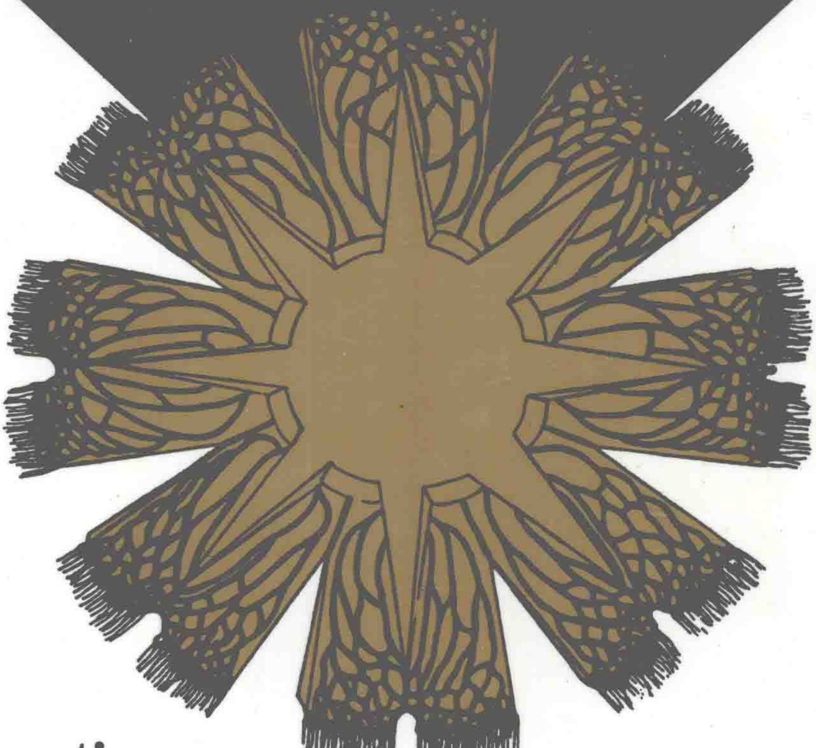
C. LADD PROSSER, EDITOR

ENVIRONMENTAL AND METABOLIC ANIMAL PHYSIOLOGY



Comparative Animal Physiology, Fourth Edition

ENVIRONMENTAL AND METABOLIC ANIMAL PHYSIOLOGY

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Edited by
C. LADD PROSSER
Department of Physiology and Biophysics
University of Illinois
Urbana, Illinois

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CONTRIBUTORS

Warren Burggren Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003

James Wayne Campbell Department of Biochemistry and Cell Biology, Rice University, P. O. Box 1892, Houston, Texas 77251

Edward J. DeVillez Zoology Department, Miami University, Oxford, Ohio 45056

Anthony P. Farrell Department of Biological Science, Simon Fraser University, Barnaby, British Columbia, Canada V5A 1S6

James Heath Department of Physiology and Biophysics, University of Illinois at Urbana-Champaign, 524 Burrill Hall, 407 South Goodwin Avenue, Urbana, Illinois 61801

Peter W. Hochachka Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, British Columbia, Canada V6T 2A9

Leonard B. Kirschner Department of Zoology, Washington State University, Pullman, Washington 99164

Brian A. McMahon Department of Biology, University of Calgary, 2500 University Drive, Calgary, Alberta, Canada T2N 1N4

James G. Morris Department of Physiological Sciences, School of Veterinary Medicine, University of California, Davis, California 95616

Dennis Powers Hopkins Marine Laboratory, Stanford University, Pacific Grove, California 93950

C. Ladd Prosser Department of Physiology and Biophysics, University of Illinois at Urbana-Champaign, 524 Burrill Hall, 407 South Goodwin Avenue, Urbana, Illinois 61801

John L. Roberts Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003

George N. Somero Environmental, Population, and Organismic Biology, University of Colorado at Boulder, 122 Ramaley, Boulder, Colorado 80309-0334

PREFACE

This book, **Environmental and Metabolic Animal Physiology,** and its companion volume, **Neural and Integrative Animal Physiology,** together comprise the fourth edition of **Comparative Animal Physiology.** Previous editions of **Comparative Animal Physiology** were published in 1951, 1961, and 1973. Each book is designed to serve as a study text for upper division and graduate courses in comparative physiology; together they constitute a reference work that provides a comprehensive introduction to the literature in specific areas of comparative physiology, biochemistry, and biophysics.

The chapters in **Environmental and Metabolic Animal Physiology** are arranged in three groups. The first four chapters deal with environmental physiology and are oriented toward ecological physiology: "Theory of Adaptation," "Water and Ions," "Temperature," and "Hydrostatic Pressure." The next four chapters deal mainly with biochemical aspects of physiology: "Nutrition," "Digestion," "Nitrogen Metabolism" and "Energy Transfer." Three chapters on holistic physiology follow: "Respiration," "O_2 and CO_2 Transport," and "Circulation."

Traditionally, animal physiology has been concerned with function in organs and cells. Whole-animal physiology has led to many medical applications; other kinds of animal physiology are veterinary physiology, and physiology of fishes, insects, parasites, and other animal groups. Cellular and molecular physiology, like biochemistry and biophysics, are reductionist approaches to function.

Comparative physiology has been defined in several ways:

(1) *The functional analysis of non-laboratory or unfamiliar animals.* Routine physiological measurements, although made on different species, contribute little to biological principles.
(2) As experimental variables, comparative physiology uses, in addition to physical and biotic parameters, different kinds of animal. *Comparative physiology is thus the study of physiological diversity.*
(3) *Comparative physiology deals with highly conserved functions and substances.* The essential biochemical and biophysical properties of organisms evolved before there were organisms we would recognize as such. Thus, comparative physiology analyzes the functioning of genetically replicating molecules; passive membrane properties and active transport reactions; and energy transfer. To these it adds the study of variation on common themes and adaptive modulation.

(4) *Another characteristic of comparative physiology is the recognition of the uniqueness of each kind of animal.* We do not speak of "higher" and "lower" animals but of degrees of complexity. Each kind of animal is adapted to its physical and biotic environment if it survives and reproduces.

Comparative physiology has made important contributions to human and veterinary medicine and to agriculture. However, the main objective of comparative physiology is to contribute to basic biological theory.

Evolution is the most unifying concept of biology. Comparative physiology, by comparing the biochemistry and physiology of related animals, can provide clues to earlier life forms. Extrapolation to ancient forms requires some knowledge of previous physical environments. Comparative physiology contributes to assessing the relative importance of gradualism and saltation, the relative importance of selection and neutral change. For example, what is the meaning of small differences in amino acid sequences in families of proteins? Physiological adaptation is a key to phylogeny.

Speciation as identification of kinds of animals is aided by comparative physiology. Several bases for the definition of species are: (a) classification by systematists based on best judgments of specialists; (b) cladistic, quantitative differences between populations; (c) biological species based on observed gene exchange; (d) new species formed by hybridization or by parthenogenesis and separated spatially; and (e) physiological species based on adaptations to ecological niche or geographic range. A modern systematist makes use of all of these concepts in describing species.

Animal distribution, ecological location, is determined by physiological adaptation to the environment—both biotic and physical. Stress tests and other physiological measurements are useful in monitoring animal distribution, especially in diverse and disturbed environments.

Medical applications have been derived from knowledge of comparative physiology. A few of many examples of contributions of comparative physiology to medicine are: (a) establishment of filtration-reabsorption and secretion in kidney function; (b) skin and gill models of active ion transport; (c) mechanisms of O_2 transport in reduced O_2, as at high altitude; and (d) induction of digestive enzymes by diet.

An organism constantly interacts with its microenvironment, physiological and biological; hence the physiology of an organism cannot be described without considering its environmental interactions. A whole organism is not equal to the sum of its parts. Out of the whole organism there emerge unique characteristics not present in any of the isolated parts. It is important, therefore, to analyze the relation between components of the environment and the whole organism and to analyze these interactions in terms of organ and cell physiology.

This book is a comprehensive survey of function systems in diverse animals. Each chapter has an extensive reference list. Most text statements are supported by citations to specific references. Selection in the reference lists has been mainly for recent research papers, reviews, and classical papers.

A certain factual background of the reader is assumed. The reader needs to have acquaintance with the principal phyla and classes of animals; a guide to animal groups is furnished in Chapter 1. A knowledge of elementary cellular physiology is assumed, and cellular phenomena are used to arrive at comparative generalizations. Background of elementary biochemistry is essential for understanding the chapters on nutrition, digestion, nitrogen metabolism, and energy transfer. Some knowledge of organ function as presented in mammalian and human physiology textbooks is assumed.

The chapters have been written by specialists. Many consultants have critically read sections and entire chapters. It is the hope of the authors and editor that this volume will continue a tradition in comparative animal physiology, will present the relevance of molecular biology to comparative problems, and will strengthen the position of holistic biology.

C. LADD PROSSER

Urbana, Illinois
September 1990

CONTENTS

Chapter 1

Introduction: Definition of Comparative Physiology: Theory of Adaptation

C. Ladd Prosser

The science of physiology is the analysis of function in living organisms. Physiology is a synthesizing science that applies physical and chemical methods to biology. Physiology developed as the theoretical basis for medical practice. Comparative physiology goes beyond medical physiology to contribute to the understanding of basic biology. Comparative physiology requires some background in zoology (classification and structure of animals), biochemistry and molecular biology, cellular physiology, and human physiology.

Comparative physiology (including comparative biochemistry, pharmacology, and biophysics) is defined in several ways according to usage. One definition of comparative physiology is that it studies the functions of unfamiliar, nonlaboratory animals. However, routine measurements on several related species contribute little toward establishing general biological principles. It has been useful to examine the physiology of some groups of animals in detail. Traditional physiology is that of mammals, particularly of humans. Physiology of higher plants gives a basis for agriculture. Other kinds of special animal physiology are fish physiology, insect physiology, and the physiology of parasites. Several-volume treatises on physiology of crustaceans, molluscs, and fishes are available.

A second definition of comparative physiology is that, in addition to familiar physical and biotic parameters of the environment, this discipline uses *kind* of animal as an experimental variable. Comparative physiology considers diversity in modes of solving life problems.

A third definition is that comparative physiology recognizes the diversity and modulation of highly conserved properties of organisms. Comparative physiology provides an intellectual bridge between molecular and whole-animal biology. Comparative physiology emphasizes the integration of the organism at all levels of organization.

Comparative physiology contributes to ecology in describing mechanisms of adaptation to diverse environments. Ecological correlates are presented in several chapters of this book.

Comparative physiology contributes to evolutionary theory in providing correlations of function with structure and chemical composition from which relatedness and origins can be deduced. Evolution over long times considers properties of phyla that have been dated by paleontological methods. Experiments on fossils are not possible but measurements on modern relatives of extinct forms make possible extrapolations to ancient animals. Analyses of adaptations elucidate the relative importance of gradualism and saltation in evolution. Evolution can be deduced from phyletic trees constructed from physiological and biochemical comparisons of closely related animals. For determining phylogenetic relatedness, sequences of amino acids in proteins and of nucleic acids in genes are examined by comparative physiologists and these measurements are correlated with function. The relative importance of neutral changes and adaptive alterations are also considered by comparative physiologists. When closely examined, small changes in amino acid sequences can be seen to have adaptive effects on enzyme kinetics.

A related subject to which comparative physiology contributes is speciation. Classification may, but need not, reflect phylogeny. The concept of species can be looked at in five ways according to context:

1. The most general meaning of species is that of the systematist and is based on morphological and biochemical identity of individuals in a group.
2. Cladistic species are determined by computer-based quantitative morphological and biochemical similarities.
3. The most general definition is the biological species according to which species are populations of similar organisms which can interbreed; reproductive isolation of species may be by several mechanisms, some of which are physiological.
4. The biological definition cannot be used for parthenogenetic animals or for those that show much hybridization or introgression; plants hybridize extensively and show population and subspecies differences that make determination of reproductive species difficult.
5. A functional definition of species is adaptational or physiological; each species must be adapted to its ecological niche and geographic range throughout its life cycle.

Modern systemists avail themselves of all five ways of assessing species. In estimates of decline of endangered species, stress studies on populations in critical environments supplement conclusions of systematists.

Animal Phylogeny

The physiology of an animal group reflects the evolutionary history of that group. A phylogenist uses data from paleontology supplemented by data from taxonomy, comparative morphology and, in increasing amount, from comparative physiology and biochemistry. The presence of homologous structures indicates a common ancestral gene pool. Physiological *homology* refers to a similar function, for example, use of a sodium pump in dissimilar organs or use of rhodopsin in eyes of diverse animals. Physiological *analogy* refers to evolutionary convergence or similar solution of a given life problem by different means, such as the

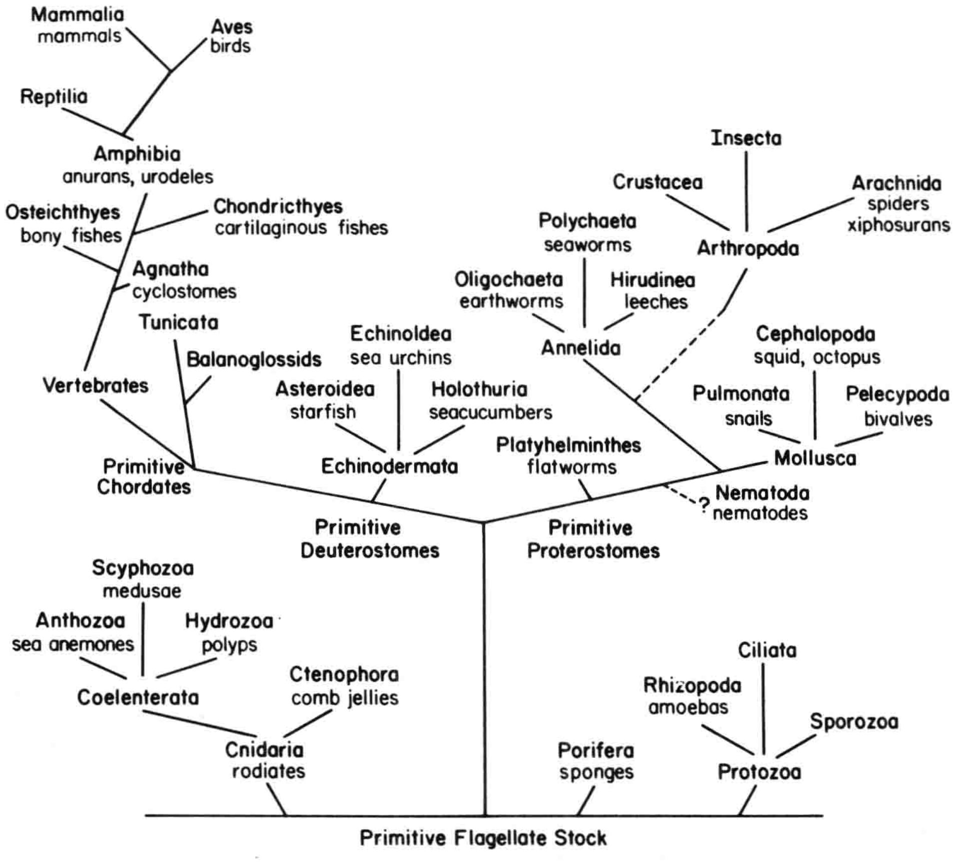

Figure 1. Phylogenetic tree of animals based on adult morphologies, fossil evidence and developmental patterns. Only those phyla and classes that are frequently used in comparative physiology are included. Common names are given in lower case. (Modified from M. J. Greenberg, Fig. 1, in *Comparative Animal Physiology*, 3rd ed.)

use of different metalloproteins for O_2 transport.

Since comparative physiologists use taxonomic types—from subspecies to phyla—as experimental variables, it is important to know something of the relationships among organisms. Physiological analyses are useful in elucidating evolutionary relationships. As an aid to students whose background in zoology may be limited, an abbreviated phyletic chart is given in Figure 1; this is based mainly on morphological, fossil, and developmental characters (5). The common names of phyla and some classes are added to the systematic names. Only the groups of animals that are frequently used in comparative physiology are included.

Classical phylogeny relies mainly on gross anatomy and embryology, and biochemical data provide general substantiation for classical phylogenetic trees. The principal phyla evolved more or less simultaneously during the Cambrian era, hence phyletic trees are polyphyletic. The most primitive of protozoans are plant–animals, the flagellates. Other modern protozoans and sponges are represented as offshoots from the direct phylogenetic line. It is postulated that cnidarians (coelenterates) and ctenophores evolved from primitive flagellate stock. At a primitive level acoelomate animals such as Nematheliminthes and Platyhelminthes emerged, although their points of origin on the phyletic tree are uncertain. Near this level, a branching resulted in two parallel lines. On one side are the proterostomes—annelids, arthropods, and molluscs. On the other side are deuterostomes—echinoderms and chordates. The cephalopods show greatest specialization among molluscs, insects among arthropods, and birds and mammals among chordates. The annelids–arthropods–molluscs show determinate or spiral cleavage, that is, the blastomeres arrange themselves in a stereotyped pattern and there is little cellular equipotentiality, each cell in cleavage—blastula stages having a fixed prospective role. In echinoderms–chordates cleavage is indeterminate. In the proterostomes the mesoderm begins with a particular cell in the blastula that starts two mesodermal bands; in these animals the blastopore gives rise to the mouth and the anus is opened secondarily. In the deuterostomes, cleavage is indeterminate, mesoderm arises as an outpouching from the archenteron, that is, from endoderm, the blastopore becomes the anus and the mouth opens secondarily.

Many essential biochemical and biophysical properties evolved during prebiotic evolution before there were organisms we would recognize as such. Structure of replicating molecules, coding of protein synthesis, mechanisms of osmotic and ionic balance, of electron transport reactions are common to all living animals. Most of the properties of nerve conduction and synaptic transmission found in complex animals occur also in the nerve nets of cnidarians. Mechanisms of osmotic, ionic, and volume regulation evolved before modern phyla, and modulation of these functions occurred at a later date; these general physiological properties are not useful in establishing origins of phyla.

There were undoubtedly many kinds of Precambrian organisms. One group of Precambrian animals, the ediacarans (700–600 My b.p.) were soft-bodied creatures that left impressions in several regions of the earth. Little is known of their physiology although they were undoubtedly anaerobic. During a long Precambrian period the oxygen concentration in the environment gradually increased by action of photosynthetic blue-green algae, modern remnants of which are stromatolites. Once oxygen levels rose to ~1%, animal diversification was extensive. Comparative physiology considers the transition from anaerobic to aerobic metabolism.

Phylogenetic relations have been deduced from amino acid sequences in similar proteins of the same family and from nucleotide sequences in ribosomal RNAs and DNAs. Proteins are aligned for similar amino acids at corresponding sites. The most extensive analyses have been with globins—mostly O_2-carrying molecules; other proteins that have been sequenced are calmodulins, Ca-binding proteins, fibrinopeptides, and cytochromes *c*. Comparisons have been mostly between classes and orders of vertebrates. Evolutionary relations based on protein homologies are well correlated with paleontological evidence (2–4). An evolutionary cladogram of globins including several phyla of invertebrates as well as vertebrates shows close relations for vertebrate α and β hemoglobins (but not myoglobin), between hemoglobins of several molluscs and insects. Insects are distantly related to crustaceans and annelids are at a distance from arthropods (4). Proteins are related to life habits and are adaptive to the environment, hence are specific for subphyletic groups and are not much used for relationships of phyla.

Ribosomes are of very ancient origin and are essential to protein synthesis in all organisms, hence are relatively unchanged in their characteristics. The ribosome comprises two subunits. The smaller of these contains a single (16S) RNA species, of ~1500 nucleotides length; the larger contains several RNA species, the small 5S RNA (~120 nucleotides in length) and the much larger 23S rRNA (~2900 nucleotides in length). Each ribosomal RNA (rRNA) folds back upon itself to produce a large number of loop structures—base paired stalks; the 16S rRNA, for example, contains ~50 loops (9). Two studies of 5S RNAs from a few species of many phyla have given very different cladograms. It was concluded that 5S RNA is not useful for tracing relations between phyla (6). Archaebacteria, eubacteria, and eukaryotes examined for homologies in 16S RNAs show clear differences (9). A cladogram based on 18S RNAs from 22 classes in 10 phyla indicates that rapid early radiation resulted in divergence of four major groups: chordates, echinoderms, arthropods, and eucoelomate proterostomes consisting of annelids, molluscs, brachiopods, and sipunculids. This cladogram, is very different from the ones based on 5S RNA but differs in only a few details from the classical phyletic trees based on embryology (1). Mitochondrial DNAs are useful for elucidating relations of closely related species but they mutate so rapidly as to be useless for phyla.

Physiological Variation

Three determinants of biological variation are genetic, environmental, and developmental. Environmentally induced variation can take place only within the limits set for an animal by its genotype. An adult character can develop only if critical genes are expressed at appropriate times and in appropriate tissues during development. Genetically and environmentally based variation can be distinguished by acclimatization and ultimately by cross-breeding. Acclimation refers to compensatory changes in an organism under maintained deviation of a single environmental factor (usually in the laboratory). Acclimatization refers to compensatory changes in an organism under multiple natural deviations of the environment—seasonal or geographical.

Adaptive Variations

Adaptive variations, both genetically determined and environmentally induced, are measured as functional differences in animals in altered, often stressful, environments. Two general classes of adaptive variations are (1) resistance adaptations, which permit function at or near tolerable limits of environmental stress; and (2) capacity adaptations, which are alterations that permit relatively normal function over a mid-range of environmental conditions (7, 8).

Examples of resistance adaptations are:

1. *Survival at Environmental Limits.* Survival tests include median lethal values for stress such as heat, cold, salinity, and oxygen supply. A prelethal effect may be a state of coma from which recovery is possible. Time-stress measurements of death or coma give quantitative criteria. The criteria of survival are different for intact animals, for tissues, for isolated enzymes (inactivation), and for lipids (phase change). Survival limits are wide for molecules (e.g., enzymes), narrower for tissues, still narrower for intact organisms, and are narrowest for populations. Integration reduces the range of

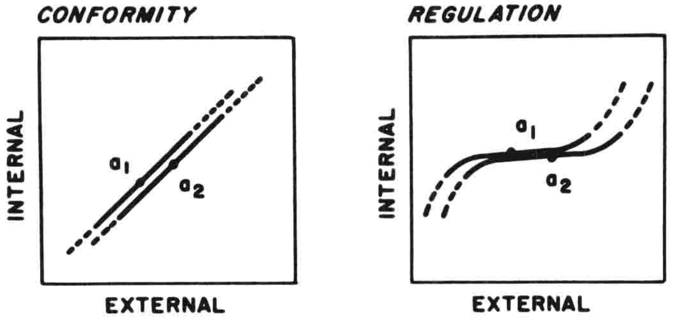

Figure 2. Diagram representing internal state as a function of external state for a given parameter, for example, temperature or salinity. Patterns of conformity and of regulation (homeostasis). Two levels of acclimation are indicated as a_1 and a_2. Solid lines indicate the range of normal tolerance and broken lines indicate the range of tolerance for brief periods. Conformers tolerate a wider range of internal variation than do regulators but regulators tolerate wider external ranges. [From Fig. 2 in Chapter 1 of (7)].

tolerance. Not all parts of an animal are equally subject to functional failure; frequently the nervous system is the most sensitive. Survival limits of organisms or parts of organisms can be modified (acclimated) by prior experience of the environmental factor.

2. *Reproduction.* Environmental limits for reproduction or for embryos are often narrower than for adults. Limits for completion of a full life cycle may differ from limits for short-term survival.

Adaptive variations of internal state as a function of the environment that are classified as capacitative are conformity and regulation.

3. *Adaptive Variations.* Some animals change internally to conform to the environment, for example, poikilothermic or poikilosmotic animals (Fig. 2); these are conformers. Other animals are regulators and maintain relative internal constancy in a changing environment (Fig. 2); these are regulators, for example, homeotherms. Regulation fails at extreme limits of an environmental stress. In general, conformers tolerate wide internal variation but narrow environmental limits, whereas regulators tolerate only narrow internal variation but wide environmental range (Fig. 2). Acclimation can shift the tolerated internal limits for a conformer; in a regulator, acclimation can change the critical limits for activation or failure of homeostatic controls. Both patterns, conformity and regulation, are homeostatic in the sense of permitting survival in a changing environment and most animals show elements of both patterns. One parameter may show regulation (ionic composition) while another shows conformity (osmotic concentration), for example, in marine and brackish water invertebrates.

4. *Recovery.* Recovery from a stressed state varies with the kind of stress and is best shown by regulators. Some osmoregulating crustaceans maintain relative constancy of hemolymph osmotic concentrations in both hyper- and hypo-osmotic media; beyond critical concentrations in the milieu at either high or low levels they lose the ability to regulate themselves and concentrations of hemolymph rise or fall in parallel with the medium (Chapter 2). Oxygen regulators maintain constant levels of oxygen consumption as

P_{O_2} is decreased to critical concentrations below which metabolism declines steeply. Homeothermic animals (birds and mammals) maintain their body temperature by a variety of behavioral, circulatory, metabolic, and insulative means over a range of ambient temperature. Below some critical temperature, regulation fails, O_2 consumption increases, and body temperature is maintained, until at a low ambient temperature metabolism is insufficient and body temperature falls (Fig. 3). At high temperatures, circulatory and insulative means maintain relative constancy of T_b until at a critical temperature metabolism increases as it does in poikilotherms.

5. *Rate Functions.* Rates can be measured for movement, for metabolism, and for enzymatic reactions measured *in vivo* or *in vitro*. For enzymatic rates, two methods are useful: (a) measurement of maximum velocity where substrate is saturating and enzyme activity is rate limiting and (b) measurement of Michaelis constants (K_ms), which give rates in the physiological range of substrate concentration. Several patterns of rate function have been described for temperature conformers; they are applicable for other parameters as well. Figures 4 and 5 diagram patterns of acclimation after transfer from an intermediate temperature (T_2) to a lower temperature (T_1) or to a higher temperature (T_3). Immediately after transfer the rate declines or rises in direct response (pattern 4). After a period of ac-

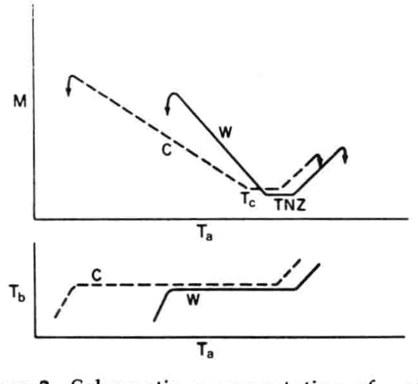

Figure 3. Schematic representation of metabolism M and body temperature T_b in homeothermic animals at different ambient temperatures T_a. TNZ is thermaneutral zone. T_c is critical temperature below which M increases in T_b maintenance. C and W refer to cold and warm acclimated animals. [From Fig. 1-7 in (8)].

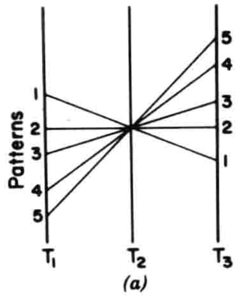

Figure 4a. Patterns of rate functions as altered by temperature acclimation in poikilothermic animals. T_2 is intermediate temperature. T_1 is lower and T_3 is higher temperature. Pattern 4 shows direct response and no compensation, merely Q_{10} effect. Pattern 3 shows partial acclimation, pattern 2 shows perfect compensation, pattern 1 shows overcompensation, pattern 5 shows inverse or undercompensation. [From Fig. 1-4 in (8)].

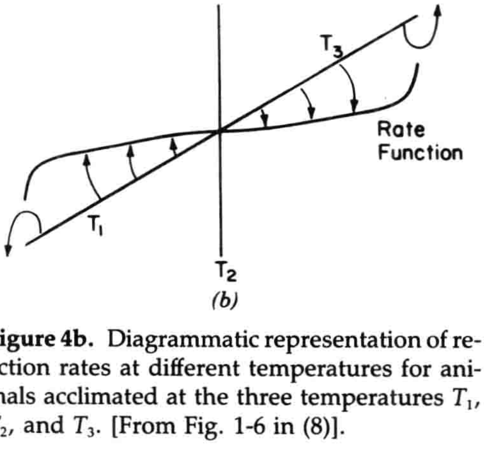

Figure 4b. Diagrammatic representation of reaction rates at different temperatures for animals acclimated at the three temperatures T_1, T_2, and T_3. [From Fig. 1-6 in (8)].

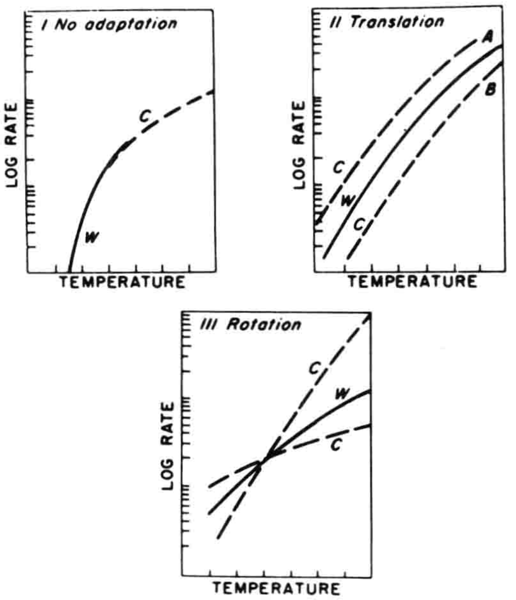

Figure 5. Three patterns of rate function in cold (C) and warm (W) acclimated poikilothermic animals. Rate functions measured at different temperatures. [From Fig. 1-5 in (8)].

climation, the rate at T_1 rises and at T_3 declines toward the original rate (T_2). If compensation is complete at steady state the rate is the same at all three temperatures (pattern 2); overcompensation occurs in some systems (pattern 1) but partial compensation is the more common pattern (pattern 3). No compensation occurs when the rate remains the same as it was immediately after the transfer (pattern 4); some rate functions show undercompensation or inverse acclimation (pattern 5). Another way of treating the data is to plot the entire rate–temperature curve. On acclimation there may be translation of the curve to right or left (constant Q_{10}) or rotation (change in Q_{10}) or a combination of the two responses (Fig. 5). Comparable changes in metabolic rates have been described during acclimation of marine and estuarine animals to various salinites and during acclimation to various levels of O_2.

Changes in the environment bring about not only metabolic acclimation but also behavioral acclimation. These are shown by taxic (direct) responses, selection of "preferred" environments in gradients, and feeding and reproductive changes. Each of these can be altered by acclimation to an environmental change.

Three time courses can be distinguished in response to environmental alteration. First, there are direct reactions to the environmental change. These may be direct metabolic responses (Q_{10}'s) or may be reflex behaviors. Changes in ions, temperature, oxygen, or foodstuffs may lead to immediate alterations in reaction rates. Capacity adaptations are often hereditary; for example, homeotherms are more sensitive in reaction rates than poikilotherms to changes in body temperature. The time for the direct response to a new rate is usually minutes or hours.

The second time period in response may require days or weeks. This is the period of acclimation or compensation and the physiological adjustment is related to the amount of environmental change and the genotype. In seasonal changes, compensatory alterations may develop gradually. In the laboratory, compensatory acclimations take place by a number of biochemical alterations, the net effect of which is homeokinesis or constancy of energy output. Homeokinesis is to be distinguished from homeostasis which is constancy of internal state.

A third time course of biological response occurs over many generations, the time for selection of genetic variants. Evolutionary changes correlated with environment alterations are influenced by (1) behavior—competition, predation, and social interaction, and (2) biochemical changes—alterations in protein struc-