The Self-Adjustment of Populations to Change

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INTRODUCTION

To demonstrate how populations may accommodate themselves to changed conditions, and so maintain themselves in being, I shall devote much of this address to discussing the results of laboratory experiments with the Australian sheep-blowfly, Lucilia cuprina Wied. It is true that the particular mechanisms of adjustment revealed are replaced by other mechanisms in many natural populations, but this would be equally true were any other kind of animal studied, whether in the laboratory or in the field. The fact that results obtained with laboratory populations can seldom be regarded as directly applicable to field populations in general is due to the existence of at least a dozen major systems of population regulation, and to the great diversity of influences which cause each population to present a somewhat different problem from all others. However, abundant evidence is provided by both field and laboratory studies showing that the populations of many different kinds of animals possess the ability to adjust themselves to great changes in their environments. These studies, together with logical deduction from certain well-established facts (Nicholson, 1954b) strongly suggest that this ability is possessed by all persistent populations. The experiments discussed simply show in some detail how this adjustment is achieved by one particular kind of animal.

An inherent difficulty with field studies is that the observable events in natural populations consist largely of end results, and the situation in the field is generally so complex that it is difficult to identify with certainty the underlying causes of many of the observed events. Help may be given here by statistical analysis of the field data collected; but such analysis does no more than establish associations between environmental factors and observed occurrences in populations. The discovery of such associations commonly suggests causes; but further study is necessary to determine whether these are, in fact, the causes of the occurrences observed. That is to say, field observations and their analysis suggest hypotheses which possibly may be checked by further field observation; but it is often more effective to employ experiments, either in the field or in the laboratory. Thus, theory and experiment are necessary complements to field observation—instead of having little relation to field studies, as some ecologists seem to argue.

The purpose of experiments with populations in the laboratory is to assist in the discovery of the mechanisms which regulate natural populations. They are based upon field observations which suggest that certain factors should be studied intensively and, to be meaningful, they need to be checked ultimately by field observation. Their special virtue is that they make possible the study of the influence of individual factors, or groups of factors, under simplified conditions, so that the effects produced by these are unobscured by the uncontrolled, and often unknown, additional factors which commonly make field observations inconclusive. Consequently, when designing a laboratory experiment with populations, no attempt is made to duplicate field conditions but, instead, the conditions are deliberately simplified by physically removing, as far as is possible, all variables which are not relevant to the problem under investigation. When the characteristic influences of individual factors have been determined, more complex situations may be studied to discover how several different factors interact. Such subdivision of complexities for the detailed study of their parts, and subsequent integration, is a characteristic feature of the scientific method.

Some Concepts and Definitions

Before describing experiments in which this procedure was followed, it is important to discuss certain concepts and definitions about which there are differences of opinion which have given rise to much misunderstanding and unprofitable argument.

Many authors use the word “population” to mean any group of individuals of the same species which has been chosen arbitrarily for study or discussion, but this usage leads to much confusion when employed in discussions of population dynamics. In an ecological context I would define the word “population” as designating a group of interacting and interbreeding individuals which normally has no contact with other groups of the same species. That is to say it is a discrete dynamic unit of a species population. This is the same sense in which geneticists use the term; and it is implicit in most serious discussions of population dynamics, particularly those having a mathematical basis.

Thompson (1956) criticises this usage of the term. On page 392 he says, “the population, like the species, in itself, is merely a concept. It exists, of course, in the real world, as a collectivity, but it is unified only in the mind, and it is therefore only in the mind that it exists as an entity.
To describe it as a self-regulating system, like an animal body, is merely playing with words". I contend that a population is something more than a concept. It has a similar objective reality to a family, or a tribe, or a nation. Because individuals within such groups react upon one another, and with the outside world, in ways they would not react were they not parts of an integrated group, each of these groups has characteristics which are more than the sum of those of the constituent individuals. In many of its relations with the outside world each such group acts as a unit; and the behavior of individuals is often strongly influenced by special interactions with other members of the same group.

It is important to make a distinction between the "environment" of a species and that of an individual. I cannot agree with the contention of Andrewartha and Birch (1954) that in ecology this word can refer only to the environment of an individual. According to the dictionary (O.E.D.) this term refers especially to "the conditions or influences under which any person or thing lives or is developed". Thus an "environment" is not an entity in its own right; instead it is the complement of some particular entity which needs to be specified before the term has any meaning. Now the influences of individuals upon one another play such a distinctive role in population regulation that, for clarity of thought and ease of discussion, such influences need to be considered separately from all other factors which influence populations. So, when discussing the environment of an individual, I distinguish between "the population", or the "other individuals", and "the environment", this word being used to refer to the totality of external factors which influence a population, unless some other sense is specifically indicated. This emphasizes the unique part played by the activities of other individuals of the same species in an individual's environment, and follows generally accepted usage in ecology.

Another term about which there is some confusion is density. In its strict sense "density" refers to the average number of objects in a unit of space. This word is used in ecological discussions instead of the simple word "number" because it refers to the inversely related conditions of crowding and of dispersion, both of which greatly influence the effects animals have upon one another, and consequently profoundly influence population regulation. However, crowding effects are often influenced, not only by the number of animals in a unit of space, but also by the quantity of some particular requisite or mimical agency present there. Consequently, the effects animals produce upon one another are often influenced by two kinds of density; namely, that of the population, and that of some requisite or enemy. In mathematical investigations the true densities of the animals and of the things with which they interact can be represented easily in equations; but in less precise verbal discussions the term "population density" frequently conveys, not merely the idea of the number of animals in a unit of space, but also that of numbers in relation to the available quantity of the limiting requisite. For example, this looser usage is generally implied when "density-dependent factors" are spoken of. The use of the term "density" in this wider sense in ecological discussions is well established by usage. In the absence of some better term, there seems no reason why it should not continue to be used in this sense, so long as its extended meaning in this context is clearly understood.

Much unnecessary argument about the mechanism of population regulation has been caused by the ambiguous use of the term "density-dependent factor". Smith (1935) originally used this term to designate a factor which is so influenced by population density that it opposes the innate tendency of populations to grow with greater intensity at high densities than at lower ones. One source of confusion is that many ecologists have extended the use of the term to factors which are not themselves influenced by density but which, nevertheless, produce increasingly adverse effects with increasing density. For example, frosts or high temperatures may cause exceptionally great mortality at high densities, but neither the frosts nor the high temperatures are influenced by density. Further examination of such situations shows that the higher mortality is due to the exposure of a greater fraction of a population to the adverse weather conditions, or to an increased susceptibility of the animals to these. The factors which are influenced by density, and so are "density-dependent", are found to be such influences as competition for unoccupied space, or for food, or disturbances of normal activities directly by crowding. The weather conditions are non-reactive, or "density-independent", but produce density-dependent effects through the medium of other factors which are influenced by density.

Some ecologists appear to assume that "density-dependency" is an innate characteristic of certain elements of the environment, notably food, space and enemies. Although such elements are unquestionably "factors" in the environments of animals, only attributes of these can be density-dependent. Thus the availability or rate of supply of food, the availability or accessibility of vacant suitable space, and the intensity of action or density of enemies can be density-dependent—but food, space and enemies in themselves cannot. Moreover, even such attributes of these basic environmental elements may not be density-dependent. For example, the rate of supply of food, and the space available to the animals are often uninfluenced by population density, and the severity of attack by enemies may be determined by some other factor which limits their numbers, such as the territorial behavior of birds. Thus "density-dependence" and "density-independ-
ence” are terms which designate the kind of influence exercised by a factor upon a population under a given set of circumstances, and they should not be associated directly with particular attributes of particular environmental elements. The same factor may be density-dependent in one situation and density-independent in another, even within the same species population.

Much of the confusion in the use of the term “density-dependent factor” appears to be due to the fact that the word “dependent” in normal usage conveys only part of the meaning intended in this context. For example, the density of a phytophagous insect may be limited by the activities of enemies at such a low level that no insect experiences any lack of food, yet there is a degree of depletion of food which is dependent upon the density of the insects. Food depletion here is not a “density-dependent factor” in Smith’s sense, for it may be increased considerably without placing any check upon multiplication. Moreover, it would be confusing to speak of such depletion as “density-independent”, for in the ordinary usage of the word it is “dependent” upon density. It is because of such ambiguities that I prefer to substitute the terms “density-governing factor” and “non-reactive factor” respectively for “density-dependent factor” and “density-independent factor”, so emphasizing the roles played by these two factors instead of the influence of population density upon them.

*Lucilia cuprina* Cultures

For some years my method of approach to an understanding of population problems has been to use laboratory colonies of the Australian sheep-blowfly, *Lucilia cuprina* Wied., under precisely defined laboratory conditions. The method consists of introducing a small number of *L. cuprina* into a cage and, from then on, maintaining predetermined conditions constant, including the supply of such depletable requisites as food and water at a constant rate. The population is left entirely to its own devices and, apart from maintaining the predetermined conditions constant, the only action taken is to keep a careful day-to-day record of the numbers of individuals of some, at least, of the various developmental stages—supplementing this at times with other observations.

This represents a considerable reduction of the complex field problem to a few of its components, which can be studied separately with facility. No attempt has been made to reproduce field conditions in the laboratory—in fact this probably could not be done. Competitors and natural enemies, which are known to play such an important part in the control of blowfly populations in the field (Fuller, 1934), have so far been excluded from the laboratory cultures; and only recently has the fluctuation of environmental conditions been introduced into some experiments. In other words *L. cuprina* has not been studied as a “sheep-blowfly” but simply as an experimental animal—a “guinea-pig”, so to speak. Later, environmental conditions were changed, generally in one particular only at a time. These experiments revealed the effects produced upon population numbers and structure by such changes, and also the mechanisms underlying readjustment of the populations to changed conditions, which is the main theme of this address.

*Lucilia cuprina* has many properties which make it a particularly suitable subject for the experimental study of population phenomena. Its life is relatively short, so permitting the observation of many generations in a year; cultures can readily be maintained in the laboratory, using conveniently small cages; and the eggs, young larvae, pupae, and adults occur freely in the cultures, which allows them to be counted, or subjected to special treatment, without interfering with the normal activities of the developing individuals. This species is also highly fecund, which permits it to withstand relatively heavy destruction, and also adverse conditions which affect fertility. As overcrowding amongst larvae causes increased mortality, whereas overcrowding amongst adults causes decreased natality, it is possible to study separately, and in combination, the two immediate causes of population limitation. In addition, it is possible to study separately the influences of changed capacity to lay eggs and of changed length of adult life; for as protein food is essential for egg-production, the rate of this can be changed by varying the quantity or quality of meat available to the flies; and as additional sugar is essential to maintain the life of the flies for periods longer than a few days, the life-span of the flies can be varied considerably by appropriate adjustment of the amount of sugar supplied.

**Competition for Food**

The present series of experiments began with a simple study of the influence of crowding upon blowfly larvae. This showed that there was not merely an increase in mortality with increasing larval density, but also that, after a critical point had been reached, further increase in density caused an actual decrease in the total number of flies emerging from a unit quantity of larval food. This important fact has been observed by several investigators who studied crowded cultures of other species of insect. Curves based on these observations have the same general character as that graphically representing the effects of crowding in larval cultures of *L. cuprina* (Nicholson 1948; 1954b, Fig. 2). It appears, however, that Utida (1941, p. 12) was the first to conclude that this relationship between the density of the parent insects and the number of mature offspring they produce should lead to oscillation in the population level. I reached the same conclusion, for reasons already given (Nicholson, 1948), being unaware at the time of Utida’s results.
To test this conclusion cultures of *L. cuprina* were set up in large cages under constant conditions in the laboratory. The temperature was maintained at 25°C. A quota of 50 grams of bullock's liver was introduced into each cage each day (or, in some experiments, every second day), and ample supplies of water and of dry sugar for the adults were always maintained in the cages. The numbers of adults in each cage were found to vary with great violence and with an evident periodicity. Examination of the larvae during these experiments clearly showed the cause of this violent change in numbers. When the numbers of adults were high such vast numbers of eggs were laid that all of the food provided was consumed while the larvae were still too small to pupate; consequently no adult offspring resulted from eggs laid during such periods (see Fig. 1). The adult numbers therefore dwindled progressively, until a point was reached at which the intensity of larval competition became so reduced that some of the larvae attained a sufficient size to pupate. These gave rise to egg-laying adults after a developmental period of about two weeks. In the meantime the population continued to dwindle, thus further reducing the intensity of larval competition, and permitting increasing numbers of the larvae to pupate and to produce adults eventually. Consequently, for about two weeks after the appearance of the first adults of the new generation, more adults continued to emerge. This caused the adult population to rise again to a high level at which too many eggs were laid to permit larval survival, so completing a cycle.

The density-governed system of reaction just described held the population in a state of stability, in the sense that it prevented both indefinite increase and indefinite decrease in numbers; but, because there was a lag of about two weeks between the initiation of corrective reaction and its operation upon the population, the population change inducing the reaction continued without change in direction for this period, so causing excessive reaction and an alternating over- and under-shooting of the equilibrium position. Consequently, the observed periodic fluctuations were true oscillations, for, as Moran (1954) says “a series shows ‘oscillating’ behavior if the fact that at any given time the population is not at its mean value implies that there will be a tendency for the series to ‘overshoot’ the mean value”.

Note that there is no damping factor in the oscillatory mechanism just described. Two of the early experimental cultures were maintained for a period of almost two years and the oscillations continued with unchanged violence up to the termination of the experiments. In each of the numerous experimental cultures of *L. cuprina* which have now been studied, it was found that, although there was commonly a great difference between mortality and natality during any given day, these two factors became equal in intensity over periods of several months. This is shown specifically in Figure 2, in which the averages of actual daily emergences and daily deaths observed over comparatively short periods are shown. Note that these average figures were greatly reduced when conditions for the adults were improved by providing an unlimited supply of sugar. When such averages were calculated for longer periods, the equality of mortality and natality was approached even more closely. Thus, in spite of the usual great disparity between mortality and natality at any given time in *L. cuprina* cultures held under constant conditions, the innate tendency of the insects to multiply was found to be counteracted exactly by density induced reaction; and the underlying mechanism of this counteraction was shown by these experiments to be competition amongst the larvae for food.

If the numbers of an animal living under constant conditions in the field were observed to fluctuate with the violence and evident periodicity shown in these *L. cuprina* cultures, one would be
tempted to look for some periodically fluctuating external influence to account for these population changes; and it is unlikely that any association would be noted between the population level and the level of the constant food supply available. Experiments have shown, however, that the average numerical level of a population controlled by food supply varies directly with the quantity of this supply. This is illustrated by Figure 1 in which one population (A) was supplied with 50 grams of liver each day, whereas the other (B) was supplied daily with only 25 grams. For ease of comparison, the scale of B is double that of A. These two graphs show clearly that the average population of B approximates half that of A, and that the violence and other characteristics of the oscillation are unaltered by the difference in the rate of food supply.

Analysis of these early experiments, in which the adult flies fed upon the same meat as the larvae, showed that larval competition was unquestionably the dominant governing factor and that this produced the oscillations observed; but there was also evidence of adult competition for food, which tended to reduce the number of eggs laid so making larval competition less severe. Further experiments were therefore set up in which adult competition was suppressed by supplying the adults with a surplus of suitable protein food (which was unavailable to the larvae) in the form of finely ground liver. Comparison of Figure 5(A) with Figure 6(E) shows that, as a result of complete removal of adult competition in the latter culture, the mean larval population was approximately doubled, whereas the adult population was reduced somewhat. There was also a small increase in the amplitude of oscillation in adult numbers, but the underlying mechanism remained as already described.

Other cultures were set up with the converse arrangement, the adults being excluded from the larval food and given a restricted and constant daily quota of ground liver (usually only a fraction of a gram) in addition to water and sugar in excess of their needs; whereas the larvae were provided with a surplus of liver in which to develop, so avoiding any larval crowding. In these experiments the adult numbers were observed to fluctuate with a similar violence (see Fig. 8.I) to that which occurred with larval competition. These violent periodic fluctuations were produced by an internal mechanism similar to that already described, with one exception. When the adult numbers were very high, instead of producing a great excess of eggs which would lead to intense larval competition, they produced few or no eggs; but the end result was the same, that is, few or no adult offspring were produced when the fly numbers were very high.

The reason for this is that an adult fly requires more than a certain small amount of protein food before it can produce any eggs. Consequently, when large numbers of flies competed for a small quantity of ground liver, few, if any, of them obtained as much as this minimum effective amount. As the numbers dwindled, through lack of replacements, competition was eventually relaxed to the point at which some of the flies obtained sufficient protein to lay eggs. Almost all the larvae which hatched from these, being supplied with a surplus of food, developed into adults in about two weeks.

Thus, in cultures governed by larval competition only, a large number of flies laid so many eggs that larval over-crowding prevented any offspring from reaching maturity; whereas in those which were governed by adult competition alone, adult over-crowding prevented any eggs being produced. The inference is evident that, if larval and adult food were supplied daily in constant limited quantities of the right relative magnitudes, each kind of competition should oppose the effect the other tends to produce. Thus, the violence of oscillation would be greatly reduced and the population would tend to oscillate about, and possibly to remain more or less constant at, a new average population level. One would expect this level to be higher than that determined by either system operating separately; for when the adult population is provided with a surplus of liver in which to develop, so avoiding any larval crowding. In these experiments the adult numbers were observed to fluctuate with a similar violence (see Fig. 8.I) to that which occurred with larval competition. These violent periodic fluctuations were produced by an internal mechanism similar to that already described, with one exception. When the adult numbers were very high, instead of producing a great excess of eggs which would lead to intense larval competition, they produced few or no eggs; but the end result was the same, that is, few or no adult offspring were produced when the fly numbers were very high.

Figure 2. Effects produced by supplying, and denying, adequate sugar for adults of L. cuprina, in a population governed by larval competition for daily quotas of 50 g of meat. Note, the histograms show the number of adults resulting from eggs laid during periods of 2 days.
high relatively few eggs are laid, and so the intensity of larval competition, and consequently food wastage, are reduced.

To test this conclusion, several cultures were set up in each of which 50 grams of a special meat medium were supplied daily for the larvae, whereas in the different cultures a different constant quantity of ground liver was supplied daily for the adults, which were excluded from the larval food. It was found that when adult food was supplied at the rate of one gram per day the oscillation was comparatively slight and had lost almost all evidence of periodicity, whereas any appreciable departure from the rate of one gram of ground liver per day in either direction resulted in an increase in the amplitude of oscillation. Part of the first mentioned experiment is illustrated in Figure 3. A represents the end portion of series of fairly regular periodic oscillations which occurred during a period of about eighteen months when the culture was supplied with unlimited ground liver for the adults, and B represents the adult population at the beginning of a further period of a year when the ground liver was restricted to the rate of one gram per day. It will be noted that, apart from the marked reduction in the violence of oscillation, the average level of a population was approximately quadrupled by changing the rate of supply of ground liver from excess quantities to only one gram per day; and also that in B eggs were laid, and gave rise to adults, every day.

An important feature of all of the experiments described so far is that (with a few minor exceptions when the adult numbers approached zero) each daily quota of food, whether provided for the larvae or adults, was completely consumed. Thus it is strikingly evident, from the illustrations given, that the number of mature offspring generated on any particular day was far from proportional to the amount of food consumed. With larval competition this was because all of the food eaten by those larvae which failed to obtain sufficient to pupate was wasted, in the sense that it did not lead to the production of adult offspring. When the limiting requisite was adult food the position was somewhat different. With increasing numbers of flies there was a progressive reduction in the number which obtained sufficient ground liver to develop eggs. The ground liver eaten by those which obtained insufficient food was not, strictly speaking, wasted, for it was certainly used in the normal metabolism of the insect; but it was ineffective in that it did not lead to the production of eggs. Here, again, increasing competition reduced the amount of food used effectively, and so reduced the number of offspring produced by the total population. It is therefore clear, that in these instances at least, the assertion of Andrewartha and Birch (1954, p. 24) that "it is the quantity of the limited resource which determines the density of the population, not the intensity of competition", is incorrect, for both limited resources and competition play important parts in this determination; and their concept of "effective food" (p. 498) is seen to be merely an observable consequence of competition, and not an alternative to that of competition, as is implied.

Although the production of oscillation in density is only of secondary importance in the problem of the self-adjustment of populations to change, the underlying mechanism has been described in some detail in order to show that, even in this relatively complex situation, density-induced reactions hold populations in a state of balance with their environments. That is to say, they prevent indefinite increase or decrease in

\[\text{Figure 3. Effects produced by restricting daily quota of ground liver for adult \textit{L. cuprina} to 1.0 g, after period of ample supply, in a population governed by larval competition for daily quotas of 50 g of meat.}\]
numbers; and they hold populations in a condition of oscillation about an equilibrium density related both to the rate of supply of the governing requisite (food in this instance) and to the innate properties of _L. cuprina_, notably the fecundity of the flies, and the minimum food requirements of the larvae for metamorphosis and of the adults for the development of mature eggs.

Thus direct observation of laboratory cultures of _L. cuprina_ showed that it is competition which
counteracts the innate tendency of this insect to multiply very rapidly, and which holds the population fluctuating about recognizable general levels. The detailed mechanism of this state of balance was clearly visible, and of such a nature as to suggest that competition could adjust populations to widely different environmental conditions. With this knowledge it was possible to foresee how certain types of environmental change would influence populations. One could, for example, foresee with a reasonable degree of accuracy how a particular change would affect the general level of the population, the violence with which it oscillated, and the age-structure of the population.

The next step, therefore, was to set up for comparison a new series of cultures, each of which was held under constant but somewhat different pre-determined conditions; or, alternatively, a single factor was changed at the end of a long period, and the population was maintained under the new conditions for a further long period. Subsequently fluctuating conditions were introduced. In every instance the populations behaved under the new conditions in the way predicted, which strongly supports the belief that the theory upon which the predictions were based is sound. Often additional effects which had not been predicted were observed, but these were always consistent with the underlying theory of the self-adjustment of populations by competition.

**Figure 6.** E, average age- and developmental stage-structure of a culture of _L. cuprina_ governed exclusively by larval competition, the adults having a separate and ample supply of ground liver; H, effects produced upon a similar culture by the destruction of 99% of the emerging adults; A, as E except that culture is governed exclusively by adult competition for a daily quota of 0.5 g of ground liver; D, effects produced upon a similar culture by the destruction of 90% of the emerging adults.

**Complementary Governing Factors**

First we will consider changes which involved the introduction of additional or “complementary” governing factors (see Nicholson, 1955, p. 27). One of these (illustrated in Fig. 3) has already been mentioned. A population, which had for long been limited by larval food and supplied with a surplus quantity of ground liver for the adults, was changed by restricting the supply of ground liver to a quota of one gram each day in the cage. This change approximately quadrupled the average level of the adult population, and altered the population pattern very greatly because of an interaction between larval and adult competition. This experiment clearly illustrates a phenomenon which is often observed, namely,
that a new factor which has adverse effects upon individuals often increases population density (see also Figs. 2, 5, 6, and 7).

The culture illustrated in Figure 4(A) was supplied with 50 grams of protein food for the larvae and unlimited water and ground liver for the adults—but the sugar was limited to a supply of two grams each day in the cage. The effect of this restriction was to shorten the life of the adults considerably when numbers were high but, when the number of adults was low, the supply of sugar was adequate to enable them to live normally. The effect of this was to alter the shape of the oscillations (compare Fig. 1 and Fig. 4A)—populations falling very rapidly at first from the peaks, after which the fall was more gradual. Thus here, in addition to the larval competition for food, there was competition amongst the adults for the special type of food which influences the length of their lives. This had a general stabilizing effect upon the amplitude of the oscillations; and it influenced the average number of adults in the population.

The culture illustrated in Figure 4(B) was set up under similar conditions to that in Figure 4(A) except that the supply of sugar was unlimited, whereas the supply of water was reduced to a daily quota of two milliliters. As water is very important to the adults, the average life-span was shortened considerably—particularly when their numbers were highest. In consequence this population laid very few eggs, so reducing larval competition and therefore increasing the average number of flies emerging each day. This raised the mean adult population to a higher level than similar populations provided with adequate supplies of water. Here the availability of water was clearly a complementary governing factor, for it reacted to density and its effect was associated with that of larval competition for food. This changed the population pattern, and also affected the mean population size.

The experiments just described illustrate the fact that when two or more factors share the function of governing a population they operate like a single density-governing factor in that their intensities are automatically adjusted to cause them collectively to destroy just the surplus of offspring produced over any long period, or to prevent its production. However, the mutual adjustment between them may cause each to exercise a profound influence upon the density, age-structure and pattern of change of the population.

**Non-reactive Factors**

Although density-induced governing reaction is essential to maintain populations in a stable state in their environments, non-reactive factors (i.e., "density-independent factors") may have a profound influence upon the actual levels at which governing reaction adjusts population densities.

An example has been given elsewhere (Nicholson, 1954a, p. 4, Situation I). In this experiment, and the one with which it was compared, the adults were excluded from access to the larval food, but were supplied with a surplus of ground liver for their own use. In the control the cover of the pot containing the larval food was so constructed that it maintained a moist atmosphere beneath it; whereas, in the one referred to as Situation I, the cover consisted of rather large-mesh plastic gauze which did not retain a moist atmosphere, and so produced unfavourable conditions for oviposition. In consequence the flies laid fewer eggs, so reducing the intensity of larval competition and permitting more adults to emerge from the larval food than emerged in the control culture, thus increasing the adult population.

In a series of concurrent experiments constant percentages of individuals at some particular stage of development were destroyed at regular intervals, and it was demonstrated that such destruction had an important legislative influence, not only upon the mean population level, but also upon the age-structure and the pattern of population change. For example, in a preliminary experiment 50 per cent of the young larvae were destroyed each day, and the effect was to more than double the mean population of adults. This was found to be due to a reduction in the intensity of larval competition which reduced food wastage and so permitted a greater number of larvae to grow to the size necessary for pupation.

Figures 5 and 6 show histograms of the mean total populations, the age-groups covering half-day periods. This interval was chosen because at the temperature (25°C.) under which the cultures were maintained, the duration of the egg-stage is approximately 12 hours. The area included within the zones marked off for each developmental stage represents the number of individuals at that stage. The histograms show the numbers of each
developmental stage which would be observed if it were possible to select a moment when all stages were represented in their mean numbers. Naturally, in a strongly oscillating population the age-structure, and the "stage-structure", would undergo marked cyclic changes with time.

A surprising feature of *L. cuprina* populations shown by the histograms is that there is virtually no natural mortality amongst even grossly overcrowded larvae until the successful larvae pupate. Even then many of the starved larvae remain alive for a day or two. Also, the histograms illustrating control populations not subjected to imposed destruction (Fig. 5A and 6E) clearly indicate the great magnitude of the "emergency reserve" of fecundity (NichoIson, 1955, p. 292) in this insect, which is represented by the large number of "starving larvae" shown. It is to this reserve that the great resilience of the species is due.

Figure 5 illustrates a particularly interesting example of compensatory reaction to destruction. The two cultures compared were maintained under identical conditions except that in (B) 50 per cent of the total population of adults was destroyed every second day (see Nicholson, 1954b p. 24). Each culture was provided with 50 grams of larval food, to which the adults had access, and adequate supplies of water and sugar were available to the adults. Comparison of (B) with (A) in Figure 5 shows that the imposed destruction had the expected effect of markedly reducing the average life of the individual flies, so increasing the proportion of immature flies incapable of laying eggs—for adults of *L. cuprina* only begin to lay eggs about three days after emergence. The immediate effect of this was approximately to halve the number of eggs produced in the total population, so reducing larval competition and permitting a greater number of larvae to pupate. Thus destruction of adults led to an increase in the number of individuals subsequently reaching the adult stage. The mortality due to the relaxed larval competition, combined with the imposed destruction of adults removed exactly the surplus of offspring produced.

 Destruction at the rate of 50 per cent of the adult population every second day actually resulted in the destruction of 79 per cent of the adults, for the flies which escaped destruction on one occasion were exposed to it again after two days. In spite of this it will be seen from Figure 5 that automatic compensatory reaction caused the mean adult population to remain virtually the same as in the control culture in which there was no imposed destruction. In contrast to this lack of change in adult numbers, the histogram shows that the age-structure of the population was altered markedly. This experiment illustrates the important fact that it is misleading to confine attention to the numbers, or densities, of animals; the age- and stage-structures of the populations must also be considered, for these are important characteristics of populations. They are often outstandingly important, for example when we are concerned with the abundance of the destructive stage of an insect pest, rather than that of its population as a whole.

In a series of experiments which has already been discussed (Nicholson, 1954a, pp. 2–6) certain constant percentages of freshly emerging adults were destroyed. Some of these experiments are illustrated in histogram form in Figure 6. Cultures E and H were governed by larval competition alone, the larvae being supplied with 50 grams of larval food to which the adults were denied access—the adults were provided with a surplus of ground liver, water and sugar. Culture H received identical treatment to culture E, except that 99 per cent of the freshly emerging adults were destroyed, so reducing the population of mature adults, and, in consequence, also the number of eggs produced in the culture. Reduced larval competition allowed a far higher percentage of the larvae to reach the size necessary for pupation, so increasing the pupal population, and also the daily production of emerging adults. As in the experiment illustrated in Figure 5, destruction of adults led automatically to an increased production of adults, which in part counteracted the immediate effect of destruction. Consequently the mean population after 99 per cent destruction, instead of being one per cent as might be expected, was approximately 10 per cent of that produced when there was no destruction.

The cultures A and D in Figure 6 were governed by adult competition alone, the larvae being provided with a surplus of liver which permitted all of them to reach full size. The adults were excluded from this larval food and were provided with the small daily quota of 0.5 grams of ground liver, together with adequate water and sugar. 90 per cent of the emerging adults were destroyed, and this reduction of the adult population reduced competition amongst the flies, thus allowing more flies to obtain sufficient liver to produce eggs, which in turn increased the number of eggs laid by the population as a whole. There being no loss of larvae due to crowding, far more pupae were produced than in the culture in which there was no destruction of adults, and so more adults emerged. This counteracted the immediate effects of destruction to such an extent that the population, instead of being only one tenth, was approximately one third of that in the culture in which there was no destruction.

The few experiments briefly described here illustrate a fact that was equally evident in all of my *L. cuprina* experiments in which some stage was destroyed, or subjected to adverse conditions. The age-structure of the populations was greatly affected by these harmful influences, and in such a way that the number of individuals in the stage preceding that destroyed was always increased as a secondary effect of the destruction. This, to a marked degree, counteracted the im-
mediate effects of destruction. Moreover, if the stage of immediate concern to the observer were that preceding the stage of destruction, it could be said that there is "over-compensation", this stage being increased by destruction, and by adverse conditions.

In Figure 7 are plotted the means of certain of the data obtained from cultures A and D (Fig. 6) together with similar data obtained from two other experiments in which 50 per cent and 75 per cent of the emerging adults respectively were destroyed. Fuller data concerning these experiments have been given elsewhere (Nicholson, 1954a). It will be seen that progressive increase in destruction leads to a progressive increase in the number of adults emerging each day.

The curve labelled "fertility" is of particular interest. It shows the changing "coefficient of fertility", which represents the number of offspring produced on the average by an individual during its life, both males and females being included in the number of individuals. It will be noted that the coefficients of fertility of the insects, without destruction, and with 50 per cent, 75 per cent and 90 per cent destruction of emerging adults, have been automatically adjusted at about 1, 2, 4 and 10 respectively, so providing a surplus of offspring just sufficient to be removed by the degree of destruction operating. Actually they slightly exceed these figures, which compensates for the small amount of pre-imaginal mortality which occurs in all cultures. Note that I am here following the usage of demographers in using the word "fertility" when speaking of the degree of reproduction actually achieved. The word "fecundity" is used when referring to the innate ability of an organism to reproduce.

These experiments clearly illustrate the fact that non-reactive factors may produce profound effects upon population densities, age-structures and patterns of change through the medium of density-governing factors. Non-reactive and density-governing factors both produce important effects upon populations. Their functions are simply different, so there is no question of one kind of factor being more important than the other.

Fluctuating Environmental Factors

On purely theoretical grounds I had concluded earlier (Nicholson, 1954b, p. 45) that oscillations in population density of internal origin should tend to conform to climatic changes, the period of which, when cyclical, tends to be impressed upon the population. With the facilities available it was not possible to subject the cultures to periodic fluctuations in a significant climatic factor. I therefore varied the availability of a reactant which is likely to be influenced by climatic changes in nature—namely, food.

To check this expectation, ten cultures were each supplied with unlimited quantities of larval food, and also of water and sugar for the adults. In eight of the cages the ground liver provided for the adults was regularly and progressively varied from day to day from 0.05 grams to 0.5 grams per day, in the way shown in the dotted graphs superimposed upon each of the population graphs in Figure 8 (C and H). The period of fluctuation in the food supply in the eight experimental cultures was respectively 10, 20, 30, 40, 50, 60, 70 and 80 days. There were two control cultures in which the food supply remained constant from day to day, respectively at 0.1 and 0.4 grams per day. Graphs indicating the population changes in two of the experimental cultures and in one of the controls are shown in Figure 8. It will be observed that the period of population oscillation in C is slightly longer than the natural period in the control (I) and that the oscillations up to about the 500th day correspond regularly to alternate periods of food fluctuation. At about this time there is a sudden change, after which the period of population oscillation is halved, so that each population peak corresponds to each period of food change. Change in properties due to natural selection probably caused this but it illustrates the fact that the period of population oscillation tends to be equal to, or to be either an exact multiple or a simple fraction of that of the fluctuating external influence.

The culture illustrated by Figure 8 H was subjected to a much longer period of food change. Near the beginning of this experiment two population peaks fitted within one period of food change; but the population changed progressively to a condition in which there was only one major population peak within this period of food change, accompanied by one or more minor peaks. It appears probable that, by chance, this population began out of step with the imposed periodic fluctuation, but progressively approached synchronization, when the period of intrinsic oscillation became completely dominated by the period of food change.

The same general effect was observed in the other six cultures in which the food supply was varied periodically. With only one doubtfully significant exception, the period of change of the external influence, or a simple fraction of this, was imposed upon the population oscillations, although the evidence was clear that these were caused by intra-population forces and reactions, and had a well-marked natural period under constant conditions.

These experiments with cultures subjected to fluctuating environments show that populations not only adjust themselves to changes in environmental favorability and to destructive influences, but also strongly tend to accommodate themselves to cyclical changes. This suggests that, although density changes observed in natural populations are commonly closely associated with seasonal and other climatic changes, the main underlying
causes of change may well be interactions within and between populations.

**Self-adjustment by Populations:**

**General Discussion**

Extrapolation from the results of such experiments as those described is justifiable provided reasonable precautions are taken. These consist mainly in determining that the same kind of adjusting mechanisms occur both in field populations and in the laboratory populations used to assist interpretation, and in taking into account any additional factor operating in the field which was not represented in the experiments. It has been argued that *Lucilia* populations are quite exceptional, and that (Thompson, 1956, p. 400) "the facts we observe with this species cannot be generalized and then taken as the foundation of a comprehensive theory of natural control". *Lucilia* is no more exceptional than any other kind of animal for, not only are there vast numbers of related flies with similar life-cycles and behavior, but there are many animals which have similar basic characteristics. I refer to all kinds of animals which use dead organic matter as their food and which "scramble" for it, the supply of such food being almost invariably independent of the activities of the animals themselves. Unless interfered with by other factors, such as attack by natural enemies, all such animals tend to overcrowd their food supply and to waste much of it, so limiting their population levels by means of the same mechanisms as those demonstrated in *L. cuprina* populations.

Support for my basic conclusions derived from experiments with *L. cuprina* is provided by two recent investigations with animals of different kinds. Using populations of *Tribolium confusum* Duval, Watt (1955) destroyed different stages of this flour-beetle at regular intervals, and at various rates. He concluded amongst other things that (p. 288) "age distributions, and numbers, of individuals remaining after removal of the harvest are the important factors in determining the consequences of harvest. Productivity increases with rate of exploitation, then crashes without warning of the impending crash by first flattening off", and (p. 289) "the populations..."
SELF-ADJUSTMENT OF POPULATIONS TO CHANGE

were homeostatic in that the individuals replaced tended to be the same age as the individuals removed”. Similarly Slobodkin and Richman (1956) using the crustacean *Daphnia pulicaria* (Forbes) as their experimental animal, concluded (p. 235) that “removal of new-born animals at varying rates from populations of *Daphnia pulicaria* tends to reduce the size of the residual populations, but not in direct proportion to either the number or percentage of new-born animals that have been removed. This lack of direct proportionality can be accounted for in terms of a shift in the age-structure of the residual population, an increase in the growth rate and reproductive rate of those that survive the fishing procedure, and in their longevity. These effects can be adequately explained in terms of what is known of the dependence of *Daphnia* populations on the food supply per individual and the fact that removal of new-born individuals increases the available food supply for the animals that remain”. Thus the basic results obtained by Watt, and by Slobodkin and Richman, agree with those obtained with *Lucilia cuprina* in that they showed compensatory and self-regulatory reactions to destruction by external factors. In all three investigations a strong tendency towards homeostasis was observed.

In spite of what has just been said, it must be recognized that there is no such thing as “the population problem”: There are many population problems. In a sense each species in each situation it occupies presents a different population problem; but such individual problems can be classified into major categories, and I have already discussed one way of doing so (Nicholson, 1954b, p. 34).

*L. cuprina* is representative of the large group of animals which “scramble” for their food, the rate of supply of which is determined by factors other than the activity of the animals. With gross crowding such scrambling leads to much wastage of the governing requisite so that, with excessive numbers of animals, there is either excessive mortality or the fertility may be temporarily reduced below the replacement rate. This tends to produce violent oscillations in the size of the populations which are not caused by environmental fluctuations, and it generally limits the average density of the animals far below that which the supply of governing requisites could maintain if there were no wastage.

In contrast to this is the category of animals which “contest” for their limiting requisite. That is to say, each successful individual lays claim to a supply of requisites sufficient to maintain it, and to enable it to produce offspring. The unsuccessful individuals are denied access to critical requisites by their successful competitors. This kind of competition eliminates, or greatly reduces, the wastage of requisites, so permitting a relatively high density of animals to be maintained and, in addition, preventing such intra-specific oscillation as occurs in *L. cuprina*. There is room for only a certain limited number of individuals; consequently those which are unsuccessful in obtaining room “overflow” into less favourable parts of the environment from which critically important requisites are absent, or present in inadequate amounts.

The contest type of competition is always the resultant of an underlying pattern of behavior which the successful individuals use to exclude other individuals from a selected place, or object, which provides the necessary requisites for the survival and reproduction of the holders. A good example is the territorial behavior of some birds, mammals, and certain other kinds of animals. When all territories have been occupied the surplus individuals are excluded from favourable habitats and are either unable to reproduce, or are exposed to exceptional hazards, or both. When, as is usual, the fate of the excluded individuals is death, the immediate causes of this vary greatly with different species and in different situations, but the ultimate cause is exclusion from favourable habitats. For example, speaking of the muskrat, in which territoriality is very strongly developed, Errington (1946, p. 146) says “for all the severity of observed predation on young muskrats, juvenile mortality was often traceable mostly not to predators, but to drowning, disease, parental carelessness, or—on occasion very dramatically—to intraspecific attacks. Losses from non-predaceous agencies were especially apt to rise as predation losses declined, and vice versa, with intraspecific strife becoming dominantly operative when predation and the usual run of miscellaneous losses all happened to be low”.

Another of the many examples Errington (1946) gives of the self-adjustment of populations of animals to their environments concerns raptorial birds (p. 172): “we can see what looks like a general tendency for maximum densities to be self-limited. For all the “dog-eat-dog” predation and intraspecific intolerances to be noted, intraspecific intolerance in one form or another seems to be a basic mechanism underlying the regulation of their numbers”. Many examples of self-limitation by populations, particularly of birds and mammals, are given by other authors, notably by Lack (1954).

In the two categories of population regulation just discussed the amount and rate of production of the governing requisite, which is critical to the animals, is independent of their activities. There is another large and important category in which the activities of the animals not only influence the degree of depletion of their governing requisites, but also determine the amount produced. These are such phytophagous animals and predators as limit their own population densities by limiting the production of their host-plants or prey, thereby reducing these to the threshold levels, at which the enemies can find
barely sufficient food to maintain their own numbers (see Nicholson, 1933; 1954b, p. 39; and Nicholson and Bailey, 1935). Note that “parasites” of the insect type are really predators, as their larvae eat their “hosts”.

This category of population regulation is of exceptional interest because of the unexpected and varied results of interaction between animals and the organisms upon which they feed. The considerations which first caused me to consider population problems seriously conveniently illustrate the situation represented by this category.

Many years ago I was puzzled by the fact that the degree of infestation of citrus trees by scale insects appeared to be quite independent of the number of citrus trees in any particular area; for this indicated that the population of scale insects was directly influenced by the number of citrus trees—in spite of the fact that there was evidently space for far more scales on the foliage and branches, and that, as the citrus trees remained healthy, the food supply was presumably capable of supporting far more scale insects than it did. It occurred to me that the puzzling phenomenon could be due to the action of natural enemies, for the citrus trees not only provided food for the scale insects, but also constituted the area over which the enemies had to search. Simple considerations indicated that, if the number of scale insects was very high, large numbers of parasites would breed from them, and that these parasites, operating in the next generation, would collectively search the greater part of the foliage of the trees, so attacking most of the scale insects and causing their numbers to fall to a low level in the following generation. Continuing this kind of argument it became clear that the numbers of scale insects and of their natural enemies should produce effects upon one another which would always tend to reduce over-large populations, and to allow very small populations to increase.

The mechanism visualized was that, if few enemies searched a large area, each would spend most of its time exploring previously unsearched areas; whereas if the searching enemies were numerous, each would spend most of its time searching previously explored areas within which most of the scale insects would presumably have been attacked already. Assuming that the enemies were fairly evenly or randomly distributed over the foliage, it was easy to construct a curve which represented quantitatively the reduction in the success of the searching individuals in exploring previously unexplored areas, in which the unattacked scales would presumably lie. This I called the “competition curve” (Nicholson, 1933, Fig. 1). Using this curve it was possible to examine a number of hypothetical arithmetical examples by assigning arbitrary “powers of increase” to the hosts and “areas of discovery” (which represented the searching abilities of the parasites) to the parasites.

To my astonishment, no matter how I varied the two basic properties, the arithmetical examples indicated that the reactions between the two kinds of insects, although always of the right kind to oppose, and to change the direction of the current displacements, gave rise to oscillations in the numbers of both hosts and parasites, and these grew in amplitude with time! In other words, this simple system of corrective reaction was over-violent and proved to be intrinsically unstable. Subsequently Bailey confirmed and extended these conclusions by the use of mathematics (Nicholson and Bailey, 1935).

Thus, in this situation, density-induced reactions were produced in populations of both kinds of interacting animals which were of the right sign to counteract departures from the equilibrium position but they were over-violent, so causing successively greater and greater over- and under-shooting of the equilibrium position. The growth in amplitude of the oscillations is probably related to the fact that two systems of oscillation are involved. The well known predator-prey oscillations of Volterra lead to systems of sustained oscillations which may be referred to as “coupled oscillations” (Nicholson, 1954b, p. 39), as they are due to a linkage between the two changing populations. Each as it passes its equilibrium density alters the direction of change of the other population; but Volterra’s populations consisted of hypothetical animals with the curious property that they interacted from the moment they were born, which means that they were born fully mature. In contrast to this, insect hosts and their parasites require a considerable time to develop, and changes in density induced by interaction produce their effects only after the lapse of a generation. This tends to give rise to “lag-oscillations”, such as were observed in the Lucilia cuprina cultures. The superimposition of these lag-oscillations upon the coupled oscillations seems to be the likely cause of growth in amplitude of successive oscillations, and of the consequent instability of this system of interaction.

Two arithmetically calculated examples are given in Figure 9 of this type of system, each example representing the interaction of a specific host and a specific parasite. That is to say, increase in the host density is limited solely by the action of one particular species of parasite, and the parasite attacks hosts of this species only, and so limits its own density by restricting that of its host. It will be seen that the violence of reaction is greater in B than in A, which illustrates the general conclusion that the violence of oscillation mounts with increase in the “power of increase” of the host (Nicholson, 1933, p. 161; Nicholson and Bailey, 1935, p. 586). The magnitude of the “area of discovery” of the parasite does not influence the character of the oscillation. In both the examples given, it is assumed that
initially one of the interacting species is at its equilibrium density whereas the other is displaced slightly from its equilibrium density. Only by making this assumption is it possible to show several successive oscillations for, otherwise, the violence of reaction is so great that one of the populations is quickly reduced to fractional numbers, and the other population follows—as is indicated in Figure 9 B. The graphs shown in Figure 9, and similar ones published elsewhere (Nicholson, 1933; Nicholson and Bailey, 1935), are not intended to show what may be expected to happen to interacting hosts and parasites in nature, but simply to illustrate the probable underlying mechanism which leads to certain interesting events which are sometimes observed in nature.

An examination of this simple hypothetical situation leads to the question which has often been asked on much more general grounds: Why is it that phytophagous animals and predators do not multiply to such numbers that they exterminate their host-plants and prey, and so also themselves? The answer is that the primary postulates are over-simplified—the inevitable operation of other factors must be taken into account.

In the first place, a simplifying initial assumption made is that the frequency of contact between host and parasite varies directly with the density of each of these interacting insects. This assumption is also made in the Lotka-Volterra equations. It is a tenable assumption, so long as the distribution of the interacting animals is fairly uniform or random. However, when the densities of interacting animals are reduced to very low levels, this comparative uniformity can no longer be true; for the offspring of the survivors must necessarily begin their existence in the places where the survivors occurred, and these places are likely to be widely spaced. The population, therefore, becomes broken up into a large number of widely separated groups. In some of these both hosts and parasites are present, and over-violent corrective reactions quickly lead to the extermination of both. In other places there are either only hosts, or only parasites. Parasites so placed will leave no offspring, unless they happen to find a surviving group of hosts. The hosts, on the other hand, will tend to multiply progressively until such time as they are found by parasites. Thus here and there small groups of hosts multiply rapidly, but inevitably are found sooner or later by parasites and exterminated; but in the meantime some hosts have dispersed into previously vacant places where multiplication begins again. This leads to an ever-changing “spotty distribution” of the interacting insects. The populations of both species are maintained at a fairly constant level in relation to the total area of distribution, this level being far below the calculated equilibrium density (see Nicholson, 1933, p. 361).

Published accounts of the successful introduction of beneficial insects to destroy insect pests, or noxious weeds, indicate that such “spotty distribution” is the typical end result of such introduction, when successful. In a recent communication Dr. S. E. Flanders, who has an unrivalled knowledge of this subject, wrote “it appears that the spotty distribution of insects is characteristic of pests under control by natural enemies. It is also characteristic of plants under control by phytophagous insects”. In Australia we have an excellent and easily observable example in the control of prickly-pear (Opuntia spp.) by the introduced moth Cactoblastis cactorum. Mr. A. P. Dodd, who played a prominent part in the introduction of this beneficial insect and in the study of the subsequent course of events, told me recently that, throughout the previously heavily infested area, prickly pear now appears only in small widely separated patches which inevitably are found before long by C. cactorum and quickly destroyed (see Dodd, 1936).

It should be noted that such systems of coupled lag-oscillation would lead to the extermination
of both kinds of interacting animals if the area occupied were comparatively small. But, when the area of occupation is very large, it is almost inevitable that some individuals would diffuse from groups of multiplying hosts into surrounding areas not occupied by parasites. These would not suffer the fate of the other insects in the group, and would establish new groups of multiplying hosts, until they, in their turn, were found by the parasites. Such temporary escape by some hosts from the system of interaction prevents the extermination of the interacting animals. In other words, the extreme sparcity of hosts is the equivalent of having refuges. The persistence of the hosts or prey made possible in this way in large areas ensures a continuing food supply for the parasites or predators.

The basic assumption made in the simple situation, that the host is not subject to limitation by anything but the specific parasite considered, can never be strictly true in natural populations; for, if the operation of any one restrictive factor were sufficiently relaxed to permit progressive multiplication of the host, it is inevitable that sooner or later the availability of some other requisite, such as food, would check this multiplication. With this consideration in mind it was concluded that (Nicholson, 1933, p. 163) "when there is an upper limit to the density an animal may reach, intraindividual oscillation may be maintained indefinitely". The underlying cause of this is that, if something other than the parasites (for example, the depletion of the food supply) prevents the host population from reaching very high levels, the necessary large number of parasites to reduce the host population to a sufficiently low level to cause fragmentation cannot be generated. Consequently the system of oscillation continues, each successive peak being mainly limited by the additional factor, such as food supply, which acts as a controlling governing factor. This is almost certainly the underlying mechanism of the persistent periodic fluctuations observed by Utida (1955) in cultures in which Callosobruchus chinensis (L.) was attacked by the braconid parasite Heterospilus prosopidis Viereck. He showed that this bean-weevil was not only affected by the density of the parasite but, at times of abundance, was limited by a density-related destruction of the eggs by trampling, by a fall in the fertility of the adults, and by mortality amongst the larvae due to direct interference when overcrowded.

One feels intuitively that there must be other possible end-results produced by such "coupled lag-oscillation" under various conditions, and that some of these, at least, must counteract the excessive intensity of the density-induced corrective reaction, so leading to systems of damped oscillations. One suggestion is that, when the parasite is not completely specific and its numbers are appreciably affected by the other species of hosts it attacks, the parasite density will not react so violently to changes in density of a particular host as it would if it attacked this host only. Such reduction in the intensity of reaction may change the system from one of growing oscillations to damped oscillations (see Nicholson, 1933, p. 164, Fig. 8).

Varley (1947, p. 181) suggests another possibility by saying "it can be shown with Nicholson and Bailey's theory that if a proportion of hosts is not available to parasitism, oscillations will be damped instead of increasing in amplitude". An unpublished mathematical investigation of this suggestion made by V. A. Bailey confirmed that there are situations in which the suggested mechanism might produce damped interspecific oscillations. However, the investigations showed that such situations are probably rare because (1) if more than the surplus of offspring produced by the host is protected from the parasites, these clearly cannot destroy the whole surplus, and so govern a population; (2) if very little more than the surplus is exposed, damped oscillations may be produced; and (3) a small further increase in the fraction of individuals exposed to the parasites leads to systems of increasing oscillation and instability. Certain other possible damping mechanisms have been explored in a preliminary way, but there is scope here for much more investigation.

In brief, if a population regulates its density by limiting the supply of an animal or plant upon which it is dependent, this tends to produce compensatory reactions of excessive intensity which cause the compensatory system to be inherently unstable. However, additional factors, which are inevitably present in the environment of a natural population, prevent this intrinsic instability from leading to extermination. Many different end-results seem to be possible, each of which is a condition of stability and can automatically compensate for the effects of any external disturbance, provided it is not excessive.

There is not sufficient time to discuss other categories of population regulation (see Nicholson, 1954b, p. 34). I can only state that in all of these, just as in the three categories already discussed, it has been found that automatic compensatory mechanisms exist which permit the populations to adapt themselves to widely different circumstances by density-induced reactions. Because of much misunderstanding upon the point, I would like to stress that my investigations and theoretical considerations based upon them, do not imply that density governing reaction should operate upon a population at all times. At times populations may multiply without check, or their numbers may be progressively reduced over a period by adverse external factors, without there being any compensatory reaction during that period. In spite of this, it is necessary, and inevitable, that density-induced reaction should
limit populations in relation to the prevailing environmental conditions from time to time at least, so determining the general levels of abundance from which the uncontrolled variations just spoken of may take place.

The foregoing considerations have shown that some kinds of animals, at least, induce reactions in their environments, and within their own populations, which bring about an automatic self-adjustment of their population densities at levels which are determined both by their own properties and by those of their environments. Theoretical considerations go farther than this (see Nicholson, 1954b, p. 59) and indicate that no population can be persistent unless it has a mechanism of density-induced compensatory reaction to maintain it in being. The question therefore arises: In what way do these findings help us to interpret events in natural populations?

**Self-adjustment of Populations in Variable Environments**

Let us first consider the simple situation of a very large area of country in which conditions change progressively from high favorability on the one side, to complete unfavorability on the other. Naturally the species will occupy all of that part of the country which is favorable to it, and in all of this, except on the line of transition between favorability and unfavorability, the animals will multiply indefinitely, if unchecked. As they increase in numbers they inevitably induce reactions opposing population growth, which sooner or later prevent further progressive growth in the population. At each point in the favorable zone the populations reach stability when the intensity of induced opposition to growth, supplementing the inherent resistance of the environment at that point, exactly counteracts the innate tendency of the animals to multiply. With the progressive increase in intrinsic environmental resistance which occurs as the unfavorable region is approached, the intensity of induced resistance automatically lessens, because of density-induced reactions. When the limit of environmental favorability is reached, the animals lose their ability to adjust themselves to further decrease in favorability—their emergency reserve of fecundity is exhausted. This, however, does not completely restrict the distribution of a population exactly at the limit of environmental favorability, for diffusion causes some animals to exist in the neighboring unfavorable areas. Such fringing areas may be occupied permanently because the continuous immigration of animals from the neighboring favorable areas compensates for the inability of the resident animals to produce sufficient surviving offspring to offset mortality.

Such fringing areas are of particular interest, for density-governing reaction does not occur in them. In spite of this, the densities of the animals are indirectly determined by such reaction. This is because the number of migrants into the fringing areas is a function of the population densities in the neighboring favorable areas, which in turn are controlled by density-governing reaction. Equilibrium is reached when the number of immigrants, together with the inadequate number of mature offspring produced by the residents, is just sufficient to compensate for the mortality which occurs in the unfavorable fringing areas. So, although it appears certain that all persistent populations are adjusted to their environments by density-induced governing reaction, such reaction may not be observable in a particular place because the place happens to be at, or beyond, the limit of favorability. Consequently, one would have to examine the neighboring more favorable areas in order to find what factors governed the population.

A more usual situation is that populations of animals are distributed over the countryside in the form of a mosaic, only certain patches of the country being truly favorable—the remainder being unfavorable in the sense that the animals may be able to survive there but not to live normally and effectively. The general reactions of a population to its environment remain as just described; but, as the favorable environment is fragmented, there is an increase in the ratio of fringing area to favorable area. Under these conditions it is probable that density-induced migration frequently plays an important part in the adjustment of population levels within the favorable areas. It appears that, in general, animals recognize areas favorable to them and occupy these by preference but, as population density within such favorable areas increases, crowding causes an increasing fraction of the population to be forced out into the fringing areas, or beyond, where the animals are exposed to less favorable conditions. These may either increase mortality, or decrease (or even prevent) the production of offspring. Such density-induced migration is therefore a reaction of the density-governing type.

The foregoing discussions about fringing populations have a bearing upon what is commonly known as "Gause's hypothesis". As Gilbert, Reynolds and Hobart (1952) point out, "Gause makes no statement which resembles any wording of the hypothesis which has arisen bearing his name", although the general idea it presents is implicit in his discussions. Various wordings have been used, the first apparently being that "two species with similar ecology cannot live together in the same place". The same concept has been expressed in other ways by various authors, and it has been pointed out that this hypothesis can readily be derived from the mathematical investigations of Lotka, Volterra and others. Andrewartha and Birch (1953, p. 174) argue that there is a "fundamental contradiction in the mathematical theory of interspecific competition of Lotka and Volterra".
and argue that (p. 177) "once the two species have come together they must continue to live together indefinitely": But their mathematical arguments are unsound (Philip, 1955).

Gilbert, Reynolds and Hobart (1952) drew particular attention to the ambiguity of the words "similar ecology" in Gause's hypothesis. One of the two basic conclusions reached in my first general article on population problems (Nicholson, 1933) resembles "Gause's hypothesis" but it avoids such ambiguity. It is (p. 147) "for the steady state to exist, each species must possess some advantage over all other species with respect to some one, or group, of the control factors to which it is subject". "Control factor" is here used in the sense of "density-governing factor". The argument upon which this conclusion was based is that the same governing factor, or group of factors, cannot be adjusted to more than one intensity at a time, so the species which induces reaction at the highest intensity must inevitably displace the others—for the intensity each would induce by itself prevents the production or survival of surplus offspring and so is the highest it can withstand permanently.

This conclusion is not based upon the assumption of "similar ecology", for if two species with very different "ecology" occupied the same area, and were governed by the reaction of the same requisite (such as a particular kind of food) one of the species would displace the other. On the other hand, if the two species had very "similar ecology", but differed in the fact that each was critically influenced by a different requisite or inimical environmental factor which governed its density, then these two could live together.

Gause's hypothesis and the conclusion that two or more species cannot be governed by the same factor are based upon the implicit postulate that the populations of the competing species are too intense. Such precise correspondence between the distributions of two or more species is unquestionably rare in nature. However, if the limits of potential distribution of the competing species were determined only by the availability of a common governing requisite, the distribution of the more potent species would extend completely over, and beyond, those of the competing species, which would consequently be displaced.

Observations upon species living under natural conditions indicate that their limits of distribution are rarely, if ever, completely determined by the availability of a particular governing requisite. Each kind of animal has many needs, so the limits of its distribution may be determined in different places by the inadequacy of different requisites, or by the presence of different inimical factors, such as unfavorable climate, excessive intensity of attack by general predators, or the presence of over-powerful competitors. It is most improbable that any two species would be influenced to exactly the same degree by all such factors, so there is a high probability that each species would be able to exist in some places in which the competing species would be unable to maintain itself. It is almost axiomatic that each species differs from all others in the nature or degree of its reactions to some, at least, of the environmental influences to which they are subject, which makes it very probable that each will have an advantage over its competitors in some places. Consequently, the probability of one species exterminating another, even when both are governed by the same factor, seems small.

It should be particularly noted that the factors which govern the density of a population and those which determine the limits of its distribution are by no means necessarily the same. For example, climatic factors and the intensity of attack of general predators, when uninfluenced by the density of the species concerned, may be primarily responsible for limitation of distribution, although within the favorable area the density of the population may be governed by some other factor, such as the depletion of food or of refuges.

Now, when each species has an advantage over its competitors in some parts of the whole region which is favorable to it, except for the presence of successful competitors in places, it will not only continue to exist but will permanently maintain fringing populations in contiguous areas in which its competitors have some advantage, the mechanism being as already described. When there is a mosaic of the conditions which favor one or other of two competing species, the fringing areas may overlap so completely that the two species occupy all parts of the region together. For example in a bushy heathland, one species may prefer to live in the bushes and the other in the open areas, but each may continuously invade the preferred habitat of the other. If, in this situation, the governing factor is availability of food, competition is incomplete, for each species searches one part of the environment more intensively than the other. In the absence of one or other of these preferred habitats, or if they were far apart, one species would displace the other from its habitat, yet each may be well adapted to live in both habitats were its competitor not present. The question arises here as to what constitutes "similar ecology", for identity in response to environmental factors and in behavior seems inconceivable otherwise than within a species.

It seems improbable, therefore, that "Gause's hypothesis" represents an important principle in nature. It remains true, however, that if one species governs itself by adjusting the availability of a particular requisite at a level just sufficient to maintain it, and that if this level is lower than the maintenance level required by some other species, this second species will be displaced, and will be exterminated if its area of distribution is completely occupied by the first species. Such displacement or extermination is most likely to
occur amongst species with "similar ecology" for they are most likely to be competitive, but displacement is not restricted to such animals. For example, an herbivorous mammal might conceivably exterminate a moth through excessive reduction of their common food supply.

**Natural Selection**

Within a species population all individuals have essentially the same properties and requirements, and so competition amongst them is complete. Consequently if by mutation or some other change in their genes, individuals appear which have an advantage over other individuals that causes them to leave more surviving offspring than individuals of the original form, this new form will inevitably displace the original from all places in which they have advantage, no matter how small this advantage may be. The replacement of the old by the new form inevitably changes the properties of the species, but the disturbance this tends to cause is automatically checked by density-governed reaction.

An example of this is illustrated by Figure 8, 1. It will be noted that the numbers at the minima of the oscillations strongly tended to become greater with time, and that the character of the oscillations began to change markedly after about the 400th day. The marked change in the population pattern indicated that the properties of the species were progressively changing. After termination of this experiment flies from this culture were compared with flies from the original culture by giving equal numbers of each a very small quantity of protein food. It was found that the flies from culture I and those from three others tested after the completion of the same general experiment, could lay large numbers of eggs, whereas those from the original laboratory culture, and also wild flies, could not produce any eggs when given the same quantity of protein.

It is evident that intense competition amongst adults for protein had led to selection of those flies which could produce eggs with a minimum intake of protein. There was evidence that there had been a similar change in properties in all ten of the cultures which were run in parallel, which strongly suggests that the change in properties was not due to mutation but rather to a new combination of the genes.

Further studies revealed the remarkable fact that the selected strains of flies could produce sufficient eggs to maintain cultures from generation to generation even when the adults were not given any protein. This, in itself, is an astonishing change of a property. This illustrates my contention (Nicholson, 1955) that natural selection operates to produce hyperadaptation. That is to say, selection does not merely operate to fit an organism to live in its existing environment, but tends to develop properties which are more than adequate, so making it possible for the species to exist in even less favorable environments.

Figure 8 shows that, in spite of this radical change in an important property, the populations still remained in being. Density governed reaction adjusted the populations about new levels and there was an accompanying change in the pattern of population change.

**Conclusion**

In brief, it is the innate ability of animals to produce a surplus of offspring which enables populations to persist in spite of adverse environmental factors which cause heavy mortality, or which seriously interfere with reproduction, provided these are not so severe that they cause the number of mature offspring to be less than the number of parents, when averaged over a long period. When adverse factors are less severe than this a population will tend to increase progressively, but increasing density induces adverse effects which oppose population growth with progressively greater severity, so preventing further growth when the intensity of this induced opposition, combined with that of the inherent environmental resistance, just counters the innate ability of the animals to multiply. Consequently any species automatically adjusts its density in different places, and in the same place at different times, in relation to the prevailing environmental conditions; and it maintains a state of stability under all conditions which are not inherently intolerable. This mechanism may enable populations to remain in being in spite of great changes in the environment, without any necessity for the development of new adaptations.

**References**


DISCUSSION

T. B. REYNOLDS, University College of North Wales, Caerns, Wales: Referring to the unfavorable environmental gradient needs qualification. The need for this qualification can actually be seen in his figure, which shows a change in the response of an experimental population to limited quantities of food.

Dr. Nicholson claims that if a barrier were erected which would isolate the populations of individuals in a marginal area from the bulk of the population, a barrier that would prevent immigration, then the populations in the marginal areas would disappear. A geneticist would predict quite the opposite: The erection of such a barrier would allow those marginal populations to adapt to those particular environmental circumstances and, in fact, immigration is precisely that factor which prevents such adaptation.

A. J. NICHOLSON: As my discussions were primarily concerned with population dynamics I assumed, for the sake of simplicity, that the properties of a species remain constant. I agree with Dr. Wallace that if a barrier appeared between a favorable area and a neighbouring area in which conditions were slightly unfavorable, natural selection might cause the development of properties adequate to enable the animals to persist in the previously unfavorable area—but I regard this as improbable. The right properties would need to be developed rapidly as the isolated population would be dwindling, and the total numbers in such an isolated fringe population are likely to be small, so making rather remote the possibility of a suitable recombination of genes being produced in time to prevent extinction. The experimental population (see Fig. 8) to which reference is made is not comparable. In this the environmental conditions were sufficiently favorable to permit the population to persist without change in properties, and selection took place simply because certain types of individuals in the evidently heterogeneous population possessed properties which were more advantageous than those of their fellows under the conditions imposed upon them in this series of cultures. There was no question of the population being in danger of extinction.

L. VAN VALEN, Columbia University, New York: On the conservation of Gause’s principle: It appears that the situation mentioned in closing, which was claimed as an exception to this principle, actually is not such. Each genetically isolated population is stated to be better adapted than the other in a region which it occupies to the exclusion of the other. These regions are connected by an intermediate zone. This obviously means that the species occupy different niches and therefore would not be in direct or indirect competition in all important aspects of adaptation, as Gause’s principle requires. These niches may appear quite similar and occur in the same region, as postulated, but a sufficient difference for coexistence was also postulated. Different susceptibility to parasites, seasonal
cycles and vertical distribution in trees are familiar examples.

A. J. Nicholson: The difficulty here is the ambiguity of the term "similar ecology". If this is taken to mean, as Dr. Van Valen's comments seem to imply, identity in the niches two or more species occupy, then Gause's principle is unsailable. But to me it seems inconceivable that such identity of adaptation can exist in two or more species—their properties must necessarily differ in some respect, for otherwise they would be indistinguishable and would be regarded as the same species. If, then, "similar ecology" is not taken to mean identity, we can consider the situation in which two or more species which can occupy the same niches, each have an advantage over the others in some places—often, for example, being more tolerant of heat and another of cold. If so, each will not only occupy those places in which it possesses advantage, but the different species will often exist together in places, the local disadvantage of one species being offset by the advantage of having reinforcement by diffusing individuals from neighbouring areas more favourable for this species. This is particularly likely in regions where there is a mosaic of varying conditions. In this sense I consider that there must be many exceptions to the claim that "two species with similar ecology cannot live together in the same place".

David Pimentel, Department of Entomology, Cornell University, Ithaca, New York: You made the statement that the flies emerging from a group of larvae who had been subjected to intense competition were about one eighth the weight of normal individuals. Have you been able to make collections of adult flies in nature and compared the relative numbers of large and small flies in nature with those in your laboratory studies?

A. J. Nicholson: Undersized specimens of L. cuprina are sometimes found in traps, but they are seldom as small as the smallest obtained in overcrowded cultures. Other factors, notably displacement of L. cuprina by other species of blowfly, interfere with intraspecific competition, and so the results of the laboratory experiments cannot be expected to apply directly to natural populations of this insect. The experiments were deliberately designed to explore the effects of intraspecific competition when uncomplicated by interspecific relations.

A. Sokoloff, Hofstra College, Hempstead, New York: 1) I should like to ask Dr. Nicholson whether he has observed a marked decrease in size of flies reared in cages where the amount of food available to larvae is limited.

2) This decrease in size undoubtedly leads to a lowering of fecundity. Since a small female lays a smaller number of eggs than a larger female, this mechanism alone would permit oscillations of numbers of flies in his populations even where food is constant and limited. This mechanism would also act as a safety-valve which would prevent the population from going into extinction.

3) In the case of blow-fly populations it would be well to compare, say, weight of individual flies which emerge from dead sheep carcasses with the weight of flies emerging from his population cages. It is certain that the emerging flies will possess a similar weight under both optimal laboratory and natural conditions despite the fact that in the dead sheep the number of larvae may exceed the available amount of food. I believe that the complex succession of scavengers must be followed by a large variety of predators which would eliminate such a large population of larvae that density-dependent relations would not occur in the dead sheep.

A. J. Nicholson: Taking Dr. Sokoloff's questions in turn:

1) In cultures of L. cuprina which were limited by competition for larval food there was commonly a marked decrease in the size of flies, particularly when larval competition was intense.

2) The small flies were observed to lay fewer eggs than normal ones, but even the smallest flies produced far more eggs than the minimum necessary for the maintenance of the population. Such density-induced reduction in egg production played its part in governing the population, but the dominant effect of larval crowding was increased larval mortality.

3) The control of L. cuprina in the field is far more complex than in the laboratory experiments discussed. A major additional factor is competition with other species of blowflies. A relatively minor factor is attack by parasites and predators, but this takes place only after the larvae leave the carcasses, so this factor plays no direct part in preventing density-dependent reactions between blowflies in the dead sheep. When carcasses were buried after only a short exposure they gave rise to much larger numbers of blowflies than did other carcasses which were exposed longer, and so had greater numbers of eggs laid upon them. Intense competition amongst blowfly larvae which causes many to die without pupating is normally observed in carcasses in the field.