Then the winged individuals of the two different sizes issued from the earth, betook themselves, so to speak, to the roof of their abode and there, after being thoroughly warmed, strolled about in various directions, without, so far as I could see, any teasing of the large by the small winged individuals; that is, without any tender preludes to mating. Then one by one both the large and the small ones took flight. Soon the surrounding air was seen to be filled with them, and the large ones were seen each to have a small one dangling from its posterior end. Not only, therefore, do they remain aloft while they are copulating, but they actually begin the act in the air. Usually the female does not long remain alone. I have reason to believe this because along with the female and attached male which I expected to capture, and which I captured without their separating from each other, I have sometimes secured at the same time two or three additional males which, jealous of the good fortune of the first, apparently wished to supplant him, or were, perhaps, waiting till he left vacant the place that was the object of their desires.

Furthermore, I have always seen the ants return one by one to their formicary as they left it. Thus it is in the air that mating begins and continues. Then it is the task of the female to support the male, contrary to what is found in the flies called demoiselles, among which the male carries the female. Nature seems to have varied her combinations in all possible ways. The female ant flies in divers directions without being abandoned by her male, and sometimes carries him out of sight. Since it is impossible to follow continuously with the eyes even those that fly lowest, and since others crossing them cause them to be lost to view, I have never been able to ascertain how long the flight and the mating may continue. I have seen some that alighted very near the formicary before separating.

It has therefore been established that the wings are necessary to the ants, both male and female, in order that they may mate, and it would seem that these organs have been given them solely for this purpose. At least it is certain that the females do not long retain their wings after they have been fecundated. The males also shed theirs, but it would seem that they retain them much longer. Their wings are not useless, except on occasions when they fly through the air without succeeding in encountering females of their own formicary; for all appearances indicate that mating occurs only among ants born together, that is, among those of the some formicary. . . .

Kormondy, E.J. 1965. Readings in Ecology.
Prentice-Hall, Inc. NJ. 219 pp.

THE PHYSICAL AND CHEMICAL ENVIRONMENT

The various physical and chemical forces impinging upon an organism can be analyzed quite apart from any consideration of the organism. This was as obvious a truth in a period when earth, air, fire, and water were considered to be the major environmental principles as it is today when sundry physical and chemical phenomena are acknowledged to be of significance. Concomitant with this recognition of a wider diversity of environmental agents has been the development of increasingly complex and sophisticated methodology and instrumentation to aid in their analysis.

Environmental analysis without consideration of the organism is relatively meaningless for the ecologist. Life is a unit of interaction, and ecology is concerned essentially with those interactions which occur at the individual, population, and community levels of organization.

Interaction may take the form of the environment regulating the organism—its distribution in time and space, its physiognomy and phenology, among other peculiarities; it may involve compensatory and behavioral adaptations on the part of organisms; it may consist of regulation and modification of the abiotic environment by organisms through the release of excrements and as agents of decomposition. This section deals with the analysis of environmental factors and certain aspects of their regulatory effect on organisms; the converse situation of organisms regulating environment is treated in the section on ecosystems. In reality, all the readings represent some aspect of organism-environment interaction.

ORGANIC CHEMISTRY IN ITS APPLICATION TO VEGETABLE PHYSIOLOGY AND AGRICULTURE

Justus Liebig—1840

Reprinted from Professor Liebig's complete works on chemistry. Philadelphia, T. B. Peterson, pp. 9, 36, 39–43, 70–71, 1841.

There are likely few contemporary chemists who would concur with the first sentence of the following passage. Ecology, however, benefited immensely from this orientation and its major by-product, the delineation of the limiting role of a minimal supply of minerals in the growth and development of plants. Thereby, Liebig laid the foundation for increased understanding of the role of the environment in the regulation of organisms.

The peculiar object of organic chemistry is to discover the chemical conditions essential to the life and perfect development of animals and vegetables, and generally to investigate all those processes of organic nature which are due to the operation of chemical laws. Now, the continued existence of all living beings is dependent on the reception by them of certain substances, which are applied to the nutrition of their frame. An inquiry, therefore, into the conditions on which the life and growth of living beings depend, involves the study of those substances which serve them as nutriment, as well as the investigation of the sources whence these substances are derived, and the changes which they undergo in the process of assimilation.

A beautiful connection subsists between the organic and inorganic kingdoms of nature. Inorganic matter affords food to plants, and they, on the other hand, yield the means of subsistence to animals. The conditions necessary for animal and vegetable nutrition are essentially different. An animal requires for its development, and for the sustenance of its vital functions, a certain class of substances which can only be generated by organic beings possessed of life. Although many animals are entirely carnivorous, yet their primary nutriment must be derived from plants; for the animals upon which they subsist receive their nourishment from vegetable matter. But plants find new nutritive material only in inorganic substances. Hence one great end of vegetable life is to generate matter adapted for the nutrition of animals out of inorganic substances, which are not fitted for this purpose. . . .

Many of the inorganic constituents vary according to the soil in which the plants grow, but a certain number of them are indispensable to their developement. All substances in solution in a soil are absorbed by the roots of plants, exactly as a sponge imbibes a liquid, and all that it contains, without selection. The substances thus conveyed to plants are retained in greater or less quantity, or are entirely separated when not suited for assimilation. . . .

The examples cited above, in which the quantity of oxygen contained in the bases was shown to be the same, lead us to the legitimate conclusion that the developement of certain plants is not retarded by the substitution of the bases contained in them. But it was by no means inferred that any one base could replace all the others which are found in a plant in its normal condition. On the contrary, it is known that certain bases are indispensable for the growth of a plant, and these could not be substituted without injuring its developement. Our inference has been drawn from certain plants, which can bear without injury this substitution; and it can only be extended to those plants which are in the same condition. It will be shown afterwards that corn or vines can only thrive on soils containing potash, and that this alkali is perfectly indispensable to their growth. Experiments have not been sufficiently multiplied so as to enable us to point out in what plants potash or soda may be replaced by lime or magnesia; we are only warranted in affirming that such substitutions are in many cases common. The ashes of various kinds of plants contain very different quantities or alkaline bases, such as potash, soda, lime, or magnesia. When lime exists in the ashes in large proportion, the quantity of magnesia is diminished, and in like manner according as the latter increases the lime or potash decreases. In many kinds of ashes not a trace of magnesia can be detected.

The existence of vegetable alkalies in combination with organic acids gives great weight to the opinion that alkaline bases in general are connected with the developement of plants. . . .

Let us consider the composition of the ashes of two fir-trees as analysed by an acute and most accurate chemist. One of these grew in Norway, on a soil the constituents of which never changed, but to which soluble salts, and particularly common salt, were conveyed in great quantity by rain-water. How did it happen that its ashes contained no appreciable trace of salt, although we are certain that its roots must have absorbed it after every shower?

We can explain the absence of salt in this case by means of the direct and positive observations referred to, which have shown that plants have the power of returning to the soil all substances unnecessary to their existence; and the conclusion to which all the foregoing facts lead us, when their real value and bearing are apprehended, is that the alkaline bases existing in the ashes of plants must be necessary to their growth, since if this were not the case they would not be retained.

The perfect developement of a plant, according to this view, is dependent on the presence of alkalies or alkaline earths; for when these substances are totally wanting its growth will be arrested, and when they are only deficient it must be impeded.

The roots of plants are constantly engaged in collecting from the rain those alkalies which formed part of the sea-water, and also those of the water of springs, which penetrates the soil. Without alkalies and alkaline bases most plants could not exist, and without plants the alkalies would disappear gradually from the surface of the earth.

When it is considered, that sea-water contains less than one-millionth of its own weight of iodine, and that all combinations of iodine with the metallic bases of alkalies are highly soluble in water, some provision must necessarily be supposed to exist in the organization of sea-weed and the different kinds of Fuci, by which they are enabled during their life to extract iodine in the form of a soluble salt from sea-water, and to assimilate it in such a manner, that it is not again restored to the surrounding medium. These plants are collectors of iodine, just as land plants are of alkalies; and they yield us this element, in quantities such as we could not otherwise obtain from the water without the evaporation of whole seas.

We take it for granted that the sea-plants require metallic iodides for their growth, and that their existence is dependent on the presence of those substances. With equal justice, then, we conclude, that the alkalies and alkaline earths, always found in the ashes of land-plants, are likewise necessary for their developement. . . .

In order not to form an erroneous conclusion regarding the processes of vegetable nutrition, it must be admitted that plants require certain salts for the sustenance of their vital functions, the acids of which salts exist either in the soil (such as silicic or phosphoric acids) or are generated from nutriment derived from the atmosphere. Hence, if these salts are not contained in the soil, or if the bases necessary for their production be absent, they cannot be formed, or in other words, plants cannot grow in such a soil. The juice, fruit, and leaves of a plant cannot attain maturity, if the constituents necessary for their formation are wanting, and salts must be viewed as such. These salts do not, however, occur simultaneously in all plants. Thus, in saline plants, soda is the only alkali found; in corn plants, lime and potash form constituents. Several contain both soda and potash, some both potash and lime; whilst others contain potash and magnesia. . . . The respective quantities of the salts required by plants are very unequal. The aptitude of a soil to produce one, but not another kind of plant, is due to the presence of a base which the former requires, and the absence of that, indispensable for the developement of the latter. Upon the correct knowledge of the bases and salts requisite for the sustenance of each plant, and of the composition of the soil upon which it grows, depends the whole system of a rational theory of agriculture; and that knowledge alone can explain the process of fallow, or furnish us with the most advantageous methods of affording plants their proper nourishment. . . .

OPTIMA AND LIMITING FACTORS

F. F. Blackman—1905

Reprinted by permission of the publisher from Annals of Botany **19**:281–295, 1905.

Blackman's major contribution to ecology was extending Liebig's "law of the minimum" to encompass the limiting effects of the maximum as well. This "law of limiting factors" as it came to be known, is developed in this selection. In the latter part of the paper, Blackman suggests but does not develop the concept which much later came to be known as "factor interaction."

In this article it is proposed to subject to critical consideration the conception of the 'optimum' as a primary general relation between physiological processes and the external or internal conditions which affect them.

In treating physiological phenomena, assimilation, respiration, growth, and the like, which have a varying magnitude under varying external conditions of temperature, light, supply of materials, &c., it is customary to speak of three cardinal points, the *minimal* condition below which the phenomenon ceases altogether, the *optimal* condition at which it is exhibited to its highest observed degree, and the *maximal* condition above which it ceases again.

As the maximum temperature for most metabolic processes is very near to the death point, exact location of it is attended with considerable experimental uncertainty and precise data are generally wanting. In practice, attention is usually concentrated upon the optimum of the condition and upon the general form of the middle part of the simple curve, which is usually accepted as a satisfactory graphic expression of the relation between the function and the condition.

In the treatment of the assimilation of carbon dioxide in all textbooks we find mention of optima of temperature, of light, and of carbon dioxide-supply for this process. After some years of experimental study of the effect of external conditions upon carbon-assimilation the writer has demonstrated that much of this treatment is quite incorrect, and from this position has passed to the general conviction that there is much that is misleading in that treatment of the effect of an external condition which involves giving definite values to its cardinal points.

We will at present confine our attention to the condition of temperature and will begin with certain *a priori* considerations derived from chemical dynamics.

The rate at which all normal chemical change takes place is increased by a heightened temperature condition.

Most reactions *in vitro* take place so quickly that it is impossible to measure their rate, but with all that go slowly in aqueous solution and resemble the processes of the organism, such as the saponification of esters, the inversion of sugar by acids, and others, it has been found that the acceleration produced by increased temperature is about the same. This has been generalized by van't Hoff into the rule that for every rise of 10°C. the rate of reaction is about doubled or trebled.

If this rule of chemical dynamics does not hold good for chemical reactions within the organism it is the duty of the physiologist to attempt, at any rate, to explain the aberration. Now it is interesting to note that this relation has actually been found to hold, as regards medium temperatures, say from 10°C. to 27°C., for quite a number of cases in animal and vegetable organisms so diverse in nature that the law clearly is *primarily* applicable to chemical change in the cell as well as the test-tube. Thus the respiration numbers of Clausen, for lupine seedlings and for *Syringa* flowers, show between 0° and 20°C., an increase of two and a half times for a rise of 10°C., the assimilation numbers obtained by Miss Matthaei and the writer for cherry-laurel leaves a coefficient of 2.1, and for sunflower leaves 2.3, while to come to more complex metabolic changes, the times required for spore-formation in *Saccharomyces pastorianus* (Herzog) and for the development of frogs' eggs (as calculated by Cohen from Hertwig's data. . .) at different medium temperatures both proceed within the limits of this rule.

As regards the rate of metabolic chemical change in the organism at high temperatures, this law clearly does not express the whole truth. If it did we should expect, with increasing temperature, all vital processes to proceed with ever-increasing velocity till the fatal temperature was reached at which some essential proteid coagulated or some other connexion was dislocated, and the whole metabolic machinery came suddenly to a standstill.

What then does happen as we approach the upper temperature-limit of substances. With equal justice, then, we conclude, that the alkalies and alkaline earths, always found in the ashes of land-plants, are likewise necessary for their developement. . . .

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What then does happen as we approach the upper temperature-limit of the working of the organism? An important new factor, the *time-factor*, comes into play.

In later years this factor hardly receives the attention that it deserves. Sachs, however, clearly pointed out that the higher the temperature the more quickly the fatal effect ensues, and that short exposure to a very high temperature may not kill, when a prolonged exposure to a slightly lower temperature is fatal. . . .

The optimum has by some investigators been regarded as the highest temperature which can be permanently sustained without depression of function, but more usually a real optimum is held to be characterized by this, that the retardation produced by exposure to super-optimal temperature must not be of the nature of permanent injury, and that therefore on cooling again to the optimum temperature there must be a return of the function to its highest value.

There has been little attempt to apply this principle experimentally, and it looks as if everything would depend on the *time* of exposure to the super-optimal temperature. Rather than by direct experiment, it is probable that the high transient values will in future have to be estimated by the convergence of the lines of evidence that we have already indicated. . . .

We start this section with the following axiom.

When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor.

I think one may fairly express surprise at the extent to which this principle has been overlooked by those who have proposed to work out the relation between a function and some *single* one of the various factors that control it.

This desirable end often cannot be really accomplished without taking deliberate thought to the other factors, lest surreptitiously one of *them*, and not the factor under investigation, becomes the real limiting factor to an increase of functional activity.

We will consider in some detail the application of this axiom to assimilation, and briefly its application to respiration and growth.

Carbon assimilation furnishes the most instructive case for the consideration of the inter-relation of conditioning factors, because these factors are largely external ones, whereas in growth they are internal and less under control.

Let us then consider first the case of assimilation. We can recognize five obvious controlling factors in the case of a given chloroplast engaged in photosynthesis.

(1) The amount of CO_2 available,
(2) the amount of H_2O available,
(3) the intensity of available radiant energy,
(4) the amount of chlorophyll present,
(5) the temperature in the chloroplast.

In theory any one of these five might be the limiting factor in the total effect, and it is comparatively easy to experiment with (1), (3), or (5) successively as limiting factors.

Many experimenters have indeed done this without premeditation. The experiments of Reinke, in which with increasing light the rate of assimilation (as measured by the bubbling of *Elodea*) suddenly ceased its proportional increase and remained stationary while the light increased yet another tenfold, I interpret as probably a case in which the supply of carbon dioxide was the limiting factor: its limit of arrival by osmosis being once reached no further increase of assimilation was possible.

The experiments of Kreusler on the effect of temperature on the assimilation of a shoot of *Rubus* gave, as higher and higher temperatures were used, at first a steady rise of assimilation up to 15°C., but after this the assimilation practically never rose further. This state of things has been shown by Miss Matthaei to be a case in which inadequate illumination limited the assimilation to that obtained at 15°C., and so further heating produced no increase. There are also contemporary examples of such misinterpretation which will be discussed elsewhere.

When the rate of a function exhibits, in experiment, a sudden transition from rapid increase to a stationary value, it becomes at once probable that a 'limiting factor' has come into play. . . .

PHYSIOLOGICAL ANIMAL GEOGRAPHY

Victor E. Shelford—1911

Reprinted by permission of the author and publisher from Journal of Morphology **22**:551–618, 1911.

Blackman's concept of limiting factors was developed from the perspective of control exerted by the environment. It is the organism, however, which responds to minimum and maximum factors; thus, the investigation of the ecological and physiological attributes of organisms assumes significance in explaining their geography. Professor Shelford's "law of toleration" incorporates both the geographic environment and the ecological physiology of organisms. This brief report does not at all suggest the significant impact Professor Shelford has had in ecology through his own work and that of his students. The duration of his productive work is recognized in the publication of The Ecology of North America (University of Chicago Press) in 1964, almost sixty years following the first paper from his graduate student days.

3. THE RELATION OF PHYSIOLOGICAL CHARACTERS TO GEOGRAPHIC RANGE

Our studies of animal distribution usually consist of a list of names of species with a statement of the distribution of each, followed by such interpretation as suits our particular purposes. Attempts actually to study the environment in any detail, or the reactions of animals to the conditions of environment are rare indeed. Furthermore, the groups most studied (higher vertebrates) are probably least dependent upon their environmental complexes; they are often decidedly migratory and because of their size least adapted to experimental study.

Some quite extensive attempts to correlate geographic range with meteorological conditions have been made but always with only implied reference to the physiological character of the organisms themselves, and usually with the use of *species* as an *index of conditions*. A few factors have been emphasized, and these usually in the sense of barriers. Merriam emphasizes temperature; Walker atmospheric moisture.

Heilprin, like most paleontologists, emphasizes food. There appears to be no adequate basis for the idea that the same single factor governs the distribution of most animals. Such a conclusion probably results from leaving the organism out of consideration.

Since the environment is a complex of many factors, every animal lives surrounded by and responds to a complex of factors, at least in its normal life activities within its normal complex. Can a single factor control distribution?

A large amount of physiological study of organisms has been conducted with particular reference to the analysis of the organism itself, but with little reference to natural environments. Many of the factors and conditions employed in such experiments are of such a nature that the animal never or rarely encounters them in its regular normal life. Other experiments are, however, attempts to keep the environment normal, except for one factor. These have demonstrated that in ordinary reactions an animal responds to the action of a single stimulus. Certain general laws govern the reaction of animals to different intensities of the same stimulus.

a. Laws governing the reactions of animals. The laws governing the stimulation of animals in the experiments of the laboratory are familiar subjects in the textbooks of physiology. With respect to a given factor used in the experiment, it has been found that there is a range of conditions within which the activities of the animal proceed without marked stimulative features. These are called optimal conditions. Take, for example, temperature. There is in most animals which have been subjected to experimentation with temperature, a range of several degrees in which the animal is not markedly stimulated (*optimum*). As the temperature is raised or lowered from such a condition, the animal is stimulated. If the temperature be continuously raised, a point is reached at which the animal dies. The temperature condition just before death occurs is called the maximum. The lowering of temperature produces results comparable in a general way to those of high temperature. The condition just before the death point is reached is called the minimum. With various limitations, unimportant in this connection, the same is true with respect to each of the various factors which an animal encounters in nature. Which factor determines the limitations of occurrence of an animal on the earth's surface? The answer to this is suggested in Liebig's Law of Minimum.

b. Law of minimum. Liebig's law of minimum is summarized by Johnstone:

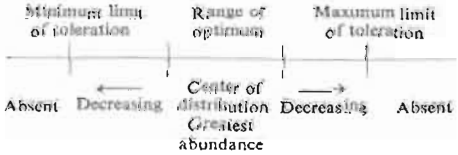
> A plant requires a certain number of food stuffs if it is to continue to live and grow. Each of these food substances must be present in a certain proportion. If it is absent the plant will die; if present in a minimal proportion the growth will also be minimal. This is true no matter how abundant the other food stuffs may be. The growth is then dependent upon the amount of food stuff present in minimal quantity.

In nature this law applies both geographically and locally. As applied to animals it includes both food and material for abode. The presence, absence and success of a species is determined by the necessary material which is absent or present in minimal quantity.

c. Law of toleration of physical factors. We have noted in the case of the tiger beetles, that for the egg-laying to take place the surrounding temperature and light must both be suitable, the soil must be moist, probably also warm, and must satisfy the ovipositor tests with respect to several factors. Egg-laying, the *positive reaction*, is then probably a response to several factors. Furthermore, after the eggs are laid, the conditions favorable for egg-laying must continue for about two weeks if the eggs are to hatch and the larvae reach the surface of the ground. The success of reproduction depends, then, upon the qualitative and quantitative *completeness* of the complex of conditions. The *negative reaction*, on the other hand, appears to be different. The absence of eggs, the number of failures to lay and therefore the number of eggs laid in any situation can be controlled by qualitative or quantitative deficiency or excess with respect to *any one of several factors*. The presence, absence, or number of eggs laid is, then, determinable by a single factor, according as it is near the optimum or near either the maximum or minimum tolerated by the species. It is, however, not necessary that a single factor deviate; the effect is similar or more pronounced if several deviate.

In nature the presence or absence, or success of a species or group of species, its numbers and sometimes its size, etc., are largely determined by the degree of deviation of a factor or factors from the range of optimum of the species or group of species. The cause of the deviation in the factor or factors is not of importance. For example, in the case of a soil inhabiting species such as Cicindela tranquebarica, to which considerable moisture is necessary, the cause of the deficiency in one case may be climatic deficiency in rainfall, in another a rapid drainage due to steep slope and porosity of soil. The former is what we have called a climatic (geographic) condition and the latter a local condition. The evidence for the law of toleration as applying to distribution is good so far as the local distribution is concerned and, since the same factors are involved in the geographic, there is no difficulty in the application of the law to geographic distribution also. The fact that in so far as our observation can go at present, the tiger beetles are found in similar conditions throughout their ranges, is also good evidence for the application of both the laws of minimum and toleration to geographic distribution. In fact the *law of minimum* is but a special case of the *law of toleration*. Combinations of the factors which fall under the law of minimum may be made, which makes the law of toleration apply quite generally; for example: food and excretory products may be taken together as constituting a single factor. From this point of view the law of toleration applies, the food acting on the minimum side, excretory products on the maximum.

d. Application of the law of toleration to geographic distribution. The so-called centers of distribution are often only areas in which conditions are optimum for a considerable number of species. The relation of the law to centers of distribution is shown in the diagram below; above the line is the scale of stimulation with the limits of toleration shown and below the parallel relation of the distribution and relative abundance.



On account of the nature and distribution of climatic and vegetation conditions, it follows that as we pass in one direction from a center, one factor may fluctuate beyond the range of toleration of a species under consideration; but as we pass in another direction it is very likely to be a *different* factor. The divisions of Merriam's zones into arid and humid portions is an illustration of this, and seems to constitute a begging of the temperature question.

4. TENTATIVE LAWS OF DISTRIBUTION

On this general basis tentative laws of distribution may be formulated.

a. Governing the limit of geographic range. The geographic range of any species is limited by the fluctuation of a single factor (or factors) beyond the limit tolerated by that species. In non-migratory species the limitations are with reference to the activity which takes place within the narrowest limits. In migratory species this activity limits the range only during a part of the life cycle.

b. Governing distribution area. The distribution area of a species is the distribution of the complete environmental complex within which it can live as determined (1) by the activity which takes place within the narrowest limits and (2) by the animal's power of migration. Barriers in which some one factor of the complex fluctuates beyond the limits of toleration of the species at all periods of its life-history may prevent the animal from reaching all the suitable habitats, but this is the result of the working of the laws rather than an exception, and faunistic animal geography begins where physiological animal geography ends.

WATER—GENERAL CONSIDERATIONS; THERMAL PROPERTIES

Lawrence J. Henderson—1913

Reprinted by permission of Lawrence J. Henderson, Jr. from The fitness of the environment. New York, The Macmillan Co., 1913.

In this "inquiry into the biological significance of the properties of matter" Henderson, a biochemist, defends the hypothesis that ". . . the actual environment is the fittest possible abode of life." In doing so, the ecologist was provided with a new framework of reference for more circumscribed study and a considerable insight into environmental influences of an overriding sort.

GENERAL CONSIDERATIONS

It was assuredly not chance that led Thales to found philosophy and science with the assertion that water is the origin of all things. Whether his belief was most influenced by the wetness of animal tissues and fluids, or by early poetic cosmogonies, or by the ever present importance of the sea to the Ionians, however vague his conception of water may, indeed must, have been, he at least expressed a conclusion which proceeded from experience and serious reflection. . . . And it is especially worthy of note that of earth, air, fire, and water the last is the only one which happens to be an individual chemical compound. From that day to this the unique position of water has never been shaken. It remains the most familiar and the most important of all things. . . .

. . . In physics, in chemistry, in

geology, in meteorology, and in biology nothing else threatens its preëminence. . . and the physiologist has found that water is invariably the principal constituent of active living organisms. Water is ingested in greater amounts than all other substances combined, and it is no less the chief excretion. It is the vehicle of the principal foods and excretory products, for most of these are dissolved as they enter or leave the body. Indeed, as clearer ideas of the physico-chemical organization of protoplasm have developed it has become evident that the organism itself is essentially an aqueous solution in which are spread out colloidal substances of vast complexity. As a result of these conditions there is hardly a physiological process in which water is not of fundamental importance. . . .

All of these circumstances. . . depend in great part upon the quantity of water which is present outside the earth's crust, and upon its often unique physical and chemical properties. . . .

Of the total extent of the earth's surface the oceans make up about three fourths, and they contain an amount of water sufficient, if the earth were a perfect sphere, to cover the whole area to a depth of between two and three miles. This corresponds to about 0.2 per cent of the volume of the globe. The occurrence of water is, moreover, not less important and hardly less general upon the land. In addition to lakes and streams, water is almost everywhere present in large quantities in the soil, retained there mainly by capillary action, and often at greater depths. The atmosphere also contains an abundance of water as aqueous vapor and as clouds. Now the very occurrence of water upon the earth, and especially its permanent presence, is due in no small degree to its chemical stability in the existing physical and chemical conditions. This stability is of great moment in the various inorganic and organic processes in which water plays so large a part. In the first place the chemical reactions in which it is concerned during the process of geological evolution, though they are no doubt in the total of great magnitude, are both slow and far from violent. Long since any very active changes of this sort, so far as the superficial part of the crust is concerned, have run their course. In the second place water is really, at the temperature of the earth and in comparison with most other chemical substances, an extremely inert body, for the union of hydrogen with oxygen is so firm that it is not readily dissolved.

Thus water exists as a singularly inert constituent of the atmosphere, as a liquid nearly inactive in chemical processes on the surface and in the soil, and everywhere as a mild solvent which does not easily attack the substances which in great variety dissolve in it. The chemical changes which do follow upon solution are not such as to produce substantial chemical transformations, and most substances can pass through water unscathed. The nature of water, then, is a great factor in the chemical stability, which, no less than the physical stability of the environment, is essential to the living mechanism. But it may be questioned if such stability would not necessarily be ultimately attained in greater or less degree with almost any other substance, as a result of the general tendency of chemical processes to reach a condition of equilibrium, and it will therefore be well to turn to more secure fields of inquiry.

THERMAL PROPERTIES

Specific heat. First among these is the heat capacity or, as it is more commonly termed, the specific heat of water. This quantity has the value of

1.000 for the interval between 0° and 1° centigrade, a number which is due to the choice of water in defining the calorie or fundamental unit of heat. The calorie, small calorie, or gram calorie is that quantity of heat which is required to raise the temperature of one gram of water through 1° centigrade, and it varies slightly with the temperature, having the relative values 1.000 for the interval from 0° to 1°, 0.998 for the interval from 4° to 5°, 0.992 for the interval from 15° to 16°, and its mean value for the interval from 0° to 100° is 1.004. The heat capacity of water is then 1.000, in that 1.000 calorie is required to raise the temperature of 1.000 gram of water through 1.000 degree centigrade. . . .

The most obvious effect of the high specific heat of water is the tendency of the ocean and of all lakes and streams to maintain a nearly constant temperature. This phenomenon is of course not due to the high specific heat of water alone, being also dependent upon evaporation, freezing, and a variety of circumstances which automatically mix and stir water. But in the long run the effect of high specific heat is of primary importance. It will be convenient to postpone consideration of the regulation and importance of the constant temperature of the ocean until the other properties of water which contribute thereto have been discussed.

A second effect of the high specific heat of water is the moderation of both summer and winter temperatures of the earth. It is not easy to estimate the total magnitude of this effect, but the manner in which it comes about is well illustrated by the differences between seaboard and inland climates or between the climate of a large part of the United States, which is a continental climate, and that of Western Europe, which is essentially an insular climate. In the most extreme form such moderation of climate is to be observed on the high seas and upon small islands. There are found the smallest known differences between the mean temperatures of different months of the year and of different hours of the day, and the least tendency to violent changes of temperature. The calculation of Zenker regarding normal temperatures may be cited as a good illustration of the nature of the case.

Latitude	Continental Climate	Marine Climate	Difference
Degrees	Degrees	Degrees	Degrees
0	34.6	26.1	−8.5
10	33.5	25.3	−8.2
20	30.0	22.7	−7.3
30	24.1	18.8	−5.3
40	15.7	13.4	−2.3
50	5.0	7.1	2.1
60	−7.7	0.3	8.0
70	−19.0	−5.2	13.8
80	−24.9	−8.2	16.7
90	−26.1	−8.7	17.4

It is unnecessary to discuss the effects upon living organisms of the equable temperature of the ocean and of the moderation of climate, for obviously we are here confronted by a true instance of regulation of the environment.

The high heat capacity of water operates in still another manner to regulate temperature upon the land and at the same time to increase the mobility of the environment of marine organisms. For directly or indirectly it is involved in the formation and duration of ocean currents, especially the movement of water in the depths from the polar to the tropical seas, and it determines the amount of heat carried by such currents. A similar and even more important "function" is the direct promotion of winds, with the resulting distribution of aqueous vapor throughout the atmosphere, a primary factor in the dissemination of water by means of the rainfall. Here the essential thing is the existence of a vast warm reservoir in the tropics and of two similar cold reservoirs at the poles.

Under these circumstances the circulation of winds, bearing away water vapor from the tropical oceans, is inevitable, and the process is intensified by the high specific heat of water.

The living organism itself is directly favored by this same property of its principal constituent, because a given quantity of heat produces as little change as possible in the temperature of its body. Man is an excellent case in point. An adult weighing 75 kilograms (165 pounds) when at rest produces daily about 2400 great calories, which is an amount of heat actually sufficient to raise the temperature of his body more than 32° centigrade. But if the heat capacity of his body corresponded to that of most substances, the same quantity of heat would be sufficient to raise his temperature between 100° and 150°. In these conditions the elimination of heat would become a matter of far greater difficulty, and the accurate regulation of the temperature of the interior portion of his body, especially during periods of great muscular activity, well-nigh impossible. Extreme constancy of the body temperature is, of course, a matter of vital importance, at least for all highly organized beings, and it is hardly conceivable that it should be otherwise. In the first place marked influence of change of temperature upon chemical reaction is almost universal, and as a rule an increase of 10° centigrade in temperature will more than double the rate of a chemical change. Secondly all living organisms contain both chemical substances and physico-chemical structures or systems which begin to be altered, and usually irreversibly altered, at a temperature which is very little above that of the human body. It is perhaps imaginable that conditions might be otherwise in beings of a very different kind, but to-day every chemist well knows that if he is to control a chemical process, almost the first desideratum is rigid regulation of the temperature at which the process takes place.

It is therefore incontestable that the unusually high specific heat of water tends automatically and in most marked degree to regulate the temperature of the whole environment, of both air and water, land and sea, and that of the living organism itself. Likewise the same property favors the circulation of water by facilitating the production of winds, besides contributing to the formation of ocean currents. Here is a striking instance of natural fitness, which in like degree is unattainable with any other substance except ammonia.

HEAT EXCHANGE NEAR THE GROUND; COLD AIR FLOODS AND COLD AIR DAMS

Rudolf Geiger—1941

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These excerpts are typical of the direction that the German meteorologist Geiger brought to ecology—namely that the environment immediately associated with the organism, the microclimate, is the critical factor, not the gross, or macroclimate typically measured. This distinction is extensively treated by J. N. Wolfe, R. T. Wareham and H. T. Scofield (1949. Microclimates and macroclimate of Neotoma, a small valley in central Ohio. Ohio Biological Survey Bulletin **41***: 1-267). An excellent application of the microclimate approach in ecology is that by John Cantlon (1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. Ecological Monographs* **23***: 241 270). David Gates has written a concise, sophisticated and ecologically oriented treatment of energy exchange (1962. Energy exchange in the biosphere. New York, Harper and Row.)*

MIDDAY HEAT EXCHANGE AT THE GROUND SURFACE

THE INCOMING RADIATIONAL TYPE

At the upper limit of its atmosphere the earth receives a vertical solar radiation amounting to about 2 calories per square centimeter each minute. This value is called "solar constant." At European latitudes normal incidence does not occur. There the horizontal surface receives at the border of the atmosphere only a portion of the solar constant. When this radiation penetrates the earth's atmosphere it suffers a series of losses. . . .

A considerable portion of the enormous incoming sun energy is reflected by the surface of the clouds and is ineffective concerning the heat economy of air and ground. As an average for the northern hemisphere and the year, this amount is 33% of the incoming radiation. In the atmosphere another portion of radiation is scattered in all directions diffusely by the air molecules themselves and by substances suspended in the atmosphere (dust, plankton). The radiation does not suffer a loss in the true sense of the word but only a deflection from its original direction. But because a portion of the scattered radiation goes back to universal space also this portion is eliminated with regard to the terrestrial heat exchange. Reflections from clouds and diffuse scattering into universal space make together 42%. The reflecting power (albedo) of the earth, therefore, is 0.42; for the inhabitant of universal space the earth looks about as bright as Venus does for our eyes.

The third loss is the absorption of radiation caused by ozone, water vapor, and carbonic acid; this is a true loss in that the radiation energy is used to increase the temperature of the absorbing gases and, therefore, is eliminated from the insolation economy. What happens with this portion is not discussed in this book.

Despite the enormous distance the sun rays have to pass through from the limit of the atmosphere down to the

bottom of the atmosphere, a mighty radiation flux penetrates down to the earth's surface partly as direct sun radiation, partly as scattered radiation from the sky. The two together represent the main portion of the solar heat at the disposal of the heat economy of earth and air. Wherever this immense energy current strikes upon the surface of the solid ground the radiation cannot penetrate this obstacle. A portion is reflected from the surface. Most of it is absorbed, changed into heat, and serves to raise the temperature of the ground.

The earth's surface, then, plays the most important part in midday heat exchange, but the layer of air next to the ground is that part of the atmosphere whose temperature relationships are most directly determined by the relationships of the surface itself. Observations of this lowest layer of air are therefore indispensable to studies of heat transfer. . . .

The temperature conditions of the layer near the ground are determined by the immense amount of heat which the surface of the ground absorbs. In summer, this surface is heated in our region up to 60°C, sometimes to 70° and 80°. . . . The temperature of the surface would be increased even much more if a heat loss—caused and maintained by the temperature contrasts—did not take place upwards and downwards. . . . One portion of the heat is conducted from the surface to the deeper layers of the ground. . . . The greater portion serves to heat the air layer near the ground and thus, indirectly, to heat the atmosphere. Partly also here, heat conduction is effective, but. . . . it does not play an important role as far as quantity is concerned. Primarily, convection and radiative pseudo conduction come into consideration. . . .

Furthermore, the ground loses much heat as a consequence of evaporation since the surface is deprived of 600 gcal if one gram of water evaporates; this is an amount of heat which would suffice to heat 6 g water from 0°C to the boiling point.

From the significance of the earth's surface for heat exchange it can be concluded that the highest temperature at about noon is at the boundary between ground and air; starting from here, the temperature decreases upward and downward. This kind of temperature distribution at noon time is called *"Incoming Radiation Type."* The real character of this type will be demonstrated by an extreme example.

Fig. 2 gives the temperature distribution which J. G. Sinclair observed at the Desert Laboratory at Tucson on June 21, 1915, at 1 PM. As we approach the ground from above, the temperature rises continuously and at an

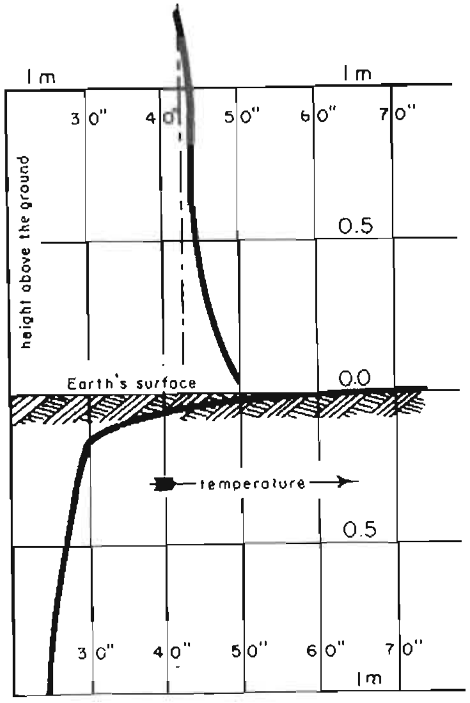

FIG. 2. *The incoming-radiation (insolation) type. (Tucson, 21 June 1915)*

increasingly rapid rate. At the surface there is a temperature discontinuity between air and earth. The surface itself possesses the highest temperature, not measured here, but in any case far above 71.5°, the measurement at a depth of 4 mm in the ground. In the first 10 cm of earth the temperature decreases with extraordinary rapidity, so that at a depth of 7 cm it is already several degrees below the air temperature. The effect of the time of day, the temporary noon-time heating, extends to a depth of only about 10 cm, as the break in the temperature curve indicates. In the lower earth layers the temperature falls again slowly.

Extremely high midday temperatures are therefore, as the illustration indicates, limited to the air and soil layers immediately bordering the earth's surface. Even under our mild climatic conditions the same holds true, though to a lesser extent. . . .

COLD AIR FLOODS AND COLD AIR DAMS

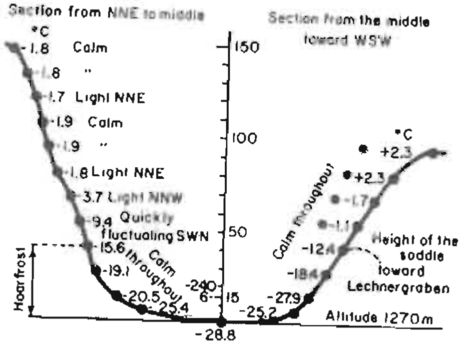

FIG. 89. *Temperature distribution in the Gstettneralm sink hole near Lunz on January 21, 1930. (After Wilhelm Schmidt)*

Fig. 89 is a cross-section of a "sink hole," a rock kettle shut in on all sides, resulting from subsidence. It is near Lunz in lower Austria and is called the Gstettneralm (1270 m above sea level). Wilhelm Schmidt initiated there a great bioclimatic cooperative project of temperature measurements on the slopes of the sink hole and was able to demonstrate relatively very low night temperatures in the kettle. The cross-section shown in Fig. 89 exaggerates the altitude somewhat. The temperatures which were taken with an Assmann aspiration psychrometer before sunrise on Jan. 21, 1930 are entered at the points of observation. Simultaneous data on wind relationships are given as well. The left side of the illustration gives the section from north-northeast to the middle of the sink hole. On the upper part of the slope for some 70 m down the temperatures are from 1° to 2° below zero. As we descend still further the temperature drops with extraordinary rapidity and on the floor of the kettle reaches −28.8°C. The cold air from the slopes accumulates there and cannot escape. The heavy frost which formed in the lowest 40 m was a visible evidence of this stratification.

In the right hand half of Fig. 89 is a cross-section from the middle toward the west-southwest. Here the sink hole is intersected by a saddle. Temperatures below freezing prevail up to the height of this saddle. Inasmuch, however, as the cold air can flow over the saddle at this point, the temperatures above the saddle increase rapidly. If we look across at the left half of the illustration we can recognize the effect of this overflow on that side of the sink hole.

The Gstettneralm and Schmidt's measurements have attained fame in that during the well-known severe winter of 1928–29 the lowest minimum temperatures of all middle Europe were observed there, −48°C. A microclimatic phenomenon has here, as so often elsewhere, taken the record away from the macroclimate. It is significant, also, that during the following winters as low as −51° was observed at the same place—an indication that it is not so much the winter weather conditions as a whole, as it is the local, temporary conditions which lead to such extreme temperatures. In the work of W. Schmidt mentioned above, we see in particular the peculiarly conclusive thermogram from the bottom of this sink hole.

Even in midsummer temperatures below freezing are reached in the sink hole, and it is self-evident that the plant world and the animal world must adapt themselves to these local conditions. At the bottom of the sink hole the plant growth consists of only a few hardy grasses and a few herbaceous plants which can maintain themselves under protection of the snow cover in winter, while in midsummer they hurry through their growing season in a few weeks. As one ascends the side of the sink hole, dwarf pines appear first, then stunted spruces and snow roses. Farther up the spruces become larger and are mingled with alpine roses. At the upper rim of the sink hole is a normal forest. The reversal of normal temperature stratification resulting from the flood of cold air is thus reflected in a reversed plant stratification. Whereas the forest usually ceases as we go upward, it comes to an end here as we descend into the sink hole. Even in the animal world there appears a similar dependence of kind and number of kinds on the relative height in the sink hole. . . .

THE UTILIZATION OF SOLAR ENERGY BY AQUATIC ORGANISMS

George L. Clarke—1939

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In discussing the variation in amount and nature of light with depth and kind of body of water, Clarke demonstrates the modification of one environmental factor (light) by another (water). In the latter half of the paper, the regulatory effect of light in limiting the distribution and photosynthesis of organisms is emphasized. Dr. Clarke's long association with the Woods Hole Oceanographic Institution (since 1931) provided the strong marine flavor to his text (1954. Elements of ecology. New York, John Wiley & Sons, Inc.).

. . . . Research in this field falls roughly into two parts, namely, (1) the determination of the amount and nature of the light actually present at various depths in all types of water bodies, and (2) the measurement of the extent to which submerged organisms are able to utilize the light present. From the biological point of view we need to know not only the range of light intensity at any point but also its spectral composition, its angular distribution, and its distribution in time.

The solar energy which falls upon a body of water is subject first of all to a "surface loss" which in the case of the ocean may amount to as much as 60 per cent in rough weather. Only about 3 to 9 per cent of this is ordinarily due to reflection (for solar altitudes greater than 30°) and the remainder has been found to be caused by a greatly increased rate of extinction in the uppermost meter of water. . . .

As the light passes from the surface downward into the water, it is reduced in intensity according to the following equation:

$$\frac{I}{I_0} = e^{-kL}$$

where I_0 is the initial intensity, I is the final intensity, k is the extinction coefficient, L is the thickness of the layer in meters, and e is 2.7. When this relationship between the reduction in the light and the thickness of water through which it has passed is expressed graphically on a semilogarithmic plot, a straight line is obtained (Fig. 1).

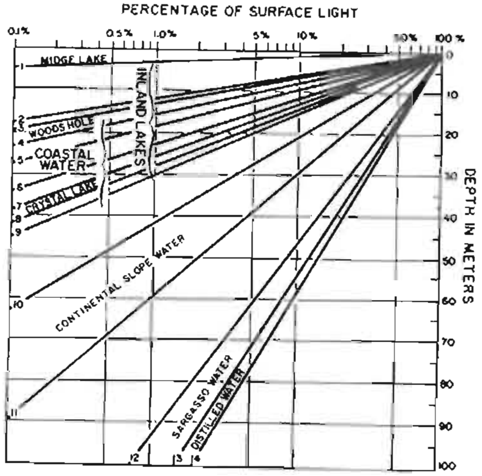

FIG. 1. *Comparison of the rates of penetration of the yellow-green component of daylight into natural waters (Photometer sensitive to wave lengths 5000–6000 Å). Curves show the relation between depth and illumination expressed as a percentage of the light at the surface. The curves represent the* average *value of the extinction coefficient for each series and no "surface loss" is included.*

The slope of the line is determined by the value of the extinction coefficient, k, which is thus an index of transparency. The extinction coefficient varies widely in the different parts of the spectrum—even for pure water—and its actual value depends upon the precise wavelength considered. In Fig. 1 the rate of absorption of red light by distilled water is seen to be very high, that for yellow light lower, and that for blue light very much lower. For example, after traversing 70 meters of distilled water blue light has suffered only a slight reduction to 70 per cent of its initial value, whereas yellow light has been reduced to 6 per cent. In the case of red light a reduction to 6 per cent has already taken place after passing through less than 3 meters of water.

Now the energy of the sun as it reaches the surface of a natural body of water is not equal in all parts of the spectrum. . . . We therefore start with unequal quantities of energy at the different wavelengths and these are absorbed at unequal rates as the light penetrates into the water. The result is that after passing through successive meters of water the spectral composition of the light present becomes rapidly and profoundly altered. The infrared and red components are reduced to small quantities within a very few meters and the ultraviolet, which was initially of small magnitude, soon drops to a minute fraction of the whole. As a consequence, after sunlight had traversed 100 meters of distilled water nothing but the blue component with a little green and violet would remain. . . .

In most natural waters the rate at which light penetrates is further decreased by the presence of varying amounts of suspended particles and dissolved material. The great diversity which results in the transparency of natural waters may be appreciated by comparing the curves of light penetra-

tion for certain typical lakes and oceanic areas in various parts of the world (Fig. 3). As will appear presently, only those measurements can be fairly compared which were made within the same part of the spectrum. In the figure observations with photometers sensitive to the yellow-green region (maximum 5500Å) are presented. Sargasso water is seen to be nearly as transparent as distilled water in this spectral region and light is reduced to 1 per cent of its surface value at about 100 meters. Beyond the edge of the continental shelf 100 miles or more from the coast in both the Atlantic and the Pacific the transparency is such that the 1 per cent value is reached at about 50 meters. In coastal waters the same value occurs at between 30 and 15 meters. Although there are a few inland lakes which are as clear as typical coastal waters, the majority of them are more turbid. In Midge Lake, for example, the illumination has been reduced to 1 per cent of its surface value at 3 meters. The extreme range of possible transparency in natural waters is thus very great.

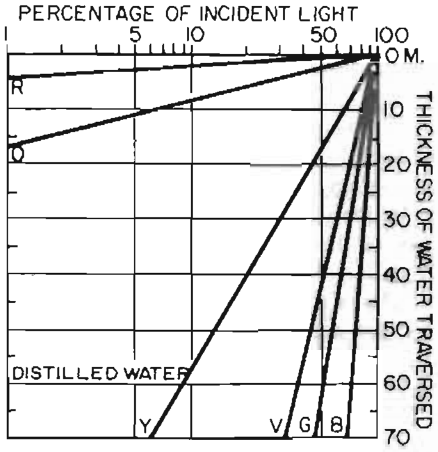

FIG. 3. *Transmission of light by distilled water at 6 wave lengths within the visible spectrum. Curves show the percentage of incident light (logarithmic scale) which would remain after passing through the indicated thickness of water.*

In the various natural waters we find that the *relative* rates of absorption of *different parts of the spectrum* are not the same as those characterizing distilled water. This situation is brought about by the fact that both the suspended and the dissolved material present have a *selective* action on light beyond that of the water itself, and the nature of the selective effect varies widely from one body of water to another. As a result it becomes necessary to measure separately the rate of penetration of each spectral region for each lake or oceanic area. . . .

The distribution in time of the illumination at any point is controlled by changes in the length of day and by seasonal variation in transparency. The latter is of vital importance since it has been shown to be chiefly responsible for the tremendous differences in amount of light received daily by organisms at only moderate depths—as much as 10,000 × at 30 meters. The agents causing changes in transparency, however, are not adequately known and present another opportunity for research.

In dealing with the utilization of the light energy by aquatic animals and plants, separate consideration will be given to the major subdivisions of the solar spectrum to which the following magnitudes may be roughly assigned: Infrared, 41 per cent; ultraviolet, 7 per cent; and visible, 52 per cent. . . . the infrared radiation is almost entirely absorbed in the uppermost meter. The chief importance of the infrared is, therefore, the rapid heating of the surface stratum.

Ultraviolet light in large amounts is injurious to plankton and other organisms, but according to ZoBell and McEwen virtually no bactericidal radiations penetrate sea water to as great a depth as 3 meters. The beneficial effects of ultraviolet in vitamin formation and in other poorly understood ways call for exact measurements of its rate of penetration. Yet serious disagreement exists on the rate of absorption of ultraviolet light even for distilled water!

. . . . Previously it had been supposed that ultraviolet was absorbed very rapidly by pure water itself, but the observations of James and Birge indicate a much lower absorption at least as far as 3600Å. It is essential to know whether this low rate continues to hold for the shorter, and more important, wavelengths or whether there is an abrupt upward turn. . . .

Turning now to the visible component of the spectrum, we find that many observations exist on the degree of activity of fish and of plankton animals in relation to its intensity. The information obtained, however, has not yet been adequately applied to the ecological relationships of the species concerned. A prominent case in point is the diurnal migration of plankton. Although research in this field has shown conclusively that the daily change in illumination is primarily responsible for the migration, the internal physiological reactions which control direction and speed of swimming are poorly understood. . . . Even less clear are the reasons why the vertical migration of one species differs from that of another and why the behavior of the same species varies profoundly from time to time and from place to place. . . .

The intensity of illumination controls photosynthesis and hence limits the depth of growth of both bottom-living and pelagic plants. For example, the lower limits for fixed plants in the following oceanic areas are: in Baltic, 20 meters; off Iceland, 50 meters; and in Mediterranean, 130–160 meters. In lakes the lower limits are: Trout Lake, 10–12 meters; Crystal Lake, 15–20 meters; and in Crater Lake, 12 meters. The maximum abundance of phytoplankton has been reported at the following depths: off Syracuse, 50 meters; off California, 25–55 meters; and in north European waters, 10–30 meters. At these depths most of the radiant energy present is in the green or blue, but red light is most effective for photosynthesis. Diatoms and other algae appear, however, to be able to use other parts of the visible spectrum effectively. The mechanism which makes this possible requires elucidation.

The relative rates of photosynthesis at various levels beneath the surface have been investigated by measuring the oxygen evolved by phytoplankton placed in bottles and suspended at different depths. Near the surface the illumination has sometimes been found sufficiently strong to inhibit photosynthesis, although the exact explanation for this is wanting. . . . Below the point of maximum photosynthesis the rate drops off to a depth at which no appreciable reaction takes place, but respiration continues at all levels to which living cells may be distributed. The intensity of light at which photosynthesis just balances respiration is termed the compensation intensity, the value of which has been reported in two recent investigations as 500 lux and 350 lux (or 0.3 per cent of noon sunlight) respectively. . . . Since the compensation intensity will naturally vary from species to species, further determinations for types important ecologically are seriously needed. The depth at which the compensation intensity is found, known as the compensation point, has been located (for short intervals) in a number of cases: Sargasso Sea, greater than 100 meters; English Channel, 45 meters; Gulf of Maine, 24–30 meters; East Sound (W. coast of Canada), 10–19 meters; Trout Lake, Wis., 8–16 meters; Woods Hole

Harbor, 7 meters. The depth of the compensation point over an average 24 hour period is, however, the significant value from the point of view of the continued growth and ecological role of each species. Marshall and Orr, working in the Clyde Sea area, found that on this basis the depth varied from 2 meters to 30 meters according to the season. . . .

It thus appears that most of the light incident on the surface of lakes or oceanic areas is absorbed by the water itself or by detritus and that only a very small part can be utilized by plants or animals. We conclude that aquatic organisms are existing under very unfavorable circumstances in regard to the utilization of solar energy. It is for this reason that the intensity, amount, and composition of the light are so frequently found to be limiting or highly significant factors in the aquatic environment. . . .

FACTORS EFFECTING VEGETATIONAL ZONATION ON COASTAL DUNES

Henry J. Oosting and W. Dwight Billings—1942

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This paper is an excellent example of procedure and interpretation in environmental analysis. The first portion considers several factors which might determine the distribution of plants on a local scale. Field measurements and observations are the basis for eliminating all but one of the various agents. Direct experimentation is then used to corroborate that factor as being of major regulatory significance in zonation. In addition to the substantial investigations of both authors, Dr. Oosting is the author of a widely used text (1956. The study of plant communities. San Francisco, Freeman and Co.).

The coast of North Carolina is discontinuously paralleled by a series of narrow, usually elongate islands. These low-lying sand "banks" may support a sclerophyllous forest in which live oak (*Quercus virginiana* L.) predominates and which includes numerous characteristic species of southern affinity. . . .

Because of the full exposure to almost constant wind from the ocean, a slight disturbance of the vegetative cover may result in extensive "blow outs" of the unconsolidated soil. Once initiated, the shifting of the sand may not be checked naturally for years. Man's activities have contributed materially to the destruction of cover. Grazing has been particularly serious, for it has indirectly transformed several of the banks into almost barren seas of shifting sand.

Today, grazing has been largely discontinued and, on government controlled areas particularly, much time and effort have been expended in attempts to stabilize the shifting dunes. Miles of brush barriers have been constructed and thousands of acres have been planted with grasses. The success of these attempts cannot yet be evaluated.

One of the most effective native sand-binding grasses is sea oats (*Uniola paniculata* L.) which is found in abundance on these coastal dune areas. The importance of this species and its associates as natural stabilizers prompted an investigation of the environmental factors governing their distribution. A portion of Bogue Bank near old Fort Macon at the entrance to Beaufort harbor, North Carolina, was chosen for intensive study. The area has been relatively undisturbed in recent years and illustrates all degrees of stability and vegetational development. The exposed position of the bank subjects it to the full sweep of the ocean wind and the pounding surf.

The ocean side of the bank is bordered by a sand beach of varying width which terminates at a low (5–15 ft.) foredune. Behind this is an extensive depression sometimes covered with small dunes in all stages of development and stability, sometimes blown out to a depth very near the water table. This area may be only 150 feet wide but is often 600 feet or more in width, and it terminates inland at a relatively high rear dune which may be 40 feet high. The rear dune forms a ridge down the center of the bank and obviously affords shelter to the leeward, for here vegetation is much less disturbed and woody species predominate, usually forming dense thickets whose tops rarely extend above the crest of the dune. . . .

THE VEGETATION

. . . Size and habit make *Uniola paniculata* and *Andropogon littoralis* the most conspicuous plants on the area. They may grow intermixed but where one is relatively abundant the other is not important. One of the objectives of the transect mapping was to determine the relative abundance of the two species in different positions on the dunes. The transect data. . . show that these two species far exceed all others in number and cover and that there are certain zonal concentrations which are probably general. Uniola exceeds Andropogon on the foredune (zones I and II) and on the crest of the rear dune (zone V). Andropogon is more abundant in the protected depression between the large dunes (zone III). On the windward slope of the rear dune (zone IV) either may predominate. On transect 1, Uniola is more important in this zone, but whenever the slope is fairly stable, as on transect 2, Andropogon predominates, especially on the lower portion bordering zone III. . . .

THE ENVIRONMENT

Soil factors. . . . It seemed plausible that soil moisture might be a factor in determining differences in vegetation. Field water content, therefore, was determined at three different times during the study. Duplicate samples were taken at depths of 10 cm. and 20 cm. at each of the 10 stations and also in the blowout area (zone IIIa). . . .

There seem to be no significant differences between the moisture contents at the various stations except for the obviously higher percentages recorded from the moist depression at station 3A on transect 1. Usually there is somewhat more moisture at the 20 cm. depth than at 10 cm. The lowest values are exhibited at the first and last stations on each transect. . . .

Observation of a visible spray of salt water from the surf suggested the possibility that wind-deposited salt on the surface of the soil might be rain-leached into the soil increasing the osmotic concentration of the soil solution. Absorption of water, transpiration rates, and water requirements have all been shown to be reduced as the salt content of the soil increases. . . . If concentrations of salts in the dune sand are sufficiently different at different stations, this might serve as a selective factor in determining the distribution of dune plants.

Soil samples of one hundred grams each were taken at the transect stations from the upper 10 cm. and the second 10 cm. Each sample was soaked in 200 ml. of distilled water for one hour and then 50 ml. portions of the water were titrated and salt calculated as NaCl. The highest salt content found was 1.81 mg. per 100 gm. of soil, which is only 0.0018 per cent of dry weight. There seems to be no reason to suppose that such minute quantities of salt could chemically or osmotically affect the growth or distribution of plants on the dunes.

Considering the amount of salt spray carried over the dunes, it is obvious that leaching must be very rapid to maintain the low salt concentrations at root depths. A possibility also exists that the dune plants may absorb some of this soil salt. Our limited data indicate a variation from day to day in the salt content of the soil and that the concentration at 20 cm. is rather consistently less than at 10 cm. (2 to 40 per cent). There is likewise variation from station to station which is paralleled on the two transects. The windward side of the foredune has the highest concentrations, the crest of the foredune the next highest. This is as might be anticipated in terms of wind-borne salt spray. The crest of the rear dune, which yields the third highest salt spray catches, is lowest in soil salts (0.94 mg. per 100 gm. of soil). . . .

Soil pH throughout the dunes area ranges from 7.4 to 7.9. Usually there is a greater amount of shell material in samples with the higher values. No consistent differences between stations or depths are apparent. . . .

Surface soil temperatures of 125–127° F. are not uncommon in the early afternoon sometime after the sun has reached its peak but at the same time air temperatures do not exceed 95–100° F.

Soil temperatures at 4 and 10 inches likewise respond to fluctuations of atmospheric temperature, but the magnitude of variation is much less than at the surface and the lag is greater. Highest temperatures recorded at a depth of four inches are 95° F. at 2:00 P. M. and at the same time 89° F. at ten inches. . . .

No soil temperature variations were noted which can be interpreted as factors in the zonal distribution of a species. . . .

ATMOSPHERIC FACTORS

Hourly determinations of air temperature taken simultaneously at all stations during a day show much variation, with no apparent correlations with zones or topography. . . .

. . . Evaporation is consistently somewhat higher at stations on transect 2 than at those on transect 1. At all stations, evaporation rates are three to four times as great by day as by night.

The greatest overall loss on both transects is at station 5 atop the rear dune, and the loss at station 2 on the foredune is almost as great. This suggests a possible correlation with the distribution of Uniola, for the species has its best development at or near these stations. The least evaporation takes place at station 3 sheltered by the foredune. Losses on the windward side of the foredune and rear dune (stations 1 and 4) are all of about the same magnitude.

By day the greatest evaporation is on the foredune (station 2) followed in decreasing order by stations 5, 4, 3 and least of all on the windward side of the foredune (station 1). The night rates of loss indicate a quite different pattern, for station 5 has the highest values followed by stations 1, 2, 3, and 4. The greater daytime evaporation in the exposed situations may contribute to the presence of Uniola and the absence of Andropogon in such places. . . .

. . . On these dunes, the relative humidity decreases from the foredune inland to the top of the rear dune. On transect 1, the humidity is invariably lower on the beach than on the foredune but the reverse is true on transect 2.

The data suggest no strong relationship between the distribution of vegetation and relative humidity on the dunes.

Both evaporation and relative humidity are profoundly influenced by the more or less constant wind from the direction of the sea. Other factors being equal, places in the lee of sheltering dunes will lose less water by evaporation than exposed positions in front of or on the crests of dunes. . . .

That the effect of this wind on dune vegetational zonation is not confined to its evaporational influence is clearly shown by the results obtained with the salt spray traps described above. The amount of salt spray and the distance it is transported are largely determined by wind. The total NaCl intercepted by 5 traps on a transect for any single run ranged from 29 mg. on a calm day to 121 mg. on a windy day when breakers were rolling. Again, the relative amount of spray striking at a station varies from day to day, and this too depends upon wind velocity.

Regardless of weather and the amount of salt transported by the wind, the salt catch values for the windward side of the foredune (station 1) are always 40 to 50 per cent of the total salt intercepted on the transect during an exposure of the traps. Then, ordinarily, the crest of the foredune is exposed to the next highest amount of spray and, surprisingly, the crest of the rear dune receives the next highest amount. Successively, the leeward side of the foredune receives relatively much less and the base of the rear dune the very least (only about 15 per cent of the total).

Apparently much of the salt spray is dropped on the foredune as the wind rises from the water. Then as it passes over the depression behind the foredune, there is no obstruction until the rear dune is reached. Some of the spray is lost between the two dunes, perhaps by gravity. However, it would appear that the real force of the wind is deflected upward by the foredune and its first obstruction thereafter is the crest of the rear dune.

Here, then, is a factor which shows some correlation with the distribution of the two major dune species. Uniola is invariably found in areas of greatest exposure, whether the soil be stable or not. Andropogon predominates on protected areas and on the seaward slope of the rear dune but not on its crest. Assuming that salt spray is the factor limiting or controlling the two species, one may suppose that the lower portion of the windward slope of the rear dune consistently receives a minimum of salt spray (as at station 4) and that only the crest of the dune is subjected to the heavy spray content of the wind rising from the foredune. . . .

PHYTOMETER STUDIES

In table V a summary is presented of the relative responses of the three grass species during the phytometer treatments. Detailed observations were made at the time of transplanting (August 1), and again 12 days after treatment was begun, 8 days later, and finally when the experiment was terminated (September 1). The symbols

used in the table indicate the condition of the plants relative to that of the last preceding observation. . . .

The phytometer experiments suggest several generalizations. Andropogon and Uniola are relatively unaffected by low soil moisture over considerable periods of time but, because of a probable lower moisture requirement, Uniola is capable of longer survival under extreme conditions. Under comparable low moisture conditions Spartina will die before the other two species show much indication of suffering. Andropogon cannot live for long when salt water is added to the soil but Uniola is much less affected. Daily watering is less favorable to all three species than watering on alternate days. Probably better growth is possible under wider intervals of watering. Salt spray is seriously injurious to Andropogon, affects Uniola only slightly, if at all, and has no effect on Spartina.

TABLE V. *Responses of plants of three dune species to watering and spraying treatments at intervals during a month. The symbols indicate: (○) unaffected; (+) improved in appearance, either in color or new growth; (−) declining, unhealthy or dying. The first symbol in each group compares the plants to their field condition, the second is compared to the first, and the third to the second*

	Uniola	Andropogon	Spartina
No treatment	○ ○ +	○ + −	○ ○ −
Water daily	○ ○ ○	○ + ○	− ○ ○
Water alternate days .	○ ○ +	○ + +	− ○ +
Seawater daily	− ○ −	− − −	− ○ +
Water daily and seawater spray daily . .	○ ○ ○	− − −	○ ○ ○

DISCUSSION AND CONCLUSIONS

The transect data serve to corroborate the zonal distribution of the major species on the Ft. Macon dune area and to show the relationship of these zones to topographic features. Such a distribution is usually explainable on the basis of exposure, soil, temperature, or moisture relationships. Here, however, the usual factors do not seem to control the situation. The soil is uniform or nearly so, soil moisture does not seem to vary characteristically for the zones nor sufficiently to have any strong influence. Temperature of the soil and air varies widely and inconsistently. Relative humidity and evaporation rates are greatest at the crests of the fore and rear dunes. None of these factors seems to be strongly correlated with the distribution of the dominant species.

The phytometer studies show that Uniola and Andropogon require very little moisture to survive and, in fact, do better under low soil moisture conditions than when watered daily. Thus, the deep depressions are left to more mesophytic species. If the depressions are periodically flooded with salt water *Spartina patens* is dominant. If moist with seepage water, the low places are predominantly occupied by *Fimbristylis castanea.* The phytometer experiments further show that the water requirement of Uniola is less than that of Andropogon. This may be a factor contributing to the predominance of Uniola on the crests of the dunes where evaporation is greatest and may partially explain its success as a pioneer dune former in dry and shifting sand. However, the relative tolerance of the two species to salt spray is such that Andropogon dies under exposures which scarcely affect Uniola. Apparently, the general distribution of the two species on the dunes is largely controlled by the extent of exposure of the habitat to wind-borne spray. . . .

FURTHER STUDIES IN PHOTOPERIODISM, THE RESPONSE OF THE PLANT TO RELATIVE LENGTH OF DAY AND NIGHT

W. W. Garner and H. A. Allard—1923

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The regulatory action of an environmental factor is perhaps no better illustrated than in plant photoperiodism, the study of which was pioneered by Garner. The response of organisms to periodic environmental oscillations (tides, lunar changes, etc.,) has yielded an extensive literature and considerable polemic. The opposing viewpoints concerning the operation of these "biological clocks" are ably summarized by F. A. Brown (1959. Living clocks. Science 130: *1535–1544) and C. S. Pittendrigh (1958. Perspectives in the study of biological clocks. Perspectives in marine biology. Berkeley, University of California Press, pp. 239–268).*

In an earlier paper considerable data were presented tending to show that the length of day exercises a remarkable regulatory action in initiating or inhibiting sexual reproduction in plants. In a number of species studied it was found that ordinarily the plant can attain the flowering and fruiting stages only when the length of day falls within certain limits, so that in such cases flowering and fruiting occur only at certain seasons of the year. In this respect some species and varieties respond to relatively long days while others respond to short days. Moreover, some plants are much more sensitive to change in length of day than are others. In the absence of the particular day length favorable to sexual reproduction vegetative development may continue for a more or less indefinite period, thus frequently leading to the phenomenon of gigantism. It was discovered, also, that exposure to a daily light period intermediate between that favorable only to vegetative development, on the one hand, and that favoring only flowering and fruiting on the other hand, tends to cause both forms of activity to progress simultaneously. This combined form of activity constitutes what is commonly known as the "everflowering" or "everbearing" behavior. It was suggested that probably the seasonal range in length of day is an important factor in the natural distribution of plants and that in agricultural practise the correct time for planting many crop plants may be largely conditioned by the prevailing length of day. To designate the response of the plant to length of day the term "photoperiodism" was suggested. . . .

LONG-DAY AND SHORT-DAY PLANTS AND THE CRITICAL LENGTH OF DAY FOR FLOWERING

. . . the plants studied tend to arrange themselves into two groups. One of these groups consists of species that are caused to flower by the action of short days while the other includes those species that are forced into flowering through the action of long days. For convenience the first named group are spoken of as short-day plants while the second group are designated as long-day plants. At first sight it would seem that these two groups of plants are diametrically opposed in their response to length of day, but detailed study of the two groups indicates that the difference is one of degree rather than of kind. In fact, classification into the two groups is more or less arbitrary. In the case of such plants as Cosmos and Bidens, flowering is inhibited by a daily light exposure much in excess of 12 hours' duration, while vegetative development promptly gives way to flowering when the light period is reduced to 12 hours or less. These plants will flower even when receiving only a few hours of light daily; in other words, it is not possible to reduce the light duration sufficiently to prevent flowering without killing the plants. On the other hand, Solidago and Hibiscus are readily prevented from flowering by reducing the light period to something less than 12 hours, although under these conditions they may continue to live and may even continue development in certain directions. These plants are not inhibited from flowering by increasing the light duration beyond the normal. The important point is that the inhibition of flowering in the first case by a long light period is not of the same sort as the inhibiting effect of a short light period in the second case; that is, the inhibition in the two cases results in different alternative forms of vegetative activity, as will be shown in later paragraphs. There are, moreover, plants which may be said to occupy an intermediate position in that it is possible to have a day length too long as well as one too short to induce flowering. *Mikania scandens* L., briefly discussed in our former paper, is an example of this type. In the wild state Mikania regularly flowers in late July and through August, and if kept in the greenhouse through the winter it also usually flowers very sparsely in the spring. Seedlings from a planting made December 10 were unable to flower under the influence of the lengthened daily light period in the electrically illuminated greenhouse, while similar plants in the control greenhouse flowered at the usual time in August of the following summer. On the other hand, this species was unable to flower through the summer or fall under day lengths of 5, 10, and 13 hours' duration. The Biloxi variety of soybeans (*Soja max* (L,) Piper), discussed in detail in the former paper, occupies a position slightly below the intermediate position of Mikania in response to day length. In this case flowering is readily inhibited by a day length in excess of 13 hours. On the other hand, with very short day lengths only a very few cleistogamous flowers and fewer seed are developed but the reproductive phases apparently can not be entirely suppressed. . . .

Not only do plants differ markedly as to the particular length of day most favorable for flowering but they also differ widely as to the narrowness of the range in day length which will permit of flowering. Experiments with Mikania, referred to above, indicate that under ordinary conditions this plant will readily flower only under a day length ranging but little beyond an hour on either side of 14 1/2 hours, which is approximately the optimum for flowering. Buckwheat flowers readily under a daily illumination period ranging at least from 5 hours up to 18 or 20 hours and probably even under continuous illumination, notwithstanding the fact that the extent of vegetative development and life duration are profoundly affected by this range in the length of the light period. While there is a certain degree of antagonism or incompatibility between the vegetative and reproductive phases of activity, the two obviously are not necessarily affected to the same degree by a given change in duration of the light period. *Viola papilionacea* Pursh will flower under all lengths of day met with in temperate regions except for a short period in midwinter. In the broadest sense the plant will flower continuously for about 10 months of the year, a conspicuous example of everblooming. During the summer months, however, only the cleistogamous type of flower is seen while in spring and fall only the showy blue, chasmogamous blossoms develop. By maintaining a light period equivalent to the long summer days the cleistogamous flowering continues indefinitely and, similarly, a considerably shorter light period will maintain the open type of flowering indefinitely, thus illustrating a narrower type of everblooming. In this case the whole effect of the range in length of day from February to the summer solstice is merely to change the type of blossom (involving change in relative fertility).

Thus, beginning with the equatorial length of day of 12 hours as the standard, it may be said that a group of plants normally will flower under any range downward to less than 6 hours, while another group will flower under any range upward to at least 18 hours and probably up to continuous illumination. Other plants will flower only within a comparatively narrow range on either side of the 12-hour standard. Still others are capable of flowering throughout these ranges, their response being quantitative rather than qualitative in character. . . .

SPRING FLOWERING AND FALL FLOWERING

The facts brought out in the preceding discussion of the relation between long-day and short-day plants and the balance between the vegetative and the reproductive types of activity throw light on the relationships existing between spring-flowering and fall-flowering plants. As is well known, many plants normally flower only during the spring, while many others regularly flower only in the fall. There are a number of plants, however, which flower in both spring and fall, although usually there is a marked difference in the extent of the flowering during the two seasons. Finally, there is a large group of plants which blossom in midsummer and a smaller group which under favorable conditions flower in winter. It is well known that in a very large number of perennials the flower buds are organized during the summer or early fall of the year preceding that in which the blossoms finally open, so that, in considering the effects of light duration, it is necessary to avoid confusing the action on the laying down of primordia and that on the final unfolding of the blossom.

Broadly speaking, in cool temperate regions short-day plants will flower chiefly in the fall rather than in the spring because of the lag in temperature rise in spring as compared with the lengthening of the day. In other words, in spring the day length is likely to become too long for flowering of short-day plants before the temperature has risen sufficiently to permit plants to become active. This is true more particularly of the annuals and those herbaceous perennials which require considerable vegetative development as an antecedent to flowering. That plants of these types which regularly flower in the fall will actually flower in the spring when the obstacle of low temperature is removed has been demonstrated in a number of cases. As a specific illustration Peking soybeans germinating in the greenhouse March 31 showed first open blossoms on May 12, or 42 days after appearance above ground, while a second lot germinating April 13, just two weeks later than the first planting, did not show open blossoms till July 16, 90 days after germination. Plantings of the Biloxi soybeans made on the same

dates failed to flower till September, since the day length was already above the critical for flowering in this variety. The Biloxi quickly flowers, however, if planted in winter or early spring in the greenhouse. Indirectly, the many experiments already described in which various plants have been forced into flowering out of season by shortening the light period or inhibited from flowering in the normal season by increasing the light period furnish proof of this relationship of spring and fall flowering in the short-day plants. As the critical light period for flowering becomes longer the chances for spring flowering of the species are increased till finally spring flowering merges with summer flowering in those species which are intermediate between the more typical short-day and long-day plants. Again, sparse flowering in spring is to be looked for in those of the short-day plants which are able to flower at all, for the reason that the change in day length is toward the optimum for vegetative activity and away from the optimum for flowering. It is under these conditions, also, that various modifications and abnormalities in flowering and fruiting, quantitative as well as qualitative, are most likely to occur. On the other hand, the short-day plants as a whole will have their energies thrown into flowering and fruiting more or less quantitatively, as it were, through the change in day length in the fall when the change is away from the optimum for vegetative activity and toward the optimum for sexual reproduction. One important qualification must be made to this principle, namely, that it holds good only so long as the day length does not become too short for the flowering and fruiting processes.

The long-day plants, on the other hand, through late spring and early summer are subjected to a changing day length which is approaching the optimal for sexual reproduction, hence it is to be expected that these plants would flower and fruit abundantly during this period. A large proportion of spring flowering plants consists of woody and herbaceous perennials in which the flower primordia are organized during the summer preceding the spring in which the blossoms unfold. In this case it seems probable that the optimal day length for flower development following the summer solstice passes by before the embryonic flower buds have made much progress in their development and the direction of the change in day length through late summer and the fall is away from this optimum for flowering and fruiting and toward or through the optimum for vegetative activity. Under these conditions further development of the flower buds would be attended with difficulty so that their growth would be slow. If the onset of cold weather is delayed, some species may flower in the fall instead of in the normal spring season. In some, and probably in most instances, however, flowering would be inhibited by the short days of late fall and winter. On the other hand, the cold weather of winter may exercise a distinctly helpful influence on the completion of the flowering process by establishing a favorable balance of income over outgo. Consequently, the earliness of flowering in the spring will depend largely on how soon the temperature rises to the point where development can actively proceed. The necessary internal conditions for flowering having been established, it remains for rise in temperature in spring to speed up the unfolding of the blossoms. Nevertheless, the increasing length of the day in the spring undoubtedly remains a factor, particularly in those species which do not unfold their blossoms till spring is well advanced. . . .

COMPENSATION FOR TEMPERATURE IN THE METABOLISM AND ACTIVITY OF POIKILOTHERMS

Theodore H. Bullock—1955

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The adaptation to an environmental variable, in this instance temperature, and the ecological significance of this compensation is one of the points developed by Bullock in this paper. This aspect of ecological physiology provides yet another dimension to the concept of tolerance and suggests caution in the assessment of the role of any given factor in the ecology of any given group.

. . . It is generally assumed that poikilotherms operate at lower rates in colder habitats and seasons. It is the purpose of this article to call attention to evidence, old and new, supporting the thesis that many cold-blooded animals are, on the contrary, relatively independent of temperature, within limits, in nature. This is to say that these species tend to maintain a certain level of metabolism and other characters measured as rates, compensating for different temperatures by homoeostatic mechanisms of various kinds.

The phenomena of temperature races and of acclimation are familiar to geneticists and physiologists, but the numerous indications in the literature that these are probably operating in ecology on a grand scale have been overlooked to such a degree that standard treatises on ecology may contain no reference to compensatory differences in metabolism or activity in different habitats or seasons. Usually there is mentioned only the phenomenon of change in tolerance to extremes, e.g. winter hardiness. Since the common examples of the latter phenomenon are species unable to maintain full activity in winter, the impression is reinforced that cold-blooded forms are victims of the environmental temperature. Many species, perhaps whole habitat groups, may fail characteristically to show compensatory adaptation of rates of activity or metabolism over a large part of the range of temperatures to which they are exposed naturally. But it will be shown below, after reviewing some of the facts already known, that a great variety of animals do show compensation normally, thereby affecting their ecologic, geographic and seasonal status —and consequently evolution—to a major degree. . . .

II. THE FACT OF COMPENSATION

. . . Moore first showed that several species of the genus *Rana* could be arranged in a series such that the more northern-ranging breed earlier at a given latitude, develop faster, have lower temperature coefficients (Q_{10}) and limits of heat tolerance. What is more pertinent in the present connexion, he later showed that the same is true of latitudinally separated populations of one wide-ranging species, *R. pipiens*. More stenotopic species like *R. catesbeiana* and *R. clamitans* do not show such physiological differentiation among their populations. Moore's data show clearly the importance of making comparisons only in the physiological temperature range or of otherwise avoiding the extremes where excessive heat or cold greatly change the rate-temperature curve. Similarly, Volpe found certain species of toads (*Bufo fowleri* and *B. americanus*) which show geographic temperature adaptation at least in the lower portion of the physiological temperature range. . . .

In this laboratory a series of studies has been directed toward the physiological ecology of temperature adaptation, and three of them bear upon the latitudinal comparison within a species. Roberts found compensatory differences in the standard metabolism between populations of a shore crab, *Pachygrapsus crassipes*, from different points on the coast. Rao reported the same with respect to the rate of ciliary pumping of water in a mussel, *Mytilus californianus*, from Puget Sound to Los Angeles. These cases, in contrast to most earlier ones, were controlled as to weight, which has a large effect. Moreover, in *Mytilus* size has a different effect in the different populations—less in the cold-adapted, more in the warm-adapted—so that northern animals can grow bigger without the activity per gram being depressed too far. Dehnel has found in three species of gastropods (*Thais emarginata*, *Crepidula nummaria*, *Lacuna carinata*) that larvae growing within capsules on their own yolk, in samples at Sitka, Alaska, grow from two to nine times faster than in samples in southern California at any given temperature, between 10 and 16°C.

In short, adaptation of metabolism and other rate functions to latitude, as though it were compensation for temperature, is widespread, within and between species.

(2) *Microgeographic physiological differences within the species.* The discovery of precisely similar differences between individuals separated by less than a metre deserves a separate heading. This was discovered recently in a student project on intertidal invertebrates by James, confirmed by Wemple, and has been reported in a preliminary note by Segal, Rao & James. Limpets (*Acmaea limatula*) have a consistently faster heart beat in samples taken from lower intertidal levels than from higher levels. The species ranges vertically less than 1.5 m. but individuals probably do not move outside of a territory extending only a fraction of this distance in height, over considerable periods. The significant parameter of the intertidal difference appears to be temperature; the higher tide specimens act as though adapted to higher average temperatures which is probable in this locality. Transplantation of limpets in the field indicates that complete acclimation is possible in a few weeks. Not only heart rate but also condition of gonads reflects the intertidal position and is reversible within a month. *Mytilus edulis* and *M. californianus* both show similar vertical differentiation, in pumping rate and in shell/body ratio. In a certain case, 75 cm. vertically is equivalent to about 330 miles latitudinally in the pumping-rate compensation of *M. californianus* of 20 g. soft parts at 16°C., as between the given geographic localities. . . .

(a) *Distribution and types of adaptation.* The distribution [of temperature compensation] among species is apparently wide but far from universal. But this statement can apply only to a given measure of the tendency. It is quite uncertain whether there is complete absence of regulatory adaptation in any organism, that is, passive submission to the role of 'Spielball der Umgebung.'

The known instances are widely scattered among the groups of animals and plants. There is considerable evidence that terrestrial and possibly fresh-water forms are relatively poorer in instances or in the degree of compensation than marine poikilotherms. Interestingly and inevitably, the terrestrial forms are the ones which exhibit *par excellence* winter hardiness (acclimation of tolerance), long known and studied but only recently analysed metabolically by Scholander, Flagg, Hock & Irving. However, several cases have been cited above among insects, pulmonates, and amphibians, as well as fresh-water fish, of metabolic adaptation to temperature by one or another measurement so that a generalization like that above must at the least be qualified. I feel confident in predicting that reptiles will also yield examples of physiological adaptation, although as Prof. R. B. Cowles has pointed out to me, these animals accomplish in part the same result behaviourally by controlling their microclimate, e.g. sunning and shading themselves, and this may be in lieu of some physiological adaptation.

We may recognize various types of animals on the basis of this tendency, at least for a given physiological character. There are the non-acclimating, the partially-, completely-, over-, and reverse-acclimating cases. Precht has formalized these as types IV, III, II, I and V, respectively. There are only a few cases of types I and V. We may distinguish slow- and fast-acclimating instances (measured in days) and as a separate group those in which 'immediate' compensation or 'temperature-independence' is manifest (measured in minutes). There appear to be species in which various genotypes exist, each adapted to a certain temperature but unable to acclimate, and others in which adaptation is phenotypic, that is, the genotype permits a wide range of acclimation. The facts at hand do not allow a simple statement as to the greater importance of the one or the other among eurythermal species. . . .

(b) *Mechanisms and levels*. . . . Consideration of these differences also suggests the probability that the separate regulatory processes are not always proportional so as to preserve the balance of the organism. Thus we have seen dehydrogenase activity altered without concomitant change in catalase. We may propose that it is the factor of balanced alteration which is the crucial one limiting the extent of acclimation in a species and its frequency among species. One might ask, if a winter-adapted animal can metabolize faster than a summer-adapted one, at summer temperature, then why does it instead normally slow down, when it could be feeding, reproducing and dominating its habitat faster? The simplest answer appears to be balance; something is not proceeding as fast as oxygen consumption, so that the whole machine is unable to keep up the high rate. Indeed, it is tempting to speculate that the hazards of balance, or the proportional change in various mechanisms, conceal the answer to the general biological question: Why are not eurythermal species more common or why are not most species distributed more widely than they are? But we must not mistake this facile statement for a fact; the actual fact of an imbalance which is sufficient to be effective in nature in limiting acclimated individuals must first be demonstrated. . . .

(c) *Significance in ecology and evolution*. The extent or adequacy of the compensatory change varies greatly. Although frogs and cunners (*Tautogolabrus adspersus*) exhibit seasonal acclimation, it is not enough to prevent them, at least in some typical habitats, from being nearly immobilized in winter. This is not to say, however, that the physiological changes are without significance.

It is easier to recognize the significance in those cases where the degree of adaptation is enough to insure almost or quite as high a rate in the one habitat or season as in the other. It is difficult to estimate the completeness of compensation based on the habitat temperatures because the latter are difficult to specify, except in certain cases such as the Arctic and tropical oceans. Without further work we cannot assume that the monthly average, daily average or any given measure short of the complete curve of temperature against time, is biologically appropriate, since we do not know how the organism weights equal departures from the average in the two directions or for different lengths of time.

One approach which offers some advantages is to plot an acclimated *R-T* curve (each point being the rate after acclimation to that temperature) superimposed on the same ordinates with the usual, acutely measured curve. The latter will typically be steeper, departing in both directions—above the acclimated at high temperatures and below it at low temperatures (Fig. 5)—at least when the animal acutely measured is one used to a non-extreme temperature. Perfect acclimation would then be shown by a horizontal, acclimated *R-T* slope and would obtain over a definite, limited temperature range. We possess data sufficient only for a few points on the acclimated *R-T* curve in any of the cases discussed above. Fry & Hart present an acclimated *R-T* curve of goldfish activity, showing a moderate degree of compensation.

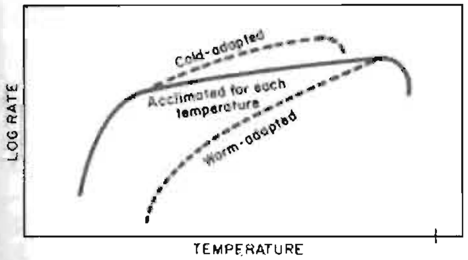

FIG. 5. *Hypothetical R-T curves showing the relation between the usual, acutely measured, temperature effect on cold-adapted and on warm-adapted individuals and the possibly more natural curve when temperature is changed slowly or time for acclimation is available at every temperature.*

This acclimated *R-T* curve should be of great biological interest as a means of comparing species in an ecologically significant way. The curve can in particular be expected to show not only a slope indicating the degree of sensitivity to temperature but a length indicating temperature range and a shape at the ends indicating the sharpness of geographic or ecological limits. This sharpness of transition from physiological to lethal temperatures might well be typically more abrupt than has been indicated by considering only the acutely measured *R-T* curve.

The acclimated curves will also show whether there is proportionally more compensatory change in adapting to low temperatures than to high. This is the result which Rao & Bullock believe to be most common though not at all universal, as shown by a higher Q_{10} in general for comparable portions of the warm-acclimated curve than for the cold-acclimated curve (i.e. portions of equal rates or ordinate levels). It is as though either curve were derived from the other, not by simple displacement (lateral or vertical or a combination) but by pivoting around a point off-scale to the right.

It is to be hoped that studies will be forthcoming permitting the plotting of acclimated *R-T* curves. But even now the large number of cases that have been cited in which adaptation has been demonstrated at two or a few places, seasons or acclimation temperatures permit the general conclusion that the phenomenon of compensatory regulation must be of great importance in extending the ecological, geographic and seasonal limits of the species. . . .

THE METHOD OF TRIAL AND ERROR IN THE BEHAVIOR OF LOWER ORGANISMS

Herbert S. Jennings—1904

Reprinted from Contributions to the study of behavior in lower organisms. Carnegie Institution of Washington Publication 16, 1904.

The chief response of lower organisms to changes in environmental factors, i.e., stimuli, was, according to Jennings, the method of trial and error. This adaptive behavioral response was in marked opposition to the nonadaptive tropistic concept advanced chiefly by Jacques Loeb (see p. 47). The considerable polemic elicited by adherents of each hypothesis subsequently lessened as the incompleteness of each became apparent and their complementarity was realized.

. . . [Trial and error] has been found by Lloyd Morgan, Thorndike, and others to play a large part in the development of intelligence in higher animals. Intelligent action arises as follows: The animal works by the method of trial and error till it has come upon the proper method of performing an action. Thereafter it begins with the proper way, not performing the trials anew each time. Thus intelligent action has its basis in the method of "trial and error," but does not abide indefinitely in that method.

Behavior having the essential features of the method of "trial and error" is widespread among the lower and lowest organisms, though it does not pass in them so immediately to intelligent action. But like the dog bringing the stick through the fence the first time, they try all ways, till one shows itself practicable.

This is the general plan of behavior among the lowest organisms under the action of the stimuli which pour upon them from the surroundings. On receiving a stimulus that induces a motor reaction, they try going ahead in various directions. When the direction followed leads to a new stimulus, they try another, till one is found which does not lead to effective stimulation.

This method of trial and error is especially well developed in free-swimming single-cell organisms—the flagellate and ciliate infusoria—and in higher animals living under similar conditions, as in the Rotifera. In these creatures the structure and the method of locomotion and reaction are such as to seem cunningly devised for permitting behavior on the plan of trial and error in the simplest and yet most effective way.

These organisms, as they swim through the water, typically revolve on the long axis, and at the same time swerve toward one side, which is structurally marked. This side we will call *X*. Thus the path becomes a spiral. The organism is, therefore, even in its usual course, successively directed toward many different points in space. It has opportunity to try successively many directions though still progressing along a definite line which forms the axis of the spiral. At the same time the motion of the cilia by which it swims is pulling toward the head or mouth a little of the water from a slight distance in advance. The organism is, as it were, continually taking "samples" of the water in front of it. This is easily seen when a cloud of India ink is added to the water containing many such organisms.

At times the sample of water thus obtained is of such a nature as to act as a stimulus for a motor reaction. It is hotter or colder than usual, or contains some strong chemical in solution, perhaps. Thereupon the organism reacts in a very definite way. At first it usually stops or swims backward a short distance, then it swings its anterior end *farther than usual toward the same side X to which it is already swerving*. Thus its path is changed. After this it begins to swim forward again. The amount of backing and of swerving toward the side *X* is greater when the stimulus is more intense.

This method of reaction seems very set and simple when considered by itself. It is almost like that of a muscle which reacts by the same contraction to all effective stimuli. The behavior of these animals seems, then, of the very simplest character. To practically all strong stimuli they react in a single definite way.

But if we look closely at this simple method of reacting, we find it, after all, marvelously effective. The organism, as we have seen, is revolving on its long axis. When, as a consequence of stimulation, it swings its anterior end toward the side *X*, this movement is combined with the revolution on the long axis. As a consequence, the anterior end is swung about in a wide circle; the organism tries successively many widely differing directions. From each of these directions, as we have seen, a sample of water is brought to the sensitive anterior end or mouth. Thus the reaction in itself consists in trying the water in many different directions. As long as the water coming from these various directions evinces the qualities which caused the reaction—the greater heat or cold or the chemical—the reaction, with its swinging to one side, continues. When a direction is reached from which the water no longer shows these qualities, there is no further cause for reaction; the strong swerving toward the side *X* ceases, and the organism swims forward in the direction toward which it is now pointed. It has thus avoided the region where the conditions were such as to produce stimulation. . . .

. . . Not until recently, it must be confessed, has the real significance of this type of behavior been fully perceived. The results seemed to a large degree negative; the reaction method clearly did not agree with the prevailing tropism theory, nor with any other of the commonly held theories as to the reactions of lower organisms. Just what the organism did was, indeed, fairly clear, but the plan of it all, the general relations involved in all the details, was *not* clear. This was partly due, perhaps, to overemphasis of certain phases of the reaction and to a tendency to consider other features unimportant. The behavior under stimuli is a unit; each factor must be considered in connection with all the others; then the general method running through it all becomes strikingly evident. . . .

In general terms we find that through this reaction by trial and error the organisms are kept in conditions favorable to their existence, and prevented from entering unfavorable regions. Through it they keep out of hot and cold regions and collect in regions of moderate temperature. Through it they tend to keep out of strong or injurious chemicals and out of regions where the osmotic pressure is much above or below that to which they are accustomed. Through it they gather in regions containing small amounts of certain chemicals, not leaving them for regions where there is either more or less of these chemicals. When oxygen is needed they collect through this reaction in regions containing oxygen; when the oxygen pressure is high, they do not react with reference to oxygen, or through this reaction they avoid regions containing much oxygen. Through this reaction organisms which contain chlorophyll, and therefore need light, gather in lighted regions or move toward the source of light; through the same reaction the same organisms avoid very powerful light. In all these cases, when there is error the organism goes back and tries a new direction, or a whole series of new directions. . . .

Examination shows that error from the standpoint of this behavior is as a rule *error* also from the standpoint of the general interests of the organism, considering as the interests of the organism the performance of its normal functions, the preservation of its existence, and the production of posterity. In general the organism reacts as error to those things which are injurious to it, while in those conditions which are beneficial it continues its normal activities. There are some exceptions to this, but in a general view it is clearly evident. There is no common thread running through all the different agents which constitute "error" in the reactions, save this one, that they *are* error from the standpoint of the general interests of the organism. . . .

This method of trial and error, which forms the most essential feature of the behavior of these lower organisms, is in complete contrast with the tropism schema, which has long been supposed to express the essential characteristics of their behavior. The tropism was conceived as a fixed way of acting, forced upon the organism by the direct action of external agents upon its motor organs. Each class of external agents had its corresponding tropism; under its action the organism performed certain forced movements, usually resulting in its taking up a rigid position with reference to the direction from which the stimulus came. Whether it then moved toward or away from the source of stimulus was determined by accidental conditions, and played no essential part in the reaction. There was no trial of the conditions; no indication of anything like what we call choice in the higher organisms; the behavior was stereotyped. Doubtless such methods of reaction do exist. In the reactions of infusoria to the electric current (an agent with which they never come into relation in nature), there are certain features which fit the tropism schema, and in the instincts the "Triebe"—of animals there are features of this stereotyped character. The behavior of animals is woven of elements of the most diverse kind. But certainly in the lower organisms which we have taken chiefly into consideration the behavior is not typically of the stereotyped character expressed in the tropism schema. The method of trial and error is flexible; indeed, plasticity is its essential characteristic. Working in the lowest organisms with very simple factors, it is nevertheless capable of development; it leads upward. The tropism leads nowhere; it is a fixed, final thing, like a crystal. The method of trial and error on the other hand has been called the "method of intelligence" (Lloyd Morgan); it involves in almost every movement an activity such as we call choice in higher organisms. With the acquirement of a *finer perception of differences* the organism acting on the method of trial and error rises at once to a higher grade in behavior. Combining this with the development of sense organs and the differentiation of motor apparatus, the path of advancement is wide open before it. . . .

FORCED MOVEMENTS, TROPISMS AND ANIMAL CONDUCT

Jacques Loeb—1918

Reprinted by permission of the publisher from Forced movements, tropisms, and animal conduct. Philadelphia, J. B. Lippincott Co., pp. 13–18, 1918.

According to Loeb, the reaction of an animal to a stimulus is a "forced movement" owing to differences in tension of symmetrical muscles. This concept of behavior conflicted with that of Jennings' "trial and error" hypothesis (see p. 44 for added comment).

INTRODUCTION

The analysis of the mechanism of voluntary and instinctive actions of animals which we propose to undertake in this volume is based on the assumption that all these motions are determined by internal or external forces. Our task is facilitated by the fact that the overwhelming majority of organisms have a bilaterally symmetrical structure, *i.e.*, their body is like our own, divided into a right and left half.

The significance of this symmetrical structure lies in the fact that the morphological plane of symmetry of an animal is also its plane of symmetry in physiological or dynamical respect, inasmuch as under normal conditions the tension in symmetrical muscles is the same, and inasmuch as the chemical constitution and the velocity of chemical reactions are the same for symmetrical elements of the surface of the body, *e.g.*, the sense organs.

Normally the processes inducing locomotion are equal in both halves of the central nervous system, and the tension of the symmetrical muscles being equal, the animal moves in as straight a line as the imperfections of its locomotor apparatus permit. If, however, the velocity of chemical reactions in one side of the body, *e.g.*, in one eye of an insect, is increased, the physiological symmetry of both sides of the brain and as a consequence the equality of tension of the symmetrical muscles no longer exist. The muscles connected with the more strongly illuminated eye are thrown into a stronger tension, and if now impulses for locomotion originate in the central nervous system, they will no longer produce an equal response in the symmetrical muscles, but a stronger one in the muscles turning the head and body of the animal to the source of light. The animal will thus be compelled to change the direction of its motion and to turn to the source of light. As soon as the plane of symmetry goes through the source of light, both eyes receive again equal illumination, the tension (or tonus) of symmetrical muscles becomes equal again, and the impulses for locomotion will now produce equal activity in the symmetrical muscles. As a consequence, the animal will move in a straight line to the source of light until some other asymmetrical disturbance once more changes the direction of motion.

What has been stated for light holds true also if light is replaced by any other form of energy. Motions caused by light or other agencies appear to the layman as expressions of will and purpose on the part of the animal, whereas in reality the animal is forced to go where carried by its legs. For the conduct of animals consists of forced movements.

The term forced movements is borrowed from brain physiology, where it designates the fact that certain animals are no longer able to move in a straight line when certain parts of the brain are injured, but are compelled to deviate constantly toward one side, which is (according to the species and the location of the injury in the brain) either the side of the injury or the opposite side. The explanation of these forced movements is that on account of the one-sided injury of the brain the tension of the symmetrical muscles is no longer the same. As a consequence, the impulses for locomotion which are equal for symmetrical muscles will cause greater contraction in certain muscles of one side of the body than in the symmetrical muscles of the other side, and the animal will no longer move in a straight line. The only difference between the forced movements induced by unequal illumination of the two eyes and by injury to the brain is that in the latter case the forced movements may last for days or throughout the whole life, while in the former case they last only as long as the illumination on the two sides of the body is unequal. If we bring about a permanent difference in illumination in the eyes, *e.g.*, by blackening one eye in certain insects, we can also bring about permanent circus motions. This shows that animal conduct may be justly designated as consisting of forced movements.

The idea that the morphological and physiological symmetry conditions in an animal are the key to the understanding of animal conduct demanded that the same principle should explain the conduct of plants, since plants also possess a symmetrical structure. The writer was able to show that sessile animals behave toward light exactly as do sessile plants; and motile animals like motile plants. The forced orientations of plants by outside sources of energy had been called tropisms; and the theory of animal conduct based on the symmetrical structure of their body was, therefore, designated as the *tropism theory of animal conduct*. . . .

Although the tropism theory of animal conduct was offered thirty years ago its acceptance was delayed by various circumstances. In the first place, the majority of the older generation of biologists did not realize that not only the methods of the physicist are needed but also the physicist's general viewpoint concerning the nature of scientific explanation. In many cases the problem of animal conduct is treated in a way which corresponds more to the viewpoint of the introspective psychologist than to that of the physicist. The attempts to explain animal conduct in terms of "trial and error" or of vague "physiological states" may serve as examples. None of these attempts have led or can lead to any exact quantitative experiments in the sense of the physicist. Other biologists have still more openly adopted an anthropomorphic method of explanation. If pleasure and pain or curiosity play a role in human conduct, why should it be otherwise in animal conduct? The answer to this objection is that typical forced movements when produced in human beings, as, *e.g.*, in Ménière's disease or when a galvanic current goes through the brain, are not accompanied by sensations of pleasure or pain, and there is no reason to attribute the circus movements of an animal, after lesion of the brain or when one eye is blackened, to curiosity or thrills of delight. An equally forcible answer lies in the fact that plants show the same tropisms as animals, and it seems somewhat arbitrary to assume that the bending of a plant to the window or the motion of swarmspores

of algæ to the window side of a vessel are accompanied or determined by curiosity or by sensations of joy or satisfaction. And finally, since we know nothing of the sentiments and sensations of lower animals, and are still less able to measure them, there is at present no place for them in science.

The second difficulty was created by the fact that the Aristotelian viewpoint still prevails to some extent in biology, namely, that an animal moves only for a purpose, either to seek food or to seek its mate or to undertake something else connected with the preservation of the individual or the race. The Aristotelians had explained the processes in the inanimate world in the same teleological way. Science began when Galileo overthrew this Aristotelian mode of thought and introduced the method of quantitative experiments which leads to mathematical laws free from the metaphysical conception of purpose. The analysis of animal conduct only becomes scientific in so far as it drops the question of purpose and reduces the reactions of animals to quantitative laws. This has been attempted by the tropism theory of animal conduct. . . .

INSTINCT, WITH ORIGINAL OBSERVATIONS ON YOUNG ANIMALS

Douglas A. Spalding—1872

Reprinted by permission of the publisher from British Journal of Animal Behavior 2:2–11, 1954. This is a reprint of the original which appeared in MacMillan's Magazine in 1872.

In spite of its diffuseness of style and frequent philosophical overtones, Spalding's paper is a classic in the study of instinctive behavior. It is remarkable for its approach, techniques and insights. An overriding theoretical framework of instinctive behavior came later in the work of Lorenz (see p. 53) but one finds there much which is first described here.

The only theory of instinct, of the nature of an explanation, is that put forward by Mr. Herbert Spencer as part of his philosophy of evolution; but, as a theory, it is only beginning to be understood and appreciated among scientific men; while some eminent thinkers question the reality of the phenomena to be explained. Professor Bain, our other psychologist, and his able following of trained disciples, simply discredit the alleged facts of instinct. Unfortunately, however, instead of putting the matter to the test of observation and experiment, they have contented themselves with criticising the few accidental observations that have been recorded, and with arguing against the probability of instinctive knowledge. . . . The position of psychologists of the too purely analytical school, however, is not that the facts of instinct are inexplicable; but that they are incredible. . . . And it is held, that all the supposed examples of instinct may be—for anything that has yet been observed to the contrary—nothing more than cases of rapid learning, imitation, or instruction.

Thus it would appear that with regard to instinct we have yet to ascertain the facts. With a view to this end, I have made many observations and experiments, mostly on chicken. The question of instinct, as opposed to acquisition, has been discussed chiefly in connection with the perceptions of distance and direction by the eye and the ear. Against the instinctive character of these perceptions it is argued, that as distance means movement, locomotion, the very essence of the idea is such as cannot be taken in by the eye or ear; that what the varying sensations and feelings of sight and hearing corrrespond to, must be got at by moving over the ground—by experience. On the other hand, it is alleged that, though as regards man the prolonged helplessness of infancy stands in the way of the observer, we have only to look at the young of the lower animals to see that as a matter of fact they do not require to go through the process of learning the meaning of their sensations in relation to external things; that chickens, for example, run about, pick up crumbs, and follow the call of their mother *immediately* on leaving the shell. For putting this matter to the test of experiment, chickens, therefore, are most suitable and convenient subjects. I have observed and experimented on more than fifty chickens, taking them from under the hen while yet in the eggs. But of these, not one on emerging from the shell was in a condition to manifest an acquaintance with the qualities of the outer world. On leaving the shell they are wet and helpless; they struggle with their legs, wings, and necks, but are unable to stand or hold up their heads. Soon, however, they may be distinctly seen and felt pressing against and endeavouring to keep in contact with any warm object. They advance very rapidly. I have seen them hold up their heads well, peck at objects, and attempt to dress their wings when only between four and five hours old. But there is no difficulty in conceiving that, with great spontaneity and a strong power of association, much might be learned in four or five hours. Professor Bain is of opinion, from observations of his own on a newly dropped lamb, that "a power that the creature did not at all possess naturally, got itself matured as an acquisition in a few hours." Accordingly, in the absence of precautions, the time that must elapse before chickens have acquired enough control over their muscles to enable them to give evidence as to their instinctive power of interpreting what they see and hear, would suffice to let in the contention that the eye and the ear may have had opportunities of being educated. To obviate this objection with respect to the eye, I had recourse to the following expedient. Taking eggs just when the little prisoners had begun to break their way out, I removed a piece of the shell, and before they had opened their eyes drew over their heads little hoods, which, being furnished with an elastic thread at the lower end, fitted close round their necks. The material of these hoods was in some cases such as to keep the wearers in total darkness; in other instances it was semi-transparent. Some of them were close at the upper end, others had a small aperture bound with an elastic thread, which held tight round the base of the bill. In this state of blindness—the blindness was very manifest—I allowed them to remain from one to three days. The conditions under which these little victims of human curiosity were first permitted to see the light were then carefully prepared. Frequently the interesting little subject

was unhooded on the centre of a table covered with a large sheet of white paper, on which a few small insects, dead and alive, had been placed. From that instant every movement, with the date thereof, as shown by the watch, was put on record. Never in the columns of a Court Journal were the doings of the most royal personage noted with such faithful accuracy. This experiment was performed on twenty separate chickens at different times, with the following results. Almost invariably they seemed a little stunned by the light, remained motionless for several minutes, and continued for some time less active than before they were unhooded. Their behaviour, however, was in every case conclusive against the theory that the perceptions of distance and direction by the eye are the result of experience, of associations formed in the history of each individual life. . . .

It would be out of place here to attempt to indicate the full psychological bearing of these facts. But this much may be affirmed, that they put out of court all those who are prepared only to argue against the instinctive perception by the eye of the primary qualities of the external world. When stripped of all superflous learning, the argument against this and every other alleged case of instinctive knowledge is simply that it is unscientific to assume an instinct when it is possible that the knowledge in question may have been *acquired* in the ordinary way. But the experiments that have been recounted are evidence that prior to experience chickens behave as if they already possessed an acquaintance with the established order of nature. A hungry chick that never tasted food is able, on seeing a fly or a spider for the first time, to bring into action muscles that were never so exercised before, and to perform a series of delicately adjusted movements that end in the capture of the insect. This I assert as the result of careful observation and experiment; and it cannot be answered but by observation and experiment at least as extensive. It is no doubt common for scientific men to discredit new facts, for no other reason than that they do not fit with theories that have been raised on too narrow foundations. . . .

If now it be taken as established that in the perceptions of the eye and the ear, chickens at least manifest an instinctive knowledge of the relations and qualities of external things, the popular belief that the special knowledge, the peculiar art and skill, so marked in the various species of animals, come to them mostly without the labour of acquisition, is at once freed from all antecedent improbability. In the way of direct evidence, the little that I have been able to observe in this wide field goes to prove that the current notions are in accordance with fact. We have seen that chickens follow the call of their mother before they have had any opportunity of associating that sound with pleasurable feelings; and one or two observations, which must be taken for what they are worth, support the general opinion that they have an equally instinctive dread of their more deadly enemies. When twelve days old one of my little *proteges*, while running about beside me, gave the peculiar chirr whereby they announce the approach of danger. I looked up, and behold a sparrow-hawk was hovering at a great height over head. Having subsequently procured a young hawk, able to take only short flights, I made it fly over a hen with her first brood, then about a week old. In the twinkling of an eye most of the chickens were hid among grass and bushes. . . .

A few manifestations of instinct still remain to be briefly spoken of. Chickens as soon as they are able to walk will follow any moving object. And, when guided by sight alone, they seem to have no more disposition to follow a hen than to follow a duck, or a human being. Unreflecting on-lookers, when they saw chickens a day old running after me, and older ones following me miles and answering to my whistle, imagined that I must have some occult power over the creatures, whereas I simply allowed them to follow me from the first. There is the instinct to follow; and, as we have seen, their ear prior to experience attaches them to the right object. The advantage of this arrangement is obvious. But instincts are not conferred on any principle of supplying animals with arts very essential to them, and which they could not very well learn for themselves. If there is anything that experience would be sure to teach chickens, it would be to take care when they had got a piece of food not to let their fellows take it from them, and from the very first they may be seen to run off with a worm, pursued by all their companions. But this has been so stamped in their nature that, when they have never seen one of their kind, nor ever been disturbed in the enjoyment of a morsel, they nevertheless, when they get something larger than can be swallowed at once, turn round and run off with it. . . .

The only theory in explanation of the phenomena of instinct that has an air of science about it, is Mr. Spencer's doctrine of Inherited Acquisition. The laws of association explain our intellectual operations, and enable us to understand how all our knowledge may be derived from experience. A chicken comes on a bee, and, imagining it has found a dainty morsel, seizes the insect, but is stung, and suffers badly. Henceforth bees are avoided; they can be neither seen nor heard without a shudder of fear. Now, if we can realize how such an association as this—how that one individual learns by experience may, in any degree, be transmitted to the progeny of that individual—we have a key to the mystery of instinct. Instinct in the present generation is the product of the accumulated experiences of past generations. The plausibility of this hypothesis, however, is not appreciated by the majority of even the educated portion of the community. But the reason is not far to seek. Educated men, even materialists—their own positive statements to the contrary notwithstanding—have not yet quite escaped from the habit of regarding mind as independent of bodily organization. Hence it is, that while familiar with the idea of physical pecularities passing by inheritance from one generation to another, they find it difficult to conceive how anything so impalpable as fear at the sight of a bee should be transmitted in the same way. Obviously, this difficulty is not consistent with a thorough belief in the intimate and invariable dependence of all kinds of mental facts on nervous organization. . . .

TAXIS UND INSTINKTHANDLUNG IN DER EIROLLBEWEGUNG DER GRAUGANS. I.

Konrad Lorenz and Niko Tinbergen—1938

Reprinted by permission of the authors and publisher from Zeitschrift für Tierpsychologie 2:1–29, 1938. Translated by Ursula Stechow, 1964.

Animal behavior studies began as an integral component of ecology; currently certain of such investigations appear to be unwanted stepchildren owing to their peculiar orientation. The thrust of animal behavior studies identified with Lorenz has led to a highly analytic approach in which the ecological context is often completely obscured. A critique of Lorenz' theory of instinctive behavior is given by D. S. Lehrman (1953. Quarterly Review of Biology **28***: 337–363).*

A. TOPOTAXIS

Most aspects of the process which we have, with A. Kühn, called taxis—and specifically topotaxis—contain side by side with directional reaction also rigid instinct patterns undergoing compulsive motion formulae, above all that of locomotion. Nevertheless, the essential criterion of topotaxis remains some singularly specific motion (the turning of an animal's entire body or of one of its parts, as for example, its eyes or head) directed and with its intensity determined by outside stimuli. . . .

The turning motion, characteristic of any kind of taxis in the widest sense of that word, and which orients the animal within its space, was called "related orientation turning" (*orientierte Bezugswendung*) by K. Bühler. The very ample term comprises any change in posture relating an organism to the spatial data of its environment. It thus includes the simplest turning "toward" or "away-from" as well as any spatial reaction resulting from cognizance of outside stimuli through highly complex mental achievements. . . .

. . . Without getting involved in the purely ideological question of whether an animal is subject, actively steering itself according to such stimuli, or object, passively directed by them, we can state that we have here objective evidence of the establishment, through outside stimuli, of purposeful activity expedient in the preservation of the species. In the simplest and best analyzed cases, this process is most certainly one of reflex activity in the true sense of that term. But even in orientation reaction, brought about by so-called higher mental processes, the activity of the central nervous system is essentially answering to, and utilizing external stimuli, and thus, at least in function, reflex-like as a phenomenon.

B. INSTINCT ACTIVITY

Instinct activities, too, show relationships to reflexes, namely in the fact that, like them, they are brought about by specific outside stimuli. Closer scrutiny, however, reveals that merely the trigger mechanism and not the further development of a formal activity is truly one of reflex. The total form of a once initiated activity seems to be independent not only of external stimuli but even altogether of the receptoral equipment of the animal. Instinct activities are not, like any form of taxis, native reaction norms, but rather native motion norms.

Improbable though it seems upon first glance, there are a number of weighty reasons for the assumption that the whole series of well-coordinated, highly expedient, species-preserving activities of an animal should be brought about, like the doings of a tabetic, without involvement of receptors (in other words, that they should not be a string of reflexes). By eliminating in various organisms all receptors of the central nervous system, E. von Holst has succeeded in bringing totally convincing evidence that in it are lodged stimulus-producing, rhythmo-automatic processes touched off through impulses coordinated already in the central nervous system and passed on as a series—and in perfect species-preserving form—to the animal's muscular system without the aid of the peripheral system or its receptors. . . .

. . . If it seems a bit premature today to equate altogether the motion automatisms investigated by von Holst to instinct activities, it must be stated with all possible emphasis that two of the most important phenomena which clearly outline instinctive behavior and which offer to any other kind of explanation well-nigh insurmountable difficulties, do allow themselves an easy berth within the assumption of such rhythmo-automatic stimulus production and the central coordination of impulses. These two phenomena are the lowering of the threshold of trigger stimuli and the thus facilitated voidance of an instinct action in a situation where not even the physico-mechanical conditions of its species-preserving purpose are met.

Even where the instinct activity is triggered by an unconditioned reflex, which would normally react only to a certain, often highly specific combination of outside stimuli, we see, occasionally quite closely, that the form of the resulting motion is independent of that of the stimuli bringing it about. If the latter fail to appear for any time longer than normal to conditions in the accustomed span of time, then very soon, diminuation will occur in the selectivity of that particular instinct activity; the animal will now, in a similar pattern, respond also to other stimulus situations merely resembling the truly adequate one previously known; the resemblance of the now activating stimuli to the ones previously alone effective, need be the less evident the longer the reaction "stoppage" lasts. In cases where the kind of stimuli triggering a specific instinct activity makes a quantitative evaluation possible at all, we find that with the increased duration of the rest period the threshold value of the necessary stimulus intensity goes into continual decline. Since both phenomena are evidently founded upon the same process in the central nervous system, I have [previously] incorporated both under the concept "threshold lowering" (*Schwellerniedrigung*). Now in many, if not even fundamentally in all instinct activities, the threshold value can literally reach the zero point where, upon a shorter or longer stoppage period, the whole series of motions is executed to perfection without appreciable influence of any outside stimuli. This we call "idling reaction" (*Leerlaufreaktion*). Threshold-lowering and *Leerlaufreaktion* speak doubly in favor of the premise of rhythmo-automatic stimulus production and central coordination of impulses.

The threshold-lowering phenomenon suggests the idea of an inner accumulation of a reaction-specific incentive—von Holst expects this to be enzyme (*Erregungsstoff*) activity—which is being continually produced by the central nervous system and which increases to the higher potential the longer the detention (which the actual execution of a particular instinct activity would bring) fails to come about. The higher the attained tension, the more intense the instinct activity when finally launched and the more difficult then for the superior instance, which is the central nervous system, to stem the instinct activity and keep it from breaking forth at the "wrong time." These ideas, as presented here in gross simplification, were developed earlier and in ignorance of von Holst's findings. . . .

For all these reasons it seems justified to raise to the status of working hypothesis our assumption that, through coordination of single acts, instinct activity is independent of each and all receptors and that it is not to be influenced by them. This may be an overly crude simplification of facts and may mean to the concept of instinct activity an uncommon narrowing down, especially since we are aware through von Holst's investigations that an impulse sent out by centrally coordinated automatism can be superseded by the reflex contraction of even one muscle. . . .

SUMMARY AND RESULTS

We investigated the question, in what way an instinct activity (in the sense of receptor-independent, centrally coordinated motion processes) might be co-functioning with one or more receptor-guided, topotactic acts and, in the united effect, produce in an animal species-preserving, purposive behavior. In the activity series by which the grey goose restores to the nest an egg that has rolled away from it, taxis as well as instinct patterns are involved, whether simultaneously or in sequence. As an initiating orientation reaction, the directional stretching of the neck sets up the stimulus situation in which instinct activity is triggered and simultaneously, the topographic placement created which is the prerequisite of the species-preserving functioning of its course, a typical case therefore of "appetence behavior" in Craig's manner of thinking. The now initiated instinct activity is a bending down and inward of neck and head by which motion the egg, lying close against the lower surface of the beak, is shoved toward the nest. Beginning with the first moment of this motion series and lasting all the way to its completion, this process runs entirely in the sagittal plane, with an additional orientation reaction participating in the general process. By thigmotactically directed lateral motion, the egg is held in balance and kept to its direction at the underside of the shoving beak.

Our assumption that the motion within the sagittal plane should be a pure instinct activity is founded upon the following facts as found: 1. It shows the phenomenon of the *Leerlaufreaktion*, characteristic of receptor-independent instinct acts. 2. The form of the motion remains continually the same. We did not succeed in obtaining marked, receptor-directed adjustments to physically changed environmental factors. Neither the details of the path over which the egg was to be rolled, nor the shape of the object to be rolled produced appreciable variety in motion activities. Wherever variations were sought by force (as for example by oversized objects) the motion jammed and was broken off. 3. The power behind the sagittal movement is, within the narrowest confines, found to be constant. Even if the object-produced touch stimuli create a small tonus effect upon the muscle that executes the motion, this effect seems, nevertheless, always to be the same regardless of the different weights of objects involved. The motion thus stops upon even the slightest overweighting of the object. 4. The activity shows the reaction-specific fatigue factor which, in contrast to taxis, is the mark of instinct activity.

The assumption that, contrary to the motions occurring in the sagittal plane, the lateral motions giving balance should be stimulus-directed orientation reactions is founded upon the following facts: 1. Lateral motions do not occur when, devoid of an object, the sagittal ones continue in an idling process. 2. Lateral motions do not come about with objects that do not allow a straying from their path. 3. Objects whose diversion occurs in a way different from that normally happening to the goose egg show a perfect adjustment of the lateral motion to the motion peculiarities of the object in question. . . .

DISCRIMINATION OF STREAM ODORS BY FISHES AND ITS RELATION TO PARENT STREAM BEHAVIOR

Arthur D. Hasler and Warren J. Wisby—1951

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Orientation, especially as it occurs in homing and migratory behavior, has offered considerable challenge to the student of animal behavior and provided ample opportunity for far-ranging speculation. A wide variety of forces (gravitation, rotation) and agents (sun, stars) and processes (sound emission, color discrimination) have been proposed as homing stimuli for different groups of animals. In this paper, olfaction is identified as being of significance in the recognition pattern of fish.

The role of sensory mechanisms in orientation of fishes, especially in relation to homing, remains a mystery notwithstanding many efforts to solve this problem. It is the object of this paper to point up again the possibility that the sense of smell may play an important part in directing fishes to their home waters. The primitive character of this sensory system, its evolutionary constancy, its extreme sensitivity in comparison to other receptor processes, and its capacity to serve as a memory-evoking mechanism, all point to a working hypothesis—that olfactory stimuli may be factors in the homing of migrating fishes. . . .

In the above observations, it could not be clearly proved that fishes orient on the basis of olfaction; nor has the idea been proposed that the home water carries a distinctive odor which through discrimination and memory may serve as a directing guide to the fishes in orienting toward and reaching its original habitat. The chief objective of our experiments was to determine whether streams do have characteristic odors and if fishes can discriminate between them, and whether they can retain in memory habits of orientation learned with respect to these odors.

It may be desirable, at this point, to define clearly the requirements of an odor which is to serve as a "sign-post" for returning salmon. First of all, it must remain relatively constant in any one stream over a period of years because an interval of three to five years may elapse between original learning of the olfactory controlled reaction and its reinstatement, upon return to the vicinity of the home water to spawn. . . .

The second condition which must be placed upon the odor is that it must have significance only to those returning migrants which had been conditioned to it during their freshwater sojourn; while being neutral to all others for it would seem that any odor, or substance, which was an attractant or repellent would induce salmon to enter a stream or tributary irrespective of whether or not they were native to the stream.

There is yet another restriction which must be placed upon a homing odor. It must remain detectable even though the stream be changed severely in chemical and physical characteristics, for salmon will continue to attempt to return to a stream even though that stream may have been seriously polluted, or gutted by floods, during the time the salmon were at sea. . . .

It was the immediate intent of this experiment to determine if it were possible to obtain an olfactory discrimination between Otter Creek and Honey Creek by the bluntnose minnow. The minnows were trained in such a manner that they learned to associate the odor of one of the streams with food and the odor of the other with punishment.

The equipment used by the authors [in] 1949 and 1950 was suitable for conducting this series of training tests. It consisted of several seven gallon aquaria, each with a siphon-airlift circulation system installed in both ends. Water was siphoned from the aquarium, returned by air pressure, and discharged into a 6-inch funnel which was suspended above the tank. The funnel was connected to a glass tube which lay across the end of the aquarium. Perforations in the tube directed the incoming water across the bottom of the aquarium. Water from the jet on one side flowed only about halfway across, because there it met the stream from the other end, and both were deflected upward. This produced two currents or convection cells, each of which involved one half of the tank. Water samples containing the odors were introduced into the aquarium by means of a separatory funnel, which was connected to the siphon tube after it left the tank.

An objection to the two-electrode punishment system, as described by the authors (*l.c.*), was overcome by introducing a third electrode. Formerly, it was difficult to punish a fish which entered the end zone more than two to four centimeters above the electrodes. Also, a fish between the electrodes was apt to be injured, as a shock was administered. With a third electrode, located about two inches above the one in the corner, it was possible to punish, without injuring, any fish entering the end zone below the level of the new electrode. Thus, a region (2″ × 2″ × 6″) bounded on the bottom by the two electrodes on the floor of the aquarium was designated as the "end zone," that is, the place where the fish were fed or punished by electric shock (2.3 volts; 20 milliamperes) depending on which odor was being introduced. Also, higher voltages could be used without adversely affecting the fish, thereby impressing the training to the negative odor.

The fish were rewarded by introducing food, pressed on perforated celluloid strips, into the end zone. Since, in this method of training, hunger is the principal motivating force, tests were timed at those intervals when hunger motivation was at its greatest. An attempt was made to test at different times each day, and to feed no more than was necessary for the well-being of the experimental animals. The fish were fed very heavily every sixth day, and tests omitted on the seventh, because a mere subsistence diet such as this would, in time, have harmed them. . . .

Fishes of two aquaria received positive training to water of Otter Creek, that is, fish were fed immediately after the test, and negative training to water of Honey Creek, that is, fish were punished by a light electrical current if they entered the end zone during the time this water was being introduced. Two other aquaria were trained to the same two odors, but with opposite meanings; Honey Creek was the positive odor; Otter Creek, the negative. If training were accomplished the fish should eventually associate food with the positive scent, and therefore enter the end zone. The negative scent would be associated with punishment and the fish should stay out of the end zone.

It should be pointed up that the fish were fatigued to the natural odors of the aquarium so that introduction of an unfamiliar water was immediately detected if in a perceptible concentration. In order to assure a forceful stimulus the creek water was diluted only by one-half when it was put into the separatory funnel. A minimal detectable concentration was not established. . . .

At the outset the fishes showed natural unlearned orientative responses for the odor of either creek, that is, they entered the end zone more often during the introduction of the odor on either the negative or the positive test than during the pretest. Not until later in the training sequence did they discriminate between them.

. . . The minnows learned equally well irrespective of whether Otter Creek (draining quartzite watershed) was positive or negative. A noticeable degree of discrimination was accomplished in a month of training. . . .

After reaching the discrimination level. . . training was continued for two more months in order to attain the maximum level of discrimination, or the plateau in the learning curve.

RETENTION OF LEARNING

. . . An attempt was. . . made to determine the length of retention of discrimination in the bluntnose minnow. Daily training was stopped and odors were presented weekly, without reward or punishment. After six weeks the fish were confusing the two odors so completely it was apparent that discrimination no longer existed.

That this method of testing does not produce a clear-cut measure of actual retention is well known to psychologists. The procedure followed involves detraining through repeated testing, and through interference habits set up by routine daily feeding between tests. That is, an animal which has been trained to associate food with an odor, will be subjected to the reverse of this training process if fed without prior introduction of the odor. Thus, the minnows, during these tests, were actually being detrained, and the results of the tests can only be considered to be an absolute minimum indication of true retention.

It should be kept in mind that the life span of the bluntnose minnow is only two years. Hence, training was started at the senile stage, whereas salmon would be conditioned to the stream odor while young. . . .

SEASONAL INFLUENCE ON CHARACTER OF ODOR

. . . To test the possibility of seasonal changes in odor, samples were collected during winter and presented to fish that had been trained to water from the same streams which had been collected in summer. The fish responded equally well to this water, indicating that the odor characteristics recognized by the fish in these two streams did not lose their identity with the change in season.

EVIDENCE OF OLFACTORY DETECTION OF STREAM ODORS

To determine if these differences in water are perceived by tissues of the fish's nose, the olfactory capsules of trained fishes were destroyed by heat cautery. After the wound had healed, these fish were again tested with the training odors. There was no response; nor did they participate in the reaction when placed in an aquarium with normal, trained minnows. It can thus be seen that a reaction to the substance is dependent on the olfactory system and on individual perception of the odor, and is not a "follow the leader" phenomenon.

That the latter is true can also be shown by placing a blinded, but otherwise normal, fish, which has received positive training to one odor and negative training to the other, in an aquarium with fishes which have received the reverse training. When one of the training odors is then introduced into the aquarium, the odd fish exhibits a response which is the opposite of that being demonstrated by the resident fishes.

NATURE OF THE ODOR

With this proof that the olfactory receptors were stimulated by a property of the creek water, it was logical to wonder what the substance was. . . .

Differences in total organic nitrogen of the two streams were quite marked. Since most odorous compounds are organic in nature, it seems quite likely that the elements detected by the minnows may be located in this fraction. . . .

SIGNIFICANCE AND APPLICATION

Most of the evidence for the reliability of parent stream behavior in fishes is found in the literature on the salmon. When it was decided to initiate a series of experiments to attempt to discover the mechanism behind parent stream behavior, therefore, they were designed to lead eventually to a series of actual tests in the field with salmon.

In this research, one major barrier to the hypothesis that fish orient to their home streams, has been explored. That is, it was shown that some streams, at least, have odor characteristics which can serve to produce persisting differential responses in certain fishes. Furthermore, the results of generalization tests indicate strongly that the odors of streams are aromatic substances present in the volatile organic fraction. However, our evidence for olfactory discrimination of stream water by fishes does not constitute proof that parent stream behavior is not also controlled by other factors. . . .

One of the characteristics which a stream must have to fulfill the conditions of our thesis is that the substance, to which the fishes are responding on their return journey, must remain detectable even though the stream be changed severely in chemical and physical characteristics. Salmon continue to return regardless of pollution, floods, and changes in weather. These things do alter the materials in the stream, but on the basis of our evidence it appears that aromatics derived from the vegetation and soils of the watershed lend a distinctive odor which can be perceived, learned and recognized again after a protracted period of non-exposure. The aromatic characteristic of a watershed, filtering into the stream, might be surmised to remain constant over long periods.

Additional collateral indications of the importance of the sense of smell in the life of a fish comes from a large series of studies by von Frisch and his students. Their results attest the extreme sensitivity of the fish nose to natural substances, for they show that fish have been found capable of recognizing one another by scent, and that they may be alarmed at extremely dilute emanations (Schreckstoff) from injured fish skin. It would seem too that the acuity of the sense of smell in fishes is of similar sensitivity as that of dogs and insects where but a few molecules stimulate the end organ. In contrast, the common chemical sense and the ability to discriminate temperature differences are crude senses when compared with the olfactory system.

Techniques have been developed whereby it is now possible to hatch and maintain salmon through the fingerling stage in aquaria at Madison. Preliminary results from a set of experiments currently in progress indicate that the olfactory system of salmon is very acute, and that they can discriminate between stream odors.

A set of field experiments must also be undertaken to furnish final proof of the hypothesis herein contained. Of a number of possible methods of solution, one promises to be of some practical value. The hypothesis could be tested by exposing salmon to a constant, artificial odor through the fingerling stage and then determining if the fish conditioned in a hatchery could be decoyed to a neighboring stream upon return from the sea. Should this be the case, it would aid in salvaging the declining salmon runs where new dams may obstruct passage to their parent streams. . . .

THE STUDY OF POPULATIONS

Discrete populations of a species are sufficiently unit-like in their characteristics and responses to permit their being objectified. Among the many facets of a population, ecologists are concerned with aspects of their growth (natality, mortality, growth form, etc.), regulation (fluctuations, oscillations, dispersal, etc.), and inter- and intraspecific interactions (cooperation, competition, etc.).

Since its inception, this field has had a strong mathematical orientation in formulating and testing descriptive and predictive models. Much of its empirical and theoretical development has had an animal focus based on data derived largely from laboratory populations of relatively few diverse kinds of organisms. The original anthropocentric orientation given the field continues, for in spite of the more esoteric and academic aspects of population ecology, the implications regarding the human population are not easily avoided.