INTRODUCTION

LIFE has been defined as "a continual struggle with the environment"; and the cynic who, from the human point of view, summed it up as "one damned thing after another" was only making the statement in another way. Throughout existence, every organism is swayed by two contending forces—one innate and conservative, urging it to appear and act as its ancestors appeared and acted: the other environmental and progressive, compelling it to change in conformity with its surroundings. The animal we know is the product of an age-long struggle to reconcile constitutional limitations with environmental exigencies.

For the œcologist, the environment includes every external influence which surrounds the living being—the climate, the soil, the topography of the country and its flora and fauna. It is the setting in which the animal or plant is placed, "the mould into which the organism fits" (38). We owe to Haeckel the useful word "Œcology" for the study of the relations of this environmental mould and its occupants; and nowadays the title "Bionomics" is sometimes given to the reactions of habit and life history to the same causes[1].

It is for the zoologist in the practice of his science to determine the part played in the moulding of the organism by the two opposing forces of heredity and environment; and he is confronted by this problem as soon as he seeks to devise a natural classification of animals. The existing systems are taxonomic, that is to say they are based on phylogenetic considerations, and express our views of the evolution of species and their morphological affinities. This is the sound foundation for a system of classification, because, while all biologists share the belief that existing forms have arisen from a common stock, the part played by the environment in this evolution is still in dispute. It is often difficult to distinguish between characters of

[1] The good old term "Natural History" has fallen into disuse, but might well be revived to include much of what is now called Bionomics.

taxonomic value and those which are environmental adaptations. Sometimes allied forms differ considerably in adaptation, and in some cases adaptational characters may assume taxonomic importance. This difficulty has so impressed some modern œcologists that, for the purposes of their study, they have proposed schemes of classification based on bionomical or physiological considerations. Such a system has its convenience in the detailed œcological survey of limited areas, and in the use of special terms to express associations of organisms possessing similar reactions to a common environmental complex, but its employment in a more general or exact way is not practicable in the present work. The taxonomist considers life from the angle of what it is and was: the œcologist wishes to study what it does and did. Data for the first point of view are available, and can be tested by more or less precise methods. Data for the second are not available, at any rate at present, and even if we possessed them, it is doubtful whether they would readily lend themselves to comparison and measurement. It is true that, within limits, reactions to environmental stimuli can be distinguished and recorded. It is possible for instance to test the reactions of certain organisms to CO_2, or to increased insolation or humidity; but a general classification based on such a primary reaction is out of the question, because it would be impossible to subject the whole animal kingdom to experiment. Such experiments are of high importance and interest, but taxonomy remains the sheet-anchor for the explorer who ventures into the œcological sea. If an œcological "classification" is necessary at all, it is preferable to group the different animals of a region by a common link, such as food, into a series of bionomical complexes as will be described later on. This would substitute for the phylogenetic tree that familiar figure of taxonomy, the concept of a net or woven cloth of intricate pattern, whose threads, no matter what their colour or size, are all mutually interdependent and essential to the strength and design of the whole fabric.

Botanists however sometimes use a form of œcological classification when they approach their subject from the point of view of environment. Thus Schimper, Warming and others write of guilds, formations, associations and so on; and Warming (45) in this sense regards the *formation* and the *association* as the œcological equivalents of the taxonomic genus and species respectively. Such conceptions and terms can be used with greater precision by the botanist than by the zoologist because of the essential difference between plants and animals. The plant is fixed, and can only meet change in the surrounding conditions by structural and physiological changes in itself. The animal is mobile, and within limits can change its environment to suit its needs by moving elsewhere.

Thus an apple tree and a swallow must both prepare for the winter. The tree sheds its leaves and lowers its metabolism. The bird migrates to Africa. In a sense the plant is the captive of its environment, and wears its chains—the structural adaptations to its surroundings—plainly for all to see. On the other hand, the animal may be compared to a prisoner on bail or ticket-of-leave. Its movements are restricted, but the fetters are less obvious. In fact the physical surroundings can be best deduced from what the plant *is*, and from what the animal *does*. Shelford (37) remarks that for œcological purposes, it is the behaviour (bionomics) of animals, and not, as is often thought, their structure which should be compared with structure in the vegetable kingdom; and he also points out that again it is behaviour which offers the truest analogy to the development of human culture.

It is the faithful correlation of plant growth with the physical environment, especially to the important factor, or complex of factors, called "climate," that leads us naturally to define the main types of land environment in terms of plant life as Woodland, Grassland and Desert. These three great divisions have meaning not only for the botanist, but for others also; and this is easily understood, for vegetation is the apparel of scenery. As Darwin wrote: "A traveller should be a botanist, for in all views plants form the chief embellishment."

But when the zoologist, forsaking botanical terms, tries to classify environments in the language of his own science, he cannot construct a workable scheme. Here and there a region, or zone of a region, is characterised by a special type of animal life; but sooner or later the classification breaks down, and he finds that he must fall back on the language of the botanist or geologist. Nevertheless, though these great formations cannot be expressed in terms of animal life, they represent real though often ill-defined conceptions to the zoologist. In certain kinds of country—forests, steppes, mountains, deserts—certain types of animals predominate, while others are rare or absent; and it is often found that the predominant forms possess a certain number of adaptations in common.

This was brought home to me more than once between the years 1914 and 1922 when it was my good fortune to visit extreme examples of Woodland, Grassland and Desert in different parts of the world; and this book is the outcome of the lack that I myself then felt of some guide to the general trend of animal life amid surroundings that were new to me and presented unexpected œcological complications and problems. For although the large formations, which are sometimes called climatic or geographic, are typical of the country over wide areas, they are not homogeneous. Each is interspersed with smaller local or edaphic formations, due to accidents of soil or topography. We speak of the Sahara or Gobi deserts as sandy wastes, although we are well aware that the typical desert scenery is interrupted by oases and watercourses. Rivers, swamps, lakes, mountains, forests, clearings, etc., by modifying the soil, rainfall, and other environmental factors, all give rise to local formations which are of great importance to the distribution and development of the flora and fauna. In fact the œcological study of any region is essentially the study of local *versus* climatic conditions.

For œcological purposes, woodland includes all the forested regions of the earth, from the stunted birch and conifer tracts of the north, or the deciduous woods of the temperate zone, to the jungles of the equator; and it often merges into open country through parkland and savanna forest. Grassland includes all fertile unforested land, steppes, prairies and pampas, where vegetation of one kind or another is present throughout the year, and agriculture is possible. Deserts are regions where, owing to the scanty water supply, the life of plants and animals is either in abeyance or non-existent for at least the greater part

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of the year, and ordinary agriculture is impossible. Deserts are of two kinds: those which are *physically* dry, with little water present in any form, and those which are *physiologically* dry, where, though water may actually be abundant, it exists in a form inaccessible to living beings. Much of the Sahara and Gobi are deserts of the first type. Some salt deserts belong to the second category, but by far the largest physiological deserts are the frozen circumpolar belts where, for the greater part of the year, the water is locked up as snow and ice, and all life must exist under physiologically dry conditions. These types of country blend and grade into each other, not only at the limits of the greater formations, but also where local conditions change within the climatic formations themselves.

In some cases it is difficult to decide whether similar formations which do not lie adjacent have arisen independently under similar conditions, or whether their present likeness is due to past continuity. In the first place we may expect to find a difference, and in the second a resemblance between the flora and fauna. An excellent example of this occurs in the Sayansk Mountains at the source of the Yenisei River in Siberia. The spurs of this range, which form the northern bastions of the Central Asiatic highlands in lat. 52°–54°, are clothed on their northern slopes, four or five thousand feet above sea-level, with forests of the same type as the low-lying coniferous "taiga" between lat. 56° and 72°. Between the climatic forest formation and the mountains is an open steppe formation with a completely different flora. Now it is well known that altitude in warm climates may produce a state of things comparable to that found on low-lying ground in high latitudes—for instance the flora of high mountain tops has a general resemblance to that of the polar regions[1]. At first sight this seems to be the case in the Sayansk Mountains; but on investigation it appears more likely that, at an earlier epoch, coniferous forest

[1] Generally speaking, the mean temperature falls 1° F. for each degree of latitude north (or south) of the equator; and the same for every three hundred feet of altitude. The observations of the Everest expeditions suggest that certain species of birds, believed to breed only in Siberia, may yet be found to nest much further south in the Himalayan region and the adjacent highlands (4).

extended over the whole region, and at the end of the Ice Age, as the glaciers retreated northwards, the part of the forest on the mountain slopes was cut off from the rest, and the steppe flora crept into the intermediate zone with the altered conditions (35). Hence while altitude compensates for latitude as a general rule, its effect in this case has been to conserve an ancient formation, not to produce a new one.

My first expedition was in 1914 when I accompanied the late Miss Czaplicka to the cold desert tundras of Siberia, and after this lapse of time I can only marvel at the youthful optimism which led me without preliminary training, north-east in the footsteps of Middendorf, and at the good fortune which attended my ignorance. However I learned there the handicap of lack of preparation, and determined that next time opportunity offered a journey abroad, I should be better equipped. The occasion arrived three years later, during war service in south-west Russia. The Danubian steppe, though but the fringe of the great Eurasian grassland formation, is most impressive to the naturalist, and no doubt intensive study of the conditions in its seasonal and topographical semi-desert tracts would throw light on certain bionomical problems which are difficult to solve elsewhere. The contrast of tundra and steppe, their analogies and differences, first suggested the present studies, and when in 1922 the opportunity to travel abroad occurred again, I purposely chose the tropical jungle of British Guiana as a collecting ground, to complete a trilogy of Woodland, Grassland and Desert extremes. The manner of the proposed survey was more difficult to settle than the matter. Long ago I had fallen under the spell of *From North Pole to Equator*, and only those who have travelled through countries similar to those which Brehm visited can fully appreciate the insight and vigour of his descriptions of scenery and weather, and his unfailing gift for selecting the outstanding characteristics of animal and plant life in the wilderness. But, with all his charm, Brehm wrote for the nature lover more than for the naturalist, and his essays serve as a spring of happy reminiscence for the returned wanderer rather than as a guide to the œcologist on the spot. I began to wonder whether it was possible to offer not only picturesque descriptions of climate and scenery to the traveller, but also to trace the influence of these on the fauna with the greater precision demanded by the student. For all travellers are not naturalists. One I knew who travelled for a long September day across the steppes, and, with eyes averted from broad horizons, ripe barley fields, and hollows mist-blue with thistles and chicory, perused the works of Mr Charles Garvice. And some students regard the world merely as a collecting ground, or as a large open air demonstration in laboratory science. I once saw a meteorologist who, for the first time, watched the glory of midnight sunshine on the snows of the arctic swamps and then remarked unmoved that "the temperature was pleasantly high considering the latitude and the season."

> Primroses by the river's brim
> Dicotyledons were to him,
> And they were nothing more.

It may be said at once that neither of the types of which these individuals are representative will find anything to interest or profit them in the following pages, which are but the outcome of the happiness I myself have found in the curious and beautiful surroundings whither the study of natural history has led me.

The aim to satisfy at once the nature lover and the naturalist presents a double difficulty, for the manner must not be too technical on the one hand, nor the matter too diffuse and descriptive on the other. The first stumbling block I have tried to avoid by relegating most of the scientific names to an accessible but unobtrusive position in the index, and by transferring long references from the text to the sectional bibliographies. In the present state of our knowledge the second difficulty is the greater of the two, for little experimental work has been done on bionomics, and the subject still rests largely on generalisation and inference. But this very fact will be the book's best justification, if thereby attention is drawn to the rampart of our ignorance, as yet scarcely breached, and an objective for another assault suggested.

The animal can be moulded to the environment either by modification of form and function (structural) or by modification of behaviour and life history (bionomical), though the distinction between the two kinds of adjustment cannot always be finely drawn. On the whole, structural adaptations are determined chiefly by topographical factors, while bionomical adaptations are in the main related to climate. Indeed, figuratively speaking, the topography of the country and the variations of the climate represent the same part in the make-up of the environment as morphology and physiology play in the study of the organism. Thus the mammalian fauna of open treeless plains, tundras, steppes, pampas, high plateaux or tropical deserts, has, irrespective of climate, certain features in common. In each the dominant forms are mobile running animals or subterranean rodents of social habits; and the structural adaptations of the limbs to leaping or digging are often similar in different parts of the world. Naturally, species adapted to climbing are absent in the open country, but, where the plain or desert is broken by cliffs and ravines, it is frequently occupied by a secondary population whose members show affinities to the inhabitants of forests elsewhere, and, like them, are able to invade all three spatial dimensions. Thus typically the hyrax is a dweller in desert rocks, but certain African species inhabit hollow trees; and the wall-creeper of Central Europe, a cousin of the little woodpecker-like tree-creeper of our woodlands, lives in crevices in crags and precipices[1]. Again, animals which run upon a shifting or slippery surface are often provided with supporting flanges along the toes. This is seen in many desert-living reptiles, notably in one of the geckoes of the Caspian region, which, forsaking the climbing habits of its congeners, has lost the characteristic sucking finger discs, and developed lateral flanges to the digits. This structural adaptation finds its parallel in the "snow shoes" of the wood-grouse of the sub-arctic forests which pass the winter amid heavy snow. The lateral scales of the toes grow out to form a horny fringe which helps to support the bird in soft drifts or on slippery branches.

These are similar modifications of structure brought about

[1] The wall-creeper lacks the stiff supporting tail feathers of the tree-creeper.

by similarities of form in the environment; but, when habit and behaviour are considered, the determining factor is more often the climate. This is the case with the vast behaviour complexes connected with migration, hibernation, with breeding habits which are due to seasonal sexual activity, and to some extent with food-getting.

Some writers consider that, in the past, animal œcologists have laid too much stress on structural adaptations. For instance, Shelford (37) regards them as of secondary importance, and emphasises the necessity of regarding the animal kingdom from the point of view of reaction to environmental stimuli. But apart from the fascination of the study of morphological adaptation, which has held naturalists both before and since Darwin's day, structural adaptations play a part in habit and behaviour analogous to that of tools in the development of human culture (11). The anthropologist studies the evolution of the weapons, boats, pottery, etc., and the crafts, customs, and ceremonies with which they are linked, as a valuable source of knowledge as to the distribution, history, and present condition of the races of mankind. Until recently at all events, the "bow-drill" was still employed occasionally in English cutlery factories to bore the ivory handles of knives. In 1914, three months after watching this ancient device in use in a Sheffield workshop, the writer saw the same tool used by a nomad Dolgan on the Siberian tundra to drill holes in a plate of mammoth ivory. Now if in this instance the anthropologist had employed strictly œcological methods, he must have confined himself to remarking that these two workmen, in such different phases of culture, could both bore holes. He would have missed the fact that they performed the task by precisely the same means. In the same way, side by side with the environmental reactions of habit and behaviour, the zoologist must take into account the modification of organs which make such reactions possible.

This view is not in accord with those of certain modern œcologists. Shelford (37) compares "an African antelope running gracefully from a pack of hunting dogs, and an old-man kangaroo leaping from a pack of dingoes," and remarks that if the naturalist "notes mainly the specific peculiarities of the movements of the limbs and body of the pursued in each case, he will be dwelling upon specificities of little œcological significance, and missing the point of view of the œcologist altogether ...it matters not if one animal progresses by somersaults so long as the two are in agreement in reaction to physical factors as indicated by the manner of spending the day, avoidance of forests, swamps, cold mountain tops, etc., entirely available to them."

But most naturalists will find the atmosphere of these œcological heights too rarefied for them; and therefore in the following pages, structure and behaviour will be considered side by side as mutually complementary to each other, though it must not be forgotten that the latter is more plastic than the former, and tends to evolve more rapidly.

A large class of structural adaptations are those correlated with the spatial level at which the animal lives, either under or on the earth, in the water, in trees or in the air. Sometimes such adaptations are common to a number of allied species or genera, and may even constitute isolated groups of considerable magnitude, such as the whales or bats. In other cases, a well-defined taxonomic order contains forms living at several levels. The Rodentia, for instance, include species which are cursorial, semi-aquatic, subterranean, arboreal and even aerial.

Another large class of structural adaptations is that concerned with obtaining food; and these may also be the diagnostic taxonomic character of a huge group occupying very diverse environments, as in the bugs, or may appear in a single genus, as in the crossbill, the skimmer, or in a more marked degree in the duck-billed platypus.

Adaptations to level are as a rule less restrictive than those concerned with food-getting, probably because the associated physiological changes are not so great. The bill of the snipe or woodcock is an instrument beautifully adapted for its purpose, but the normal range of these birds is correspondingly restricted to regions where the soil is soft enough for probing for food and contains abundant earthworms. On the other hand, the ant-