was known about thermal biology or that no one had attempted a conceptual synthesis. Neither impression would be accurate. In many respects, thermal biology has progressed tremendously, as one can conclude from reading an early synthesis of this topic (see Cossins, A. R., and K. B. Bowler. 1987, Temperature Biology of Animals. New York, Chapman and Hall). In other respects, though, thermal biology continues to lag behind other disciplines. Let me explain. When it comes to documenting patterns, few disciplines have made more progress than thermal biology. But if we judge progress by our understanding of the processes that generate these patterns, then we have much progress to make. While proximate explanations abound, ultimate explanations remain scarce. This problem stems from the paucity of quantitative models of thermal adaptation. Thermal biologists have described patterns and documented effects to the point that empirical knowledge has far outstripped theoretical understanding. Most papers in thermal biology focus on empirical descriptions or rely on verbal arguments about adaptation. In comparison, consider the discipline of foraging biology that I referred to above; herein lies a trove of quantitative models and experimental tests about evolutionary hypotheses. The basic ideas about the evolution of foraging behavior were formulated in the 1960s and have been gradually developed to the point that the evolutionary impacts of many factors—from constraints on digestion to risks of predation—have been explored in great detail. Few evolutionary processes in thermal biology have been modeled to the same degree, and no major synthesis of evolutionary thermal biology has emerged. My aim is not to cast blame (for I would certainly share in this blame). Rather, I want to see thermal biology keep pace with other biological disciplines. And to do so, we must develop a quantitative theory of thermal adaptation.

Upon closer inspection, a wealth of evolutionary models lie waiting for thermal biologists to adopt as their own. Beginning with Levins (Levins, R. 1968, Evolution in Changing Environments: Some Theoretical Explorations. Princeton, Princeton University Press), biologists have been modeling the evolution of quantitative traits in variable environments for more than four decades. With the growth of this theory, an increasing emphasis has been placed on genetic, developmental, and ecological issues. Many of the models can be applied to understand aspects of thermal adaptation. Although some of these models are mathematically intense, I have distilled from them the essence of what they tell us about adaptation to temperature. For thermal biologists, this book contains a synthesis of theory that should guide research in the coming decade. For evolutionary biologists, the book contains an evaluation of current models of evolution in variable environments.

Throughout the book, you may notice a taxonomic bias. This bias stems from two factors. First, intentional bias resulted from my conceptual focus. The book revolves around the concept of a thermal performance curve, which describes the relationship between body temperature and organismal performance. Most of the book draws on studies of ectotherms because we can measure their performance curves more readily than we can measure those of endotherms. Students of endotherms will find the most relevant theoretical and empirical content in Chapter 4, but other chapters contain relevant theory. Second, some bias inevitably results from the lack of suitable data for certain taxa. In each chapter, I focused on the data most relevant to the theory. Consequently, certain chapters are rich with examples involving animals, plants, or microbes, but no chapter contains an even coverage of all of these groups. I hope this taxonomic bias reflects my effort to evaluate the theory more than my ignorance of the literature (although the latter seems inevitable given the exponential growth of knowledge).

Above all, I tried to produce the kind of synthesis that I had longed for when I was a graduate student. If I succeeded in this effort, my success was due partly to the biologists who mentored me in my formative years: Justin Congdon, Art Dunham, Henry John-Alder, and Peter Petraitis. My views were also shaped by discussions or collaborations with George Bakken, Lauren Buckley, Ray Huey, Rob James, Joel Kingsolver, Bill Mitchell, Carlos Navas, Amanda Niehaus, Peter Niewiarowski, Warren Porter, Leslie Rissler, Mike Sears, Frank Seebacher, and Robbie Wilson. Many colleagues were kind enough to comment on sections of the book or provide information about their research: David Atkinson, George Bakken, Lauren Buckley, Brandon Cooper, Lisa Crozier, Marcin Czarnołeski, Wilfried Gabriel, George Gilchrist, Lumír Gvoždík, Gabor Herczeg, Luke Hoekstra, Ray Huey, Jose Martín, Bill Mitchell, Mike Sears, Ben Williams, and Robbie Wilson. Their suggestions and insights contributed greatly to the final product. Other colleagues provided original images or permission to adapt figures: Martin Ackermann, Steve Beaupre, Gabriel Blouin-Demers, Lauren Buckley, Andy Clarke, Lisa Crozier, Michael Dillon, Wilfried Gabriel, Ted Garland, George Gilchrist, Bruce Grant, Brian Helmuth, Ray Huey, Jacob Johansson, Joel Kingsolver, Mark Kirkpatrick, Michael Kopp, Sue Mitchell, Carlos Navas, Mark New, Camille Parmesan, Steve Piper, Mike Sears, Tim Shreeve, Gian-Reto Walther, and Kazunori Yamahira. Finally, the preparation of this book was greatly accelerated by the help of Angela Borchelt and Phaedra Seraphimidi, who obtained copyright permissions for the figures adapted from other sources.

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