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PREFACE

The Eighteenth Symposium of the Society for Experimental Biology was held in September 1963, at the Zoological Laboratory, Cambridge. We are greatly indebted to Professor C. F. A. Pantin for the hospitality provided by his Department and for the willing help of its assistant staff. King's College was most generous in providing accommodation for members of the Symposium.

The topics discussed were concerned only with the homeostatic mechanisms of animals. Even so the field covered was very wide; this was inevitable with the subject, as is emphasized by the following definition to which all contributors agreed before the meeting:

Homeostasis in its widest context includes the co-ordinated physiological processes which maintain most of the steady states in organisms. Similar general principles may apply to the establishment, regulation and control of steady states for other levels of organization. It must be emphasized that homeostasis does not necessarily imply a lack of change, because the 'steady states' to which the regulatory mechanisms are directed may shift with time. But throughout the change they remain under more or less close control.

Such a concept can therefore be applied to organizations at cellular, organ system, individual and social levels. It may be considered in relation to time intervals ranging from milliseconds to millions of years. Its essential feature is the interplay of factors which tend to maintain a given state at a given time.

Following a consideration of the environment, and some of the stresses to which animals are subjected, and the way their physiological mechanisms maintain homeostasis, the Symposium went on to consider the changes in homeostasis which occur with time. The second part of the Symposium was devoted to a consideration of feedback mechanisms which are important in all aspects of homeostasis. This part of the Symposium emphasized not only the considerable advantages to be gained by applying methods of analysis similar to those used by engineers, but it also put these studies into perspective in relation to the problems which arise in their use with living systems.

Several innovations were introduced by the Symposium Committee with the agreement of the S.E.B. Council:

(*a*) Before the meeting contributors submitted abstracts which were made available to all those attending the meeting. These abstracts were valuable in furthering the discussion of papers both before and after their presentation. They have also provided a record of the meeting prior to the publication of this volume.

(*b*) Several speakers kindly agreed to open the discussion of particular papers; they were subsequently invited to summarize their contributions and several are contained within this volume. Such formal discussion was not found to hinder the spontaneous discussion which has formed such a characteristic feature of S.E.B. Symposia for so long.

(*c*) There has also been a slight change of format in this volume, in that each paper begins on a right-hand page. This has been introduced in order to facilitate the production of reprints. Each author has been given a larger but restricted number of reprints which is the same for all papers.

Many people helped in the organization of this Symposium, by suggesting speakers and in other ways. I should like to thank Professor J. Z. Young for his encouragement in the early stages of its organization and Professors C. H. Waddington and P. F. Scholander for suggesting several speakers. Dr J. Edelman was Symposium Secretary at the time of the meeting and gave valuable support. I wish also to thank Mr A. E. Dorey who acted as Local Secretary, and Dr P. J. Mill for his assistance with editing this volume.

Finally, I should like to thank the Secretaries, sub-editors and printers of the Cambridge University Press for their considerable help, especially as it was given during a period of re-organization.

G. M. HUGHES

Editor of the eighteenth Symposium of the Society for Experimental Biology

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HOMEOSTASIS AND THE ENVIRONMENT

By C. F. A. PANTIN
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We are reminded in our Preface that homeostasis—or strictly the machinery by which homeostasis is achieved—'includes the co-ordinated physiological processes which maintain most of the steady states in organisms. Similar general principles may apply to the establishment, regulation and control of steady states for other levels of organisation.' We shall hear much of the homeostatic machinery of the individual but little of that of communities and ecological systems. Organisms in nature occur not by themselves, but as elements in a particular kind of material configuration. These configurations include material objects which endure, such as hills and other solid structures. But they also contain reversible dynamic equilibria (such as those of the solutes in sea water), together with open steady states which maintain themselves by the constant flow through them of matter and energy. These steady states include non-living systems such as rivers, and also living organisms themselves.

The class of configuration with which a particular species is associated has certain geographical and climatic conditions which are necessary for maintenance of the individual organisms and which in turn are influenced by those organisms. Enforced seasonal changes are met by these through appropriate behaviour patterns and life histories, so that the ecological system can survive. Animal migrations involve patterns of this sort. Longer term geological climatic changes, as in the equatorial drift of communities during glacial periods, again are met by migration, ensuring thereby the maintenance of the class of ecological system. Such behaviour patterns and so on can in fact be considered as homeostatic devices evolved in the ecological system as a whole for its preservation.

All this has indeed an important consequence for conservation. We cannot in fact conserve nature. The consequence of everything we do, from the experiments of the nuclear physicists to the preservation of species by use of insecticides, is part of nature. We can, however, observe the natural world at a particular stage and say that certain ecological configurations and certain species are worth preservation for aesthetic or practical reasons, or for the pure addition to knowledge which can be made from their study so long as they exist. Hedgerows are well worth preserving even though these accidental consequences of a particular form of agriculture presumably had no existence at least until Neolithic times.

When we try to conserve a species or a habitat, what in fact we do is to try to determine the homeostatic devices which are needed to prevent extinction. In an African National Park this may mean enforcing a population balance which would not take place without our intervention, for instance by controlling the numbers of hippopotamus by shooting. Or we may counter migration consequent upon periodic drought by artificial irrigation, thereby artificially limiting and stabilizing the position of an ecological system so that a configuration which formerly ranged over vast areas can be maintained within the limits of a National Park. From this point of view, the principles of 'Nature Conservation' are essentially similar to the principles by which an isolated limb or part of an entire organism can be artificially maintained: we try to maintain the boundary conditions so that the situation for the part or limb is equivalent to that which would obtain if it were still attached to a much larger complex organism.

At least to the extent to which a particular ecological configuration maintains itself through the homeostatic behaviour patterns of the organisms which are comprised in it we may say that the configurations themselves resemble organisms, though of a higher order. The homeostatic systems arise through the operation of natural selection even though growth, reproduction and evolution are not of the same character in these higher order systems as in the species of individual organisms which are among their components. But even if we confine our attention to the inanimate components of an ecological configuration we still find powerful systems tending to conserve that configuration; which systems might well be termed homeostatic.

Some of the most striking examples of homeostatic mechanisms which have been discussed concern the maintenance of some constancy of composition in the body fluids of animals. Many years ago Macallum (1926) pointed out the close correspondence between the composition of these and that of sea water. He drew evolutionary conclusions from this.

Geological evidence seems to point to the essential stability of the composition of the sea and of our oxygen-rich atmosphere (Goldschmidt, 1954; Mason, 1952). As Rubey (1951) says:

> Several lines of evidence seem to indicate some actual changes in the composition of sea water and atmosphere with time. Yet, the more closely one examines the evidence, the more these changes appear to be merely second-order differences. Everything considered, the composition of sea water and atmosphere has varied surprisingly little, at least since early in geologic time.

Just as we have studied the mechanisms which maintain the constancy of the composition of body fluids, so we may examine the conditions which maintain the sea or the atmosphere as environments in which life can be maintained. In the first place, as Henderson (1913) pointed out in his remarkable book, *The Fitness of the Environment*, the physical properties of the environment present to us a unique collection of properties essential for the maintenance of that class of systems to which living organisms belong. These properties cover different qualities, from the special properties of carbon and the properties of water to the special set of physical conditions on this planet. As Henderson says, there is no obvious linkage between many of these special conditions: that is, given that one is true we have no reason to suppose that the truth of the others could be inferred from it. This does not imply that systems with certain essential features characteristic of life as we know it may not exist in different conditions elsewhere in the universe—as, for instance, conceivably in liquid ammonia systems in the outer planets—or even in certain classes of machine to be constructed on our own—but that the possibility of the whole set of these depends upon unique properties of the material universe which show no necessary linkage.

If I may quote from an earlier paper of mine on the properties of sea water in relation to life (Pantin, 1931):

On this view the similar composition of the body fluids in different animals is related to the fact that physically similar systems which constitute protoplasm require in all cases more or less similar collections of special elements. The close relation of the composition to that of sea water is very significant: but we may consider it from the following standpoint. It is possible that were the world such that the composition of sea water differed widely from that actually found, primitive marine organisms could never have developed in intimate contact with such an environment. Had sea water possessed a composition other than that required for the easy maintenance of protoplasmic systems, we, as observers, would not have existed.

This conception renders the whole problem an example of Henderson's *Fitness of the Environment* (1913). It has at least the advantage that it focusses attention on the physical mechanism by which the composition is maintained and thus lays the problem open to experimental investigation.

Since Henderson's day, the number of known unique properties favourable for the existence of living organisms has increased, from the remarkable properties of the DNA molecule to the unique properties of sodium, including the sodium of the ocean, to maintain cellular ionic composition through the operation of the sodium pump. But apart from the suitability of the properties of its constituents for the maintenance of living organisms there is the equally striking phenomenon of the maintenance of the composition of the atmosphere and ocean within steady limits. Undoubtedly the existence of certain dynamic equilibria, that is, the existence of certain reversible systems, helps to keep the properties of the ocean within their present limits. Thus the pH of sea water throughout the seas stays close to the narrow range pH 8·0–8·3. Sea water is roughly 0·0026N for bicarbonate and its buffering restricts variation of pH. Nevertheless, though the sea maintains itself at a fairly steady pH 8·0–8·3 (Harvey, 1928), seeing that for bicarbonates, $pK_1 = 6{\cdot}47$ and for carbonates $pK_2 = 10{\cdot}32$ (Clark, 1922), even allowing for the high proportion of Na^+ in the ocean, the pH of sea water is well to one side of the maximum regions of buffering. The carbon dioxide content of the ocean is in fact the consequence of a complex series of interacting open steady states involving evaporation and the water cycle through rivers to the sea together with the quantity of carbonate rocks in the surface of the earth, all in close relation to the water during its cyclical changes of state on the earth's surface consequent on the receipt of solar energy; and the stable pH of the ocean and its carbon dioxide content are related to the stability of the composition of the atmosphere.

Selection is the key to the acquisition of internal stability in organisms. But the peculiarly stable conditions in the ocean did not arise through the action of natural selection upon the progeny of a number of reproducing and heritably varying little seas. How does stability arise in the ocean?

The sheer volume of the atmosphere and hydrosphere play some part in smoothing out temporary and local variations in composition of atmosphere and ocean. The operation of Le Chatelier's principle generally ensures that the effect of small changes imposed on a system in dynamic equilibrium will tend to be reduced. But when considering open steady states, the maintenance of constancy is less simple. Thus, the water in the ocean is maintained as part of a steady state involving the whole hydrosphere of salt and fresh water, and water locked up in sediments, in ice, and present in the atmosphere. The volume of this water has been estimated at about 1600×10^6 km.^{3}: whilst annual terrestrial precipitation of water in all forms is estimated to be about 400×10^3 km.^{3} That corresponds to an average rate of turnover of about once in 4000 years; which is trivial compared with geological time. The considerable fluctuations of sea level in the relatively short period of the Pleistocene show how sensitive the volume of the ocean must be to the conditions of its steady state (Poldervaart, 1955).

Likewise we may turn to other steady states which control conditions in the atmosphere and hydrosphere. The most important is that which controls the amount of oxygen and carbon dioxide. The high proportion of oxygen in our atmosphere appears to be the consequence of photosynthesis. The greater extent of sea than of land and the richness of the phytoplankton suggests that photosynthesis in the sea is at least as important as that on land. Indeed Krogh's observations that the partial pressure of carbon dioxide in oceanic water is generally below that of the air suggests that photosynthesis in the former is the greater (Harvey, 1928). Manifestly, in a steady state, the average production of oxygen must be equal to the average consumption of carbon dioxide. For some reason, that is maintained by a gross difference in the partial pressure of the two gases. If we take atmospheric carbon dioxide as 3 parts per 10^4 and oxygen as 2100 parts per 10^4, there is a 700-fold difference—to the enormous advantage of aerobic animal life including our chemists and engineers.

What controls this difference in partial pressure is not, I believe, known. One may well suggest that in part it is a reflexion of the different conditions of the primary organisms responsible. Photosynthetic organs, whether in land plants or in marine diatoms, are highly adapted structures in which the biochemical machinery is brought into the closest proximity to carbon dioxide supply. On the other hand, most of the conversion of oxygen into carbon dioxide can with reasonable probability be ascribed to bacteria (rather than to animals) commonly living in situations in which oxygen can only reach them by diffusion at a considerable external partial pressure.

But whatever the conditions, the concentrations of oxygen and carbon dioxide of the atmosphere and hydrosphere are maintained by what must seem a highly vulnerable steady state. I have no exact estimates for the uptake of carbon dioxide by plants on the earth's surface, but if one accepts figures quoted by Strasburger (1930), while there are some $2 \cdot 1 \times 10^{12}$ tons of carbon dioxide in the atmosphere, land plants alone consume some $0 \cdot 05 \times 10^{12}$ tons per year. Such calculations suggest that the average rate of oxygen and carbon dioxide turnover in the atmosphere is a matter of decades. Even if such calculations are out by several orders of magnitude, it is still clear that the maintenance of an oxygen-rich atmosphere such as our own for the immense periods of geological time seems to call for some natural controlling devices which play the same part as do the 'homeostatic' controls in living organisms.

A system such as the ocean is thus the result of the interaction of a series of open steady states. The system has properties that adapt it singularly well for the maintenance of living systems. The open steady states in it seem to be vulnerable, in that their turnover is rapid compared with the great duration of geological time through which they seem to have endured; and yet with such a rapid turnover one might expect that small changes in conditions would have resulted in large changes in the whole system.

This collection of properties, which has some parallel to that characteristic of the homeostatically controlled body-fluid of a single organism, cannot be the result of natural selection in the ordinary sense. On the other hand, any configuration of matter and energy will tend to change with time. It might continuously change its character for ever; or it might achieve a state which was a stage in a cyclical relaxation oscillation; or it might reach a state in which any deviation leads to a correcting change towards a mean position. In either of these last two cases the configuration will, for a time, tend to be maintained and will survive. Limited relaxation oscillations and corrected deviations from the mean are the characteristic classes of homeostatic control in living organisms. Thus there is here a factor operating with something of the effect of natural selection in that a configuration will pass through a series of varied states until one is reached which gives the required stability, and this state will necessarily endure.

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THE ROLES OF PHYSIOLOGY AND BEHAVIOUR IN THE MAINTENANCE OF HOMEOSTASIS IN THE DESERT ENVIRONMENT

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There is an endless fascination in attempting to understand the ways in which animals are able to live and reproduce under physically difficult circumstances. However, in the temperate parts of the world where biologists have attained a high population density, the physiological capacities of animals are usually not of great ecological importance as determinants of the distributional limits. Other largely inferential factors such as competition, predation, food supply, or suitable habitats, restrict the distribution of animals to areas much smaller than those permitted by their physiological capacities *per se* (see Bartholomew (1958), Gordon (1962), for discussion and documentation).

There are, of course, parts of the world where the physical environment is so demanding and inhospitable that it directly limits animal distribution. One of the most widespread of these physically demanding environments exists in the low-latitude deserts which dominate the continental areas and oceanic islands in the horse latitudes of both hemispheres, and extend long tongues north and south on the lee sides of mountain ranges, particularly in the New World.

A POINT OF VIEW

It is my purpose in this paper to discuss and evaluate some of the ways in which vertebrates have come to terms with this difficult physical environment, but, to develop a point of view, I will first describe briefly a way of looking at organisms that is useful to the student of the ecologically relevant aspects of physiology, particularly in studying problems of homeostasis. The complexity of contemporary biology has inevitably led to extreme specialization and 'tunnel vision', and to poor communication between disciplines. In this situation, members of each specialized field begin to feel that their own work is fundamental and that the work of other groups, although sometimes technically ingenious, is either irrelevant or at best peripheral to the understanding of basic problems and issues. The biochemist is apt to feel that all important biological problems will be solved at the molecular or submolecular level, while the ecologist feels that the molecular biologist is preoccupied with details of machinery whose significance he does not appreciate. There is a familiar solution to this problem, widely recognized intellectually but sometimes difficult to accept emotionally. This is the idea that there are a number of levels of biological integration and that each level offers unique problems and insights, and further, that each level finds its explanations of mechanism in the levels below, and its significance in the levels above.

This elementary philosophical idea is relevant here because physiological ecology demands preoccupation with many levels of biological integration, continuously and usually simultaneously. Any attempt to attain an adequate understanding of the relation of an organism to its environment presents a problem of such enormous complexity that the biologist must, unfortunately, be reconciled from the beginning to obtaining an incomplete answer. The task, which all scientists face, of isolation and simplification of problems, is particularly acute for the student of physiological ecology. He cannot reduce the problem until only a single variable remains; he cannot restrict the data to a single level of biological integration, or, as is done in most other biological disciplines, even to several adjacent levels. Further, he cannot limit his data-gathering to the techniques of any one specialized field. As well as seeing the whole of the problem with sufficient clarity to enable him to ask the right questions, the student must have enough intellectual brutality not to be deterred by the knowledge that few men are able to handle these complexities. More than most students, he must recognize that biology is a continuum.

ORGANISM AND ENVIRONMENT

It is unavoidable that we biologists, because of our limitations, divide ourselves into categories of specialization and then pretend that these categories exist in the biological world. As everyone knows, organisms are functionally indivisible and cannot be split into the conventional compartments of morphology, physiology, behaviour and genetics. Each of these is only one aspect of the organism as a whole and since it is the organism which deals with the physical environment, where do we start? First, we must decide what an organism is. Obviously, it is not just a museum specimen, nor is it just an animal or plant caged in the laboratory, or observed in the field. It is useful to think of the organism as an interaction between a complex, self-sustaining physicochemical system and the substances and conditions which we usually think of as the environment. As Claude Bernard pointed out almost a century ago, organism and environment form an inseparable pair; one can be defined only in terms of the other. The separation of organism from environment seems natural to us, because we are organisms and we think of ourselves as separate from the environment. It is clear that the organism exists as a dynamic equilibrium and thus, as long as it is alive, it is the example *par excellence* of the phenomenon of homeostasis.

CLIMATE AND ECOCLIMATE

Although organism and environment form a single functional unit it is convenient to maintain a verbal distinction between them. Fortunately, we can do this if we never treat the two ideas separately and if we always remember that, when dealing with a population of a given species, it must not be related to the gross environment; instead, we must relate it to the specific and limited environment with which the organisms in question are maintaining a dynamic equilibrium. This point of view is particularly important when dealing with terrestrial animals, for on land, in contrast to the sea, there is an almost infinite series of physical situations available, and terrestrial animals can by their behaviour select from this array of environmental conditions in an intricate and precise way. Terrestrial animals, because of their mobility and capacity for complex behaviour, including acceptance and rejection, can actively seek out and utilize those specific and limited facets and aspects of the physical environment that allow their anatomical and physiological attributes to function adequately for survival and reproduction. Consequently, by their behaviour these animals can fit the environment to their functional capacities. From this point of view, it follows that there is no such thing as 'the environment', at least in the terrestrial situation, but rather an enormous series of environments. Indeed, it is probable that, in a given part of the world, as many terrestrial environments exist as there are species.

For a large mammal, such as a human being, the climate, in the usual meteorological sense of the word, would appear to be a reasonable approximation of the conditions of temperature, humidity, radiation, and air movement in which terrestrial vertebrates live. But, in fact, it would be difficult to find any other lay assumption about ecology and natural history which has less general validity. Ostriches, kangaroos, prong-horned antelope, and shepherds may live in the meteorologists' climate but few other vertebrates do.

Most vertebrates are much less than a hundredth of the size of man and his domestic animals, and the universe of these small creatures is one of cracks and crevices, holes in logs, dense underbrush, tunnels and nests—

a world where distances are measured in yards rather than miles and where the difference between sunshine and shadow may be the difference between life and death. Climate in the usual sense of the word is, therefore, little more than a crude index to the physical conditions in which most terrestrial animals live.

Each species selects from the variations in the local macroclimate and microclimates a particular combination of physical conditions—its ecoclimate—appropriate to its functions and capacities. Each species or other adaptive group in a given area has its own ecoclimate and, if one is to study the relations of an animal to its physical environment, interpretations must be made in terms of ecoclimate.

The ecoclimate of each species or organism must be measured separately and the measurements that are taken and the places where the measurements are made must be carefully selected on the basis of accurate knowledge of the natural history of the population concerned. It is obvious that, because of the great diversity of physical conditions which are available in the terrestrial environment, an individual animal can exploit its physiological capacities most fully by utilizing its behaviour to place itself in those situations with which it can cope by physiological regulation, or by restricting its period of exposure to intolerable physical conditions, so that its limits of physiological tolerance are not exceeded in spite of its inability to maintain an adequately steady state. The rest of this paper will consider a few especially instructive instances of the interplay of behaviour and physiology by which various desert-dwelling reptiles, birds and mammals either maintain a steady state, or restrict to acceptable rates and periods of time the changes in their physiological state in situations with which they cannot cope fully by physiological means.

Adequate general coverage of the adaptations of the different groups of vertebrate animals to conditions of desert life is available in the literature (Schmidt-Nielsen & Schmidt-Nielsen, 1952; Schmidt-Nielsen, 1964; Chew, 1961; Bartholomew & Cade, 1963); this paper will not attempt an exhaustive summary, but instead will discuss selected patterns of adjustment to the desert environment in relation to homeostasis.

THE DESERT ENVIRONMENT

The heat and aridity of low-latitude deserts pose an ecological challenge so severe that few kinds of vertebrates can occupy the deserts permanently. The few species which do occur in deserts are often present in some numbers, however, a situation similar to that found in other areas, such as the arctic, where the limiting factors are physical rather than biotic. The