Chapter VI

THE DESTRUCTION OF ONE SPECIES BY ANOTHER

(1) In the two preceding chapters our attention has been concentrated on the indirect competition, and we have to turn now to an entirely new group of phenomena of the struggle for existence, that of one species being directly devoured by another. The experimental investigation of just this case is particularly interesting in connection with the mathematical theory of the struggle for existence developed on broad lines by Vito Volterra. Mathematical investigations have shown that the process of interaction between the predator and the prey leads to periodic oscillations in numbers of both species, and all this of course ought to be verified under carefully controlled laboratory conditions. At the same time we approach closely in this chapter to the fundamental problems of modern experimental epidemiology, which have been recently discussed from a wide viewpoint by Greenwood in his Herter lectures of 1931. The epidemiologists feel that the spread of microbial infection presents a particular case of the struggle for existence between the bacteria and the organisms they attack, and that the entire problem must pass from the strictly medical to the general biological field.

(2) As the material for investigation we have taken two infusoria of which one, *Didinium nasutum,* devours the other, *Paramecium caudatum* (Fig. 27). Here, therefore, exists the following food chain: bacteria ® *Paramecium ® Didinium*. This case presents a considerable interest from a purely biological viewpoint, and it has more than once been studied in detail (Mast ('09), Reukauf ('30), and others). The amount of food required by *Didinium is* very great and, as Mast has shown, it demands a fresh *Paramecium* every three hours. Observation of the hunting of *Didinium* after the Paramecia has shown that *Didinium* attacks all the objects coming into contact with its seizing organ, and the collision with suitable food is simply due to chance (Calcins '33). Putting it into the words of Jennings ('15*) Didinium* simply "proves all things and holds fast to that which is good."

All the experiments described further on were made with pure lines of *Didinium* ("summer line") and *Paramecium*. In most of the experiments the nutritive medium was the oaten decoction, "with sediment" or "without sediment," described in the preceding chapter. Attempts were also made to cultivate these infusoria on a synthetic medium with an exactly controlled number of bacteria for the Paramecia, but here we encountered great difficulties in connection with differences in the optimal physicochemical conditions for our lines of *Paramecium* and *Didinium*. The introduction of a phosphate buffer and the increase of the alkalinity of the medium above pH = 6.8-7.0 has invariably favored the growth of *Paramecium,* but hindered that of *Didinium*. Satisfactory results have been obtained on Osterhout's medium, but here also *Didinium has* grown worse than on the oaten medium. Therefore, absolute values of growth under different conditions can not be compared with one another though all the fundamental laws of the struggle for existence remained the same. The experiments were made in a moist thermostat at a temperature of 26°C.

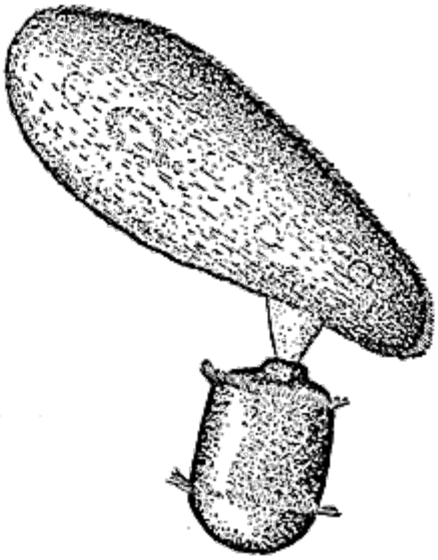

Fig. 27. *Didinium nasutum* devouring *Paramecium caudatum*

(3) Let us first of all analyze the process of interaction between the predator and the prey from a qualitative point of view. It is well known that under natural conditions periodic oscillations in the numbers of both take place but in connection with the complexity of the situation it is difficult to draw any reliable conclusions concerning the causes of these oscillations. However, quite recently Lotka (1920) and Volterra (1926) have noted on the basis of a purely mathematical investigation that the properties of a biological system consisting of two species one of which devours the other are such that they lead to periodic oscillations in numbers (see Chapter III). These oscillations should exist when all the external factors are invariable, because they are due to tile properties of the biological system itself. The periods of these oscillations are determined by certain initial conditions and coefficients of multiplication of the species. Mathematicians arrived at this conclusion by studying the properties of the differential equation for the predator-prey relations which has already been discussed in detail in Chapter III (equation 21a). Let us now repeat in short this argument in a verbal form. When in a limited microcosm we have a certain number of prey (N_1), and if we introduce predators (N_2),[1] there will begin a decrease in the number of prey and an increase in that of the predators. But as the concentration of the prey diminishes the increase of the predators slows down, and later there even begins a certain dying off of the latter resulting from a lack of food. As a result of this diminution in the number of predators the conditions for the growth of the surviving prey are getting more and more favorable, and their population increases, but then again predators begin to multiply. Such periodic oscillations can continue for a long time. *The analysis of the properties of the corresponding differential equation* shows that one species will *never be capable of completely destroying another:* the diminished prey will not be entirely devoured by the predators, and the starving predators will not die out completely, because when their density is low the prey multiply intensely and in a certain time favorable conditions for hunting them arise. Thus *a population consisting of homogeneous prey and homogeneous predators in a limited microcosm, all the external factors being*

constant, must according to the predictions of the mathematical theory possess periodic oscillations in the numbers of both species.[2] These oscillations may be called "innate periodic oscillations", because they depend on the properties of the predator-prey relations themselves, but besides these under the influence of periodic oscillations of external factors there generally arise "induced periodic oscillations" in numbers depending on these external causes. The classic example of a system which is subject to innate and induced oscillations is presented by the pendulum. Thus the ideal pendulum the equilibrium of which has been disturbed will oscillate owing to the properties of this system during an indefinitely long time, if its motion is not impeded. But in addition to that we may act upon the pendulum by external forces, and thereby cause induced oscillations of the pendulum.

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[1] It is assumed that all individuals of prey and predator are identical in their properties, in other words, we have to do with homogeneous populations.

[2] According to the theory, such oscillations must exist in the case of one component depending on the state of another at the same moanent of time, as well as in the case of a certain delay in the responses of one species to the changes of the other.

If we are asked what proof there is of the fact that the biological system consisting of predator-prey actually possesses "innate" periodic oscillations in numbers of both species, or in other terms that the equation (21a) holds true, we can give but one answer: observations under natural conditions are here of no use, as in the extremely complex natural environment we do not succeed in eliminating "induced" oscillations depending on cyclic changes in climatic factors and on other causes. Investigations under constant and exactly controlled laboratory conditions are here indispensable. Therefore, in experimentation with two species of infusoria one of which devours the other the following question arose at the very beginning: does this system possess "innate" periodic oscillations in numbers, which are to be expected according to the mathematical theory?

(4) The first experiments were set up in small test tubes with 0.5 cm^3 of oaten medium (see Chapter V). If we take an oaten medium without sediment, place in it five individuals of *Paramecium caudatum,* and after two days introduce three predators *Didinium nasutum,* we shall have the picture shown in Figure 28. After the predators are put with the Paramecia, the number of the latter begins to decrease, the predators multiply intensely, devouring all the Paramecia, and thereupon perish themselves. This experiment was repeated many times, being sometimes made in a large vessel in which there were many hundreds of thousands of infusoria. The predator was introduced at different moments of the growth of population of the prey, but nevertheless the same result was always produced. Figure 29 gives the curves of the devouring of Paramecia by *Didinium* when the latter are introduced at different moments of the growth of the prey population (in 0.5 cm^3 of oaten medium without sediment). This figure shows the decrease in the number of Paramecia as well as the simultaneous increase in number and in volume of the population of *Didinium*. (We did not continue these curves beyond the point where *Didinium* attained its maximal volume.) It is evident that the

Paramecia are devoured to the very end. As it is necessary that the nutritive medium should contain a sufficient quantity of bacteria in order to have an intense multiplication of Paramecia, we arranged also experiments in the test tubes on a daily changed Osterhout's medium containing *Bacillus pyocyaneus* (see Chapter V). In Figure 30 are given the results of such an experiment which has led up, as before, to the complete disappearance of both *Paramecium* and *Didinium*. Thus we see that in a homogeneous nutritive medium under constant external conditions the system *Paramectum-Didinium* has no innate periodic oscillations in numbers. In other words, *the food chain:* bacteria + *Paramecium* + *Didiniurn* placed in a limited microcosm, with *the concentration of the first link of the chain kept artificially at a definite level, changes in such a direction that the two latter components disappear entirely and the food resources of the first component of the chain remain without being utilized by any one*.

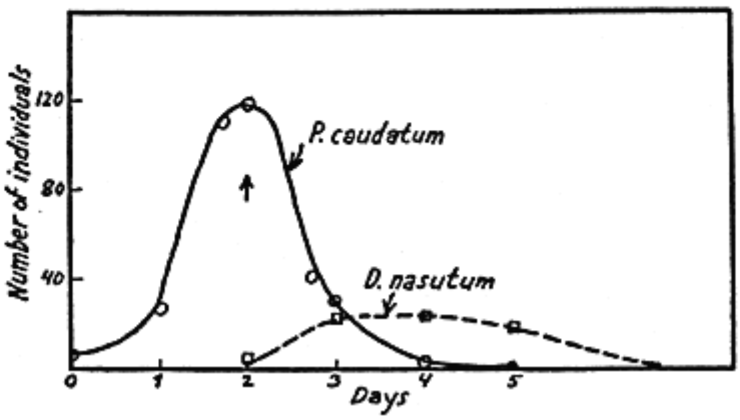

Fig. 28. The elementary interaction between *Didinium nasutum* and *Paramecium caudatum* (oat medium without sediment). Numbers of individuals pro 0.5 c.c. From Gause ('35a).

We have yet to point out that the study of the properties of the predator-prey relations must be carried out under conditions favorable for the multiplication of both prey and predator. In our case, there should be an abundance of bacteria for the multiplication of Paramecia, and suitable physicochemical conditions for the very sensitive *Didinium*. It is self-evident that if at the very beginning we set up unfavorable conditions under which *Didinium* begins to degenerate, and as a result is unable to destroy all the prey, or if the diminishing prey should perish not in consequence of their having been devoured by the predators but from other causes, we could not be entitled to draw any conclusions in respect to the properties of the predator-prey relations in the given chain.

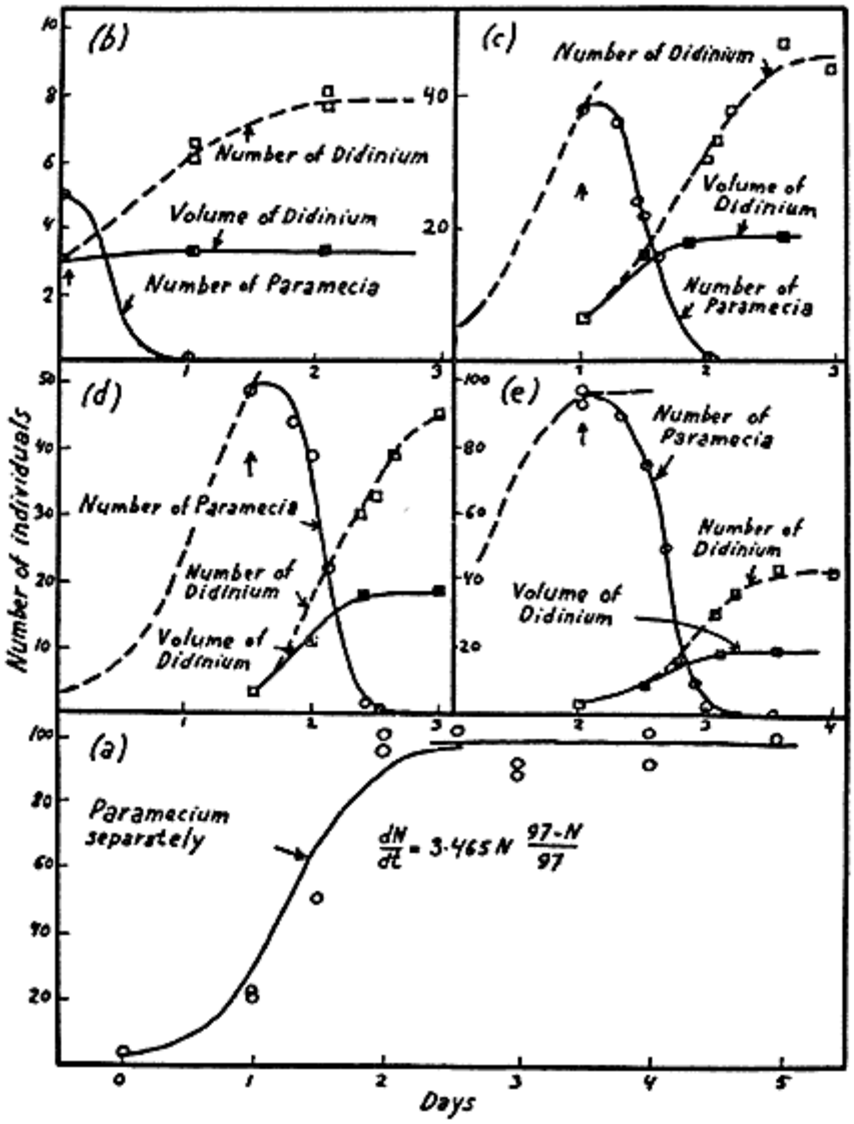

Fig. 29. The destruction of *Paramecium caudatum by Didinium nasutum*. (a) Growth of *P. caudatum* alone. (b) *Didinium is* introduced at the very beginning of growth of Paramecia population. (c) *Didinium* is introduced after 24 hours. (d) *Didinium* is introduced after 36 hours. (e) *Didinium* is introduced after 48 hours. Numbers of individuals pro 0.5 c.c.

(5) We may be told that after we have "snatched" two components out of a complex natural community and placed them under "artificial" conditions, we shall certainly not obtain anything valuable and shall come to absurd conclusions. We will therefore point out beforehand that under such conditions it is nevertheless possible to obtain periodic oscillations in the numbers of the predators and prey, if we but introduce some complications into the arrangement of the experiments. As yet we have only separated the elementary interaction between two species, and noted some of its fundamental properties.

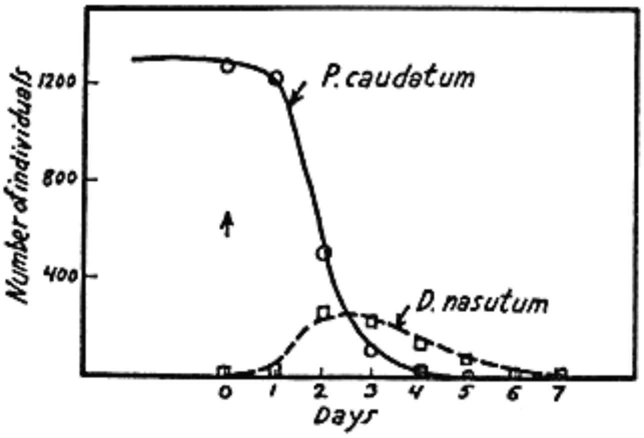

Fig. 30. The elementary interaction between *Didinium nasutum* and *Paramecium caudatum* (medium of Osterhout). The environment is not completely favorable for *Didinium,* and it begins to die out too early. Numbers of individuals pro 5 c.c. From Gause ('35a).

However, why is the theoretical equation of the mathematicians not realized in our case? The cause of this is apparently that a purely biological property of our predator has not been taken into account in the equation (21a). According to this equation a decrease in the concentration of the prey diminishes the probability of their encounters with the predators, and causes a sharp decrease in the multiplication of the latter, and afterwards this even leads to their partly dying out. However, in the actual case *Didinium* in spite of the insufficiency of food continues to multiply intensely at the expense of a vast decrease in the size of the individual. The following data give an idea of the diminution in size of *Didinium:* three normal individuals of this species placed in a medium free of Paramecia continue to multiply intensely, and in an interval of 24 hours given on an average 7.1 small individuals able to attack the prey. This vast increase of the "seizing surface" represents, metaphorically speaking, those "tentacles by means of which the predators suck out the prey completely." Translating all this into mathematical language, we can say: the function characterizing the consumption of prey by predators [$f_1(N_1, N_2)$], as well as the natality and the mortality of predators [$F(N_1, N_2)$],* are apparently more complicated than Lotka and Volterra have assumed in the equation (21a), and as a result the corresponding process of the struggle for existence has no periodic properties. We shall soon return to a further analysis of this problem along mathematical lines.

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* See Chapter III, equation (21).

II

(1) We have but to introduce a slight complication into the conditions of the experiment, and all the characteristic properties of our biological system will be

altogether changed. In order to somewhat approach natural conditions we have introduced into the microcosm a "refuge" where Paramecia could cover themselves. For this purpose a dense oaten medium "with sediment" was taken (see Chapter V). Direct observations have shown that while the Paramecia are covered in this sediment they are safe from the attack of predators. It must be noted that the *taxis causing the hiding of Paramecia in this "refuge" manifests itself in a like manner in the presence of the predators as in their absence.*

We must have a clear idea of the role which a refuge plays in the struggle for existence of the species under observation, as a lack of clearness can lead further on to serious misunderstandings. If *Didiniurn* actively pursued a definite *Paramecium* which escaping from it hid in the refuge, the presence of the refuge would be a definite parameter in every elementary case of one species devouring another. In other words, the nature and the distribution of refuges would constitute an integral part of the expressions $f_1(N_1, N_2)$, and $F(N_1, N_2)$ of the corresponding differential equation of the struggle for existence.

Such a situation has recently been analyzed by Lotka ('32a). We might be told in this case that in experimenting with a homogeneous microcosm *without refuges* we have sharply disturbed the process of elementary interaction of two species. Instead of investigating "in a pure form" the properties of the differential equation of the struggle for existence we obtain a thoroughly unnatural phenomenon, and all the conclusions concerning the absence of innate oscillations in numbers will be entirely unconvincing. But for our case this is not true. We have already mentioned that *Didinium* does not actively hunt for Paramecia but simply seizes everything that comes in its way. In its turn *Paramecium* fights with the predator by throwing out trichocysts and developing an intense rapidity of motion, but *never hiding in this connection in the refuge of our type*. In this manner, we have actually isolated and studied "in a pure form" the elementary phenomenon of interaction between the prey and the predators in a homogeneous microcosm. The refuge in our experiment presents a peculiar "semipermeable membrane," separating off a part **of** the microcosm into which *Pararnbecium* can penetrate owing to its *taxis, in general quite independently of any pursuit of the predator,* and which is impenetrable for *Didinium*.

When the microcosm contains a refuge the following picture can be observed (see Fig. 31): if *Pararnecium* and *Didinium* are simultaneously introduced into the microcosm, the number of predators increases somewhat and they devour a certain number of Paramecia, but a considerable amount of the prey is in the refuge and the predators cannot attain them. Finally the predators die out entirely owing to the lack of food, and then in the microcosm begins an intense multiplication of the Paramecia (no encystment of *Didinium* has been observed in our experiments). We must make here a technical note: the microcosm under observation ought not to be shaken in any way, as any shock might easily destroy the refuge and cause the Paramecia to fall out. On the whole it may be noted that when there appears a refuge in a microcosm, a certain threshold quantity of the prey cannot be destroyed by the predators. The elementary process of predator-prey interaction goes on to the very end, but the presence of a certain number of undestroyed prey in the refuge creates the possibility of the microcosm becoming later populated by the prey alone.

(2) Having in the experiment with the refuge made the microcosm a heterogeneous one, we have acquired an essential difference of the corresponding process of the struggle for existence from all the elementary interactions between two species which we have so far examined. In the case of an elementary interaction between predator and prey in a homogeneous microcosm very similar results were obtained in various analogous experiments (see Table 6, Appendix). In any case the more attention we give to the technique of experimentation, the greater will be this similarity. In other terms, in a homogeneous microcosm the process of the struggle for existence in every individual test tube was exactly determined by a certain law, and this could be expressed by more or less complex differential equations. For every individual microcosm the quantities of the predator and the prey at a certain time t could be exactly predicted with a comparatively small probable error.

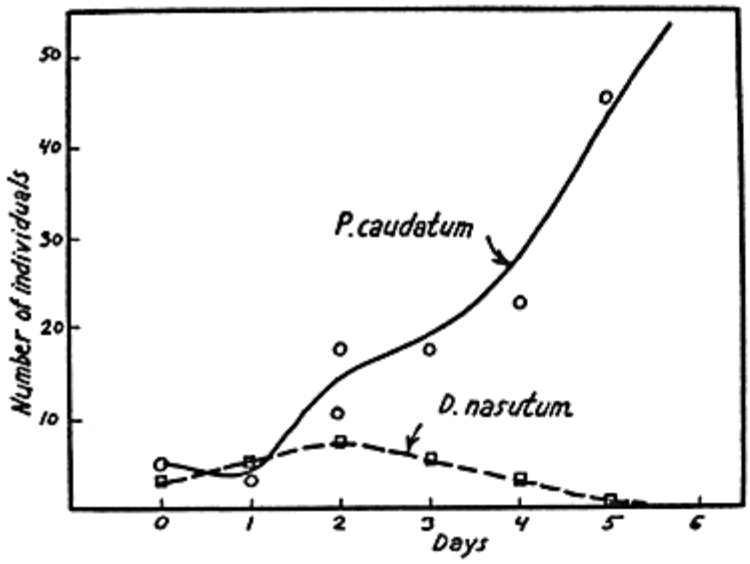

Fig. 31. The growth of mixed population consisting of *Didinium nasutum* and *Parameciqxm caudatum (*oat medium with sediment). Numbers of individuals pro 0.5 c.c.

Such a deterministic process disappears entirely when a refuge is introduced into the microcosm, because the struggle for existence is here affected by a multiplicity of causes. If we take a group of microcosms with similar initial conditions the following picture is observed after a certain time: (1) in some of the microcosms in spite of the existence of a refuge all the prey are entirely devoured (they might have accidentally left the refuge, hidden inadequately, etc.). Or else (2) as shown in Figure 31 a certain number of prey might have in the refuge been entirely out of reach of the predators, and the latter will perish finally from lack of food. (3) Lastly, prey may from time to time leave the refuge and be taken by the predators; as a result a mixed population consisting of prey and predators will continue to exist for a certain time. All this depends on the circumstance that in our experiments the absolute numbers of individuals were not large, and the amplitude of fluctuations connected with multiplicity of causes proved to be wider than these numbers.

(3) Let us consider the corresponding data. In one of the experiments 30 microcosms were taken (tubes with 0.5 cm^3 of oaten medium with sediment), in each of them five *Paramecium* and three *Didinium* were placed, and two days after the population was counted. It turned out that in four microcosms the predators had entirely destroyed the prey whilst in the other 26 there were predators as well as prey. The number of prey fluctuated from two to thirty-eight. In another experiment 25 microcosms were examined after six days; in eight of them the predators had died out entirely and prey alone remained. Therefore, in the initial stage for every individual microcosm we can only affirm with a probability Of 48s that it will develop in the direction indicated in Figure 31. Certain data on the variability of populations in individual microcosms are to be found in Table 7 (Appendix). Further experimental investigations are here necessary. First of all we had to do with too complicated conditions in the microcosms owing to variability of refuges themselves. It is not difficult to standardize this factor and to analyze its role more closely.

In concluding let us make the following general remarks. When the microcosm approaches the natural conditions (variable refuges) in its properties, the struggle for existence begins to be controlled by such a multiplicity of causes that we are unable to predict exactly the course of development of each individual microcosm.[3] From the language of rational differential equations we are compelled to pass on to the language of probabilities, and there is no doubt that the corresponding mathematical theory of the struggle for existence may be developed in these terms. The physicists have already had to face a similar situation, and it may be of interest to quote their usual remarks on this subject: "Chance does not confine itself here to introducing small, practically vanishing corrections into the course of the phenomenon; it entirely destroys the picture constructed upon the theory and substitutes for it a new one subordinated to laws of its own. In fact, if at a given moment an extremely small external factor has caused a molecule to deviate very slightly from the way planned for it theoretically, the fate of this molecule will be changed in a most radical manner: our molecule will come on its way across a great number of other molecules which should not encounter it, and at the same time it will elude a series of collisions which should have taken place theoretically. All these 'occasional' circumstances in their essence are regular and determined, but as they do not enter into our theory they have in respect to it the character of chance" (Chinchin, '29, pp. 164-165).

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[3] This means only that the development of each individual microcosm is influenced by a multiplicity of causes, and it would be totally fallacious to conclude that it is not definitely "caused." All our data have of course no relation to the concept of phenomenal indeterminism.

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(4) If we take a microcosm without any refuge wherein an elementary process of interaction between *Paramecium* and *Didinium is* realized, and if we introduce an artificial immigration of both predator and prey at equal intervals of time, there will appear periodic oscillations in the numbers of both species. Such experiments were

made in glass dishes with a flat bottom into which 2 cm^3 of nutritive liquid were poured. The latter consisted of Osterhout's medium with a two-loop concentration of *Bacillus pyocyaneus,* which was changed from time to time. The observations in every experiment were made on the very same culture, without any interference from without (except immigration) into the composition of its contents. At the beginning of the experiment and every third day thereafter one *Parameciurn* + one *Didiniurn* were introduced into the microcosm. The predator was always taken when already considerably diminished in size; if it did not find any prey within the next 12 hours, it usually degenerated and perished. Figure 32 represents the results of one of the experiments. Let us note the following peculiarities: (1) At the first immigration into the microcosm containing but few Paramecia the predator did not find any prey and perished. An intense growth of the prey began. (2) At the time of the second immigration the concentration of the prey is already rather high, and a growth of the population of the predator begins. (3) The third immigration took place at the moment of an intense destruction of the prey by the predators, and it did not cause any essential changes. (4) Towards the time of the fourth immigration the predator had already devoured all the prey, had become reduced in size and degenerated. The prey introduced into the microcosm originates a new cycle of growth of the prey population. Such periodic changes repeat themselves further on.

Comparing the results of different similar experiments with immigration made in a homogeneous microcosm, we come to the same conclusions as in the preceding paragraph. Within the limits of each cycle when there is a great number of both *Paramecium* and *Didinium* it is possible by means of certain differential equations to predict the course of the process of the struggle for existence for some time to come. However, at the critical moments, when one cycle of growth succeeds another, the number of individuals being very small, "multiplicity of causes" acquires great significance (compare first and second cycles in Fig. 32). As a result it turns out to be impossible to forecast exactly the development in every individual microcosm and we are again compelled to deal only with the probabilities of change.

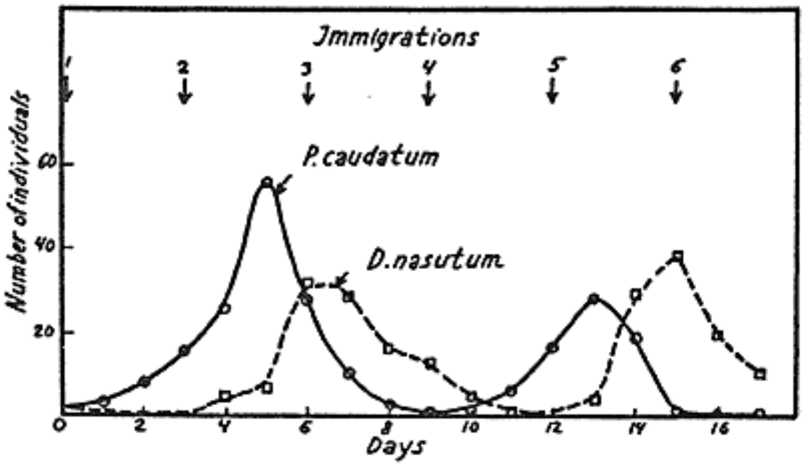

Fig. 32. The interaction between *Didinium nasutum* and *Parameciurn caudatum in* a microcosm with immigrations (1 *Didinium* + 1 *Paramecium).* Causes of too low peak

of *Didinium* in the first cycle of growth are known. From Gause ('34a).

(5) Let us briefly sum up the results of the *qualitative analysis* of the process of destruction of one species by another in a case of two infusoria. The data obtained are schematically presented in Figure 33. In a homogeneous microcosm the process of elementary interaction between the predator and the prey led up to the disappearance of both the components. By making the microcosm heterogeneous (refuge) and thus approaching the natural conditions we began to deal with a "probability" of change in various directions. The predator sometimes dies out and only prey populate the microcosm. By introducing immigration into a homogeneous microcosm we obtain periodic oscillations in the numbers of both species.

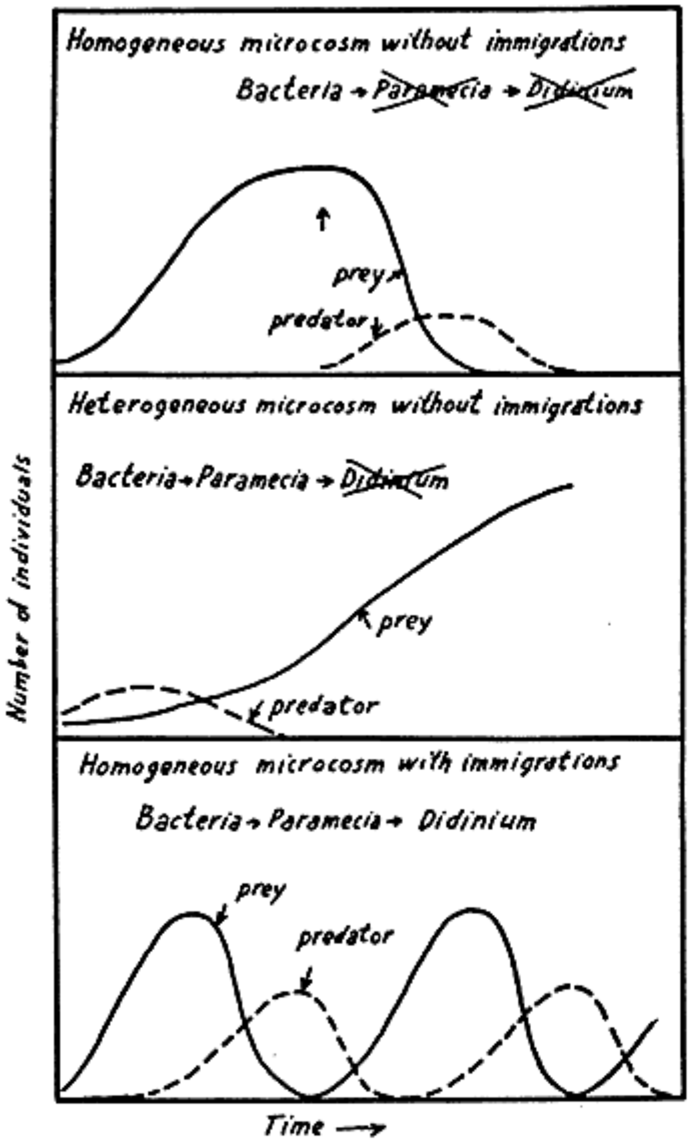

Fig. 33. A schematic representation of the results of a qualitative analysis of the predator-prey relations in the case of two Infusoria.

III

(1) The above given example shows that in *Paramecium* and *Didinium* the periodic oscillations in the numbers of the predators and of the prey are not a property of the predator-prey interaction itself, as the mathematicians suspected, but apparently occur as a result of constant interferences from without in the development of this interaction. There is evidence for believing that this is characteristic for more than our special case. Jensen ('33) in his monograph on periodic fluctuations in size of various stocks of fish concluded that he has not found any periodicity identic to those treated by Volterra. The same conclusion was arrived at by S. Severtzov ('33) dealing with vertebrates. There are also plenty of entomological observations showing the possibility of a complete local extermination of hosts by parasites. We may according to Cockerell ('34) recall some observations on Coccidae (scale insects) made in New Mexico. Certain species occur on the mesquite and other shrubs which exist in great abundance over many thousands of square miles of country. Yet the coccids are only found in isolated patches here and there. They are destroyed by their natural enemies, but the young larvae can be blown by the wind or carried on the feet of birds, and so start new colonies which flourish until discovered by predators and parasites. This game of hicle-and-seek results in frequent local exterminations, but the species are sufficiently widespread to survive in parts of their range, and so continue indefinitely. Such local exterminations in grayfish have been recently observed by Duffield ('33).

(2) Experimental epidemiology is the one domain where the problems of a direct struggle for existence have already been submitted to an exact analysis in laboratory conditions. Therefore let us consider in brief the results there obtained. If we took a microcosm of any size populated by homogeneous organisms, not allowing any immigration or emigration, and if we caused it to be fatally infected, we should obtain a complete dying out of the organisms (if among them there were no immune ones, and if they were unable to acquire any immunity). In other terms, we should have before us the well-known elementary interaction of two species. However, the process of dying out does not usually go on to the end owing to the heterogeneity of population and presence of immune individuals, which are in a certain degree equivalent to the individuals protected in the refuge: they are not carried away by the process of destruction which goes on to the end among the non-immune ones. The nature of this "refuge" is very complicated, and it is interesting to quote here the following words of Topley ('26, pp. 531-532): "Most of us who have been concerned at all with the problem of immunity have been accustomed to take the individual as our unit. When we take as our unit not the individual but the herd, entirely new factors are introduced. Herd resistance must be studied as a problem *sui generis*. One factor peculiar to the development of communal as opposed to individual immunity may be referred to here. A herd may clearly increase its average resistance by a process of simple selection, by the elimination through death of its more susceptible members.... That some process of active immunization will be associated with the occurrence of non-fatal infection may safely be assumed, though its degree and importance may be very difficult to assess, so that we must allow for the possibility that the spread of infection which is killing some of our hosts is immunizing others.

"A very imperfect analogy may help to depict the position. Suppose we take a number of stakes of different thickness, plant them in the ground and expose them to bombardment with stones of varying size from catapults of varying strengths. After a certain time we shall find that a number of the stakes have been broken. This will not have happened to many of the thicker stakes, but other survivors will consist of thinner stakes, around which ineffective missiles have formed a protective armour. Survivors of the latter class are in a precarious state; subsequent bombardment may displace the protective heap, and perhaps add its impetus to that of the new missile. Survivors of the former class may eventually be destroyed by a missile of sufficient momentum."

(3) The experiments of epidemiologists dealing with the influence of immigration on the course of an epidemic among mice in a limited microcosm are also very interesting. One can distinctly see here that a continuous interference from without acting upon a definite population causes periodic oscillations in the epidemic which disappear immediately as the interference ceases. Let us quote Topley again: "When susceptible mice gain access to the cage at a steady rate the deaths are not uniformly distributed in time, nor do they occur in a purely random fashion. They are grouped in a series of waves, each wave showing minor fluctuation. The equilibrium between parasite and host seems to be a shifting one. As the result of some series of changes, the parasite appears to obtain a temporary mastery, so that a considerable proportion of the mice at risk fall victims to a fatal infection. This is followed by a phase in which there is a decreased tendency for the occurrence of fatal infection, and the death-rate falls. As fresh susceptibles accumulate this succession of events is repeated, and the deaths increase to a fresh maximum, only to fall again when this maximum is passed." But if only "no such immigration occur the epidemic gradually dies down, leaving a varying number of survivors."

We can conclude that *the process of elementary interaction between the homogeneous hosts and the homogeneous bacterial population possesses no "classical" periodic variations*. Without wishing to adopt at once the preconceived opinion that such a phenomenon is generally impossible, we ought in any case require a clear demonstration of its possibility. This demonstration will be really given below.

IV

(1) Turning back again from empirical observations to the general principles let us note that there can exist two different types of innate periodic oscillations in the systems, as Hill ('33) has noted recently in connection with physiological problems. One of them which was assumed by Lotka-Volterra and which we have searched above must be called a "classical" fluctuation and it is entirely analogous to well-known oscillations in physics arising as the consequence of the reaction with one another of properties analogous to inertia and elasticity. A changing system tends, on one hand, to maintain its state of motion because it possesses mass, whilst on the other the force of elasticity increases according to the removal from equilibrium and ultimately reverses the motion or change. In the classical theory of biological population the predator tends to multiply indefinitely, but by a removal in this way from an equilibrium with the prey the change in the predator population becomes reversed, later again replaced by an increase, and so on (equation 21a).

There is, however, another type of oscillation with which physiologists are concerned and to which apparently belong the spread of epidemics and fluctuations in our protozoan population. A certain potential or a certain state is here built up by a continuous process and the conditions become less and less stable until a state is reached t which a discharge (or epidemics) must take place. It is evident that the interaction between the two components instead of periodically leads here to an interruption of contact (depending from specific biological conditions in the case of epidemics and from a disappearance of predators and prey in our Protozoa), and then ceases until the next critical threshold. Such oscillations with an interruption of contact bear in physics the name of "relaxation oscillations."

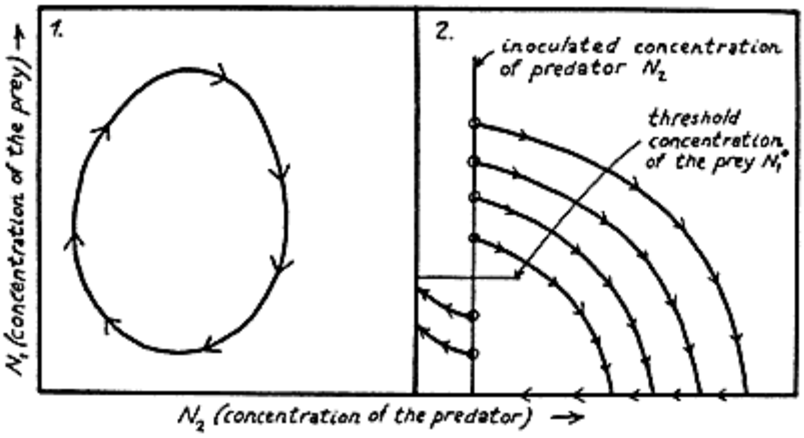

Fig. 34. Diagrams illustrating two types of innate periodic fluctuations in numbers of animals. 1. "Classical" fluctuation of Lotka-Volterra. 2. "Relaxation fluctuations."

It is easy to visualize the difference between these two types of oscillations employing the illuminating graphs so often used by Lotka. On the coordinate paper we usually plot time on the abscissae and densities of predators (N_2) and prey (N_1) on the ordinates. But if we abstract from time and plot N_2 on the abscissae and N_1 on the ordinates we obtain a clear idea of the nature of interspecific interaction. As Figure 34 shows in the case of classical oscillation we must have a closed curve.[4]

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[4] The transformation of the usual time-curves into such graphs is illustrated by a numerical example reproduced in Fig. 35. The upper part of it presents a theoretical case of the classical Volterra's oscillation in the usual form. If we note the values of N_1 and N_2 at different moments of time, and then plot N_1 against the corresponding N_2, we shall obtain the closed curve reproduced below.

Let us now turn our attention to the graph for the relaxation interaction. Suppose we introduce a definite amount of the predator, N_2, at different densities of the prey (N_1). Then, before the critical threshold of the latter is reached (N_1°, Fig. 34), an epidemic of *Didinium* cannot start and the curves return on the ordinate. After the critical threshold is reached there appears a relaxation which leads to the destruction of the prey--the curves cross the abscissa.

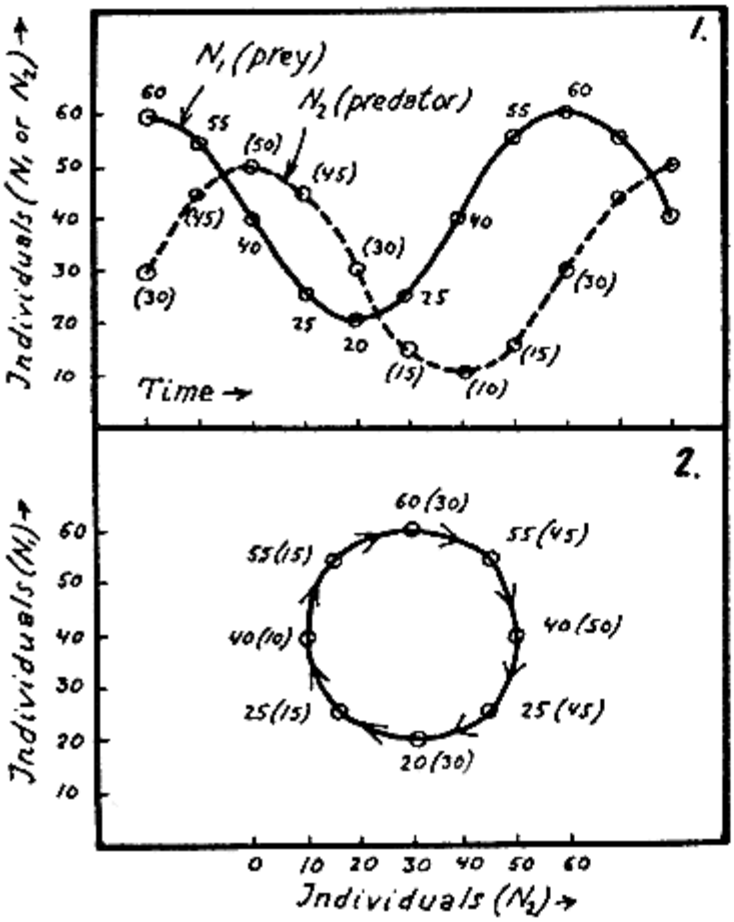

Fig. 35. Diagram illustrating the transformation of the usual time-curves (1) into relative graphs of interaction (2) for the "classical" Lotka-Volterra fluctuation in numbers.

(2) This little amount of theory enables us to formulate our problem thus: How do the biological adaptations consisting of a very active consumption of *Paramecium* by *Didinium* disturb the conditions of the classical equation (21a) and transform it into that of an elementary relaxation? For all the technical details the reader is referred to the original paper (Gause and Mtitt, '35), and we will discuss here only its essential ideas.

In a first approximation to the actual state of affairs we can write an elementary equation of relaxation. It can be admitted [on the basis of the observations on *Paramecium* (N_1) and *Didiniurn* (N_2)] that if N_2 *is* large the mortality of the predators is negligible when $N_1>O$. In addition, the increase of predators only slightly depends on N_1 (with an insufficiency of prey the predators continue to multiply at the expense of a decrease in size of the individuals; in this connection the consumption of prey but slightly depends on N_1).

Introducing these assumptions into the equation (21) we write $-\frac{dN_2}{dt} = 0$, where

$N1 \neq 0$ and $-\frac{dN_2}{dt} = d_2N_2$ where $N_1 = 0$.* To reduce the dependence upon N_1 of the members characterizing the interaction of species, we substitute $\sqrt{N_1}$ to N_1 † Then

$$\left.\begin{array}{ll} \frac{dN_1}{dt} = b_1N_1 - k_1N_2\sqrt{N_1} & \\ \frac{dN_2}{dt} = b_2N_2\sqrt{N_1} & (N_1 \neq 0) \\ \quad = -d_2N_2 & (N_1 = 0) \end{array}\right\} \ldots\ldots\ldots\ldots\ldots\ldots(21b)$$

---

[*] This condition is already sufficient for an exclusion of the "classical" periodic fluctuations.
†Special experiments show that this substitution is satisfactory (Gause and Witt, '35).

Figure 36 shows that the solution of the equation 21b (the integral curves on the graph N_1, N_2) actually coincides with biological observations on *Paramecium* and *Didinium*. It is therefore safe to assume that the general equation of the destruction of one species by another (21) takes in our special case the form (21b) instead of the classical expression of Lotka-Volterra (21a).

(3) The equation of relaxation (21 b) represents but a first approximation to the actual state of things, and is true only if N_1 or N_2 are large. Looking at the trend of the experimental curves on the surface N_1, N_2 with small densities (Fig. 37) we notice that they pass from the right to the left and cross the ordinate (Fig. 37, a). This means that "an epidemic" of predators cannot break out if the concentration of the prey has not attained the threshold value a_h. Below it predators disappear[5] and leave a pure population of prey, but above it we find usual relaxations.

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[5] In these experiments were used predators possessing no 'residual growth,' e.g. already diminished in size. See experiments with immigrations where predators usually did not find any prey in the microcosms containing very few Paramecia, and consequently perished.

Taking into account all these features we can write for *Paramecium* and *Didinium a* complicated equation of relaxation representing an adequate expression of what actually exists. We admit that the mortality of predators appears not only with N_1 = O, but that a slight mortality generally exists increasing with a diminution of the concentration of N_2, and that the intensity of hunting also increases with an insufficiency of prey.

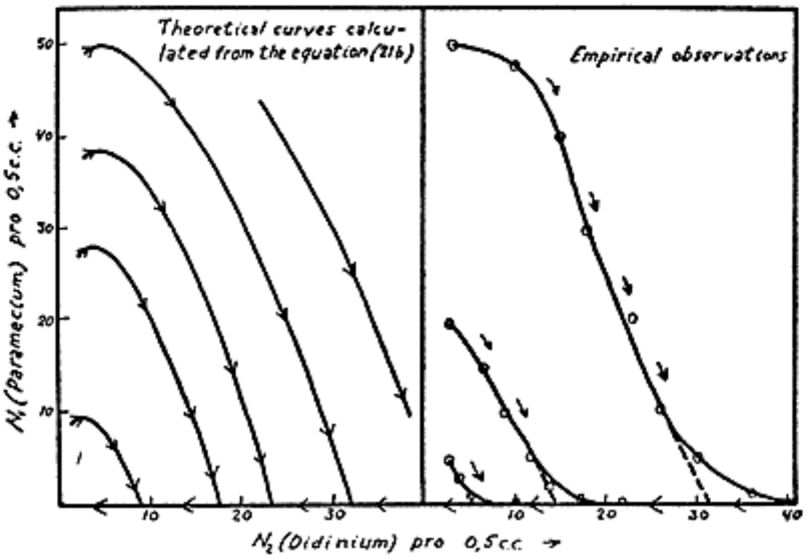

Fig. 36. The solution of the equation 21b (to the left) and empirical observations on *Paramecium* and *Didinium* (to the right). No "residual growth" of the population of predators (in the absence of the prey) is taken into account in the theoretical equation. From Gause and Witt, '35.

The solution of this complicated equation[6] is represented on Figure 38. It is a further concretization for *Paramecium* and *Didinium* of the principle of relaxation represented on Figure 34. An epidemic of predators cannot start below the threshold in the concentration of the prey, but above it we find usual relaxations. A characteristic feature of our food-chain is an extraordinarily low value of the threshold.

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[6] The equation given by Gause and Witt ('35) (21c) is:

$$\left.\begin{array}{ll} \dfrac{dN_1}{dt} = b_1N_1 - f_1(N_1)N_1N_2 & \\ & (N_1 \neq 0) \\ \dfrac{dN_2}{dt} = b_2N_2\sqrt{N_1} - f(N_2) = -d_2N_2 & (N_1 = 0) \end{array}\right\}$$

....(21C)

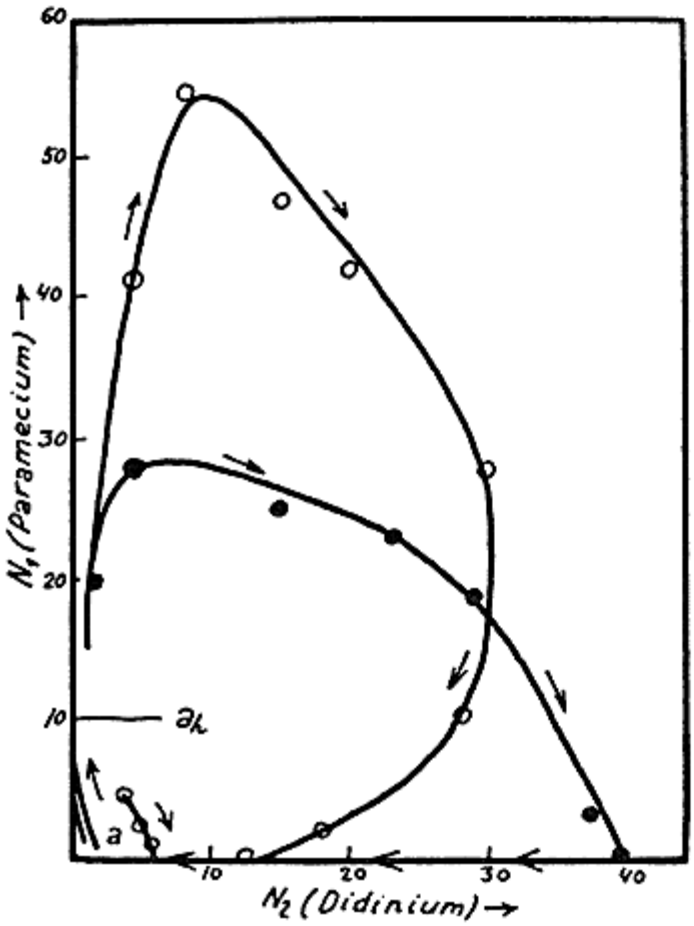

Fig. 37. The interaction between *Paramecium* and *Didinium* at different densities of population. The absence of the "residual growth" (comp. Fig. 36 right) as well as the differences between both curves are connected with slightly unfavorable conditions of the medium.

A mathematical analysis of the properties of the complicated equation of relaxation given in Fig. 38 shows that there is a point on the map of the curves of interaction which is usually called "singular point." The powers of mortality, natality and interaction of prey and predators are so balanced that the "classical" oscillations in numbers are theoretically possible around it. But in the case of *Paramecium* and *Didinium* the coordinates of this singular point are exceedingly small. In other terms the zone of possible classical oscillations is displaced here to such small densities that these oscillations are completely annihilated by the statistical factors which are much more powerful in this zone.

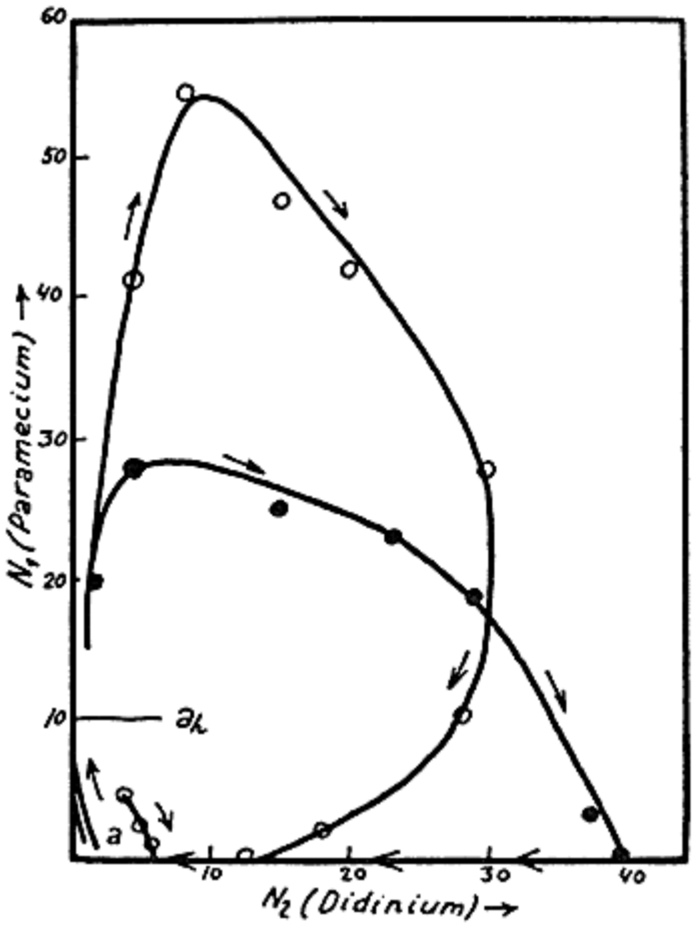

Fig. 38. The solution of the complicated equation of relaxation (21c). a_h represents the threshold concentration of the prey.

(4) In conclusion let us consider the appearance of periodic variations in numbers under the influence of immigrations (a slight and synchronous inflow of N_1 and N_2 after intervals of time t). In other terms we have to deal here with the problem of the influence of small impulses. At the origin (a, Fig. 37) they lead to a return of the curve to the ordinate. Relaxations arise when the concentration of N_1 rises above the threshold. From Figure 38 it is easy to calculate how a delay of the inflow after the threshold has been reached increases the dimensions of the relaxations (the importance of this problem for epidemiology has been pointed out by Rermack and McKendrick ('27)). When relaxation is going on, slight impulses do not disturb it seriously until crossing of the abscissa by tile integral curves, and later on up to their intersection with the line of horizontal tangents (Fig. 38). After this the impulses lead to a return on the ordinate and the process begins again.

V

(1) The theory of the preceding section shows that the consumption of one species by another in the population studied is so active that the classical oscillations in numbers are transformed into an elementary relaxation and the coordinates of the singular point

around which such oscillations could be theoretically expected are exceedingly small. This fact except its independent interest enables us to predict that were we in a position to reduce the intensity of consumption we could increase the coordinates of the singular point, and in this way observe the classical oscillations of Lotka-Volterra. The situation is entirely analogous to that of classical physiology. The rate of propagation of nervous impulses is under usual conditions too high and it is sometimes desirable to decrease it, to cool the nerve, in order to be able to observe certain phenomena. How can one decrease the intensity of consumption of one species by another?

The simplest way is to investigate a system where this intensity is naturally low. This has been recently made by Gause ('35b) who analyzed the properties of the food chain consisting of *Paramecium bursaria* and *Paramecium aurelia* devouring small yeast cells, *Schizosaccharomyces pombe* and *Saccharomyces exigaus*. Special arrangements allowed of controlling artificially the mortality of predators by rarefying them, and of avoiding the settling of yeast cells on the bottom by a slow mixing of the medium. Figure 39 shows that under such specialized conditions fluctuations of the Lotka-Volterra type actually take place, and in this manner the conditions of the equation (21a) are realized in general features.

It must be remarked that the equation (21a) does not hold absolutely true because the oscillations do not apparently belong to the "conservative" type. In other terms they do not keep the magnitude initially given them but tend to an inherent magnitude of their own (compare the first and second cycles on Figure 39, 1 and 2). This problem, however, requires further investigations.

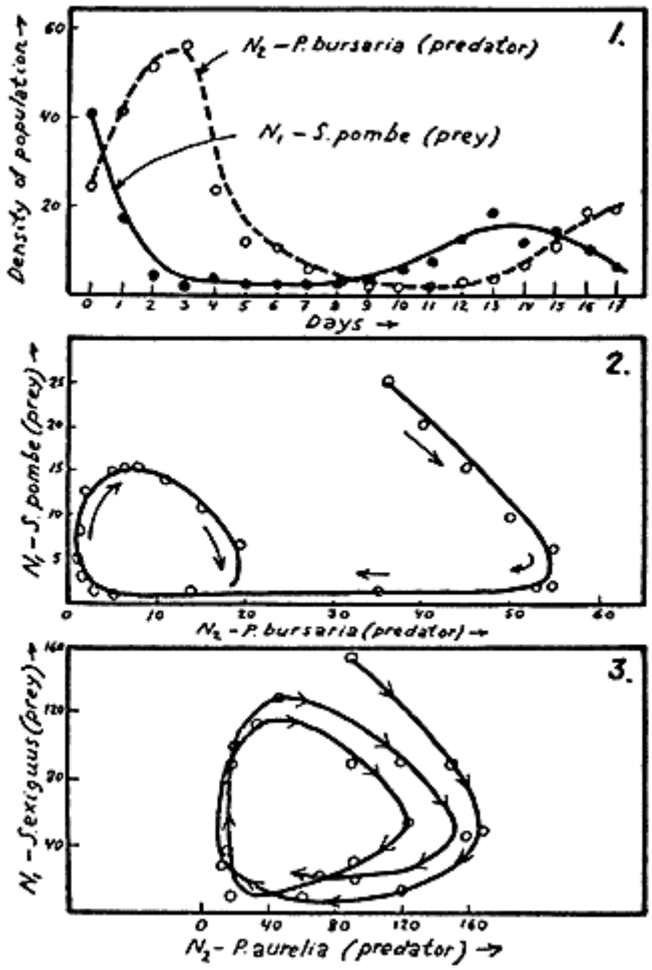

Fig. 39."Classical" periodic fluctuations in a mixed population of *Paramecium bursaria* and *Schizosaccharomyces pombe* in the usual (1) and in the relative form (2). (3) Periodic fluctuations in a population of *Paramecium aurelia* and *Saccharomyces exiguus* in the relative form. According to Gause, '*35b*.

(2) It is interesting to compare our data with some observations made at the Rothamsted Station (Cutler, '23, Russell, '27) which also attracted the attention of Nikolson ('33). There is reason to suspect that the fluctuations in the numbers of soil organisms observed by Cutler and referred to by Russell are interspecific oscillations. "Bacteria do not fluctuate in numbers when grown by themselves in sterilized soil; they rise to high numbers and remain at approximately a constant level. Their numbers fall, however, as soon as the soil amoebae are introduced, but no constant level is reached; instead there are continuous fluctuations as in normal soils. There is a sharp inverse relationship between the numbers of bacteria and those of active amoebae; when the numbers of amoebae rise, those of bacteria fall." It is hardly possible therefore to avoid the conclusion that Cutler had to deal here (in a complicated form) with classical periodic variations of the Volterra type.

In conclusion let us note that this final demonstration of the possibility of "classical" oscillations showed that very specialized conditions are required for their realization, and it is therefore easy to understand why in real biological systems with their typical adaptations leading to very intensive attacks of one species on another the so much discussed "relaxation interaction" between the species apparently predominates.

VI

(1) In Chapter III we have pointed out that the connection between the relative increase of the predator and the number of prey is not a linear one, and that this is of significance for the processes of one species devouring another. We can now be convinced that this connection is actually non-linear.

Recently Smirnov and Wladimirow ('34) have investigated under laboratory conditions the connection between the density of the hosts N_1 (pupae of the fly *Phormia groenlandica)* and the relative increase of the parasite $\frac{1}{N_2}\frac{dN_2}{dT}$ [the progeny of one pair (male + female) of a parasitic wasp, *Mormoniella vitripennis,* per generation]. The experimental data they obtained are represented in Figure 40. As the density of the hosts increases, the relative increase of the parasite increases also until it reaches the maximal possible or "potential increase" (b_2) from one pair under given conditions. That the curve showing the connection between $\frac{1}{N_2}\frac{dN_2}{dT}$ and N_1 can actually be expressed by the equation [Chapter III (23)]:

$$\frac{1}{N_2}\frac{dN_1}{dt} = b_2(1 - e^{-\lambda N_1})$$

can be seen in the following manner: by plotting as ordinates the values log (b_2 - $\frac{1}{N_2}\frac{dN_2}{dT}$) corresponding to different values of abscissae N_1, we should obtain a straight line which, as Figure 40 shows, is actually observed. The slope of this straight line is characterized by the coefficient l , which thus expresses the rate at which the relative increase of the parasites approaches its maximal value with the increase of the density of hosts.

(2) To summarize: We expected at the beginning of this chapter to find "classical" oscillations in numbers arising in consequence of the continuous interaction between predators and prey as was assumed by Lotka and by Volterra. But it immediately became apparent that such fluctuations are impossible in the population studied, and that this holds true for more than our special case. The corresponding analysis showed definitely to what biological adaptations this impossibility is due. This has enabled us to find a particular system possessing no such adaptations and in this way to observe "classical" fluctuations under very specialized conditions.

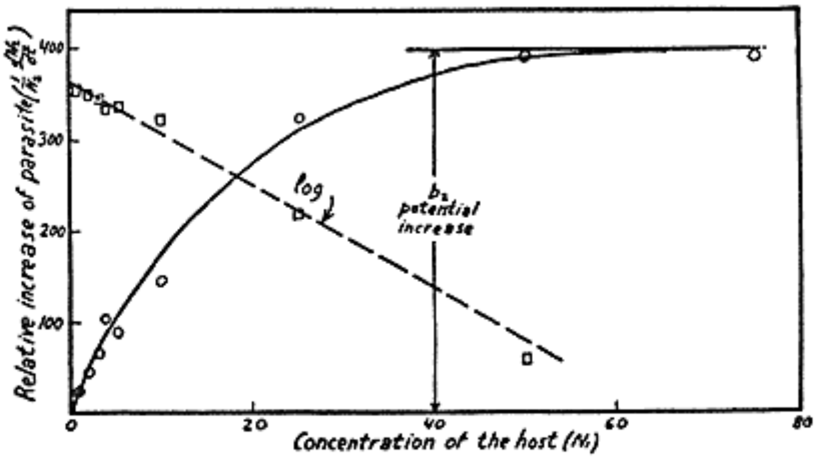

Fig. 40. Connection between the progeny of one pair of the parasite, *Mormoniella vitripennis,* and density of the host, *Phormia groenlandica,* according to Smirnov and Wladimirow. From Gause, '34c.

It is to be hoped that further experimental researches will enable us to penetrate deeper into the nature of the processes of the struggle for existence. But in this direction many and varied difficulties will undoubtedly be encountered.