Research on Populations of Tribolium confusum and its Bearing on Ecological Theory: A Summary

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SPECIAL REVIEW

RESEARCH ON POPULATIONS OF *TRIBOLIUM CONFUSUM* AND ITS BEARING ON ECOLOGICAL THEORY: A SUMMARY

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(*With* 1 *Figure in the Text*)

THE series of studies on populations of the flour beetle (*Tribolium confusum* Duval), which this paper is intended to summarize, was initiated by R. N. Chapman (1928). Previously, this beetle had received considerable attention from entomologists (including Chapman), chiefly on account of its importance as a pest in stored cereals. Park (1934) has summarized most of the important facts connected with the general biology of *Tribolium*, and the following is intended to supplement his paper, on which, for the sake of completeness and to serve as an introduction, the remarks in § 1 are based.

1. Beetles of the genus *Tribolium* belong to the family Tenebrionidae, subfamily Ulominae. All members of this subfamily occur either as pests in stored products or else under the bark of trees and in rotting logs, and the two flour beetles, *T. confusum* Duval and *T. ferrugineum* Fab. (= *castaneum* Hbst.), have also occasionally been taken in these situations (Good, 1933). *T. confusum* can exist in a variety of cereal products, though not on the whole grain. Sweetman & Palmer (1928) have shown that vitamin B, which is present in most flours, is essential for its development. Good (1933) concluded that there might be from 6 to 11 larval instars, 7 or 8 being the most usual. Park summarizes Brindley's (1930) data on larval sizes and lengths of stadia and gives admirable figures of larvae, pupae and adults. Sex is easily determined in the pupal stage. The adults are reddish brown in colour and darken with age; their mean length is 3·4 mm.; males weigh on an average 1·48 mg. and females 1·78 mg. The period of development varies considerably according to conditions of temperature and humidity. Brindley (1930) found that the average was 30 days, from egg to adult, at 29° C. and 73 % relative humidity (R.H.). The adults have a relatively long life, again varying with environmental conditions but averaging about a year when these are favourable.

Park also deals with those papers which throw further light on the general biology of the beetle, particularly those of Chapman (1928) and Holdaway (1932), but they may more properly be considered separately in relation to other work on population problems with which he was not concerned in his paper.

2. Chapman (1928) first considered a fundamental property of natural populatich, by way of analogy, is stated in terms similar to those used for the relationship between electric current, potential and resistance as follows: "the quantity of organisms which may be found is the result of the balance between *biotic potential,* or the potential rate of reproduction, and the environmental resistance." On the basis of this hypothesis two experiments with *Tribolium confusum* were devised.

(*a*) The first was to test "whether a condition of equilibrium would be reached in which the population, as expressed in the number of individuals per gram of flour, would remain constant regardless of the size of the environment". A series of environments was set up of 4, 8, 16, 32, 64 and 128 g. of whole-wheat flour, the depth of flour in each case being the same. Into each environment adult beetles, one pair (male and female) to every 4 g. of flour, were introduced. Temperature and humidity were kept uniform. By using sieves of bolting silk of various meshes it is possible to remove eggs, larvae, pupae and adults from the flour separately. Counts were made at intervals of the numbers of the various stages present, and it was found that in each environment there was initially "a rapid increase in numbers, which was followed by a condition of relative stability....The mean number of individuals per g. of flour in all environments after the attainment of stability was 43·97" ± 2·88. Thus the first proposition was verified. "A condition of equilibrium is attained in which the biotic potential is equalled by the environmental resistance and the population remains relatively constant," continuing with regular fluctuations in its various components, about a steady mean.

(*b*) Secondly, Chapman desired to test "whether the effective rate of reproduction of single pairs of beetles was inversely proportional to environmental resistance, which, in this case, is a function of the total size of the environment". A single pair of newly emerged adults was placed in each of a series of environments having the same quantitative relationship with each other as those in the first experiment. "In this case, in the same period of time, one pair of beetles gave rise to 178 individuals in an environment of 4 grams and another to 4500 in 128 g. The intermediate environments had populations of intermediate sizes." Within the period of the experiment only the smaller environments had reached equilibrium, with the same number of individuals per g. of flour as in the first experiment, while the larger environments were showing similar trends. Thus it was claimed that "the increase of a population is proportional to the size of the environments and, therefore, inversely proportional to the environmental resistance". It was, however, demonstrated by Allee (1931) and Park (1932) and also independently by MacLagan (1932) that, for the early stages of population development in *Tribolium,* this conclusion was not valid. These studies will be considered below. However, as regards the maintenance of the final asymptotic population, Chapman's explanation of the mechanism of environmental resistance is undisputed. He showed that the adults and larvae are cannibalistic, eating eggs and sometimes young larvae and pupae. The frequency with which eggs are eaten depends on their relative abundance in the population. The number of eggs present in the population represents its biotic potential. "A high potential is ever present" but is prevented from realization in the balanced population by egg eating, "and when the environmental resistance" (egg eating) "is lowered by the death of adults, eggs hatch and produce new adults to take the place of those which have died".

3. Gause (1931) analysed Chapman's data and showed that the growth of the *Tribolium* population takes the form of the Verhulst-Pearl logistic curve (see Pearl, 1925). Further mathematical studies of *Tribolium* populations have also been made by Stanley (1932, 1932 *a*), who considered individuals in the population as "moving or stationary particles amenable to the formulations of the kinetic theory of gases" and was able to obtain theoretical curves showing "substantial agreement with the biological data". The present writer is unable to do more than notice these papers (the mathematical reader should consult them himself), but it is still necessary to emphasize the importance to ecologists of exact quantitative methods in dealing with animal populations, so amply vindicated by the results of the researches now under discussion.

4. Before passing on to a consideration of the relationship between population density and rate, reproduction and to the effect of conditioning of the environment on the asymptotic population, it is necessary to examine the work of Holdaway (1932) in which further light is thrown on the effect of environmental changes on environmental resistance. Holdaway investigated the growth of populations of *Tribolium confusum* under different conditions of R.H. He found that the magnitude of the asymptotic, or balanced, population varies according to the amount of atmospheric moisture in the external environment, there being an optimum condition at about 75 % R.H. Above this level of humidity the balanced population decreases in magnitude as saturation is approached and, with complete saturation, reaches zero owing to the formation of fungi which prevent development. By maintaining a population at 25 % R.H. until it had stabilized itself and then transferring it to an atmosphere of 75 % R.H., he was able to show that population growth recommences in the new environment and continues until it has reached a higher level of stability. Further, it was shown that the rate of growth of the population increases with humidity, although the effect of humidity changes on the various stages of development of the beetles was not the same. The "viability of the eggs and pupae is at a maximum at low humidities, while for larvae it is at a minimum. As regards the duration of the various stages there is little effect on eggs and pupae....The larval stage is the one in which duration is most affected by atmospheric moisture. It increases with decrease in humidity." It is not possible to summarize here all of Holdaway's results. They demonstrate the necessity of studying development as a whole in relation to environmental change; that, in fact, studies on the effect of environment on separate stages in an animal's life do not necessarily indicate what the ultimate effect will be on the whole population. Of particular importance, however, in relation to the size of the balanced population is the eating of eggs and pupae. Holdaway suggests that the feeding stages of *Tribolium*, i.e. larvae and adults, may utilize the non-feeding stages, i.e. eggs and pupae as sources of moisture. This might account for the increase in size of the asymptotic populations with increasing humidity; for at 75 % R.H. the flour itself contains more moisture than at 25 % R.H., and consequently there is less need for larvae and adults to feed on eggs and pupae, and therefore a greater survival of these stages. He succeeded in showing that the percentage survival of eggs after 10 days of population growth at 75 % R.H. was 81 and after 30 days 54. The corresponding figures for a population kept at 50 % R.H. are 70 and 41. "It can then be affirmed that the mechanism by which atmospheric moisture regulates *Tribolium* populations is an alteration in intensity of the normal biotic control which the species can exert on itself; or in other words, the effect of the physical factor, humidity, on the insect population is *per medium* of a biotic effect, the intensity of which is regulated by the physical effect of atmospheric moisture on the moisture content of the flour."

5. We may now turn to the work of Park (1932), following Allee (1931) and MacLagan (1932). Chapman (1928) gives data for the density of beetles in six environments of 32 g. of flour each, which had been started with 1, 2, 3, 4, 8, 16 and 32 pairs of beetles respectively. All these populations reached equilibrium with density the same as in the experiments described. The three workers mentioned above re-analysed this data and found that in the earlier stages of population growth there is an optimum density for rate of reproduction. Park (1932) and MacLagan (1932) repeated the experiment and confirmed the results of these calculations. The rate of increase of a population of *Tribolium* can be expressed as the "progeny per beetle per day" or as "eggs and/or larvae per female per day". The following is taken from MacLagan's (1932) Table 1 and is recalculated from Chapman's data:

Beetles per g.	0·062	0·125	0·25	0·5	1·0	2·0
Progeny per beetle per day (11 days)	1·59	3·90	3·18	2·82	2·36	1·82
Progeny per beetle per day (23 days)	1·56	3·80	3·0	1·56	1·04	0·80

It is quite clear from this table that populations having an initial density of 0·125 beetles per g. of flour reproduce more rapidly than those with either lesser or greater densities. In Park's repetition of this experiment the result was essentially similar to that given above, with the optimum for reproduction rate at an initial density of 0·125 beetles per g. MacLagan's result, however, has additional interest in that his experiment was performed under somewhat different environmental conditions at 30° C., instead of 28° C., and at a somewhat higher humidity. In plotting reproductive rate against initial population density he obtained a curve of essentially the same form as Park's but the optimum had shifted to an initial density of 2 beetles per g. In commenting on this result MacLagan remarks that "in this instance, at least, the changed optimum density was not due so much to a difference in physical environmental factors (although perhaps partly so) as to the evolution of a strain of beetles which were not only better adapted to withstand crowded conditions but actually found the conditions of life under such circumstances more agreeable". This is of importance in that it indicates a factor, the ignoring of which has occasionally given rise to needless controversy. The behaviour of a *Tribolium* population depends not only upon the immediate conditions of the experiment but also to a large extent on the previous history of the individuals composing it. MacLagan's stock culture had been maintained for 6 months before the experiment under conditions of intense crowding.

It is now necessary to consider the explanations put forward for the existence of an optimum density for rate of reproduction. Park (1933) suggested that it arose from the interaction of two factors; the first, egg-eating, which is most intense in cultures of high density, and the second, the stimulating effect of copulation on the frequency of egg production. He found that the fecundity of females which had been associated with a large number of males was greater than that of females of the same age which had had only limited opportunities for copulation. This factor alone would tend to give populations of high density a greater rate of reproduction. On the other hand, the denser the population, the greater the amount of egg eating. This would tend to produce successively decreasing reproductive rates in dense populations. The two factors together combine to produce a maximum reproductive rate at an intermediate density.

MacLagan (1932), however, put forward other suggestions to account for this optimum density and carried out experiments to analyse its effect in populations of the grain weevil, *Sitophilus* (*Calandra*) *granarius*. This insect differs from *Tribolium* in that it feeds on the whole grain. Its eggs, "instead of being distributed at random in the floury medium, are inserted into the grains of the particular cereal being used".

Experimental environments were set up with 0·25, 0·5, 1·0, 2·0, ..., 32·0 weevils per g. of wheat grains. In each environment the numbers of males and females were equal. After 64 days the populations were counted and the increase in each expressed in terms of adult progeny per weevil. From these results it is seen that "the two variables, population density and progeny per weevil, exhibit a hyperbolic relationship". It is pointed out, however, that "to be strictly correct, the environmental unit of space, so far as oviposition is concerned in *S. granarius*, is *the number of available grains* per female weevil rather than the total volume per weevil". Thus the progeny per weevil in each environment is also plotted against the initial number of grains available. It is found that the relationship is not rectilinear and it becomes evident that "although the progeny per female weevil decreases as the number of grains at her disposal decreases, she utilizes a greater percentage of the total available number, that is, the less space available the more efficiently does the female weevil utilize it, so far as oviposition is concerned, at least up to a certain degree of crowding". Beyond a certain point, however, the amount of oviposition continues to decrease until it ceases altogether when the density is 4 female weevils to one grain in a population of equal numbers of males and females. It is suggested that this change in the amount of oviposition occurs when crowding is such that it causes "undue interference in the act of oviposition resulting from repeated physical contacts".

Another fact which emerges from these experiments is that "the densities productive of maximum oviposition and maximum space utilization for the latter purpose, are by no means synonymous". Female weevils only laid the maximum number of eggs when the number of available grains was eight times that actually utilized. This occurs when there are 400 grains per female weevil. Maximum space utilization, however, occurs at 12·5 grains per weevil, though even then only 50 % of the grains are used. Further, it was found that if the number of grains per weevil was increased beyond 400 (where the greatest rate of reproduction occurred) there followed a reduction in the number of progeny, thus clearly indicating an optimum density for rate of oviposition.

In pursuit of further understanding of the density effect MacLagan tested the effect of one species upon another when both inhabited the same environment. As before, the weevil *Sitophilus granarius* was used, this time in conjunction with the moth *Sitotroga cerealella* which also breeds in wheat. Knowing from previous experiments the biotic potential of the weevils at different densities it is possible in these experiments to express the result of interspecific action as the percentage reduction in progeny per weevil caused by the presence of the moth. In original environments of 1000 grains the following result was obtained:

Weevils	Moths	Percentage reduction in expected progeny of weevils
10	20	24·0
10	40	8·3
40	10	Negligible

The interest of these figures lies in the fact that in no instance does the moth produce as great a reduction of progeny as would have been produced by an equivalent number of weevils. "Thus whatever the ultimate nature of the factor responsible for these reactions, it is not species specific, so that the effect can be brought about through the presence of other species in the environment, despite the absence of direct competition for food or oviposition space."

Another experiment in which the total volume available to the weevils was increased by the addition of glass beads to the wheat grains, in equal numbers, thus doubling the volume while leaving oviposition space unaltered, gave a negative result.

Before discussing the conclusions of these experiments it is necessary to note a further publication, that of MacLagan & Dunn (1936). In the paper summarized above it was pointed out that the frequency of copulation might be affected differentially by crowding. Accordingly these workers carried out experiments with another grain weevil, *Sitophilus oryzae*. Six-hourly observations were made each day for 5 days of the number of females *in copula* in cultures of different densities. The results summarized below are extracted from their Table 1.

Weevils per grain	0·005	0·02	0·04	0·08	0·64	1·28	2·56
Percentage females (*in copula*)	22·8	31·97	33·06	24·23	5·89	2·56	2·01

This table clearly indicates an optimum density for copulation frequency. This optimum can be shifted by altering the physical or biotic factors in the environment. "For instance, by halving the number of males, the optimum is shifted to a more intense degree of crowding", and "by doubling the number of males the optimum is shifted to a less intense degree of crowding".

Further experiments with *Sitophilus oryzae* on the effect of density on oviposition confirm the results obtained by MacLagan (1932) with *S. granarius*. The rate of oviposition decreases continuously, in hyperbolic form, from lower to higher densities.

MacLagan & Dunn reach a conclusion which is paralleled by Holdaway's remarks concerning optima for the different developmental stages of *Tribolium*. "Living organisms are not always the highly coordinated physiological units they are often represented to be...and some should be regarded as heterogeneous assemblages of diverse physiological processes, each with its own optimum, rather than harmonious physiological units." Thus with the grain weevils copulation, oviposition and space utilization all contribute to the amount of reproduction and all find their maximum manifestation at different densities. MacLagan and Dunn conclude that the operation of density on population activity is largely through the medium of thigmotropism and is thus automatic.

Commenting on Park's (1933) explanation of the *Tribolium* optimum for reproduction rate MacLagan & Dunn remark that he "overlooked the possibility of a decreased copulation frequency above a certain degree of crowding, although this provides the key to the situation, as the decrease in population is greater than can be completely accounted for by eating of the eggs".

6. Turning once more to *Tribolium* studies we must note a paper of Chapman & Baird (1934). The purpose of these authors was to determine whether the behaviour of such populations is sufficiently constant to warrant "the biotic constants" of the beetle, such as time of hatching of eggs, duration of larval and pupal life, amount of oviposition, egg eating, etc., being used in mathematical calculations. Running series of parallel cultures they found that the variations between them were small and that the biotic constants obtained were "sufficiently exact to warrant the use of mathematical formulae for calculating the potential trends of the population". They criticize Park (1933) in that his results differ numerically from their's and also show a higher degree of variation. Park, however (1935), has answered this criticism. "Why should the beetle populations of Park, most probably genetically different from those of Chapman and undoubtedly under certain different ecological conditions, give the same 'biotic constant' of reproduction as do those of Chapman?" It has already been noted that the previous history of the population is a factor which must be taken into account in describing population behaviour. We may note a remark of Tippett (1931) which emphasizes a fact often ignored by biologists. "In the biological sciences, the measured quantities are subject to uncontrollable variation", but "the statistician regards his variations as being essential properties of the population and they are as real as the average is." Thus we may note that if there are differences in the average values obtained in two populations having different histories, we may equally expect that the variabilities characterizing those average values will also differ. It is necessary to determine "biotic constants" afresh for each different stock of *Tribolium* used.

7. We are indebted mainly to Park (1934*a*, 1935) for our knowledge of another aspect of *Tribolium* populations. Recalling Chapman's original paper, it was shown that a population of *Tribolium*, whatever its original condition, ultimately reached a condition of stability with a density of 43·97 individuals per g. of flour. This stable condition is only maintained if the floury medium is renewed at fairly frequent intervals. If the flour is not renewed the activities of the beetles in producing excreta, etc., changes its composition and this has a deleterious effect on the population. The flour becomes "conditioned" and with increasing "conditioning" the population decreases and ultimately dies.

Park (1934*a*) first investigated the effect of conditioned flour on reproduction. 18 environments of 32 g. of conditioned flour were set up with one pair each of adult *Tribolium* of the same age and history. The conditioned flour had been previously populated by all stages of the beetle for a period greater than two life cycles. As controls 18 environments were set up, identical with the first set, save that the flour was fresh. Counts were made every 10 days, at which times the flour in the controls was renewed. The eggs and larvae produced were removed at each counting. It was found that whereas the controls maintained a constant level of productivity, the experimental populations produced a decreasing number of offspring at successive counts. Moreover, the initial production of offspring, for the first 10 days was lower than that of the controls. After 10 days two-thirds as many eggs were produced in the conditioned flour as in the fresh; after 60 days, only one-ninth as many. Since, however, the relative proportions of eggs and larvae present in experimental and control stock were the same, it is evident that infertility of eggs is not responsible for the reduction in rate of reproduction. It may be due either to increased egg eating in conditioned flour or else to a decrease in fecundity of the beetles. Before passing to that question, however, we have to consider a second experiment designed to test whether "these experimental beetles may be returned to normal conditions by their return to fresh flour, or, are their reproductive processes so permanently inhibited that the number of eggs thereafter produced will remain permanently few?"

The same populations were used as above, but the experimental beetles were now transferred to fresh flour and for 40 more days were subjected to the same treatment as the controls, with changes of fresh flour every 10 days. At the 100th day they had reached nearly the same level of productivity as the controls, having commenced to increase their output of offspring with the change to fresh flour at 60 days. Meanwhile it became noticeable that the productivity of the controls had decreased slightly, an effect to be correlated with ageing of the parents.

Park (1935) next tested the effect of conditioned flour on egg-eating. 40 male beetles which had lived for 15 days following emergence in fresh flour were placed one each in 40 bottles containing 32 g. of fresh flour with 30 eggs randomly distributed in it. Another 40 bottles were set up in the same way, but with conditioned flour, the beetles in this case having passed 15 days since emergence also in conditioned flour. On the tenth day counts were made of the number of eggs remaining in each bottle. The eggs in each bottle were again made up to 30, the flour in the fresh flour bottles was renewed and the process repeated every tenth day for 50 days. The result showed that the beetles in the fresh flour consumed twice as many eggs, on an average, as those in conditioned flour. Evidently, then, egg eating cannot account for the reduced rate of reproduction in conditioned environments. "It may be that conditioned flour lowers the general physiological level of the organism and thus reduces its food intake." Or, on the other hand, eggs may be more difficult to locate in the conditioned flour.

The reduction of the population in the latter medium must then be due to a decrease in fecundity of the females. This was shown as follows. Virgin females are able to lay eggs, which, owing to the absence of copulation and, hence, fertilization, are infertile. The average number of eggs laid by virgin females in 5 days, in fresh flour, was 50·3; in conditioned flour, 16·8. An experiment with mated beetles yielded similar results. Egg counts were made daily in 20 sets containing single pairs of fresh-flour beetles and likewise with a similar set of conditioned-flour beetles. At each count the eggs were isolated in order to test their fertility. The egg rate per female per day in fresh flour was 1·5; in conditioned flour 0·17. Further, it was shown that egg laying by the conditioned-flour females was extremely erratic, and it seems evident that the organisms "are fundamentally influenced by such conditioning". A continuation of the experiment in which the type of flour supplied to the beetles was reversed showed that conditioning does not "irrevocably alter the fecundity of *Tribolium*", a conclusion to be expected in consideration of Park's earlier experiment, concerning the recovery of a conditioned population when returned to fresh flour.

Park (1935) now tested the effect of male conditioning on fecundity. In environments similar to those described above he made the following matings:

Fresh-flour male × fresh-flour female.
Fresh-flour male × conditioned-flour female.
Conditioned-flour male × fresh-flour female.
Conditioned-flour male × conditioned-flour female.

The conditioned-flour females had low egg rates irrespective of the history of their mates, but while both the fresh-flour females had high egg rates, there was a significant difference between them, the fresh-flour females mated with conditioned-flour males having lower rates than those with fresh-flour males. A conditioned-flour male can, then, affect the fecundity of a fresh-flour female.

In examination of the isolated eggs mentioned above it was found that there was no significant difference in fertility between fresh-flour eggs and those from conditioned-flour females. However, examination of the larval stages through which fresh-flour and conditioned-flour larvae pass makes it quite clear that conditioning greatly increases the mortality of metamorphosis as well as slowing down the rate of development.

The conditioning of the flour, i.e. the alteration in the composition of the environment by the activities of the population inhabiting it, is therefore of great importance in controlling the abundance and length of life of the population as a whole. The exact nature of the physiological effects of conditioned flour, which produce these changes in the behaviour of individuals, is not yet known. It has been shown, however (Park, 1936*a*), that the decrease in fecundity produced by conditioned flour is not "symmetrically proportional" to the amount of conditioning. This was shown by testing the fecundity of beetles in varying mixtures of fresh and conditioned flour. There was no significant difference between the fecundities of beetles in environments with $\frac{3}{4}$ fresh and $\frac{1}{4}$ conditioned and $\frac{1}{2}$ fresh and $\frac{1}{2}$ conditioned flour, though both were intermediate between entirely fresh and $\frac{3}{4}$ conditioned and $\frac{1}{4}$ fresh flours.

As a first step in the investigation of *Tribolium* physiology Park (1936) has shown that conditioned flour has no appreciable effect on the oxygen consumption of individuals, although it is shown that females require more oxygen than males, a fact possibly to be correlated with their greater weight.

8. To turn now to an entirely different aspect of the *Tribolium* researches we come to the work of Chapman (1933) and Chapman & Whang (1934). The work of Gause (1934) has now popularized our knowledge of competition fluctuations in animal population, and there is no need to discuss their mechanisms here.

In a population of *Tribolium* initiated with a small number of adults the following changes take place. First there is a steady increase in the number of eggs present. After some days (the exact period depending on the physical conditions) the first laid eggs begin to hatch and there follows an increase in the number of larvae, and coincidentally with the increase in larvae there is a decrease in the number of eggs present. The next stage is that in which the larvae commence to pupate, and the pupa population increases simultaneously with a decrease in the population of larvae. The egg population again rises, and now pupae begin to hatch producing an increase in the adult population which eventually reaches a steady state, while larval and egg populations continue to fluctuate about a stable mean. These fluctuations are best explained by treating the larvae and adults as predators of the eggs, which are themselves being produced by the adults. Thus the first decrease in eggs takes place when the larvae hatch, and it continues, owing to the predatory action of the larvae, until the larval population is reduced by pupation, which, of course, allows the egg population again to rise (Fig. 1).

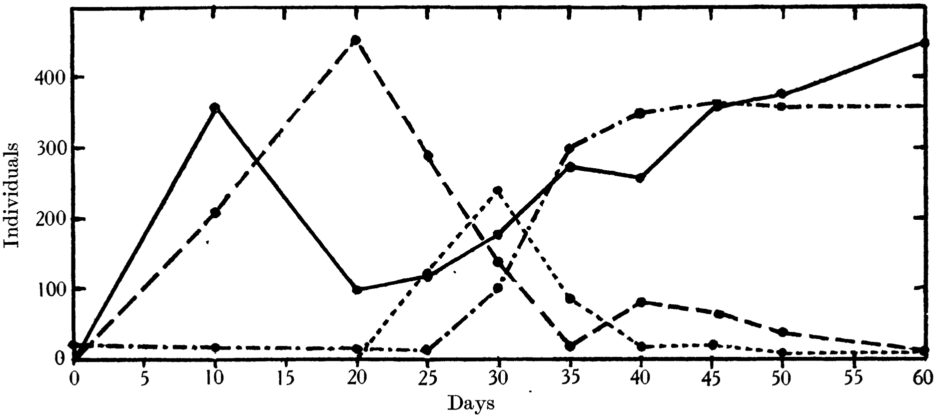

Fig. 1. Population trend of *Tribolium confusum* at 32° C. and 75 per cent. R.H.
Eggs ————; Larvae — — —; Pupae - - - - -; Adults — · —.

(Redrawn, by permission, from **Chapman** (1931), *Animal Ecology, with especial reference to insects*, p. 213.)

Confirmation of this view is obtained in experiments described by Chapman (1933). The Sporozoon *Adelina* is parasitic in *Tribolium* larvae, causing their death during the instar immediately preceding pupation. Thus in parasitized cultures no adults are produced, and the population gradually declines owing to the natural death of adults and the consequent failure to maintain the egg population. During this decline the populations of eggs and larvae fall into fluctuating rhythms which alternate with one another. Eggs are continually being produced by the surviving adults thus *tending* to an accumulation of eggs. Meanwhile larvae hatch from the eggs, on the remainder of which they feed. There is here the mechanism of fluctuations between predator and prey of the Lotka-Volterra type, and such fluctuations were found to occur in both accidentally and experimentally parasitized cultures. The parasite, by removing the pupal and adult stages from the population, has the effect of once more starting the larva-egg fluctuation with which a *Tribolium* population commences.

Inasmuch, however, as Park (1932) and MacLagan (1932) had demonstrated that there is an optimum for oviposition at low densities, it is possible that the initial decline in the egg population may be due to a decrease in oviposition following an increased density due to the presence of larvae. Chapman & Whang (1934) set up artificial populations composed entirely of males to which they added eggs at constant rates equivalent to the egg-laying rate in normal populations of the same size. There was here a constant "oviposition" rate. They found that the decrease in the egg population coincident with the hatching of larvae took place exactly as in a normal control culture, save that the peak in the egg curve was slightly higher than the controls. It is possible, however, that although the difference between experiment and control was within the limit of statistical error, the slightly lower value for the control was due to a decrease in oviposition. But whether this is so or not, Chapman & Whang have clearly demonstrated that egg consumption by larvae is responsible for the main trend of the egg population, in the early stages.

It is necessary to note here that this account of fluctuations in *Tribolium* populations is probably too simplified. Considerations of space have made a full discussion impossible, but it may be noted that since fluctuations imply changing densities it is probable that in addition to the egg-eating factor (which itself needs further analysis) differential crowding effects on reproductive rates at successive phases of the fluctuations, must also be taken into account.

Prof. Chapman has kindly informed the writer that the populations mentioned in his paper (1933) have now maintained synchronous fluctuations over a period of approximately 5 years, and that he and his associates have carried out further experimental analyses which should throw more light on this complex problem.

SUMMARY AND CONCLUSIONS

To conclude, we may review briefly the chief characteristics of natural populations as seen in the light of such studies as those here discussed.

In its growth the population tends to take the form of the logistic curve (Pearl, 1925). This curve expresses a tendency to geometric increase which is less and less realized as the population approaches saturation, owing to the increase in environmental "resistance" with increasing density. Such a form of population growth is only manifested in unmodified form under constant physical conditions and where there are no interspecific effects. In nature a variable physical environment causes modifications which are brought about in many ways. In *Tribolium* it has been shown that alteration in the external environment may change rates of growth, perhaps with opposite effects in different stages of the life cycle; it may likewise affect the amount of crowding which represents the optimum for rate of increase of the population. Under constant conditions any population imposes on itself a limit to increase and eventually reaches a state of relative stability about which it fluctuates. With a natural population which has reached equilibrium, changes in the physical environment may alter the value of this stable density and the population proceeds to readjust itself. Alternatively, the population itself, even when external conditions of temperature, humidity, etc., are constant, may so alter the environment by its own activity as to make yet other disturbances of the equilibrium. Provided the environment is such that the species concerned is able to live and reproduce in it, the factors *immediately* controlling the growth and behaviour of its population are biotic and proceed either from within the population itself or from without by the action of competing species. These biotic factors are themselves modified in intensity or in kind by external changes in physical factors.

It is the task of the ecologist first to assess the values of the physical environment in altering the behaviour of populations by its effect on individual and communal activity, and secondly, to interpret population phenomena in quantitative terms of increase and decrease in relation to intra- and interspecific competition. Population studies on various insects, mites and Protozoa (Gause, 1934) have greatly enlarged our knowledge of these phenomena. It is to be hoped that the value of this knowledge may be increasingly realized and put to use in quantitative field studies, and that soon it will be no longer necessary to agree with Gause that "as yet to many ecologists the ideas of biotic potential and environmental resistance are not connected with any quantitative conceptions".

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