

ENVIRONMENTAL PHYSIOLOGY OF ANIMALS

Environmental Physiology of Animals

SECOND EDITION

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Preface to Second Edition

The first edition of this book found a useful place in many libraries and on the shelves of teachers and students as a text for a wide range of undergraduate courses, and we are glad that our targeted market found it readable, interesting and suitably up-to-date in its approach. Our general aim of integrating animal physiology into a more holistic approach, one that includes both an ecological setting and an appreciation of the range of behavioral responses open to individual animals before specific physiological responses need to come into play, has clearly met a need and found a receptive audience.

However, we met with two general criticisms that, although not aimed at the content or the written style, were enough to put off some of the potential users. Firstly, many readers while appreciating the consistent style of illustration found the book visually rather dull. We have been able to address that in this second edition by adding a colour to the production, making the figures both clearer and we hope more attractive. Secondly, and perhaps more importantly, many lecturers reported that they could not adopt this book as their core text for physiology courses because of the omission of material on excitable tissues and control systems. Leaving these topics out of the original book was a conscious decision designed to retain the strongly environmental flavour of the treatment—after all nerves, muscle and hormones are not inherently very variable between different habitats. Furthermore there are excellent treatments of nerve and muscle available at suitable levels in existing books on neurobiology. However, many students are unable or

unwilling to purchase more than one book in a particular area of their studies, so there is clearly a need to offer a fully comprehensive coverage in one volume. Here then we have added in the two new chapters that were requested: Chapter 9 covers nerves, sense organs, muscles and the integration of all of these components into functional sensory and motor systems, while Chapter 10 covers the hormonal control systems operating across the animal kingdom. We hope that these provide coverage at the level needed for any comparative physiology course. Chapter 9 is unusually long, reflecting the enormous advantages made in the last two decades to bring the realms of neurobiology into the molecular age; it should in itself also prove suitable for many junior courses on excitable tissues.

Other chapters in the book retain the same format but have been updated where appropriate with recent insights, and additional molecular and evolutionary evidence has been included as it emerges. The suggested reading has been enhanced with recent reviews.

This new edition will therefore provide a core text for students taking a wide range of physiological modules in colleges and universities, and it should also serve as a useful reference for many lecturers striving to keep updated on the interactions of animal physiology with their own related areas of ecology, behavior and environmental biology.

Pat Willmer



Preface to First Edition

There are many books dealing with physiological functioning and the comparative adaptations of animals. Why should one more be added to the list?

We hope that there are three key reasons why this book is different.

1 Above all, we seek to be novel by setting the issues in a strongly environmental context; the largest part of this book is devoted to analyzing the problems for each kind of environment in turn. In one chapter you can find out how different kinds of seashore animal cope with the ionic problems of salinity change, the thermal problems of both cold sea water and warm drying aerial exposure, and the respiratory hazards of alternate aerial and underwater breathing. Inevitably we include more varied material, from a wider range of animal types; you will find less of a focus on terrestrial reptiles, birds, and mammals than in most other books (after all, they represent less than 1% of all animals!).

2 We try to put together issues other than just conventional physiology, to look at mechanisms and responses with perspectives from the related and overlapping fields of ecology, behavior, and evolutionary biology. Thus you can find out how the seashore animals also deal with the mechanical problems of tides and waves, how their senses may need to be modified, the difficulties of finding a mate and producing viable offspring, and some of the imposed (anthropogenic) problems that man has introduced to different habitats. The book thus has more environmental biology, more ecology, and a greater evolutionary perspective than many others.

3 Wherever possible we include modern molecular biological insights into adaptive problems, and take the level of analysis to the cell, the membrane, and the enzyme.

In essence we want to look at how animals cope with particular kinds of environment, putting together the biochemical, physiological, behavioral, and ecological adaptations that allow animals to

survive there. We believe that this will be a useful contrast to current texts; most of these instead take each system of the animal body in turn (such as ionic and osmotic issues, energy balance, temperature, circulating fluids, nerves, hormones) and then give examples of how they operate in different kinds of animals or in different kinds of habitat. We believe that our approach will prove useful for a much broader range of environmental biology courses, as well as more traditional environmental physiology courses.

Some readers will have little physiological background initially, and will want to understand physiological processes in detail, so in Section B we also offer an updated review of comparative physiology, looking at mechanisms and functions system by system, but incorporating new information on how adaptation is operating at a molecular level. We leave out most of the “examples” here, and concentrate on principles. This section provides most of the material needed for understanding comparative physiology, though it does not deal with processes largely unaffected by environment (the basic mechanisms of neural, hormonal, and muscle physiology, for example, which are broadly conserved in all animals and where excellent texts for specialist courses already exist).

Other readers may already know a good deal about physiological principles, and can use Section B merely as a reference point and reminder when considering particular environments. For them, Section C provides all the key material on environmental adaptation, relevant to a wide range of environmental biology issues. It covers far more than traditional animal physiology textbooks. Extensive cross-references to principles in Section B give the reader a chance to check their understanding of the core physiology.

Thus we hope this book presents material that will be useful to a wide range of readers, in varying kinds of environmental biology courses and at different levels. Above all we hope it will help provide an integrated understanding of environmental adaptation.



Acknowledgments

In this textbook we give further reading sections at the end of each chapter, mostly to modern review material. We have cited sources from which material in the illustrations has been drawn wherever a figure has been used in unmodified form, but we do not cite every source of information in the text. At this level, copious references break up the flow and markedly lengthen the text, making it harder to read. However, we realize that this carries two important risks: firstly for the reader, who might not be able to follow up on points of interest and find out more; and secondly for the scientists who carried out the work and might feel their contributions are going unrecognized. We hope that both of these risks are reduced by modern information technology, making it easier to access literature searches and track down the primary references. Thus we expect that the work we quote from, whether a classic paper or a very recent new insight, can usually be traced quickly and its authorship established. However, we take this opportunity at the outset to offer an enormous general acknowledgment and a debt of thanks to all those whose studies have contributed to this text.

More specifically, we offer personal and very grateful thanks to those who have read and commented on the manuscript for us. Simon Maddrell (University of Cambridge, UK) and Jim Childress (University of California, Santa Barbara, USA) took on the heroic task of reading the whole book, and gave us tremendously helpful inputs. Others read parts of the text as follows: Jon Harrison (Arizona State University, USA) (Chapters 3–8); David Scholnick (University of Colorado at Boulder, USA) (Chapters 3–8); John Spicer (University of Sheffield, UK) (Chapters 4–8); John McLachlan (University of St Andrews, UK) (Chapter 2); Lynn McLroy (University of St Andrews, UK) (Chapters 4, 5, 6, and 8); Clare Maynard (University of St Andrews, UK) (Chapter 12); Alex Rowe (University of Edinburgh, UK) (Chapter 17); David Paterson (University of St Andrews, UK) (Chapter 12); and Ray Huey (University of Washington, USA) (Chapters 15 and 16).

We also thank those who have provided invaluable assistance in locating sources of both information and illustrations over the course of several years. Here Sandy Edwards has been an invaluable and endlessly patient colleague, and Christina Lamb has also offered enormous help with seeking out references, while Peter Slater, Gordon Cramb, Mike Fedak, Anne Magurran, Su Bryan, Jim Aiton, and Susie Whiten have helped out beyond the call of duty. Finally, colleagues at Blackwell Science, especially Ian Sherman and Katrina McCallum, have had a huge and greatly valued impact on the successful production of this book.

To all these, and to many other colleagues and students over the years who have encouraged us in thinking about and writing this book, we are very grateful.

Acknowledgments for second edition

Many readers of the first edition, including our own students, have offered comments that we have tried to address or incorporate here. PGW is especially grateful to those friends and colleagues who have read all or part of the new chapters or who have loaned their books and academic papers or made suggestions for new material that might be added. Special mention should be made of Peter Slater, Keith Sillar, and Susie Whiten for their help and commentaries, and we also thank those who reviewed Chapters 9 and 10 for us: Lovise Milligan (University of Western Ontario), Guillermo Paz-y-Miñoc (University of Nebraska), Michaela Hau (Princeton University), and Carol Lee (University of Wisconsin).

Once again, we thank Sandy Edwards who acted as a tireless gopher and aide-de-camp on many occasions, and our colleagues at Blackwell Publishing, especially Sarah Shannon, Rosie Hayden, and Jane Andrew who have once again made the production a relatively painless affair!

Abbreviations

ACE	angiotensin-converting enzyme	DLH	descending loop of Henle (in vertebrate kidney)
ACh	acetylcholine	DMSP	dimethylsulfonylpropionate
ACTH	adrenocorticotrophic hormone	2,3-DPG	2,3-diphosphoglycerate
ADH	antidiuretic hormone	DVC	discontinuous ventilation cycle
ADP	adenosine diphosphate	E	electric membrane potential
AFGP	antifreeze glycoprotein	E_x	equilibrium potential due to a particular ion <i>X</i>
AFP	antifreeze protein	ECF	extracellular fluid
AKH	adipokinetic hormone	ECV	extracellular volume
ALH	ascending loop of Henle (of vertebrate kidney)	EDNH	egg development neurosecretory hormone
AMP	adenosine monophosphate	EH	eclosion hormone
ANP	atrial natriuretic peptide	EHWN	extreme high water, neap (of tide)
AP	action potential	EHWS	extreme high water, spring (of tide)
AQP	aquaporin	ELWN	extreme low water, neap (of tide)
ATP	adenosine triphosphate	ELWS	extreme low water, spring (of tide)
ATPase	adenosine triphosphatase	Epo	erythropoietin
AVP	arginine vasopressin	EPP	end-plate potential
AVT	arginine vasotocin	EPSP	excitatory postsynaptic potential
BAT	brown adipose tissue ('brown fat')	ER	endoplasmic reticulum
BMR	basal metabolic rate	ETS	electron transfer system (in mitochondria)
BOD	biological oxygen demand	EWL	evaporative water loss
BP	boiling point	FAD	flavin adenine dinucleotide
CaM	calmodulin	FAP	fixed action pattern
CAM	cell adhesion molecule	F-1,6-BP	fructose 1,6-bisphosphate
CaMK	calmodulin kinase	FP	freezing point
cAMP	cyclic adenosine monophosphate	FPD	freezing point depression
CCK	cholecystokinin	FSH	follicle-stimulating hormone
CD	collecting duct	GABA	γ-amino butyric acid
CEH	critical equilibrium humidity (above which water vapor is absorbed)	GDP	guanosine diphosphate
CEWL	cutaneous evaporative water loss	GH	growth hormone
CFC	chlorofluorocarbon	GHIH	growth hormone-inhibiting hormone
cGMP	cyclic guanosine monophosphate	GHRH	growth hormone-releasing hormone
CNS	central nervous system	GIP	gastric-inhibitory peptide
CO	carbon monoxide	GIT	gastrointestinal tract
CoA	coenzyme A	GnH	gonadotropic hormone
CPG	central pattern generator	GnRH	gonadotropin-releasing hormone
CPK	creatine phosphokinase	GTP	guanosine triphosphate
CREB	cAMP response element binding protein	H	hydrogen
CRH	corticotropin-releasing hormone	Hb	hemoglobin
DAG	diacylglycerol	HBTS	high body temperature setpoint
DCT	distal convoluted tubule (in vertebrate kidney)	Hc	hemocyanin
DH	diuretic hormone	Hif-1	hypoxia-inducible factor 1
		HLW	high-level waste

HO	heme oxygenase	NADH	reduced nicotinamide adenine dinucleotide
HSP	heat shock protein	NIS	non-indigenous species
5-HT	5-hydroxytryptamine	NK	natural killer (cell)
HTH	hypertrehalosemic hormone	NMJ	neuromuscular junction
HVA	homeoviscous adaptation	NO	nitric oxide
HWN	high water, neap (of tide)	NOS	nitric oxide synthase
HWS	high water, spring (of tide)	NST	nonshivering thermogenesis
ICF	intracellular fluid	O	oxygen
Ig	immunoglobulin	OML	oxygen minimum layer
IGF	insulin-like growth factor	OMP	ovary maturing parsin
IL	interleukin	ORC	olfactory receptor cell
ILW	intermediate-level waste	P_b	barometric pressure
IMP	inosine monophosphate	P_c	critical partial pressure
INA	ice-nucleating agent	P_i	inorganic phosphate
INP	ice-nucleating protein	P_{Na}	permeability to sodium
IP₃	inositol triphosphate	P_{O_2}	oxygen partial pressure
IPPC	Intergovernmental Panel on Climate Change	P_{osm}	osmotic permeability of a membrane
IPSP	inhibitory postsynaptic potential	P_w	permeability to water
JH	juvenile hormone	P_X	permeability for a particular ion <i>X</i>
K_m	Michaelis–Menten constant	PAH	<i>para</i> -aminohippuric acid
LAP	L-aminopeptidase	PAL	present atmospheric level
LBTS	low body temperature setpoint	PAR	phosphoarginine (arginine phosphate)
LC	light chain	PCB	polychlorinated biphenyl
LCT	lower critical temperature	PCr	phosphocreatine (creatine phosphate)
LDH	lactate dehydrogenase	PCT	proximal convoluted tubule (in vertebrate kidney)
LGN	lateral geniculate nuclei	PDE	phosphodiesterase
LH	luteinizing hormone	PEP	phosphoenolpyruvate
LHRH	luteinizing hormone-releasing hormone	PFK	phosphofructokinase
LLW	low-level waste	PIP2	phosphatidylinositol biphosphate
LPH	lipotropin	PK	protein kinase
LTD	long-term depression	PKA	protein kinase A
LTP	long-term potentiation	PKC	protein kinase C
LVP	lysine vasopressin	ppb	parts per billion
LWN	low water, neap (of tide)	ppm	parts per million
LWS	low water, spring (of tide)	ppt	parts per thousand
M_b	body mass	PRL	prolactin
MAO	monoamine oxidase	PSD	postsynaptic density
MAP	mitogen-activated protein	PSMO	polysubstrate mono-oxygenase
MDH	malate dehydrogenase	PSP	postsynaptic potential
MDOC	minimum depth of occurrence	PTH	parathyroid hormone
MEPP	miniature end-plate potential	PTTH	prothoracicotropic hormone
MF	methyl farnesoate	Q_{10}	temperature coefficient
MHC	major histocompatibility complex	RBC	red blood cell
MHWN	median high water, neap (of tide)	REWL	respiratory evaporative water loss
MHWS	median high water, spring (of tide)	RH	relative humidity
MIH	molt-inhibiting hormone	RI	refractive index
MLR	mesencephalic locomotor region	RIA	radioimmunoassay
MLWT	median low water (of tide)	RMR	resting metabolic rate
MMR	maximum metabolic rate	RP	resting potential
mPSP	miniature postsynaptic potential	RPD	redox potential discontinuity
MR	metabolic rate	RQ	respiratory quotient
mRNA	messenger RNA	rRNA	ribosomal RNA
MSH	melanocyte-stimulating hormone	RVD	regulatory volume decrease
MWL	median water level (of tide)	SA	sinoatrial
mya	million years ago	SCP	supercooling point
nAChR	nicotinic acetylcholine receptor	SDA	specific dynamic action (heating effect during digestion)
NAD	nicotinamide adenine dinucleotide		

SDE	specific dynamic effect	THP	thermal hysteresis protein
SIN	sensorimotor integration neuron	TMAO	trimethylamine oxide
SMR	standard metabolic rate	TNZ	thermoneutral zone
SR	sarcoplasmic reticulum	T6P	trehalose 6-phosphate
STT	shivering threshold temperature	TRH	thyroid-releasing hormone
T3	triiodothyronine	tRNA	transfer RNA
T4	thyroxine	TSD	temperature-dependent sex determination
T_a	ambient temperature	TSH	thyroid-stimulating hormone
T_{abd}	abdominal temperature	TTX	tetrodotoxin (sodium-channel blocker)
T_b	body temperature	UCP	uncoupling protein
T_s	surface temperature of body	UCT	upper critical temperature
T_{pref}	preferred body temperature	UT	urotensin
T_{th}	thoracic temperature	$\dot{V}_{O_2}$	rate of oxygen consumption
TBT	tributyl tin	VIP	vasoactive intestinal peptide
Tc	cytotoxic T (cell)	VMI	vasomotor index
TEA	tetraethylammonium (potassium channel blocker)	VNO	vomeronasal organ
Th	T-helper (cell)	VP	vapor pressure
		WLR	water loss rate

PART
1

Basic Principles

1

The Nature and Levels of Adaptation

1.1 Introduction: comparative, environmental, and evolutionary physiology

This book is about how animals cope with the problems posed, and exploit the opportunities offered, by their particular environments. Traditionally the mechanisms for coping with the environment have been treated as issues of **comparative physiology**, which is concerned with investigating both general principles of organismal function (the similarities that exist between all organisms) and the exceptions to the general rules. Comparative physiologists may be interested to look for different ways in which animals solve particular challenges of living in different habitats. Do these different solutions also depend on factors such as animal size or design, or the biological materials used? Much of this traditional physiology relies on laboratory study of either classic laboratory animals (mainly mammals, and certainly with vertebrates very dominant and only a sporadic use of other taxa) or of extremely specialized animals pushed to their extreme performance. This can tell us a great deal about mechanisms, since organisms living in extreme environments illustrate the range of evolutionary possibilities amongst living animals, so that species with an extreme development of a particular physiological property are therefore often useful as model systems. But this study of extremes should not make us lose sight of the “norm” of performance or of more “generalist” animals. We also need to be wary of the tendency of laboratory-maintained animals to become rather unrepresentative, as there are famous cases where within a few months or a few generations after “domestication” such animals have dramatically changed their physiological performance.

For these reasons it is very important to study animals in the context of their own habitat and their real needs, so that “comparative physiology” has tended to be replaced by **environmental physiology** or **ecophysiology** or **physiological ecology**, which in a real sense add traditional natural history to the study of comparative physiology. The primary aim of ecological or environmental physiologists is to understand how animals function in and respond to their natural environments, at all stages of their life cycles. Indeed it quickly becomes apparent that many animals, for most of their lifetime, do not need extreme physiological adaptation and rely instead on behavioral strategies to avoid the worst of their difficulties.

However, ecophysiology has in turn become subject to an increase in conceptual rigor, partly as a result of important critiques of the story-telling nature of the “adaptationist program” (the assumption

that everything has an adaptive function). We need to move beyond anecdotal science, where after collecting lots of examples of particular features their functions are to be gleaned merely by their apparent correlations with environmental features. Understanding the processes by which particular ecophysiological features arose, and the values of physiological parameters as outcomes of natural selection, may be termed **evolutionary physiology**. Evolutionary physiology is a discipline still somewhat in its infancy, but learning rapidly from other areas of evolutionary biology and from the analytical techniques of population biology and (especially) molecular biology. It involves a more explicit attempt to integrate both short-term and long-term genetic perspectives into physiological ecology. Within species, understanding the genetic basis of physiological traits, and the magnitude and causes of physiological variation, may reveal how they can be shaped in the relatively short term by natural selection. Evolutionary physiology also examines the evolution of traits over longer time periods, across species or higher taxa. Here the crucial point is that the traits we see represent an interaction between ancestral traits and selection, set in the context of ancestral environments. We can only understand this by following the evolution of these traits through a family tree or phylogeny. A phylogenetic analysis allows the evolutionary physiologist to address two crucial issues: firstly, how does the physiology of an ancestral species affect what is possible in its descendants, and secondly, how rapidly can physiological traits evolve? The recent explosion in our knowledge of the relationships between organisms, much of it based on DNA or RNA sequence analysis, provides a wealth of opportunity in this area. Thus, not only can we use explicitly evolutionary analyses to help us understand patterns of mechanistic physiology, but we can now also track the evolution of molecular components of physiological adaptation as a short cut for many years of complex laboratory analysis of comparative species differences. Evolutionary physiology may develop all the more quickly set in a strong environmental context, taking both past and present environments into account; for unless there has been substantial climatic or geological upheaval, or migration, animals tend to inherit their environment as well as their genes from their immediate ancestors. Furthermore, organisms from more extreme environments are particularly likely to show clear examples of evolutionary adaptation as a result of intense selective pressures.

This book is written in the conviction, increasingly common in all kinds of biological literature, that the trend needs to be taken yet

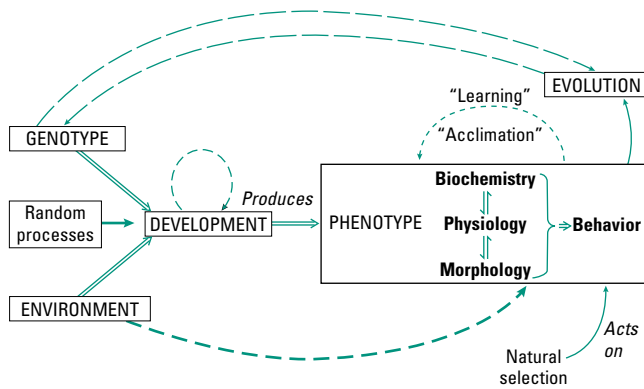


Fig. 1.1 The genotype and environment interact through developmental processes to give a particular phenotype, a suite of biochemical, physiological, and morphological traits. The phenotype also includes behavior, which is limited by all the other phenotypic characters. Selection acts at the whole organism level, and therefore mainly on behavior. Biochemical and physiological traits are normally only subject to selection if they have detectable and stable effects at the level of behavioral performance (e.g. escape speed, reproductive behaviors, food-gathering efficiency, etc.) that in turn affect reproductive fitness.

further; that physiology cannot be isolated from behavioral strategies and from ecological and life-history strategies, while also taking account of evolutionary and molecular studies. Thus, environmental adaptation has to be an interdisciplinary and fully integrated study as biological sciences come of age. A schematic view of the interrelationships of genotype, environment, and phenotype is shown in Fig. 1.1, stressing this wider viewpoint; note especially the intervening effect of developmental processes, and the key role of behavior, both as the outcome of phenotypic characters and as the level at which natural selection often acts most strongly. Genotypic variation (long-term evolutionary change) can only be subject to selection if it affects reproductive success, mediated by changes in performance and behavior, though the more immediate changes may concern biochemical, physiological, or morphological features, which are what we normally see as “adaptations”. All these issues are discussed further in this chapter.

1.2 The meaning of “environment”

The two basic concepts in natural selection are fitness and environment. Fitness is strongly linked to adaptedness and therefore to adaptation, and all these concepts are subject to intensive analysis by ecologists and evolutionary biologists (see section 1.3). However, the concept of the environment is usually largely ignored, perhaps because it is seen as unproblematic. Nevertheless it is worth considering just what we do mean by an animal’s environment.

At an obvious level, the environment means the kind of habitat in which an animal lives—the deep sea, a tropical forest, a hot desert, or whatever. In this sense an environment is equivalent to the concept of a **biome**, with grossly similar kinds of living space having similar physical characteristics all lumped together. Knowing whether an animal lives in water, in air, or amphibiously, or in cold, seasonal, or warm latitudes, certainly tells us a lot about the problems it will encounter and the kinds of design and strategy it is likely to show.

Environments are obviously rather more complex than this though, and each species of animal has a more precisely defined environment within a biome, perhaps in the deep-sea benthos, or predominantly arboreal in a forest, or in the litter layer of a fresh-water pond. By considering the environment at this level, with some elements of biotic interaction coming in as well as mere physical factors, we gain rather more knowledge about the animal’s requirements. Indeed for the parasitic animals considered in Chapter 17, properties of the host organism and of other parasites may be far more important than abiotic factors.

At a third level, each individual animal has its own environment: the totality of all the external factors it experiences, both biotic and physical. This environment is commonly modified by its own behavioral choices and indeed by its very presence. At this level we are really considering microenvironments, or microhabitats, or (on land) microclimates. This is also the level that really matters in terms of environmental and evolutionary physiology. Just because an animal lives in a “type” of environment as perceived and classified by humans, it does not necessarily experience that environment in the way that we see and experience it. Each animal chooses where to spend its time, to forage or to rest, or to seek mates, from a range of possible options. These options change on a very fine spatial scale and a very rapid temporal scale for small animals, but much more coarsely for large animals (for them the environment is sometimes described as “coarse-grained”). In many cases an animal will choose the least stressful microhabitat, whether in and amongst the ameliorating effects of vegetation, or within a burrow or nest, or merely within the boundary layer of relatively still fluid above a substratum. The presence of the animal will modify local conditions, by adding excretory products (including CO_2) or depleting oxygen, or modifying humidity and temperature; an environment containing an animal is no longer the same as the environment before the animal moved in. Thus the environment we want to know about is that of the organism itself and its immediate surroundings, measured on a temporal and spatial scale appropriate to that animal. An animal then becomes part of an interactive system that includes its own internal physicochemical state and the physical and chemical conditions of its immediate surroundings.

At whatever level we consider them, environments can be helpfully categorized in terms of three important interacting parameters: the basic stress intensity, the magnitude and timescale of fluctuations, and the energy or resource availability.

1.2.1 Environmental stress

Environments are enormously variable in relation to the stress that they impose on their inhabitants, and this stress may be both **abiotic** (physical and chemical factors) and **biotic** (direct and indirect effects of other organisms, including competition and habitat modification). Since life on Earth evolved in seas that were thermally and osmotically relatively stable, and all cellular machinery was fundamentally selected from its inception to work best in stable, rather cool marine conditions, it is often useful to see the abiotic stress as being dependent on how much conditions have diverged from those starting points. Thus life in cool sea water is relatively “easy”, life in a seasonal pond is somewhat tricky, and life in hot desert conditions is spectacularly difficult. Other extreme environments

would include polar lands, mountain peaks, hypersaline lakes, hot springs, and deep-sea thermal vents. But biotic stress may sometimes work in the opposite direction, in that “easy” habitats may also have large and diverse populations of other organisms and so impose more competition and predation pressure. Either of these kinds of stress may put an organism at a disadvantage in having to expend more of its own energy to survive, whether in physiological regulation, or avoidance tactics, or competitive or defensive activities.

1.2.2 Magnitude of fluctuations

Environments may be very stable on all timescales relevant to living organisms, the classic case perhaps being deep seas. Or they may vary on an evolutionary and geological timescale of tens or hundreds or thousands of years as land masses move, sea levels rise and fall, materials erode and deposit elsewhere, and rivers change their courses. There may also be changes with a regular annual, lunar, or daily cyclicity. Finally, there are changes on a much shorter timescale of hours or minutes or seconds, as the weather changes. Note again that the magnitude of the change is a relative phenomenon, particularly linked to the size of the perceiver. Short-term changes are especially important in relation to very local microenvironments and therefore to very small animals; the difference between the environment above a leaf and the environment below it may be profound, and both may change within seconds in relation to varying solar radiation (insolation), air movements, and rainfall. Changeable environments put a high selective premium on versatility or tolerance in animals, rather than on precise adaptations to particular conditions. This may be particularly true where man has intervened in the natural ecosystem to put new stresses on animals, whether from habitat destruction, climate modification, or the introduction of many kinds of toxic chemicals.

1.2.3 Energy or resource availability

Energy is rarely freely available to animals (as it may be to plants), but it is certainly more easily obtained in some habitats than in others. Traditionally it has been thought that where energy is severely restricted, as it may be in deserts and in polar regions, the results are simple communities with short food chains, largely made up of animals with low metabolic demands.

By contrast, in rather stable environments with high primary productivity and rapid energy flow (exemplified by tropical rain forests or coral reefs), species may develop more specific habitat preferences, leading to specialization and producing diverse and complex animal communities. The corollary of all this is that stable high-energy communities would favor adaptive radiation, whereas rates of evolutionary change may be rather low in low-energy communities.

Varying resource availability between environments is also important in leading to **resource polymorphism** (or trophic polymorphism), where differences in behavior, life-history strategy, or morphology occur within a single species. Striking polymorphisms may occur where interspecific competition is relaxed, and/or there are unfilled niches that can be rapidly exploited, and we will meet many examples of this in Part 3.

1.2.4 Selection and the environment

Interactions between all three of these components of an environment tend to determine the kinds and diversity of animals that occur, and the type of selection that operates. Traditionally two main types of selection are recognized, representing either end of a continuum: ***r*-selection**, which occurs in unpredictable environments, and ***K*-selection**, which occurs in more predictable environments (Table 1.1). The prefix *r* refers to the rate of population increase, which tends to be maximized in *r*-selected species, while *K* represents the carrying capacity of the environment. Typically, *r*-selected animals are the small, rapidly reproducing, early maturing, and short-lived species, producing large numbers of relatively low-investment progeny, many of which will not survive, often reproducing just once and then dying (semelparity) and with potentially wide swings in population size; while *K*-selected animals are large, slowly reproducing, and long-lived, producing just a few young and investing heavily in each, often reproducing repeatedly (iteroparity), and with relatively stable population sizes. The *r*-selected animals should live in disturbed habitats as early successional species, have large geographic ranges and relatively nonspecialist interactions with other species; they are colonists and opportunists, in environments of high stress and high levels of fluctuation. *K*-selected animals should be more common in climax communities, having complex coevolved relationships with other organisms; they do best with low abiotic environmental stress (though often high biotic stress) and low levels of fluctuation. These designations therefore relate to features both of the environment and of the organisms inhabiting those environments, especially their life-history strategies.

This dichotomy is useful as a way of thinking about different kinds of lifestyle and the kinds of environments and features that might be expected to go together. However, it has many imperfections, and many animals do not fit even into a continuum between the two extremes, having instead some very *r*-selected features and some very *K*-selected features. Some authors prefer to use a three-way model, where *K*-selection is the norm in predictably favorable habitats but is replaced by ***A*-selection** (adversity selection) in more extreme environments where conditions are predictably unfavorable. *A*-selection occurs in habitats that are of high environmental stress but with a low magnitude of fluctuation, and with low energy availability. Animals here have high stress resistance, low fecundity, late maturity, and long lifespans, with very low levels of biotic interaction. *A*-selection might be expected in many kinds of extreme environment: deserts, polar regions, montane habitats, caves, anoxic muds, etc. This may also link to the argument about rates of speciation in different environments. In practice maximum adaptive radiation tends to be exhibited, not in thoroughly *K*-selected environments, but in areas of abiotic stability where energy is moderately available but not unrestricted (e.g. we find tens or hundreds of closely related species in African lakes, in some areas of deep sea, and in some patches of tropical forest). Here organisms do not become too specialist, but they can speciate rather rapidly by switching between a wide range of possible resources. The opposite environmental combination of abiotic instability with high resources (perhaps exemplified by a temperate estuary) may produce an alternation between periods of relatively low diversity when species are coping with fluctuating adverse conditions, and periods

Table 1.1 Types of selection on animals.

	<i>r</i> -selection	<i>K</i> -selection	<i>A</i> -selection
<i>Environment</i>			
Stability	Low	High	High
Abiotic stress	High	Low	High
Energy	Low	High	Low
<i>Individuals</i>			
Body size	Small	Large	Small or large
Lifespan	Short	Long	Long
Maturity	Early	Late	Late
<i>Reproduction</i>			
Pattern	Semelparous	Iteroparous	Either
Generation time	Short	Long	Either
Fecundity	High	Low	Low
Offspring	Many, small	Few, large	Either
Parental care	Absent	Common	Possible
<i>Populations</i>			
Density	Fluctuating	High	Low, or fluctuating
Stability	Fluctuating	Steady	Fluctuating
Range	High	Low	Either
Competition	Low	High	Low
Biotic interactions	Few, simple	Many, complex	Few, simple
<i>Overview</i>			
	Small	Large	Very varied
	Rapid reproductive output	Slow reproductive output	Usually slow
	Colonists	Climax communities	Simple climax
	Generalists	Specialists	Specialists

of abrupt change when abiotic conditions alter too drastically, potentially leading to a phase of rapid evolution and the generation of whole new groups of related species (cladogenesis).

1.3 The meaning of “adaptation”

Adaptation is a central concept in biology and one that attracts enormous controversy. It is often used in several different senses, to describe both a pattern and a process; and more often than not it is used rather loosely.

1 Firstly, adaptation is often used as a term for the **characters** or **traits** observed in animals that are the result of selection; for example, the presence of hemoglobin might be said to be an adaptation to allow a greater oxygen carriage in blood.

2 Alternatively, and most “correctly”, adaptation might be defined as a **process**; the means by which natural selection adjusts the frequency of genes that code for traits affecting fitness (most simply, the number of offspring surviving in succeeding generations). For example, increasing hemoglobin concentrations within a taxon might be seen as an adaptation to potentially low oxygen (hypoxic) environments. Evolutionary adaptation then becomes almost synonymous with natural selection itself—necessary attributes for both include variability, repeatability, heritability, and differential survivorship of offspring. Adaptation in this sense is a process that normally occurs extremely slowly, over hundreds or thousands of generations, and is not usually reversible. However, in extreme environments or (as we shall see in Part 3) where selective pressures from human interference are strong, it can sometimes occur very quickly.

3 “Adaptation” is also used to describe short-term **compensatory changes** in response to environmental disturbance. This kind of

change is the outcome of **phenotypic plasticity**, where pre-existing traits are differentially expressed as appropriate to the local conditions. Here the terms **acclimation** or **acclimatization** are technically more correct (see section 1.5); evolutionary biologists would not use the term adaptation at all in this context.

Great caution must be exercised in using the terms “adaptation” or “adaptive”, and in the simplistic interpretation of individual traits at the molecular, cellular, tissue, or organ levels, in relation to particular environmental factors. A trait should only be considered an adaptation if there is some evidence that it has evolved (has been changed through its evolutionary history) in ways that make it more effective at its task, and thus enhance **fitness**. In other words, a trait should only be deemed to be an adaptation if it is a consequence of selection for the task it performs; an incidental ability to perform the task is not enough, and nor is the mere existence of a good general fit between organism and environment. Evidence that a characteristic is an adaptation is quite hard to come by, and may be of three kinds:

1 Correlation between a character and an environment or use. This is the commonest approach, and where it involves interspecific comparisons of extant species it forms the core of comparative physiology. However, it has inherent dangers, which are discussed in more detail in the next section.

2 Comparisons of individual differences within a species. Geographic patterns in the frequencies of different gene variants (alleles) in natural populations can be mapped over environmental gradients.

3 Observation of the effects of altering a character. An organ can be experimentally altered, or a behavior prevented, and the effects on the efficiency of some particular function in some particular environment observed. In modern physiology we can improve matters by either knocking out or overexpressing a specific gene (rather than a phenotypic character) and observing the effects; indeed, if we know enough about the evolution of a given gene we may be able to

piece together the changing physiology that goes with it. This has been possible with a few very well-studied systems such as the lactate dehydrogenase (LDH) gene alleles that are involved in key anaerobic adaptations and that show clines with latitude and temperature (see Chapter 8). But the danger remains of interfering with other processes and thereby breaking the link between cause and effect.

These approaches generally involve **correlative evidence**, which is never really conclusive. Clear evidence for adaptation is not always possible, and the literature is still dominated by inference; nevertheless this is reasonably well founded by sheer weight of evidence under criterion 1 above. Most of the material in Part 3 of this book presents adaptations supported by this kind of inference, which may be logically imperfect but is nevertheless very probably correct. In fact, unlike many of the characters that evolutionary biologists deal with, many physiological traits have direct and clearly quantifiable effects in terms of the survival of organisms, and many would argue that it is not necessary to show “adaptation” (as enhanced survivorship in the field) to make clear inferences about physiological adaptiveness.

However, it is important to realize at the outset that not all differences in physiology between species are adaptive. Remember that traits do not evolve “for a reason”; they evolve entirely by chance and are selected after they arise if they enhance the success (fitness) of their possessor. They may persist merely because they do no harm or are linked with some other beneficial trait. They may not have been selected because of the advantage they now seem to endow, but perhaps for some other and now quite unapparent reason; these kinds of traits are sometimes called “exaptations” rather than adaptations (e.g. Darwin noted that the sutures between bones in mammalian skulls may now be adaptive for allowing the birth of relatively large-brained offspring in some species, but they were selected for long ago in evolutionary history for quite different reasons). In addition, many traits were fixed because of natural selection in an ancestral species but are now present for reasons that have little to do with the current selective regime on the species being considered; this phenomenon is termed “phylogenetic inertia”, and may be attributable to the fundamental conservatism of development, of physiological mechanisms, and of underlying genes.

Remember also that natural selection does not necessarily provide maximal or even optimal solutions: **optimality** is a relative concept, and a particular design need only be sufficient to do better than the existing alternatives. Therefore it is impossible to say that any one design is “optimal”, or to predict whether a better optimum might exist. The use of optimality in adaptation debates has therefore led to considerable confusion and criticism. It is likely that there will be some sort of match between biological structures and functional requirements, but how good this match should be is not clear. A great many features of animal design, including physiological mechanisms and pathways, have to meet more than one, and sometimes several, conflicting functional demands. They are therefore very likely to represent a working compromise between these competing demands. Adequacy or sufficiency in one function, without unduly disrupting others, may well be the most common evolutionary outcome.

Even where design features appear to serve only one function we should not expect perfect or optimal form or performance. Natural selection filters phenotypic success through genotypic transmission

only in relation to differential survivorship, relative to other possible phenotypes and genotypes. Optimal construction and performance are therefore not the inevitable outcomes of selection, and the match of optimality to actual design may be largely a reflection of the strength of the selective force. Genetic drift may also tend to reduce the rate of improvement in characters, especially in small populations with low immigration. The potential for optimal adaptation may also be limited by developmental constraints, and by genetic constraints where traits are correlated or linked.

This is why it is so helpful to consider the whole organism and its integrated functioning within its habitat, rather than individual characters or particular physiological systems in isolation. The approach adopted in this book, looking at all aspects of coping with a particular type of environment, may be more useful as a background to modern evolutionary physiology than the “systems” approach more commonly presented, that deals with each system in turn and only adds in the other bodily systems and the environment as afterthoughts.

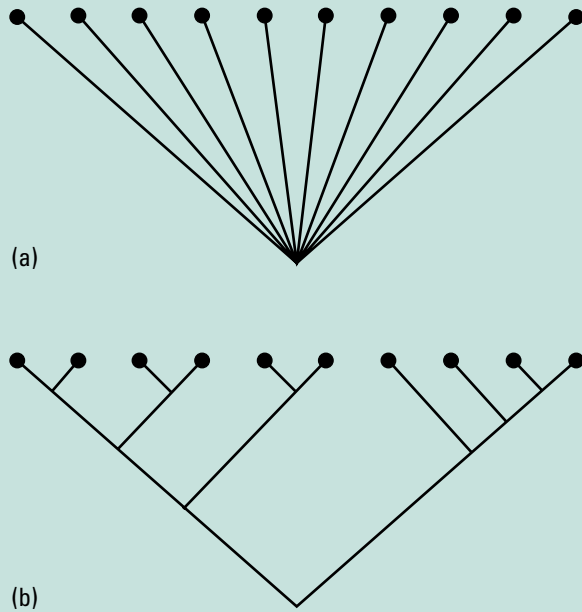
1.4 Comparative methods to detect adaptation

Comparisons between and amongst sets of species are the most common ways of looking for adaptations; indeed, it is fair to say that adaptations are essentially “comparative” phenomena and can only be measured comparatively between or within species. Many studies choose two or more species differing in behavior or ecology and compare them, to determine whether they show phenotypic differences that could be interpreted as adaptations to their different selective regimes. In a very loose sense, this is called the “comparative method”, and it has served biology well in giving “evolutionary” explanations of why things are the way they are—in the biological sciences, experiments repeating actual evolutionary events are usually impossible!

However, there is an inherent problem in looking at patterns across species. As soon as two species have diverged from a common ancestor, differences will appear between them for many traits. Some of these changes will be due to chance shifts in gene frequencies (genetic drift). This is particularly true if one or both species experience low population size (a “genetic bottleneck”), in which drift can be especially significant. Differences in a given trait therefore do not represent proof of selective modification in either of the species. So what do we need if we want to link differences in environment with differences in physiology? Imagine one species from a warm environment and one from a cold environment, differing in their physiologies. The difference may have nothing to do with environment but could just be due to genetic drift. However, if selection has modified one of the species, how can we tell which has acquired a novel physiology, and thus determine the direction of evolutionary change? We can only work this out if we know the physiology of the common ancestor, usually inferred using a technique called **outgroup comparison** (Box 1.1). Then we can say which species has changed, and by how much, giving us a correlation between temperature and physiology.

While one pair of species may show a change in one direction with temperature, another (phylogenetically distinct) pair may show the opposite change; thus we still do not have a general rule. In

Box 1.1 Statistics and biological comparisons



Typically, statistical methods assume that data points are independent, but this would be the case only if we studied 10 “ideal” species that were genuinely unrelated or were absolutely equally related, as shown in the top figure; here, instantaneous speciation resulted in 10 independent lineages leading to 10 living species.

Thus, if we were to test for a correlation between the mean values for these species for two phenotypes (e.g. relative heart mass and maximal oxygen consumption), or perhaps one phenotype and an environmental factor (e.g. blood hemoglobin concentration and altitude), we could claim the nominal $n - 2 = 8$ degrees of freedom for hypothesis testing.

If, instead, the 10 species were actually related as shown in the lower figure, with a hierarchical evolutionary relationship following descent with modification, we would have something fewer than 8 degrees of freedom available for hypothesis testing. The trait of interest might only have arisen or changed once or twice, and then been inherited by several descendant species. These could not be treated as separate examples of adaptive acquisition of that trait. Various analytical methods now exist that explicitly use the phylogenetic topology and branch lengths to allow valid hypothesis testing.

fact a single two-species comparison never gives sufficient evidence for adaptation (statistical tests of correlation always require a minimum of three data points); but unfortunately such comparisons are remarkably common as a way of proceeding in comparative physiology. However, if many distinct evolutionary radiations show the same change in physiology linked to the same difference in environment then there is evidence for a general correlation between the two. The more radiations there are that show the pattern, the stronger the case. Crucially, because each radiation starts with a different common ancestor, each represents an independent test of whether trait and environment are related. Without a phylogenetic perspective, we make the error of assuming that all species represent

statistically independent data points in our analysis, even though we know that the more closely related ones are more likely to share common features and common past environments (see example in Box 1.1).

Taking a phylogenetic perspective also helps us to avoid two common errors made in comparative physiology. First, knowledge of phylogeny may reveal that we have less support for a relationship than we thought (Fig. 1.2). Second, it may show that there are significant associations present, where a naive analysis would miss them (Fig. 1.3).

So, in addition to physiological data, a **phylogenetic comparative analysis** requires an accurate phylogeny to work with. For an increasing diversity of animal groups, reasonably reliable phylogenetic trees have been generated, increasingly based on DNA sequence data. Using outgroup comparison we can then infer the phenotypes of ancestors for each radiation—the branch points or “nodes” on the phylogenetic tree. Once we have worked out the characters at the “nodes”, then the magnitude and direction of changes that have occurred along each branch segment of the phylogenetic tree can be calculated. If we also have independent information on divergence times, available traditionally from the fossil record or more recently by applying the idea of a molecular clock to the sequence analyses, then the rates of evolution of characters can also be studied. This approach also permits statistical testing for correlations in the changes of two or more characters, which may allow us to see how the sequence of changes that occurs during the evolution of a complex character may predispose some other trait to change in a particular direction. If associations between particular characters and particular environmental factors are revealed, then justified and sensible inferences about adaptation are possible.

It must be noted, however, that this is an idealized program. For the majority of animals we do not yet have broadly agreed phylogenetic trees, nor is there a complete consensus on how these can be achieved. An incorrect phylogeny can lend statistical support to bogus relationships or can obscure genuine ones; thus the comparative method can also appear to support physiological correlations that may yet turn out to be wrong. Phylogenies based on morphological data are particularly prone to errors resulting from convergent evolution, and this may be rife in animals that are adapting to similar environmental constraints, where physiological convergence is especially likely and may be especially revealing from a functional viewpoint. Thus comparative evolutionary physiology has some substantial hurdles to overcome; and the core of our knowledge of physiological function must not be underrated just because it does not measure up to “phylogenetic correctness”. Nevertheless, understanding evolutionary ecophysiology at this kind of level is certainly an outcome much to be desired, and the limitations of more traditional and “anecdotal” species comparisons should be borne in mind throughout the reading of this book.

1.5 Physiological response on different scales

1.5.1 Different timescales

We considered the nature of adaptation in section 1.3 above, but we also need here to distinguish it from other kinds of physiological

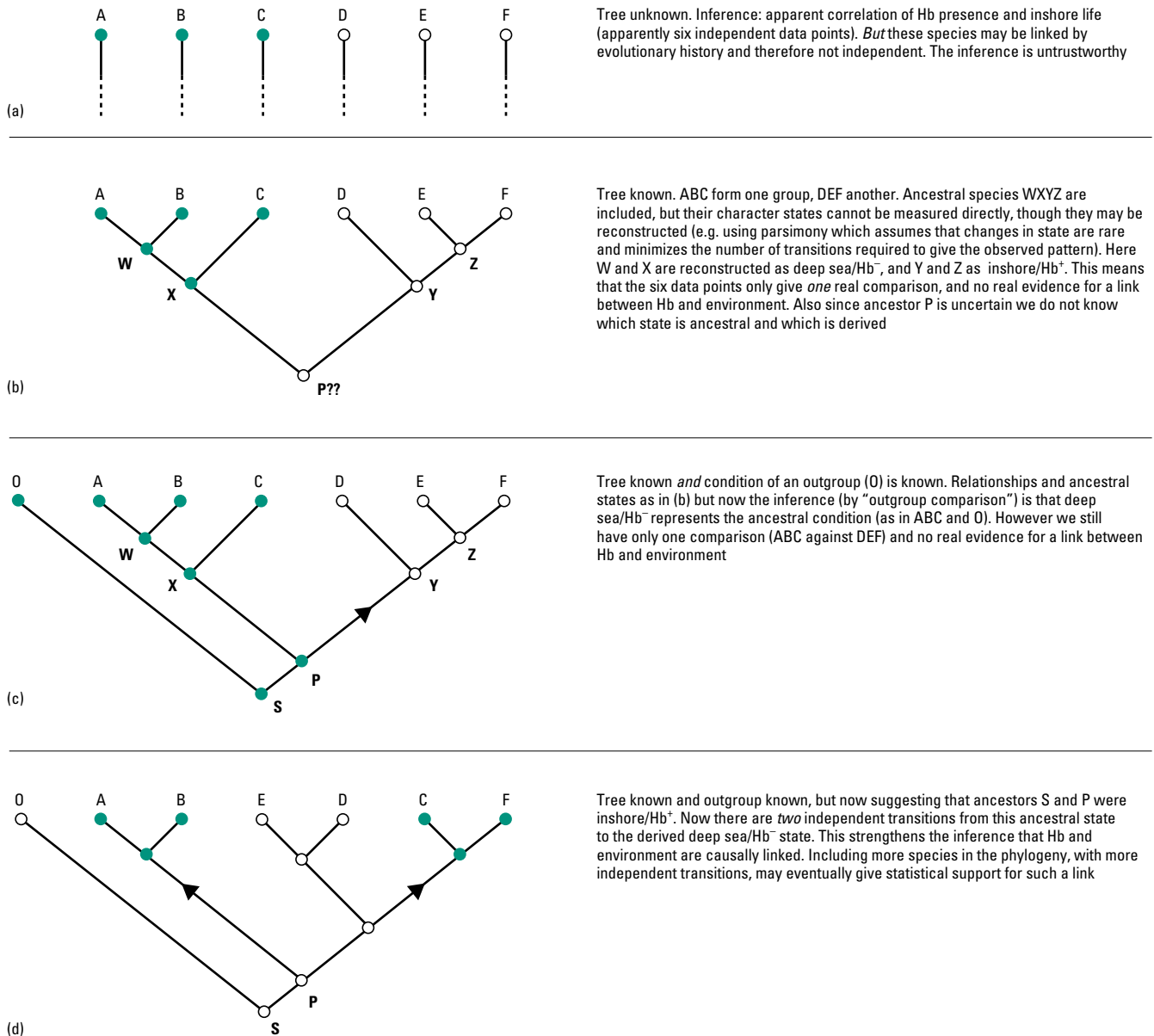


Fig. 1.2 The effects of phylogenetic trees on possible interpretations of a single character distribution (presence or absence of hemoglobin, Hb), showing the utility of outgroup comparisons. Green circles show deep-sea taxa with Hb absent; open circles show inshore taxa with Hb present. Triangles show the sites of changes of state.

response: acclimation, acclimatization, and acute adjustments such as changing heart rate. The process of adaptation is usually a long and slow one occurring over generations, and is rarely reversible. In contrast, **acclimatization** is a more rapid phenomenon whereby a physiological or biochemical change occurs within the life of an individual animal, resulting from exposure to new conditions in the animal's environment. Thus migration up a mountain may lead to acclimatization to low oxygen and low pressure; movement south-

wards out of Arctic areas may force acclimatization to warmer temperatures; and year-long survival in one place may require acclimatization to alternating summer and winter conditions. The term **acclimation** is normally used for similar processes occurring in the laboratory, in response to experimentally imposed changes in conditions. Both acclimatization and acclimation may be reversible. Thus a polar bear is presumed to be adapted to polar temperatures; a human polar explorer may become (at least partly) acclimatized to them; and a laboratory mouse may be forced to acclimate to them. The human and the mouse are both likely to revert gradually to "normal" when conditions change again.

In practice the terms acclimatization and acclimation are often used interchangeably in modern literature, especially since the term "acclimatory" is a useful shorthand for a short-term nongenotypic

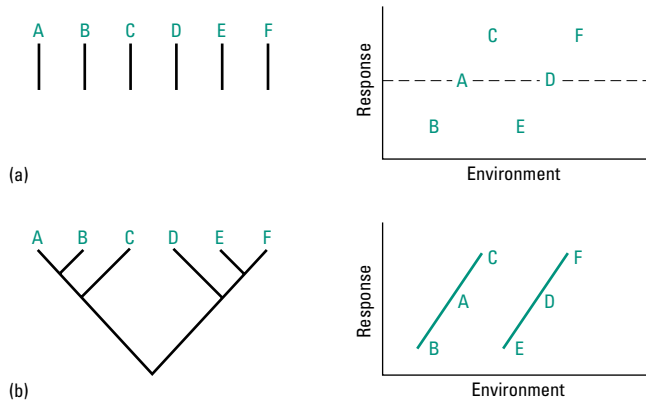


Fig. 1.3 The importance of understanding phylogenetic relationships in making inferences about adaptation and environmental effects on continuous variables. (a) Six species are considered as if they are independent entities; there appears to be no consistent effect of environment. (b) The phylogenetic tree is known showing that ABC form one radiation and DEF another. Now we can see that *within each radiation* there is a trend for the physiological response to increase in relation to position on the environmental axis. Given more radiations showing similar patterns we could reasonably analyze the effect of the environmental parameter in bringing about a specific adaptive response. (From Huey 1987, courtesy of Cambridge University Press.)

response that has no equivalent derived from the word “acclimatization”. Thus we will often speak of acclimatory responses in animals within their natural environments.

Short-term changes

Very short-term changes in physiological state, such as an increase in heart rate or ventilation or urine flow, are usually acute responses following some behavioral effect such as exercise or a bout of feeding. On a slightly longer timescale, it follows from the discussion above that responses to environmental change occurring within hours or days or weeks are normally acclimatization rather than adaptation. But changes occurring regularly and repeatably, on a seasonal, monthly, or daily basis, are also often acclimatizations rather than adaptations. Remember, though, that these changes in phenotype may be underpinned by genotypic change, in the sense of differential expression of particular genes, even if they are not brought about by any irreversible or heritable change in the genotype itself.

Developmental effects

Embryonic, larval, and juvenile phases in a life cycle may occupy very different environments from adults, and may have very different environmental responses. Such changes of phenotype during development and ontogeny operate on a slightly longer timescale and are more permanent than the acclimatory responses dealt with above. They are of course ubiquitous, and are commonly linked to changes in the environment of the embryo and/or the juvenile that affect its form and function. For example, it is possible to raise littermates of desert rodents either without drinking water or with free access to it; the drought-raised adults have increased relative medullary thickness (the ratio of the cortex to the medulla within the kidney, where it is the medulla that generates the urine-

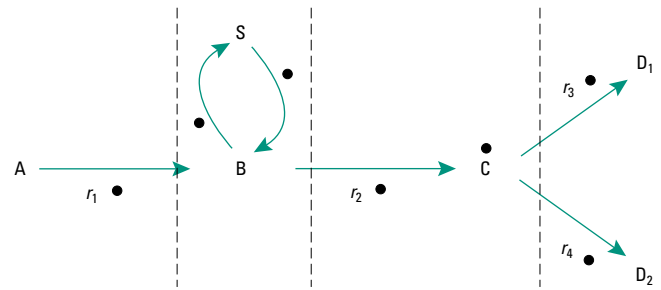


Fig. 1.4 Developmental plasticity and its interaction with the environment. The normal developmental program of a hypothetical animal runs irreversibly through immature stages $A \rightarrow B \rightarrow C$, and then may switch to alternative adult phenotypes D_1 or D_2 . The environment ($\bullet$) acts at several stages. Firstly, it controls the rates of transition between stages (r_1 – r_4). Secondly, it determines whether an optional developmental arrest (S) occurs at stage B. Thirdly, it determines which of the adult phenotypes is produced. (Adapted from Smith-Gill 1983.)

concentrating mechanism) and significantly higher urine concentrations. This kind of phenomenon is usually termed **phenotypic** or **developmental plasticity**, and again operates through differential gene expression.

The environment of an organism interacts with its developmental program to play a major role in determining the expressed phenotype (see Fig. 1.1). A whole range of environmental factors can act upon development, from the first meiotic division through to the later assumption of juvenile and then adult form. These factors may be abiotic, such as temperature, pressure, pH, humidity, salinity, and photoperiod. But there are also biotic factors acting, and these may be external, such as resource availability or population density, or internal, such as hormones. Many of these factors may interact to affect the phenotype produced, usually in a highly complex fashion (Fig. 1.4).

Environmental cues most conspicuously work by activating switches in the patterns of gene expression that make up the developmental program. This may lead either to the initiation of a developmental arrest, or to the production of alternative phenotypes differing in morphological features, behaviours, and life-history characters. Diapause in insects (a resting stage permitting survival through a regularly recurring season of adverse conditions) provides a good example of a triggered developmental arrest; many other animals in more hostile environments also show periods of arrested development. A striking example of a developmental switch to produce alternate phenotypes is temperature-dependent sex determination (TSD) in reptiles, dealt with in some detail in Chapter 15. Species with TSD are generally found in thermally patchy environments, which allows for the production of both sexes. The sex of the embryo is determined by the cumulative effects of the nest temperature in the period from shortly after egg laying through the first half of embryonic development.

Phenotype variation also arises due to the effects of environmental factors on the rates and degrees of expression of the developmental program. In contrast to developmental switches, which as we have seen produce discontinuous phenotypes, environmental effects on the rate of development produce a continuum of phenotypes. This kind of phenotypic plasticity has been called “continuous lability”,

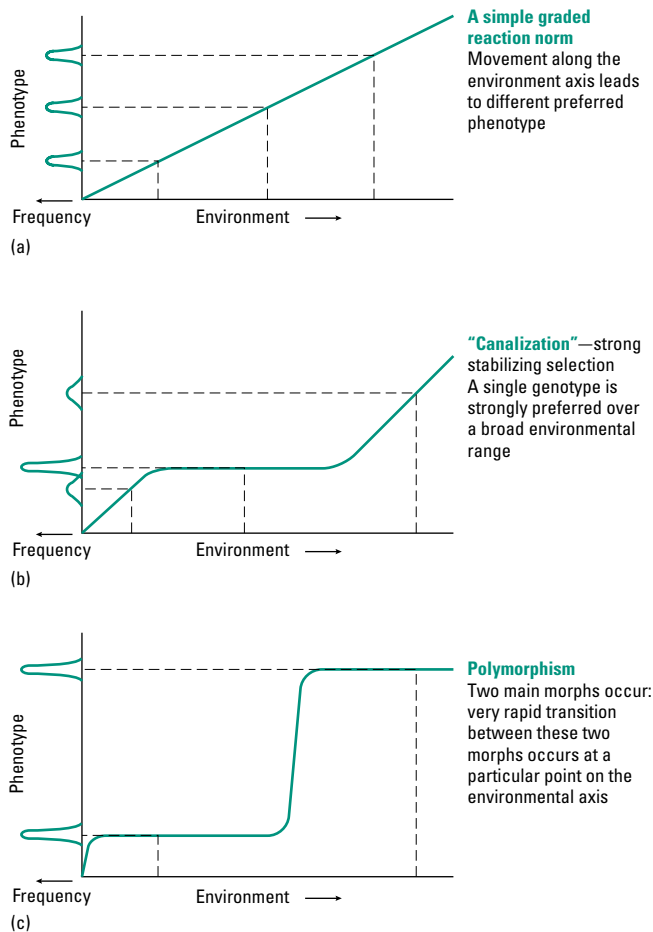


Fig. 1.5 “Reaction norms” as a way of understanding the effects of environment on phenotype.

or “phenotypic modulation”. The effects of environment on development vary between traits and at different embryological stages. For example, temperatures close to the upper and lower thermal tolerance limits of a species in the first quarter of the developmental period produce a high probability of abnormal phenotypes, but later on may have little effect. Similarly, at any given point during embryogenesis the organs and tissues will have reached different points in their developmental programs and may therefore exhibit somewhat different environmental sensitivities. In some cases, differential sensitivities of tissues manifest as a change in the relative timing of growth and maturation of different parts of the body, and this is referred to as “developmental heterochrony”.

The profile of phenotypes produced by a particular genotype in different environments is usually called the “norm of reaction” or **reaction norm** (Fig. 1.5), and this can clearly be of very variable shape. Morphogenetic processes which show little or no developmental plasticity are said to be “canalized”, i.e. they are fixed at a given level by strong stabilizing selection and produce a very narrow range of phenotypes. Characters that show discontinuous plasticity (and thus appear polymorphic) might be explained by a continuous underlying response to the environment at the cellular or genetic level, which has a distinct threshold for phenotypic expression; in

this case, the reaction norm would have steeply S-shaped regions (Fig. 1.5c).

There is some indication that the phenotypic variation induced by variable environments can be subject to strong selection, i.e. that there may be selection for plasticity itself as an adaptation. Perhaps the most compelling evidence for this comes from studies of temperature effects in amphibian life cycles. Field and laboratory experiments have shown that temperature can account for most of the observed variation in growth and differentiation in populations of the frog *Rana clamitans* along an altitudinal gradient. Growth in montane frog populations has a reduced temperature sensitivity relative to lowland populations, which serves to offset the effect of low temperature. Lowland frogs taken to high altitude have their growth retarded by low temperature to such an extent that the tadpole stage is extended by a whole season relative to the resident montane tadpoles. Such transplant experiments indicate that the phenotypic modulation of this particular trait is under genetic control. Another striking example of plasticity as adaptive in itself comes from Galápagos iguanas, where body size is linked to algal food supply, which in turn varies with environmental factors, notably El Niño (ENSO) events. During an ENSO cycle, large males die quickly, but many individuals respond with a reduction in size (shrinking by up to 20% of body length), thus significantly improving their chances of survival.

Longer term genotypic/evolutionary effects

This is the most important timescale of adaptive effects, and perhaps the only timescale where we should strictly use the term adaptation. Natural selection acts on phenotypes, regardless of their genetic basis, so there can be selection for the results of phenotypic plasticity, as well as for the results of genes producing discrete phenotypes. But the evolutionary response to selection is always at the level of the genotype, with genetic change occurring from one generation to the next. Therefore intraspecific genetic variability and hence heritable variation in fitness are essential prerequisites for long-term evolutionary change. We take a more detailed look at the mechanisms of adaptation at this level in Chapter 2.

1.5.2 Different functional levels

Avoidance, conformity, and regulation

When an animal is confronted with changes in its environment, it normally shows one of three categories of response: avoidance, conformity, or regulation. Traditionally physiology has largely concerned itself with the last of these, dissecting the mechanisms and the underlying biochemistry of the regulation of cells, tissues, and the whole body. Thus **homeostasis** (the maintenance of a constant internal environment) always takes an extremely prominent place in physiology textbooks, together with the regulatory systems needed to achieve it. But homeostasis can often be achieved more cheaply by avoidance and behavioral tricks; and it may not need to be achieved at all, with many animals surviving and flourishing with a conforming lifestyle, involving much less energy and resource expenditure. The distinction of these different kinds of adaptive and acclimatory responses constitutes a key message early on in this

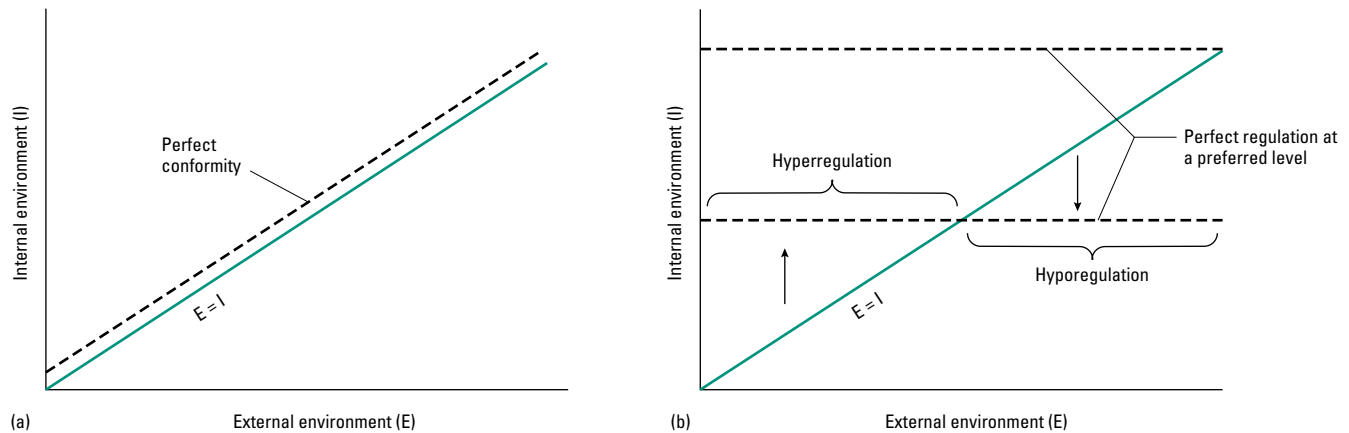


Fig. 1.6 The relation between the internal environment of an animal and the external conditions, showing the basic principles of (a) conforming ($E = I$) and (b) regulating ($I = \text{constant}$).

book. In the context of environmental adaptation it is appropriate to treat the other levels of response as being at least as important, and homeostasis merely as one of several options.

The strategies accompanying these three responses may be summarized as follows:

1 Avoiders have some mechanism for getting away from an environmental problem either in space (e.g. seeking unstressed microhabitats in crevices or burrows, or larger scale migration) or in time (using torpor or diapause, or producing a resistant egg, pupa, or cyst to survive difficult times).

2 Conformers undergo changes of internal state similar to the changes of state imposed externally. (They are therefore sometimes termed “tolerators”, although this is a little confusing since regulating animals are also “tolerating” the external conditions in the sense

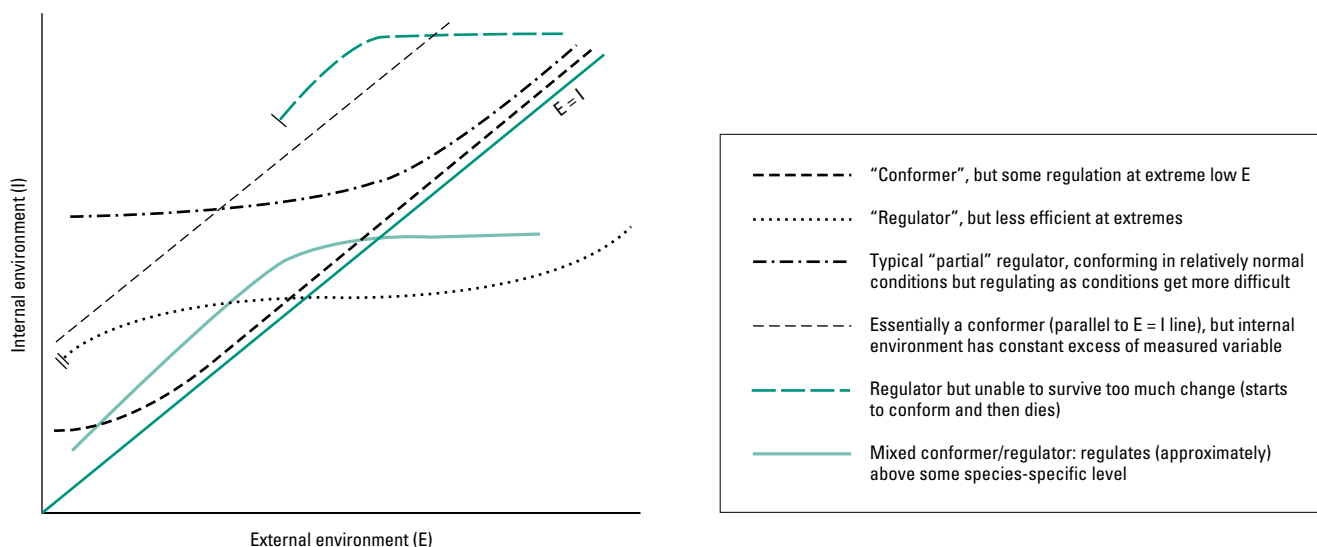
that they are surviving in them.) Conformers do not attempt to maintain a homeostatic condition for the whole body.

3 Regulators maintain some or all of the components of their internal environment close to the original or “normal” level, irrespective of external conditions.

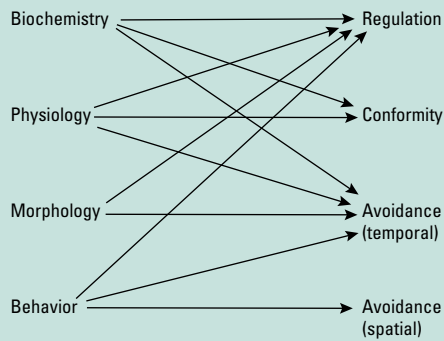
Figure 1.6 compares the general patterns of conformity and regulation. This kind of analysis may apply to a whole range of environmental and internal state variables, including temperature, osmotic concentration, oxygen levels, and pH. Thus we can identify animals that are ionoconformers, osmoconformers, thermoconformers, or oxyconformers, and plot similar kinds of diagrams to those in Fig. 1.6a, and other animals that are osmoregulators, etc., as in Fig. 1.6b. There will be many such examples later in this book, with hyperregulation being rather common and hyporegulation rather rare for most of the key variables.

However, it should be stressed that these categories are not absolute and do merge into each other; commonly we find that there are limits to both regulating and conforming (Fig. 1.7) and that there are no such things as perfect regulators or perfect conformers. For example, osmoconforming animals tend to show some regulation at extremely low salinities, so that their blood is not so dilute that the cells are irreversibly damaged by excessive swelling;

Fig. 1.7 Conformity and regulation in the real world: a variety of options for partial conforming and partial regulating.



Box 1.2 Levels at which adaptive responses can occur



while osmoregulators sometimes lose an ability to regulate at lower salinities and become conformers. Oxyregulators tend to have a critical (species specific) point beyond which they revert to conforming. Thermoregulators may lose an ability to control their body temperature at both high and low ambient temperatures. Particular species may regulate for some parameters and conform for others.

Behavior, physiology, biochemistry, and morphology

There are four major different but interacting functional levels at which avoidance, conformity, or regulation can be effected (Box 1.2), corresponding to the four subdivisions of phenotypic traits in Fig. 1.1. These levels are often seen as being hierarchical, though from a modern perspective, in which all changes are viewed as being fundamentally mediated by genes and biochemistry, this hierarchy is somewhat artificial.

Avoidance in space is primarily an attribute brought about by behavior. For a small animal it might involve a search for an appropriate habitat, using phototactic or chemotactic responses. The “microhabitat” effect is central here, animals making choices in favor of less stressful local conditions within an apparently harsh macroenvironment. For a larger migratory species the behavioral component might need to be supplemented with physiological adjustments, for example accumulation of food reserves. Avoidance in time may require more complex responses at all levels: an animal entering torpor may accumulate food, construct or find a refuge (thus also avoiding in space), then huddle in a ball to reduce its exposed surface area; it may reduce its core temperature and lower its metabolic rate; it may acquire a thicker insulating layer; and it may mobilize or generate new forms of enzymes and new components in its membranes.

Conforming is largely concerned with changes at the physiological and biochemical levels. If the internal conditions are allowed to vary markedly, whether in terms of temperature or salinity or oxygen supply, then tissues and cells will need to have biochemical systems in place that can continue to function in the new conditions, especially in terms of appropriate enzymes and stabilized membranes. Just enough must be done to keep the animal functional (though usually at a very low level) in extreme conditions,

avoiding potentially irreversible damaging effects of freezing or hypoxia or osmotic water loss (and also the damaging effects of coming out of these states, since, for example, reoxygenation has hazards of its own). In general the physiological and biochemical changes will be small and cheap to institute, so that conformity (while having the cost of reduced activity, growth, or reproduction) may have the benefit of economy.

Regulating, by contrast, may require substantial and expensive changes at all these hierarchical levels. Behavior, as we shall see repeatedly throughout Part 3 of this book, may remain as the first line of defense; even the best mammalian endotherms continue to use a whole range of behaviors (basking, burrowing, wallowing, huddling, erecting or concealing appendages, etc.) to regulate their temperature. However, behavior will be augmented by substantial physiological and biochemical adjustments; in the case of thermoregulation these may include changes of blood flow or respiratory rate, an increase in shivering or nonshivering thermogenesis, or the production of heat-shock proteins or antifreeze molecules.

It is impossible to give unconditional generalizations about patterns of avoidance, tolerance, and regulation across the animal kingdom. But to a first approximation it would be fair to say that different strategies do tend to be found in different phyla, with different body designs, and in different habitats, as follows:

1 Smaller and soft-bodied animals are more likely to be avoiders and conformers. They can use microhabitats more effectively, with concealment in protected crevices or burrows, or on and in other organisms. Because they have a high surface area to volume ratio, they will experience relatively rapid fluxes (whether the flux is of water, ions, thermal energy, or respiratory gas) across their surfaces, and working to restore a status quo against these fluxes would be very expensive. They also have little inbuilt protection against swelling and shrinking, and lack the complex outer layers that can be modified to give some insulation or impermeability. In predictably variable habitats, such as estuaries, cyclic avoidance is common (burrowing in mud, hiding in a crevice) and conforming is also often a good solution, with the cyclic environmental changes somewhat smoothed out. But in terrestrial habitats where there is both continuous high environmental stress and high fluctuation, conforming may not be an option and exceptional strategies for avoidance (torpor, estivation, encystment, cryptobiosis, etc.) are more common.

2 Animals with hard outer layers (exoskeletons), of small and medium size, may have better options for some regulation and a greater independence of their environments. Arthropods of all kinds are more likely to show partial regulation of osmotic concentrations, their exoskeletons giving them an inevitable “built-in” resistance to shrinkage or swelling. The outer surfaces can have very much reduced permeability, and may be partly thermally insulated by the addition of fine cuticular hairs, so that all fluxes are slowed and a degree of regulation becomes economically feasible. But behavioral avoidance, aided by the efficient limbs (and sometimes wings) that can be built from an exoskeleton, remains a major part of the overall strategy for coping with environmental change, especially in the more rapidly changing terrestrial habitats.

3 Large animals are much more likely to be regulators in all environments, with the important exception of the relatively equable and unchanging open oceans (where only vertebrates have a serious

problem and need to regulate, due to their history of secondary invasion as discussed in Chapter 11). Larger animals operate in a larger scale (coarse-grained) environment, where rapid changes (due to local water or air movements, or localized patches of sunshine) are relatively unimportant. They have lower surface area to volume ratios so that rates of change of state internally are much slower, giving them an “inertia” effect that smoothes out the fluctuations and gives time for regulatory mechanisms to operate. They may have better opportunities for energy storage (and indeed storage of other resources such as water and even thermal energy). They may also have “room” for more complex internal regulatory centers, both neural and hormonal. In terrestrial habitats where environmental changes are inherently faster, all of these factors may work together to make regulation the only real option for a large animal. Again, though, remember that regulation does not just mean physiological and biochemical effects; behavior often still forms the first line of regulatory response.

There are very different costs and benefits of each strategy in terms of energy usage and lifestyle. Avoidance by shutting down in time is cheap but effectively causes the animal to opt out of the race for a while and achieve no growth or reproductive output. Avoidance in space by migration may be transiently very expensive but allows the animal to keep on increasing the species biomass in another environment. Avoidance of poor physical environments by either means may give additional benefits, for example by also avoiding predation or competition. Conformity at the extremes of temperature, salinity, or hypoxia that are experienced may allow only a minimal “ticking over” lifestyle, but over a broad range of less extreme variation it is a cheap way of insuring a reasonably productive lifestyle most of the time. Regulation is usually rather expensive; osmotic regulation underpinned by ionic pumping takes a moderate proportion of the total energy budget of estuarine and freshwater animals, while thermal regulation in terrestrial endotherms may take as much as 90% of the total budget. The pay-off comes primarily in the level of performance and greatly extended activity periods during times and at places of environmental adversity; food can be gathered more or less continuously, and all the avoiders and conformers that are relatively inactive become potential prey. With all this extra food, regulators can grow and reproduce faster and/or more reliably and be such successful competitors that despite high costs they may become dominant in many ecosystems.

1.5.3 Different spatial levels

Adaptive responses may occur fundamentally at a molecular level, but they “appear” at various different spatial levels in the whole animal. Some responses are essentially subcellular, and others affect the morphology or activity of whole cells. Yet others manifest as effects on entire tissues or organs, for example changes in muscle size, heart volume, or arrangements of vascularization.

However, there is another sense in which different spatial scales of response are important. Animals are made up of several distinct compartments (Fig. 1.8), each of which may show different kinds of adaptive/acclimatory response. The individual cells contain their own fluid environment (**intracellular fluid**, ICF), and they in turn are directly bathed in tissue fluid or **extracellular fluid** (ECF). In many animals the ECF is distinct from a circulating fluid termed

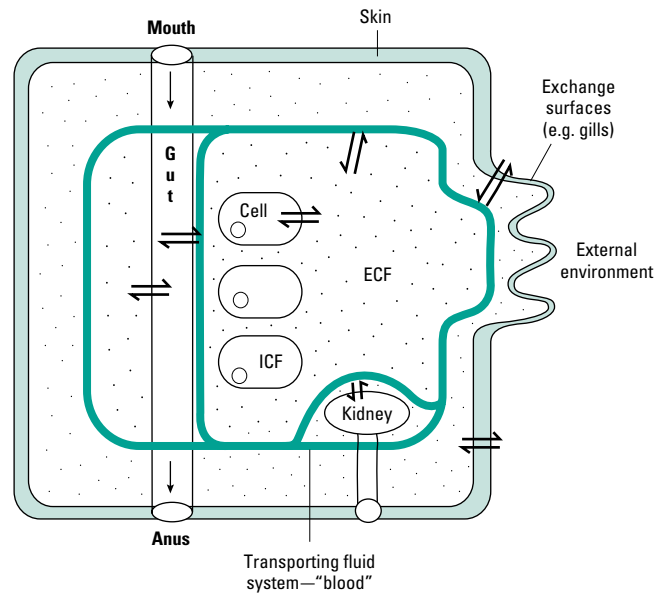


Fig. 1.8 A model of the major body compartments in an animal and exchange routes between them. ECF, extracellular fluid; ICF, intracellular fluid.

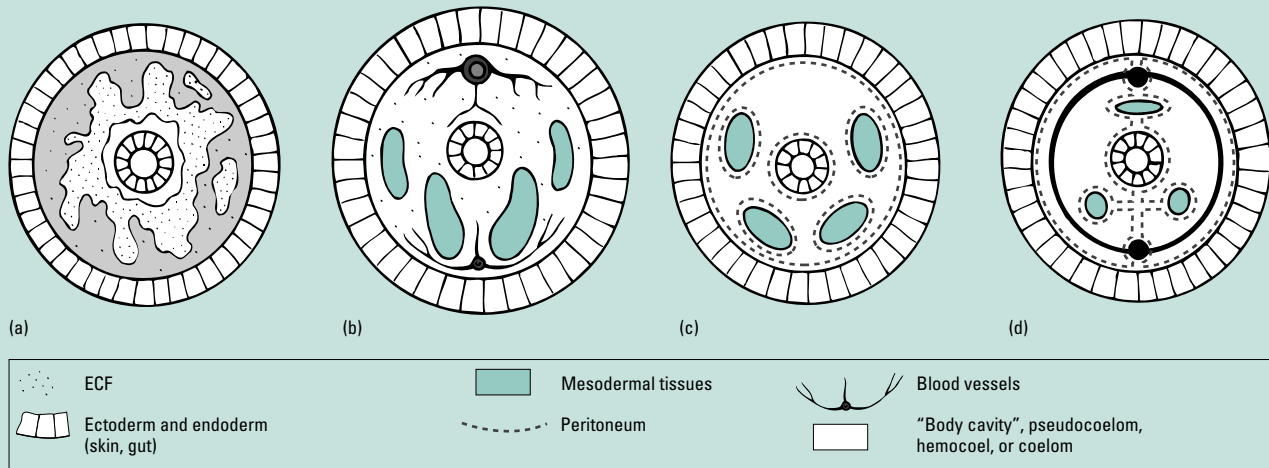
blood or **hemolymph**, and this may be chemically different from the ECF. (In fact, the relations between these fluids and animal design and body cavities are quite complex and there are other kinds of possible arrangement; see Box 1.3. However, this simple version of a three-compartment system is adequate for the kinds of animals we are normally concerned with.)

In terms of the whole animal, adaptations may therefore occur at several sites:

- 1 At the outside surfaces to maintain differences between the outside world and the circulating blood. Here the adaptive features tend to relate to the “skin”, whether this is a relatively unspecialized epidermal cell layer or a complex multilayered structure with keratinous, chitinous, or lipid-containing elements. Sometimes the adaptations relating to exchange processes will be concentrated in or even confined to particular parts of the skin, such as the gill surfaces, with other areas of skin relatively inert and impermeable.
- 2 Between the circulating fluid and the ECF. This mainly occurs in vertebrates, where some constituents of blood pass out from capillaries into the ECF and others may be returned to the blood system via the lymph vessels.
- 3 Between the ECF and the cells. Here the adaptive surface is the cell membrane itself, controlling exchanges between the ECF and ICF. Total concentrations inside cells must be similar to those outside or the cell will shrink or swell osmotically; cell membranes cannot withstand substantial pressure differences. However, the exact makeup of the cell fluid is very different from that of the ECF, as we shall see in Chapter 4.
- 4 Within cells. Cells themselves are, of course, strongly compartmentalized and internal membranes may be responsible for regulating exchanges between the cytoplasm and the nucleus, mitochondria, or endoplasmic reticulum.

Adaptation to the environment may require modification at all these spatial levels. For many invertebrate marine animals the ECF

Box 1.3 Patterns of body fluids and body cavities



(a) The extracellular fluid (ECF) bathes all cells directly, sometimes opening out into large cavities or sinuses in some parts of the body. These are technically "acoelomate" or "pseudocoelomate" animals, lacking the secondary body cavity of "higher" animals.

Common—found in platyhelminths, nematodes, other small worms.

(b) The ECF between cells and within tissues may be continuous with a larger open space that forms a body cavity (hemocoel). The fluid in this cavity may be constrained into vessels in some parts of the body, forming a heart and some major arteries, but always opens again into the main cavity; the fluid is often termed hemolymph, and it is normally the same in composition as the ECF. (A coelomic cavity may also be present but is usually small and unimportant.)

Common—found in crustaceans, insects, arachnids, most molluscs.

(c) The ECF is quite distinctly separated from the body cavity fluid (by a complex tissue layer called the peritoneum) and may differ from it chemically. Here the body cavity is usually termed a coelom and the fluid within it is coelomic fluid; the animals are coelomate.

Uncommon—found in sipunculans and other small worm phyla, echinoderms (but in these some coelomic fluid is also moved around in vessels).

(d) The arrangement is coelomate as in (c) but the coelomic fluid and ECF are supplemented with another fluid, contained entirely within vessels, and termed blood. Some leakage from the blood into the ECF occurs and this may become lymph and be recycled back into the blood system.

Common—found in annelids, cephalopod molluscs, all vertebrates.

and blood are effectively identical with sea water and adaptation concerns only levels 3 and 4. But for nonmarine animals there is always extensive regulation both at level 1, i.e. the skin of the whole animal, and at the cellular levels.

1.6 Conclusions

Environmental adaptation is a complicated business, integrating all aspects of animal biology. It requires an understanding of animal design and animal physiology above all, but this must be put in context with a detailed understanding of the environment (measured on a suitable temporal and spatial scale), and with an appreciation of ecological and evolutionary mechanisms. There is a need to move away from purely descriptive accounts and oversimplified comparisons, and to set the encyclopedic knowledge already accumulated about what animals can do into a realistic framework of why and how they came to be as they are. Equally there is a need to look beyond the confines of traditional isolated physiological "systems" (circulation, excretion, respiration, etc.) and to see the whole picture of what is needed in order to live in a particular environment:

the physiological needs of course, but also the mechanical, sensory, reproductive, and life-history adaptations that together make up a successful fully functional animal.

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