Preface

Studies of thermoregulation and thermal effects have been one of the most prolific and enduring topics in functional biology for the past century (for reviews, see Hochachka & Somero, 1984; Prosser, 1986; Cossins & Bowler, 1987). The popularity of thermal biology stems from its great significance for biological systems. Temperature has pervasive effects on biological rate processes: rapid changes in body temperature alter nearly all physiological functions by approximately 6–10% per degree Celsius over a broad thermal range. Organismal and population-level traits that depend on those processes, such as energy utilisation, growth and reproduction, are also therefore greatly affected by temperature change. Thus virtually everything that an organism does is influenced by and dependent on its thermal condition.

Despite the major impact of temperature on functional capacities, biological systems have evolved in and adapted to almost every thermal environment on earth. Adult metazoans have successfully colonised environments ranging from −70 °C to 50 °C, while the thermal tolerance of dormant stages and prokaryotes is even greater. Individual organisms and their offspring usually encounter a range of temperatures during their life-cycle, varying from daily cycles to seasonal or longer-term climate change. Responses to a given temperature or temperature change can vary markedly between species and between different life-history stages of the same species. Much of the literature of thermal biology has been concerned with determining thermal tolerances and describing patterns of function at different temperatures. The latter may be considered reaction norms, the term given to the range of phenotypes produced when organisms (or particular stages of organisms) are exposed to different environments, such as a temperature gradient. The differences in phenotype produced in distinct environments are termed phenotypic plasticity. Physiologists and cell biologists have been particularly interested and successful in investigating mechanisms that organisms use to cope with extreme thermal environments (e.g. freezing avoidance in polar fishes, hibernation in

mammals) or mechanisms associated with the functioning of tissues with a specialised thermoregulatory function (e.g. brown adipose tissue, counter-current heat exchangers, billfish brain heaters) (for other examples, see Schmidt-Neilsen, 1983). For a few species, comparative physiologists have had some success in understanding some of the cellular and molecular mechanisms underlying phenotypic plasticity to temperature change. For example, changes in the maximum swimming performance of fish following several weeks acclimation to a new temperature regimen have been explained in terms of changes in muscle structure and function: integrating studies at the organismal, physiological and biochemical levels (Johnson & Bennett, 1995; Johnston *et al.*, 1995). Much less tractable has been an understanding of the evolutionary or adaptive significance of phenotypic plasticity. Very few studies have rigorously attempted to test hypotheses about the impact of temperature acclimation on fitness (see Huey and Berrigan, pp. 205–238.

Over the past decade, there has been great interest in studies that explicitly attempt to analyse the evolution of functional characters, an interest signalled by the emergence of the term evolutionary physiology. There are many possible approaches to studying the evolutionary basis of patterns of temperature tolerance and thermal physiology. Most of our knowledge on this subject is derived from comparative studies of different natural taxa, generally populations or species. Recent emphasis has been placed on phylogenetically-based comparative studies that enable adaptive hypotheses to be tested, putative ancestral conditions to be assigned and rates of evolution to be calculated (Feder, 1987; Huey, 1987). These comparisons rely on an independently-derived set of taxonomic relationships and depend on assumptions about parsimony which may not hold true in particular cases.

Another approach to studying evolution is provided by quantitative genetics. In studies relating to thermal responses, genetically-related individuals (isogenic lines, clones, half- or full sib families) are typically exposed to different thermal environments and the response of particular traits is plotted as a reaction norm. Statistical techniques are then used to partition phenotypic variation into effects related to genotype, environment and genotype–environmental interactions and to estimate genetic correlations and heritabilities (de Jong, 1995). Multivariate extensions of quantitative genetic equations that describe responses to selection can yield predictions about the rates and direction of evolution, given certain simplifying assumptions (Turelli, 1988).

Direct experimental studies of evolution are also possible, in which

replicated experimental populations are exposed to different environments, in this case temperatures, for many generations, while maintaining control populations for comparison. This approach enables a statistical analysis of genetically-based phenotypic changes attributable to evolution in the new thermal environment. The power of such an approach is that the experimenter can directly measure characters in their initial, immediate and derived conditions. Models used for experimental evolution are necessarily restricted to organisms with short generation times which can be readily maintained in long-term culture, such as bacteria and fruit flies. A short-coming of 'natural selection' in the laboratory is that environmental conditions are often overly simplistic if the intention is to model evolution in natural environments, which are highly variable with many covarying biotic and abiotic factors.

Molecular genetics offers a variety of mechanistic approaches to the study of the plasticity of genes (Pigliucci, 1996). Recently, a number of studies have begun to map genes coding for quantitative trait loci, thereby going beyond the purely statistical analysis of populations (Mitchell-Odds, 1995). Mutants can be produced that delete or interfere with a well-characterised pattern of phenotypic plasticity. Alternatively, animals or cells can be exposed to different temperatures, and specific changes in RNA or protein patterns can be identified using differential PCR, subtraction *in situ* hybridisation or 2-D gel electrophoresis. A growing number of genes have been identified that respond to temperature change with far reaching consequences for the organism; examples include genes responsible for sex determination in reptiles and the heat shock gene family which confer thermotolerance (for a review, see Pigliucci, 1996).

Recent discoveries in developmental biology are also emerging as candidates to explain both microevolutionary and macroevolutionary events. It has been suggested that the sudden emergence of the major metazoan body plans during the late Neoproterozoic and early Cambrian was related to innovations in developmental control mechanisms that included the *Hox* gene cluster (Valentine *et al.*, 1996). In addition, homologous developmental pathways have been documented in numerous embryonic processes which may be organised in discrete regions or morphogenetic fields. It has been proposed that changes in the properties of these fields can lead to evolutionary novelty as can changes in the amount, type, or duration of gene products or mutations affecting DNA-protein binding (for a recent review on the synthesis of evolutionary and developmental biology, see Gilbert *et al.*, 1996). Environmental factors, including temperature, also have the potential to alter the properties of morphogenic fields, i.e. the range of diffusion of molecules

or the activity of certain components (cells and proteins) leading to changes in the resulting phenotypes. While not necessarily adaptive in itself the phenotypic variation generated during development may be subject to strong selection.

Recent concerns about the impact of human industrialisation on the rate of climate change have placed studies of thermal biology centre stage in the latter part of this century. It is clear that future progress in understanding phenotypic and evolutionary adaptations to temperature change will require a synthesis from hitherto more or less separate fields of evolutionary biology, molecular genetics, developmental biology, ecology, comparative physiology and organismal biology; no single approach will be sufficient. As a contribution to this synthesis, we invited some of the leading workers in thermal biology from across the spectrum of these disciplines to a meeting of the Society of Experimental Biology held in St Andrews on the occasion of the Centenary of the Gatty Marine Laboratory. This volume is the written record of that symposium. Although the emphasis of the volume is on animals, studies on bacteria and plants have been included in several of the chapters, where they help to illustrate general principles. We are grateful for the financial support of the Company of Biologists and the National Science Foundation which enabled us to assemble such high quality speakers.

Ian A. Johnston (St Andrews) Albert F. Bennett (Irvine)

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