Chapter I

THE PROBLEM

(1) The struggle for existence is one of those questions which were very much discussed at the end of the last century, but scarcely any attempt was made to find out what it really represents. As a result our knowledge is limited to Darwin's brilliant exposition, and until quite recently there was nothing that we could add to his words. Darwin considered the struggle for existence in a wide sense, including the competition of organisms for a possession of common places in nature, as well as their destruction of one another. He showed that animals and plants, remote in the scale of nature, are bound together by a web of complex relations in the process of their struggle for existence. "Battle within battle must be continually recurring with varying success," wrote Darwin, and "probably in no one case could we precisely say why one species has been victorious over another in the great battle of life.... It is good thus to try in imagination to give to any one species an advantage over another. Probably in no single instance should we know what to do. This ought to convince us of our ignorance on the mutual relation of all organic beings; a conviction as necessary as it is difficult to acquire. All that we can do, is to keep steadily in mind that each organic being is striving to increase in a geometrical ratio; that each at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life and to suffer great destruction" ('59, pp. 56-57).

(2) But if our knowledge of the struggle for existence has since Darwin's era increased to an almost negligible extent, in other domains of biology a great progress has taken place in recent years. If we look at genetics, or general physiology, we find that a decisive advance has been made there, after the investigators had greatly simplified their problems and taken their stand upon the firm basis of experimental methods. The latter presents a particularly interesting example about which we would like to say a few words. We mean the investigations of the famous Russian physiologist I. P. Pavlov, who approached the study of the nervous activity of higher animal by thoroughly objective physiological methods. As Pavlov ('23) himself says, it is "the history of a physiologist's turning from purely physiological questions to the domain of phenomena usually termed psychical." The higher nervous activity presents such a complicated system, that without special experiments it is difficult to obtain an objective idea of its properties. It is known, firstly, that there exist constant and unvarying reflexes or responses of the organism to the external world, which are considered as the especial "elementary tasks of the nervous system." There exist besides other reflexes variable to an extreme degree which Pavlov has named "conditional reflexes." With the aid of carefully arranged

quantitative experiments in which the animal was isolated in a special chamber, all the complicating circumstances being removed, Pavlov discovered the laws of the formation, preservation and extinction of the conditional reflexes, which constitute the basis for an objective conception of the higher nervous activity. "l am deeply, irrevocably and ineradicably convinced, says Pavlov, that here, on this way lies the final triumph of the human mind over its problem--a knowledge of the mechanism and of the laws of human nature."

(3) The history of the physiological sciences for the last fifty years is very instructive, and it shows distinctly that in studying the struggle for existence we must follow the same lines. The complicated relationships between organisms which take place in nature have as their foundation definite *elementary processes of the struggle for existence*. *Such an elementary process is that of one species devouring another, or when there is a competition for a common place between a small number of species in a limited microcosm*. It is the object of the present book to bring forward the evidence, firstly, that in studying the relations between organisms in nature some investigators have actually succeeded in observing such elementary processes of the struggle for existence and, secondly, to present in detail the results of the author's experiments in which the elementary processes have been investigated in laboratory conditions. The experiments made it apparent that in the simplest ease we can give a clear answer to Darwin's question: why has one species been victorious over another in the great battle of life?

(4) It would be incorrect to fall into an extreme and to consider the complicated phenomena of the struggle for life in nature as simply a sum of such elementary processes. Leaving aside the existence in nature of climatic factors which undergo rhythmical time-changes, the elementary processes of the struggle for life take place there amid a totality of most diverse living beings. This totality presents a *whole,* and the separate elementary processes taking place in it are still insufficient to explain all its properties. It is also probable that changes of the totality as a whole put an impress on those processes of the struggle for existence which are going on within it.

Nobody contests the complexity of the phenomena taking place in the conditions of nature, and we will not enter here into a discussion of this fact. Let us rather point out all the importance of studying the elementary processes of the struggle for life. At present our position is like that of biophysicists in the second half of last century. First of all it had been necessary to show that separate elementary phenomena of vision, hearing, etc., can be fruitfully studied by physical and chemical methods, and thereupon only did the question arise of studying the organism as a system constituting a whole.

(5) Certain authors at the close of last century occupied themselves with a purely logical and theoretical discussion of the struggle for existence. They proposed different schemata for classifying these phenomena, and we will now examine one of them in order to give just a general idea of those elementary processes of the struggle for life with which we will have to deal further on. To the first large group of these processes belongs the struggle going on between groups of organisms differing in structure and mode of life. In its turn this struggle can be divided into a direct and an indirect one. The struggle for existence is direct when the preservation of life of one species is connected with the destruction of another, for instance that of the fox and the hare, of the ichneumon fly and its host larva, of the tuberculosis bacillus and man. In the chapter devoted to the experimental analysis of the predator-prey relations we will turn our attention to this form of the struggle. In plants, as Plate ('13) points out, the direct form of the struggle for existence is found only in the case of one plant being a parasite of the other. Among plants it is the indirect competition, or the struggle for the means of livelihood that predominates; this has also a wide extension among animals. It takes place in the case when two forms inhabit the same place, need the same food, require the same light. We will later give a great deal of attention to the experimental study of indirect competition. To the second group of phenomena of the struggle for life belongs the intraspecies struggle, between individuals of the same species, which in its turn can be divided into a direct and an indirect one.

(6) In this book we are interested in the struggle for existence among animals, and it is just in this domain that exact data are almost entirely lacking. In large compilative works one may meet an indication that the struggle for existence "owing to the absence of special investigations has become transformed into a kind of logical postulate," and in separate articles one can read that "our data are in contradiction with the dogma of the struggle for existence." In this respect zoologists are somewhat behind botanists, who have accumulated already some rather interesting facts concerning this problem.

What we know at present is so little that it is useless to examine the questions: what are the features common to the phenomena of competition in general, and what is the essential distinction between the competition of plants and that of animals, in connection with the mobility of the latter and the greater complexity of relations into which they enter? What interests us more immediately is the practical question: what are the methods by means of which botanists study the struggle for existence, and what alterations do these methods require in the domain of zoology?

First of all botanists have already recognized the necessity of having recourse to experiment in the investigation of competition phenomena, and we can quote the following words of Clements (`24, p. 5): "The opinions and hypotheses arising from observation are often interesting and suggestive, and may even have permanent value, but ecology can be built upon a lasting foundation solely by means of experiment.... In fact, the objectivity afforded by comprehensive and repeated experiment is the paramount reason for its constant and universal use."

However, the experiments so far made by botanists are devoted to the analysis of plant competition from the viewpoint of ontogenic development. The competition began when the young plantlets came in contact with one another, and all the decisive stages of the competition took place in the course of development of the same plants.

In such circumstances the question as to the causes of the victory of certain forms over others presents itself in the following aspect: By the aid of what morphological and physiological advantages of the process of individual development does one plant suppress another under the given conditions of environment? Clements has characterized this phenomenon in the following manner: "The beginning of competition is due to reaction when the plants are so spaced that the reaction of one affects the response of the other by limiting it. The initial advantage thus gained is increased by cumulation, since even a slight increase of the amount of energy or raw material is followed by corresponding growth and this by a further gain in response and reaction. A larger, deeper or more active root system enables one plant to secure a larger amount of the chresard, and the immediate reaction is to reduce the amount obtainable by the other. The stem and leaves of the former grow in size and number, and thus require more water, the roots respond by augmenting the absorbing surface to supply the demand, and automatically reduce the water content still further and with it the opportunity of a competitor. At the same time the correlated growth of stems and leaves is producing a reaction on light by absorption, leaving less energy available for the leaves of the competitor beneath it, while increasing the amount of food for the further growth of absorbing roots, taller stems and overshading leaves" (Clements, '29, p. 318).

(7) It is not difficult to see that for the study of the elementary processes of the struggle for existence in animals we need experiments of another type. We are interested in the processes of destruction and replacing of one species by another in the course of a *great number of generations*. We are consequently concerned here with the problem of an experimental study of the growth of mixed *populations,* depending on a very great number of manifold factors. In other words we have to

analyze the properties of the *growing groups of individuals* as well as the interaction of these groups Let us make for this purpose an artificial microcosm, i.e., let us fill a test tube with a nutritive medium and introduce into it several species of Protozoa consuming the same food, or devouring each other. If we then make numerous observations on the alteration in the number of individuals of these species during a number of generations, and analyze the factors that directly control these alterations, we shall be able to form an objective idea as to the course of the elementary processes of the struggle for existence. In short, *the struggle for existence among animals is a problem of the relationships between the components in mixed growing groups of individuals, and ought to be studied from the viewpoint of the movement of these groups*.

For the study of the elementary processes of the struggle for existence in animals we can have recourse to experiments of two types. We can pour some nutritive medium into a test tube, introduce into it two species of animals, and then neither add any food nor change the medium. In these conditions there will be a growth of the number of individuals of the first and second species, and a competition will arise between them for the common food. However, at a certain moment the food will have been consumed, or toxic waste products will have accumulated, and as a result the growth of the population will cease. In such an experiment a *competition* will take place between two species *for the utilization of a certain limited amount of energy.* The relation between the species we will have found at the moment when growth has ceased, will enable us to establish in what proportion this amount of energy has been distributed between the populations of the competing species. It is also evident that one can add to the species "prey" growing in conditions of a limited amount of energy the species "predator," and trace the process of one species being devoured by the other. Or, in the experiments of the second type, *we need not fix the total amount of energy as a determined quantity,* and only *maintain it at a certain constant! level,* continually changing the nutritive medium after fixed intervals of time. In such an experiment we approach more closely to what takes place in the conditions of nature, where the inflow of solar energy is maintained at a fixed level, and we can study the process of competition for common food, or that of destruction of one species by another, in the course of time intervals of any duration we may choose.

(8) Experimental researches will enable us to understand the mechanism of the elementary process of the struggle for existence, and we can proceed to the next step: to express these processes mathematically. As a result we shall obtain coefficients of the struggle for existence which can be exactly measured. The idea of a mathematical approach to the phenomena of competition is not a new

one, and as far back as 1874 the botanist and philosopher Nageli attempted to give "a mathematical expression to the suppression of one plant by another," taking for a starting point the annual increase of the number of plants and the duration of their life. But this line of investigation did not find any followers, and the experimental researches on the competition of plants which have appeared lately are as yet in the stage of nothing but a general analysis of the processes of ontogenesis.

In past years several eminent men were deeply conscious of the need for a mathematical theory of the struggle for existence and took definite steps in this domain. It often happened that one investigator was ignorant of the work of another but came to the same conclusions as his predecessor. Apparently every serious thought on the process of competition obliges one to consider it as a whole, and this leads inevitably to mathematics. A simple discussion or even a quantitative expression of data often do not suffice to obtain a clear idea of the relationships between the competing components in the process of their growth.

(9) About thirty years ago mathematical investigations of the struggle for existence would have been premature, or in any case subject to great difficulties, due to the absence of the needed preliminary data. Of late years, owing to the publication of a number of investigations, these difficulties have disappeared of themselves. What is it that these indispensable preliminary researches represent?

There is no doubt that a rational study of the struggle for existence among animals can be begun only after the questions of the multiplication of organisms have undergone a thoroughly exact quantitative analysis. We have mentioned that the struggle for existence is a problem of the relationships between species in mixed growing groups of individuals. We must therefore begin by analyzing the laws of growth of homogeneous groups consisting of individuals of one and the same species, and the competition between individuals in such homogeneous groups. During the second half of the last century and the beginning of the present much has been said about multiplication, and "equations of multiplication" have even been proposed of the following type: the coefficient of reproduction--the coefficient of destruction = number of adults. (Vermehrungsziffer--Vernichtungsziffer = Adultenziffer; see Plate ('13) p. 246.) Usually, however, things did not go any further, and no attempts were made to formulate exactly all these correlations. Recently the Russian geochemist, Prof. Vernadsky, has thus characterized from a very wide viewpoint the phenomena of multiplication of organisms ('26, p. 37 and fool.): "The phenomena of multiplication attracted but little the attention of biologists. But in it, partly unnoticed by the naturalists themselves, several empirical generalizations became established to which we have become so accustomed that they appear to us almost self-evident.

"Among these generalizations the following must be recorded. Firstly, *the multiplication of all organisms can be expressed by geometric progressions*. This can be evaluated by a uniform formula:

$$2^{bt} = N_t$$

where t is time, b the exponent of progression and N_t the number of individuals existing owing to multiplication at a certain time t. Parameter b is characteristic for every kind of living being. In this formula there are included no limits, no restrictions either for t, for b, or for N_t. The process is conceived as infinite as the progression is infinite.

"This infinity of the possible multiplication of organisms can be considered as the subordination of *the increase of living matter in the biosphere to the rule of inertia*. It can be regarded as empirically established that the process of multiplication is retarded in its manifestation only by external forces; it dies off with a low temperature, ceases becomes weaker with an insufficiency of food or respiration, with a lack of room for the organisms that are being newly created. In 1858 Darwin and Wallace expressed this idea in a form that had been long clear to naturalists who had gone into these phenomena, for instance, Linnaeus, Buffon, Humboldt, Ehrenberg and von Baer: if there are no external checks, every organism can, but at a different time, cover the entire globe by its multiplication, produce a progeny equal in size to the mass of the ocean or of the earth's crust.

"The rate of multiplication is different for every kind of organisms in close connection with their size. *Small organisms, that is organisms weighing less, at the same time multiply much more rapidly than large organisms (i.e., organisms of a great weight).*

"In these three empirical generalizations the phenomena of multiplication are expressed without any consideration of time and space or, more precisely, in geometrical homogeneous time and space. In reality life is inseparable from the biosphere, and we must take into consideration terrestrial time and space. Upon the earth organisms live in a limited space equal in dimensions for them all. They live in a space of definite structure, in a gaseous environment or a liquid environment penetrated by gases. And although to us time appears unlimited, the time taken up by any process which takes place in a limited space, like the process of multiplication of organisms, cannot be unlimited. It also will have a limit, different for every kind of organisms in accordance with the character of its multiplication. The inevitable consequence of this situation is a limitation of all the parameters which determine the phenomena of multiplication of organisms in the biosphere.

"For every species or race there is a maximal number of individuals which can never be surpassed. This maximal number is reached when the given species occupies entirely the earth's surface, with a maximal density of its occupation. This number which I will hence forth call the 'stationary number of the homogeneous living matter' is of great significance for the evaluation of the geochemical influence of life. The multiplication of organisms in a given volume or on a given surface must proceed more and more slowly, as the number of the individuals already created approaches the stationary number."

These general notions on the multiplication of organisms have lately received a rational quantitative expression in the form of the logistic curve discovered by Raymond Pearl and Reed in 1920. The logistic law mathematically expresses the idea that in the conditions of a limited microcosm the potentially possible "geometric increase" of a given group of individuals at every moment of time is realized only up to a certain degree, depending on the unutilized opportunity for growth at this moment. As the number of individuals increases, the unutilized opportunity for the further growth decreases, until finally the greatest possible or saturating population in the given conditions is reached. The logistic law has been proved true as regards populations of different animals experimentally studied in laboratory conditions. We shall have an opportunity to consider all these problems more in detail further on. Let us now only note that the rational quantitative expression of growth of groups consisting of individuals of the same species represents a firm foundation for a further fruitful study of competition between species in mixed populations.

(10) Apart from a great progress as regards the mathematical expression of the multiplication of organisms, an important advance bas taken place in the theory of competition itself. The first step in this direction was made in 1911 by Ronald Ross, who at this time interested in the propagation of malaria. Considering the process of propagation Ross came to the conclusion that he was dealing with a peculiar case of a struggle for existence between the malaria plasmodium and man with a participation of the mosquito. Ross formulated mathematically an equation of the struggle for existence for this case, which closely approached in its conception those equations of the struggle for existence which the Italian mathematician Volterra proposed in 1926 without knowing the investigations of Ross.

Whilst Ross was working on the propagation of malaria the American mathematician Lotka ('10, '20a) examined theoretically the course of certain chemical reactions, and had to deal here with equations of the same type. Later on Lotka became interested in the problem of the struggle for existence, and in 1920 he formulated an equation for the interaction between hosts and parasites ('20b), and gave a great deal of interesting material in his valuable book, *Elements of Physical Biology ('25)*. Without being acquainted with these researches the Italian mathematician Vito Volterra proposed in 1926 somewhat similar equations of the struggle for existence. At the same time he advanced the entire problem considerably} investigating for the first time many important questions of the theory of competition from the theoretical point of view. Thus three distinguished investigators came to the very same theoretical equations almost at the same time but by entirely different ways. It is also interesting that the struggle for existence only began to be experimentally studied after the ground had been prepared by purely theoretical researches. The same has already happened many times in the fields both of physics and of physical chemistry: let us recollect the mechanical equivalent of heat or Gibbs' investigations.

(11) The study of the struggle for existence will undoubtedly rapidly progress in the future, but it will have to overcome a certain gap between the investigations of contemporary biologists and mathematicians. There is no doubt that the struggle for existence is a biological problem, and that it ought to be solved l)y experimentation and not at the desk of a mathematician. But in order to penetrate deeper into the nature of these phenomena we must combine the experimental method with the mathematical theory, a possibility which has been created by the brilliant researches of Lotka and Volterra. This combination of the experimental method with the quantitative theory is in general one of the most powerful tools in the hands of contemporary science. The gap between the biologists and the mathematicians represents n significant obstacle to the application of the combined methods of research. Mathematical investigations independent of experiments are of but small importance due to the complexity of biological systems, narrowing the possibilities of theoretical work here as compared with what can be admitted in physics and chemistry. We are in complete accord with the following words of Allee ('34): "Mathematical treatment of population problems is necessary and helpful, particularly in that it permits the logical arrangement of facts and abbreviates their expression by the use of a sort of universal shorthand, but the arrangement and statement may lead to error, since for the sake of brevity and to avoid cumbersome expressions, variables are omitted and assumptions made in the mathematical analyses which are not justified by the biological data. Certainly there is room for the mathematical attack on population problems, but there is also continued need for attack along the lines of experimental physiology, even though the results obtained cannot yet be adequately expressed in

mathematical terminology."