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The Causes of Fluctuations of Populations of Insects

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The fluctuations of insect populations and the levels which they attain are of primary interest to society in general, for they often determine the value of our crops, the welfare of our domesticated animals and the health of our communities. The environmental factors which influence these population levels and their fluctuations, and the mechanisms through which they act upon the populations are of primary importance to the entomologist.

Fifteen years ago, when I first became interested in this subject and became convinced that it was of the greatest importance in entomology, I searched the literature for titles pertaining to it. However, one of the most interesting and stimulating papers that I found was not indexed in such a way that I could find it in my systematic search of papers on populations. I stumbled upon it accidentally. It was under the title "Presidential Address" by F. Muir of the Hawaiian Entomological Society, delivered on the 18th of December, 1913. Muir considered the effect of parasites and predators upon populations and the struggle for existence. By a few simple arithmetical calculations he showed the theoretical trends of hosts with and without parasites, and illustrated the rôle which predators might play in maintaining populations at a constant level.

Since this time a considerable amount of literature has accumulated on this subject. In general we might divide this literature into two groups: the one written from a viewpoint which is primarily mathematical, and the other group written by biologists whose considerations have been based mainly upon observational data and whose conclusions have been reached largely through philosophizing on the basis of their observations. There have been a few biologists who have indulged in enough mathematics to

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make it difficult to know to which group their papers belong; but in general the biologists have revolted against the mathematics. They have had the general feeling that these phenomena are too complicated to be represented by mathematics. On this point I cannot resist the temptation to digress and call your attention to a quotation from the classic works of Fourier, the French savant who was faced with the same argument when he was struggling with the application of mathematics to thermodynamics. He was faced with the contention that mathematics was applicable to surfaces and solids and not to anything as diffuse as heat and its transmission, just as we are now faced with the contention that mathematics may be applied in engineering, but not to such problems as the biotic control of insect pests.

"Profound study of nature is the most fertile source of mathematical discoveries. Not only has this study, in offering a determinate object to investigations, the advantage of excluding vague questions and calculations without issue: it is besides a sure method of forming analysis itself, and of discovering the elements which it concerns us to know, and which natural science ought always to preserve: these are the fundamental elements which are reproduced in all natural effects.

"We see, for example, that the same expression whose abstract properties geometers had considered, and which in this respect belong to general analysis, represents as well the motion of light in the atmosphere, as it determines the laws of diffusion of heat in solid matter, and enters into all the chief problems of the theory of probability.

"The analytic equations, unknown to the ancient geometers, which Descartes was the first to introduce into the study of curves and surfaces, are not restricted to the properties of figures, and to those properties which are the object of rational mechanics; they extend to all general phenomena. There cannot be a language more universal and more simple, more free from errors and from obscurities, that is to say more worthy to express the invariable relations of natural things.

"Considered from this point of view, mathematical analysis is as extensive as nature itself; it defines all perceptible relations, measures times, spaces, forces, temperatures; this difficult science

is formed slowly, but it preserves every principle which it has once acquired; it grows and strengthens itself incessantly in the midst of the many variations and errors of the human mind.

"Its chief attribute is its clearness; it has no marks to express confused notions. It brings together phenomena the most diverse, and discovers the hidden analogies which unite them. If matter escapes us, as that of the air and light, by its extreme tenuity, if bodies are placed far from us in the immensity of space, if man wishes to know the aspect of the heavens at successive epochs separated by a great number of centuries, if the action of gravity and of heat are exerted in the interior of the earth at depths which will always be inaccessible, mathematical analysis can yet lay hold of the laws of these phenomena. It makes them present and measurable, and seems to be a faculty of the human mind destined to supplement the shortness of life and the imperfection of the senses; and what is still more remarkable, it follows the same course in the study of all phenomena; it interprets them by the same language, as if to attest the unity and simplicity of the plan of the universe, and to make still more evident that unchangeable order which presides over all natural causes."

To agree with Fourier it is not necessary to forget the extreme complexity of our subject matter. A divergence of interest along the two lines indicated is quite natural. We have on the one hand the problem of devising the mathematical expressions which indicate all the possible relationships which may arise. In these expressions it is expedient to use quite arbitrary values to represent the numbers of organisms present and the rates of their development. On the other hand, to apply these mathematics, it is necessary to devise means determining how many organisms are present and how rapidly they are developing. Appalled though we may be by the complexity of the problem we, as entomologists, are committed to it. Our attempts to control the populations of insect pests may be likened to the efforts of the alchemists of old, rather than to the rational procedure of a modern engineer in synthetic chemistry. I say this as an admission rather than as an accusation, for I am directing an experiment station that has three expeditions exploring for parasites at the present time. We are willing to try anything in the hope that we may produce a pot of gold in a

pineapple field. I see no other way of proceeding at the present time, neither do I see way of escape from the perplexing problem of the behavior of populations with which we are faced. If we are to uphold our branch of science we must get away from trial and error.

It will not be possible to make a complete survey or give an exhaustive discussion of all the literature on this subject. Following Muir we have Thompson calculating the trends of host and parasite populations in order to determine what the possibility of control would be if different parasites were introduced for certain pests. It is true these calculations of the number of generations required for parasites to overcome hosts are highly theoretical. On the other hand, in the development of these theories Thompson called attention to many fundamental phenomena and many interesting conceptions of population phenomena. The argument of many biologists that it is too theoretical is not to be given too much attention for we may be reminded that the science of physical chemistry rests fundamentally upon the work done by Willard Gibbs, which even at the time of its publication was considered to be too theoretical to be of any particular value.

The most encouraging development in the application of mathematics to the phenomena of animal population is the advent into the field of the distinguished mathematician, Professor Vito Volterra, of the University of Rome. His interest was attracted to the field through a conversation with M. D'Ancona, who had been studying the fluctuations of the populations of fish in the Adriatic Sea. A summary of Volterra's work up to 1928, translated into English, has been included as an appendix to my volume "Animal Ecology." Since that time his theories have been further developed and presented in a series of lectures at the Sorbonne in Paris. They have appeared in printed form under the title "Lecons sur la Théorie Mathématique de la lutte pour la vie," published in 1931.

I would grant the contention of the biologists that Volterra has made many assumptions with regard to the forces of reproduction and death. However, we must admire the logic in his treatment of the subject, beginning with the biological association of two species which contend for the same food, the consideration of association

of two species, one of which feeds upon the other, and his addition of one complicating factor after another until he comes to the case of any number of whatever species, some of which feed upon others, and finally his treatment of conservative and dissipative biological association.

Among his deductions are included what he calls the three fundamental laws of fluctuation. They are stated as follows:

1. *Law of the Periodic Cycle.*—The fluctuations of the two species are periodic, and the period depends only upon the coefficients of increase and decrease and the initial conditions.

2. *Law of the Conservation of the Averages.*—The averages of the numbers of individuals of the two species are constant whatever may be the initial values of the numbers of individuals of the two species just so long as the coefficients of increase and decrease of the two species and those of protection and of offense remain constant.

3. *Law of the Disturbance of the Averages.*—If an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the average of the number of individuals of the species that is eaten increase and that of the individuals of the species feeding upon the other diminishes.

These deductions are worthy of our consideration. Do the numbers of populations of two species fluctuate periodically when other conditions are remaining constant? Will the numbers of individuals of a species rise to a point of saturation if conditions remain constant? If we use some mechanical or chemical means of combating an insect pest and destroy the pest and its parasites together, will the result be an increase in the pest and a decrease in its parasites?

The only constructive reaction to these propositions is to formulate a method of experimentation whereby the truth or fallacy of Volterra's deductions can be demonstrated. Some biologists, notably those of the school of Raymond Pearl, of Johns Hopkins University, have been attempting to express in mathematical form the results of various experiments with populations. Gause (1932) of the Timiriasev Institute for Biological Research, Moscow,

Russia, is one of these. He has formulated expressions of the effect of various environmental factors upon the populations of *Tribolium confusum,* grasshoppers and yeasts.

Turning our attention now to the entomologists themselves, we find a group in Germany interested in the general phenomena of population growth, particularly as it affects outbreaks of insects. Martini (1931), Zwolfer (1932), Bodenheimer (1930), and Eidmann (1931) have published papers based mainly upon evidence gathered during epizoötics of insects. In the main they, like other zoologists, have looked to great changes in physical factors to explain the changes in population levels. Eidmann is inclined to agree with Elton that sun-spot cycles have a profound influence upon the fluctuations of animal populations. From his study of the outbreaks of certain forest insects he has concluded that they are correlated with sun-spot maxima. He believes these come in general about every ten years, and that every third one represents a high maximum. Such phenomena obviously are not subject to experimental verification; and the whole matter of sun-spot cycles and its effect upon biological phenomena rests upon a rather uncertain foundation.

Not only have many entomologists looked to the physical factors for explanation of the changes in population levels, but some of them have contended that physical factors are the only causes of fluctuations of populations; and have even denied that a condition of equilibrium between various members of a population could exist. Such problems, however, cannot be settled by assertions or denials. Neither can satisfactory proof come from observations on fluctuations of populations in the past. Conclusive evidence must come from careful experimentation. With this in mind a search was made for an insect which would be susceptible to laboratory experimentation. It should live in a stable environment; its food should not be perishable. It should be small so that large numbers could be kept in a small space and it should develop rapidly, passing through many generations in a short period of time. After the consideration of many species, the confused flour beetle, *Tribolium confusum,* was selected.

Since that time a group of students has worked with populations of this beetle under controlled conditions to determine

whether there was a hope of confirming the hypothesis of biotic potential and environmental resistance through the use of this species. In the field of genetics Drosophila was chosen for intensive study, with the result that the inheritance of characters was not only traced to specific chromosomes, but genes were described and located, and their behavior recorded. More significant still, the fundamental principles derived from the study of Drosophila were found to hold not only for other animals, but for plants as well.

The ambitious program for the intensive study of Tribolium populations, therefore, got under way with the hope that generalizations might be made which would apply in insects in general. It was shown (Chapman, 1928) that populations of Tribolium under controlled conditions would come to a point of saturation and maintain this with only slight fluctuations. This was regardless of whether the population was high or low at the start, or whether the environment was large or small. This substantiated Volterra's "first law" of the fluctuations of populations.

Proceeding to the analysis of the situation, Sweetman and Palmer (1928) showed that in a medium of whole-wheat flour the development of *Tribolium confusum* was very constant when temperature and moisture remained constant. It was shown that the addition of excess wheat embryo or other food accessories to the medium made no difference in the rate of development so long as the whole-wheat flour was used as a ration. It was thus demonstrated that the environmental factors of temperature, moisture and food could be satisfactorily controlled to the point of producing a constant effect on the beetles.

Chapman and Baird, unpublished manuscript, made a study of the biotic constants of Tribolium over a series of temperatures with controlled relative humidity. It was found that when dealing with populations of Tribolium, the times for the hatching of a group of eggs, the development of larvae and of pupae were very constant. Indeed, the coefficients of the various phenomena were quite comparable with those of physical processes. Experiments with the growth of populations under different conditions of temperature have shown that the rate of increase of a population is very precisely correlated with the biotic constants. One

can predict when the egg, larval, pupal and adult populations will change on the basis of the biotic constants when the temperature and humidity under which they are developing are known. The mathematical consideration of the growth of the population has been dealt with by Stanley (1932) in a recent paper. It will be sufficient at this point to call attention to the uniformity of the stages of population growth and the fact that populations, under the same conditions, have practically identical fluctuations as they approach equilibrium. (Fig. 1.) In his detailed analysis of the trend of the populations, Stanley was not satisfied with simple empirical formulae. He contended that the situation with regard to the population at any one time was the result of its previous history and that any damage that it might suffer was irreparable within finite time.

In the course of the study of populations under constant conditions, it was found that by varying temperature and humidity the rates at which the populations moved to their equilibrium values could be varied; and to a less extent the level which they finally attained could be influenced by these physical factors, as was pointed out by Holdaway (1932) in his study of the effect of moisture. After being satisfied with the results of experiments on the constancy of populations under constant conditions and having the results verified by workers in other institutions, as by Allee (1931) and Park (1932), the next step was to proceed on an experimental basis to offset the equilibrium of these populations. It was the plan to introduce a parasite into the system and see what effect this would have upon the equilibrium. But just before the plans for this experiment were completed, something went wrong with the cultures that had been in equilibrium. They broke down; at first in a very disorderly way. Their behavior was so disturbing that there seemed to be nothing to do but watch the disorder proceed. However, eventually they fell into a rhythmic fluctuation; and, most remarkable of all, two populations which had been handled in duplicate assumed the same synchronous rhythm as their levels sank lower and lower. (Fig. 2.) At last it was decided to kill all the individuals of both cultures and examine them carefully, whereupon it was found that they were infested with a sporozoan Protozoa belonging to the genus Adelina. This

parasite infests the larvae and kills them at about the time of pupation.

The synchronous rhythmic fluctuations were so striking and so much like those postulated by Volterra for the fluctuations of species that it was decided to sterilize all the equipment and start over with cultures set up at the equilibrium levels; and then to infest them with Adelina and watch the progress of the populations. Four cultures were set up: two at 27 degrees, and two at 32 degrees Centigrade. The growth of the parasite was inhibited at 32 degrees, and at times some of the beetles succeeded in pupating and emerging as adults. Since these cultures were set up with about 374 adults each, which were of random age, the adults of populations could be expected to gradually die out, inasmuch as they would not be replenished by new individuals. Since the life of an adult Tribolium is about a year, the oldest members of these populations should die almost at once and the youngest would all be dead in a year's time. It is interesting to note that during the 360 days during which these cultures were carried on at 27 degrees the adult population curve dropped off as a straight line. And at the end of this period of time these two populations were within ten individuals of the same number. Due to the cannibalistic habits of the larvae and adults, eggs are eaten when there are high populations of larvae to accidentally encounter them in the flour. The result is that when larvae are few, eggs are many. When the eggs hatch, the larvae proceed to the eating of eggs, with the result that the egg curves go down. The curves for larvae and eggs are then similar to those for predator and prey. As time goes on, the fluctuations of these two curves with their opposite tendencies become more and more marked, and the synchronism of the two duplicate populations is very striking. Here then is a case where physical factors were maintained constant; and the interaction of the biotic factors not only produced regular fluctuations, but in the two duplicate populations these fluctuations were strikingly similar in period and amplitude. They are not only like each other, but like the original populations which were accidentally infested.

It is unfortunate in this case that we did not have a method of recording the abundance of the protozoan parasite. Neverthe-

less, the fluctuating curves of eggs and larvae bear the relationship of prey and predator. They demonstrate periodic fluctuations of populations under physical conditions which are maintained as nearly constant as possible in a Carrier cabinet with a temperature and relative humidity control, and food changed at regular intervals. The experiment constitutes a demonstration of Volterra's first law of fluctuations; the law of the periodic cycle.

Inasmuch as the laws of fluctuations all assume that the coefficients of increase, or biotic potential, are constant, another series of experiments was set up to determine what effect a difference in the number of eggs laid or in the reproduction potentials of the insect might have upon the rates at which the populations increase and the level which they ultimately attain. The theory of biotic potential and environmental resistance rests upon the hypothesis that the rate of reproduction on the one hand, and the resistance of the environment on the other, determine the trend of populations.

It was found, as one might naturally expect, that in any population of female Tribolium there would be a normal distribution of egg-laying ability. Some females have a relatively high egg-laying rate and others a much lower egg-laying rate. Therefore, groups of females were selected, some of which had a high egg-laying rate, and others of which had a low egg-laying rate. These were set up in duplicate. The trends of these populations can be followed in Figure 2. The egg curves for populations 1 and 2 (those of the high egg-laying rates) rise more rapidly than those of populations 3 and 4; and maintain a much higher level during the first phase of population growth, as might be expected. If it were not for the cannibalistic habits of the larvae, these egg populations would have maintained these constant levels until the new adults began to lay. However, as the larval populations came up, the egg populations went down. As anticipated, the larval populations, in the case of those with a high egg-laying rate, rose to a level about equal to that which had been maintained by the eggs, and the same was true of the populations represented by the low egg-laying rate.

It was inevitable then that the numbers of pupae in the populations 1 and 2 would be higher than for 3 and 4. And, in turn, it

was inevitable that the number of adults in the first two populations should be greater than in the last two, as the populations entered the second phase of their growth. The first two populations agree very closely in all their behavior. In the early part of their history any difference that became evident in one stage was reflected by a difference in the succeeding stage. Culture No. 1 produced a few more eggs at first than Culture No. 2. Culture No. 2 later produced a few more eggs than Culture No. 1; and this in turn was followed by a larger number of larvae in Culture No. 2; and then by a larger number of pupae. At an age of 90 days there were about 10 per cent more adults in the second culture than in the first. But since the adults are carnivorous and eat their own eggs, Culture No. 1 soon had about a hundred more eggs than No. 2, and then more larvae; and this was soon followed by more pupae, and then more adults. When the F_1 daughter adults emerged and the populations entered their third phase of growth, the two populations were equal and from that time on remained practically identical.

Turning our attention now to the history of the two populations which were selected for low egg-laying rate, we find some interesting discrepancies. Through an unfortunate error in the early history of population No. 4, a portion of the record was omitted. From the level to which the larval populations arose, it may be assumed that the egg curve must have reached a level higher than that of Culture No. 3.

During the second phase of the population growth, we find the greatest difference between the adult populations of the cultures selected for high and low egg-laying rates. This is what one would expect, for these individuals are the direct result of the eggs laid by the original adults. Unless the daughters inherited their mothers' egg-laying propensities, we might expect that the differences between the populations would disappear. The most striking thing in the entire experiment is the fact that when the F_1 daughters began to lay, the egg curve of Culture No. 3 rose higher than that of any other culture in the experiment; while that of No. 4 was lower than any other. It must be kept in mind that these egg curves do not represent solely the rate of egg laying, but they are the net result of the laying and eating that is being

done in the population. Therefore, a culture with a small number of adults may have a large number of eggs present in it, and vice versa. Culture No. 4 with its small number of eggs soon outstripped all others in the population of larvae, and after 120 days it had an enormous advantage over the others, with a resultant high population of pupae. When the F_2 adults began to emerge the population curve for No. 4 mounted rapidly until it reached the level of Nos. 1 and 2. Thus, the advantage of the high egg-laying rate on the part of the grandmothers was entirely wiped out by the time the F_2 generation appeared on the scene. Culture No. 3, since the emergence of the F_1 daughters, held the record for highest number of eggs present in any population, yet it was unable to reach the population level of the other cultures. At the age of 120 days the adults' curve was mounting as rapidly as that of population No. 4. But, although it has had the high egg population, it has not been able to maintain a high larval population. It consequently found itself at 140 days with a low pupal population. Cultures 1, 2, and 4 reached the saturation point during the third phase of their growth, and from this point on the eggs will have little chance of escaping being eaten during the period required for hatching. In Culture No. 3, however, the chances of hatching are better, for there are fewer adults present. Consequently, it has been able to make slow but steady gains, and is at the present time at a level less than 10 per cent below that of the other three populations. This discrepancy of less than 10 per cent is negligible as compared with the data used by the observational biologists. In fact, the adult curves described for these four cultures from the beginning agree more closely with each other than the data used by many of our mathematically inclined contemporaries. But with the experimental technique one is permitted to examine into the smallest discrepancies and to seek their explanation. One must remember that the numbers which have been given as population values are exact counts of the entire populations and not estimates. They seem to indicate that, complicated though the problem may be, it is not beyond the possibility of attack.

To summarize, the Tribolium studies have thus far demonstrated that:

1. Populations will rise to a point of saturation which is independent of the size of the environment and of the initial population, so long as other environmental conditions remain constant. This is a substantiation of Volterra's "Law of the Conservation of the Averages."

2. Populations consisting of members, some of which feed upon the others, fluctuate periodically regardless of the fact that the physical conditions of the environment are constant. This is essentially a substantiation of Volterra's "Law of the Periodic Cycle."

3. If a population is started from individuals with a reproductive potential below that of the mean for their species, the immediate effect is to retard the rate of population growth, but the population will ultimately reach its normal saturation because the daughters of the next generation will tend to conform to the mean reproduction potential for their species. Any advantage or disadvantage which individual members of a population may possess will be lost in the next generation unless inherited.

As remote as these beakers of flour beetles may seem from the problems of pineapple and sugar cane fields, they may after all be no more remote from the practical things of life than the geneticist's cultures of Drosophila in milk bottles, which have made more fundamental contributions to the practical problems of breeding animals and plants than all the research on domesticated animals put together. Progress will admittedly be slow, but the results seem to be nature's own answer to the question of what factors influence population fluctuations.

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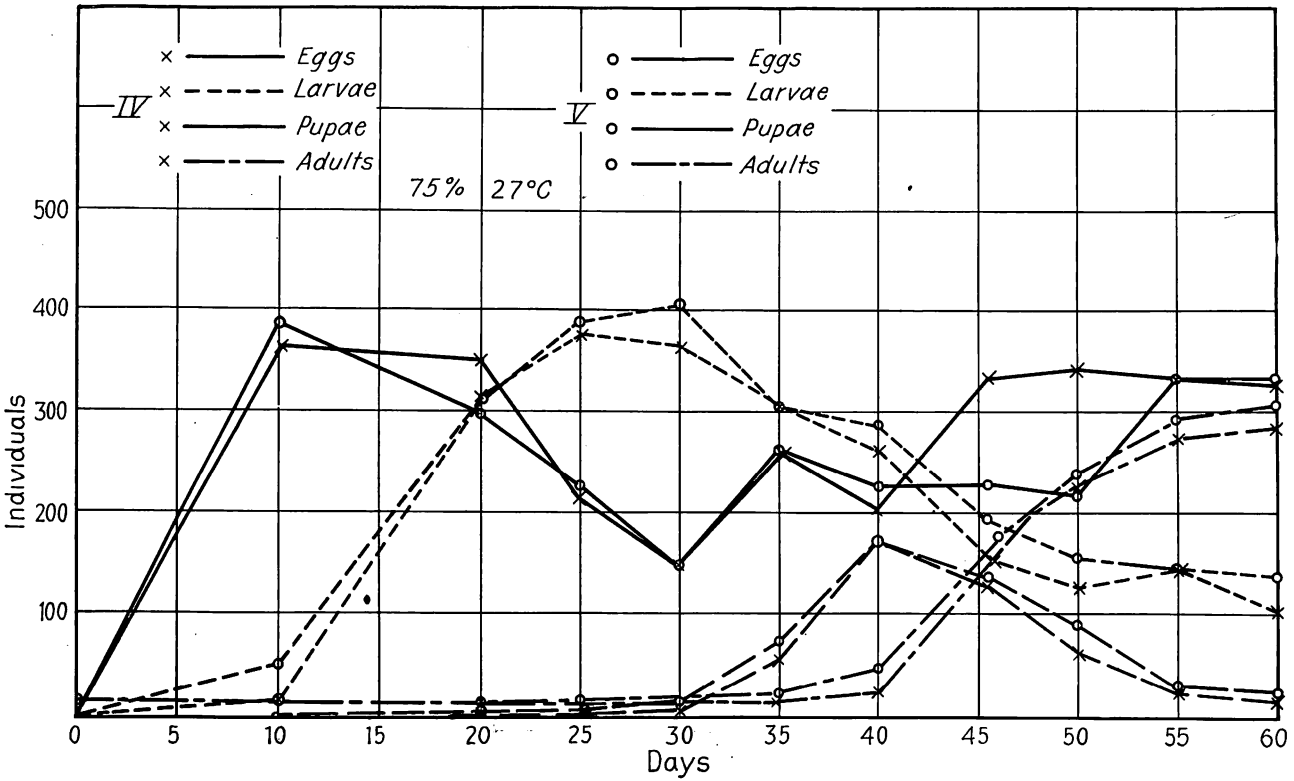

Fig. 1. Population trend of *Tribolium confusum* Duval at 27 degrees C. and 75 per cent of relative humidity. Two populations, IV and V compared.

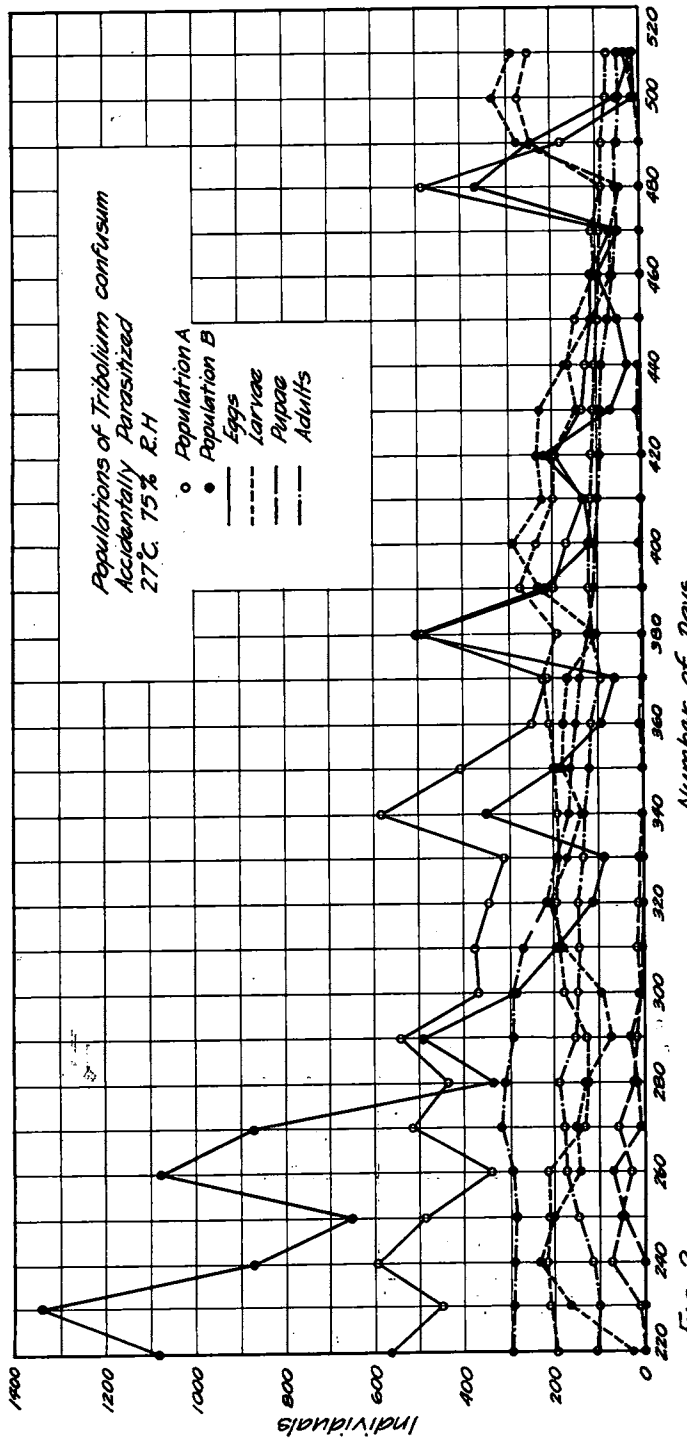

Fig. 2. Populations of *Tribolium confusum* accidentally parasitized. Duplicate populations A and B compared.

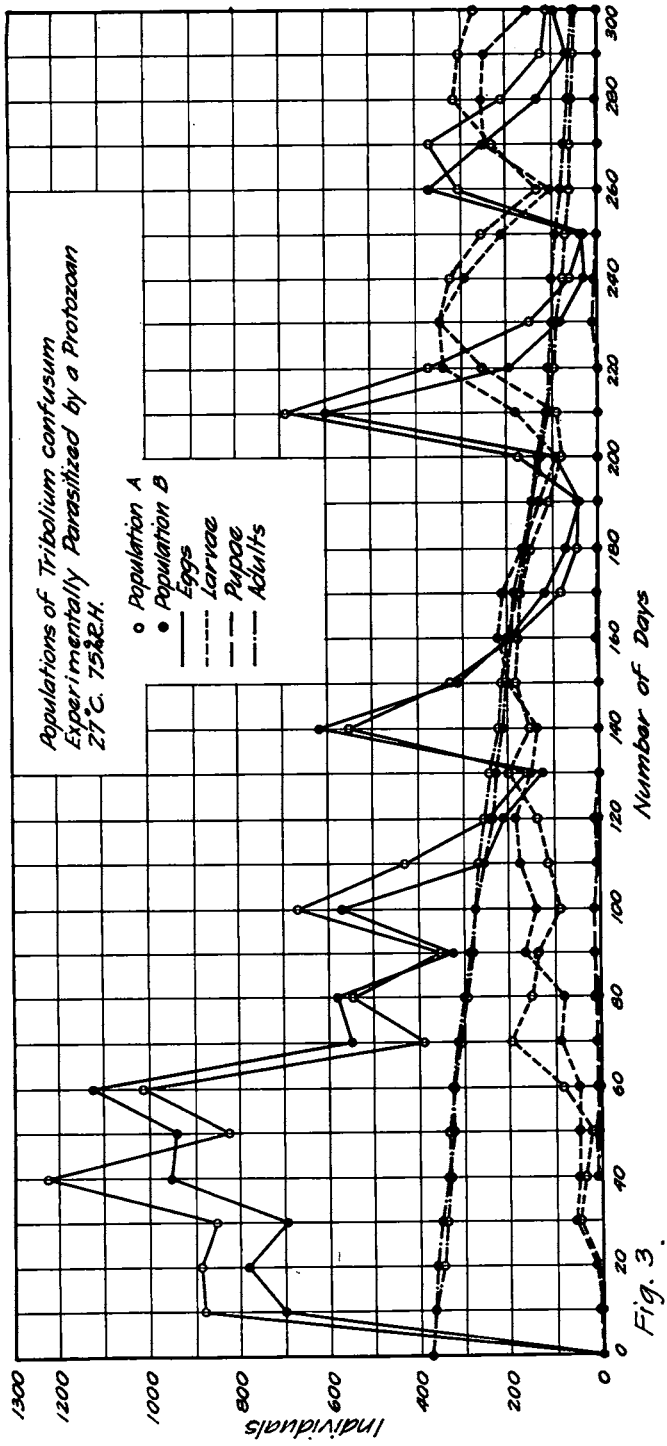

Fig. 3. Populations of *Tribolium confusum* experimentally parasitized by a protozoan, *Adelina*, at 27 degrees C. and 75 per cent of relative humidity. Duplicate populations A and B compared.

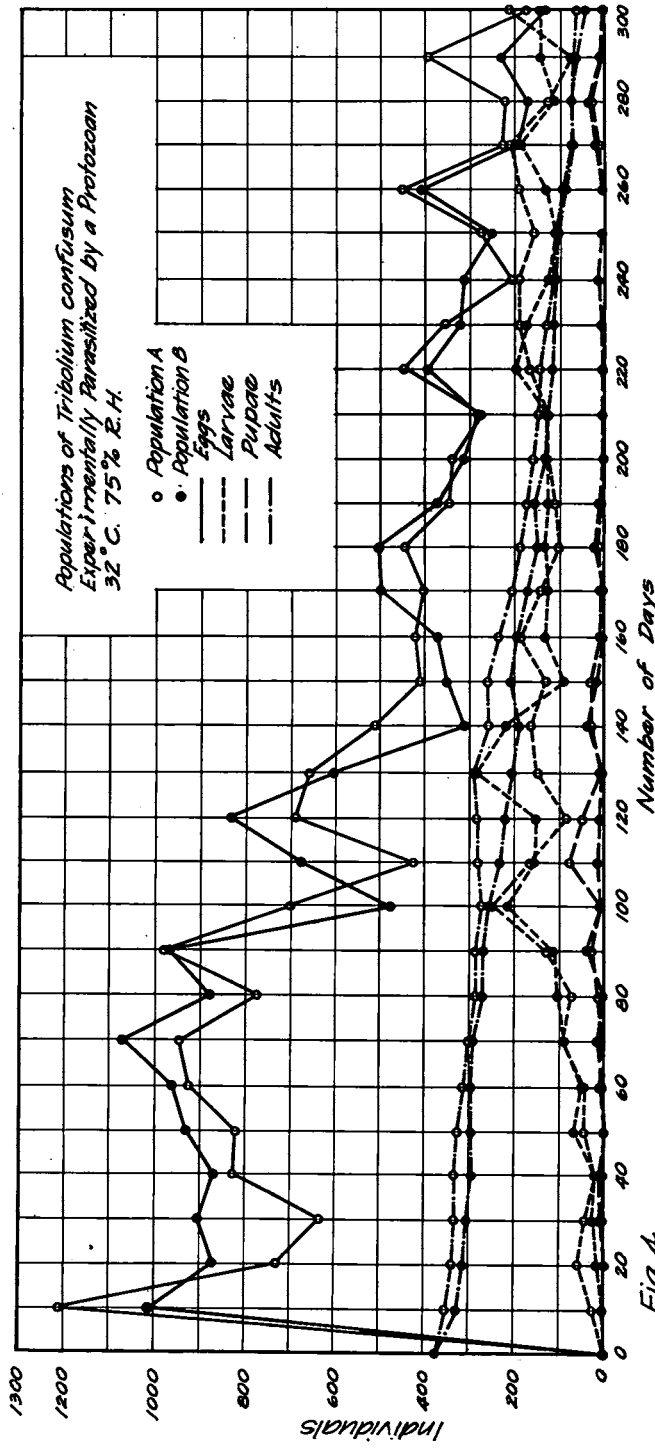

Fig. 4. Populations of *Tribolium confusum* experimentally infested with *Adelina* at 32 degrees C. and 75 per cent of relative humidity. Duplicate populations A and B compared.

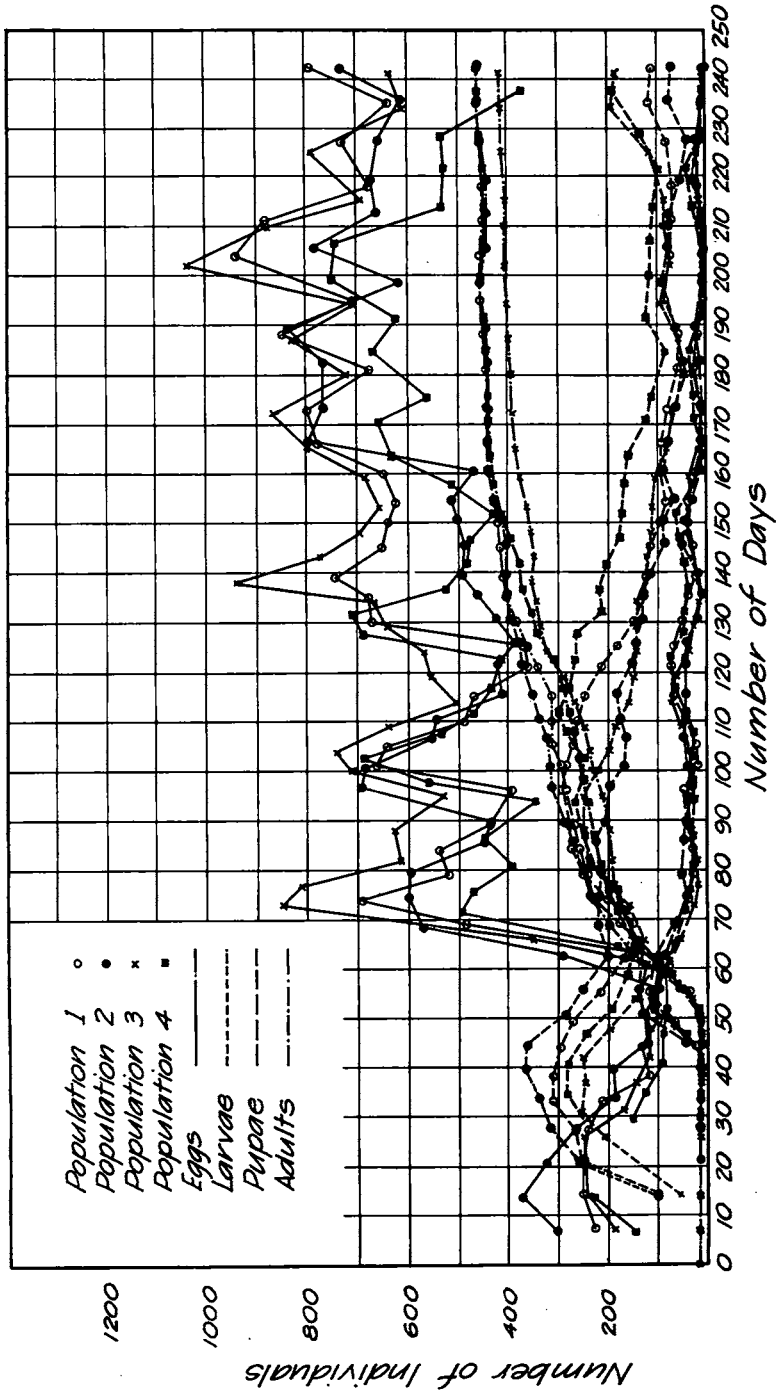

Fig. 5. A comparison of populations of *Tribolium confusum* originally selected for high and low egg laying rates. Populations 1 and 2 were started with females having a high egg-laying rate. Populations 3 and 4 were started with females having a low egg-laying rate.