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AN OUTLINE OF THE DYNAMICS OF ANIMAL POPULATIONS

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[*Manuscript received December* 14, 1953]

CONTENTS

Summary

This article is itself a summarized statement concerning the various influences which affect population densities and the population systems these lead to. Known facts concerning animal populations have been analysed, systematized, and critically examined, using the experimental and mathematical

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approaches in the simpler situations.   The more outstanding conclusions are listed below.

Populations are self-governing systems.   They regulate their densities in relation to their own properties and those of their environments.   This they do by depleting and impairing essential things to the threshold of favourability, or by maintaining reactive inimical factors, such as the attack of natural enemies, at the limit of tolerance.

The mechanism of density governance is almost always intraspecific competition, either amongst the animals for a critically important requisite, or amongst natural enemies for which the animals concerned are requisites.

Governing reaction induced by density change holds populations in a state of balance in their environments.   The characteristic of balance is sustained and effective compensatory reaction which maintains populations in being in spite of even violent changes in the environment, and which adjusts their densities in general conformity with prevailing conditions.

Far from being a stationary state, balance is commonly a state of oscillation about the level of the equilibrium density which is for ever changing with environmental conditions.

Destructive factors do not add to mortality when they continue to operate over long periods, but merely cause a redistribution of mortality, for the intensity of competition automatically relaxes sufficiently to make room for the destruction they cause.   Such compensatory reaction causes the effect of destructive factors upon density to be much less when balance is reattained than that which they produce when they first operate.

Although population densities can be governed only by factors which react to density change, factors which are uninfluenced by density may produce profound effects upon density.   This they do by modifying the properties of the animals, or those of their environments, so influencing the level at which governing reaction adjusts population densities.

Population growth and maintenance are influenced in different ways by the four kinds of density governed reaction and the three kinds of governing requisites recognized, so giving rise to the twelve situations diagrammatically illustrated in Figure 6, and to the different patterns of population growth and maintenance characteristic of these.

Interaction between populations and their governing requisites often leads to oscillations in density even in a constant environment.   Five kinds of population oscillations are recognized, namely, relaxation, coupled, lag, coupled-lag, anl fragmented oscillations.

Periodic environmental influences, such as the seasons, tend to impose their period upon oscillations of internal origin, and so to obscure their existence in spite of the fact that they may be dominantly responsible for the violence of the population changes observed.

Oscillations and fluctuations of the different populations in a community tend to interfere with one another, so giving rise to irregularities which may have no evident relation to varying external conditions.

Two or more species cannot be governed by the same factor, or group of factors, in the same place at the same time; but species with similar requirements may live together in some places, provided each has an advantage over all the others in some parts of the region they occupy.

Density governance is an important part of the mechanism of natural selection; for, as individuals with advantageous properties are selected, this causes an intensification of induced reaction which ultimately eliminates other individuals and their offspring which do not possess these advantages.

I. INTRODUCTION

Populations, like rivers, continue to exist only because new matter continually replaces the matter they inevitably lose. Flux is an inherent essential of their continued existence; and their distribution and size are functions of the rate of accession of suitable new matter, and of the local influences which determine how much of this they can take up. Population dynamics is the branch of biology concerned with the forces (that is to say, the measurable influences) which govern movement of matter through populations, from the environment and back again. Only by reaching an understanding of these forces can we expect to account for the distribution and densities, and for the changes in the distribution and densities, of populations which are observed in nature.

The primary force is solar energy, for all energy used by organisms, whether for the transport of matter or for other purposes, can be traced back to this source. The photosynthetic activity of plants traps some of this radiant energy, so enabling plants to build into themselves the inorganic materials from which the matter used by all organisms is ultimately derived. Photosynthesis, then, is the primary mechanism which makes available to organisms both the matter and the energy they use. Many different factors influence the way the matter is channelled through organisms, and from one organism to another, the energy expended in this process being obtained by the breakdown of organic materials, the products of which are ultimately excreted. Thus the energy originally trapped by photosynthetic processes is dissipated, and the matter originally elaborated by plants is returned to the inorganic environment as an inevitable result of metabolic processes. The matter remains available for re-use by organisms; but the energy is lost and has to be replaced by new solar radiation if life is to continue.

The forces which govern metabolism and reproduction, and also the forces which have governed the evolution of the innumerable kinds of organisms which exist, are clearly of fundamental importance in population dynamics; but we can regard these as the appropriate subjects of study in the separate, but closely related, sciences of the dynamics of individual organisms and the dynamics of evolution respectively. It is sufficient for the purposes of the present discourse to accept the fact that organisms have the properties we know them to possess, without specifically considering how these came into being, or the details of the metabolic processes which govern matter and energy exchange between individual organisms and their environments.

Animals not only build up and maintain their tissues by using organic food obtained directly or indirectly from plants, but they use some of it to produce offspring. This ability of organisms to multiply when conditions are favourable is of outstanding importance in all population problems, for it is the means by which populations can readily expand when the supply of the things they need increases. When this supply contracts, mortality tends to adjust the population to the new environmental conditions, for the death of some individuals permits the survivors to obtain more adequate quantities of these essentials. Thus reproduction and death are the properties of organisms which are ulti-

mately responsible for the ability of populations to adjust their densities to the prevailing supply of the things needed.

Although it is true that the size of any population tends to vary directly with the amount of food the constituent individuals collectively use, it must not be assumed that food supply is the only thing which can limit population size. It often happens that populations are limited by other factors (such as natural enemies, or the availability of suitable space) at levels far below those which the food supply would permit. Moreover, as will be shown later, population densities do not necessarily vary in direct proportion to the amount of food the constituent individuals use, for some may be wasted in greater or lesser measure according to the circumstances.

Throughout the ages organisms have been continually producing adaptations which enable them to occupy previously vacant space—or to displace other kinds of organisms from the space, or parts of the space, these previously occupied. This has led on the one hand to the occupation of more and more of the earth's surface, and on the other to diversification of organisms. This expansion of the area occupied by plants has caused an increase in the amount of solar energy used, and so also of elaborated organic matter, which is potential food for animals. The diversification of plants by adaptation to different kinds of habitats has constituted a further diversification in the habitats available to animals. Adaptation to these new habitats, and to the new habitats phytophagous animals themselves constitute or create, has led to the further diversification of animals. Because of this diversity the energy and matter primarily obtained by plants is channelled through complexes of associated organisms which vary in composition greatly from place to place; and the forces which govern this channelling are those which, influenced by the properties of the various species, and those of their environments, determine the spatial distribution and densities of these species.

The analysis presented in the following pages of the factors and mechanisms which determine the distribution and densities of populations is given only in bare outline, for the field covered is enormous. The views put forward make some contact with almost everything that has been written about populations, and so comparison of these with the views expressed by other authors must, with few exceptions, be left to later more detailed publications dealing with particular aspects of the subject. This outline has been produced expressly for the purpose of providing a framework into which can be fitted more detailed articles concerning the experimental and theoretical investigations I have carried out over a number of years.

As many of the concepts outlined in the following discussion are either new, or differ in some respect from those used by other authors, it has unfortunately proved necessary to use new terms to represent them. For this purpose English words have been selected which can be used to convey the ideas intended without any departure from ordinary English usage. Their meanings conform to those given in the Shorter Oxford English Dictionary.

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II. Characteristics and Classification of Significant Environmental Factors

It is axiomatic that organisms can live and multiply only when all their numerous essential requirements are satisfied. An environmental element or group of elements, which satisfies any one of these requirements is a *requisite*. Food and favourable living space are primary requisites for all organisms, but each can be subdivided into many distinct elements. In particular situations it may be convenient to recognize that food consists of various distinct requisites, such as protein, carbohydrates, salts of particular kinds, or other chemical constituents; or to specify the requisites as, for example, plants belonging to particular species, particular parts of those plants, or these parts when at a particular stage of development. With favourable space it may be necessary to specify separately such requisites as warmth and moisture (within known limits of tolerance), refuges, nesting sites, and suitable media in which to live. The degree to which essential things are grouped together or separated when defining requisites depends upon the needs of each particular investigation. For example, with a monophagous predator it is sufficient to define the food requisite as the prey species, without referring to the numerous chemical constituents which each play an essential part as food.

There is a quantitative or qualitative lower limit to the favourability of any requisite. When (even in the absence of competition by other individuals of the same species) this *threshold value* is not exceeded by any one requisite the population cannot persist, no matter how favourable any or all of the others may be. This happens, for example, if the right food is present but so sparse that individuals cannot obtain sufficient to maintain themselves and to produce offspring at the replacement rate; if temperature is below the limit of tolerance of the species under the prevailing conditions; or if the degree of freedom from attack by natural enemies is insufficient to permit survival of offspring at even the replacement rate. Clearly, therefore, the spatial distribution of any species is limited at all points at which the favourability of any one of its requisites falls below the threshold value under the prevailing conditions. It should be noted that the threshold value of a particular requisite for a given species is not a constant, for it varies somewhat with environmental conditions. For example, it is well known that with certain insects the limits of tolerable temperature vary markedly with the humidity conditions.

Within regions where all the requisites of a given species exceed their thresholds of favourability the species population not only can exist, but inevitably grows. However, sooner or later a check to continued population growth is inevitable, for the growing population progressively depletes such things as food and favourable space, and it may otherwise impair the favourability of the environment, as by the accumulation of harmful metabolites, or by inducing heavier attack by natural enemies. These effects of population growth reduce the favourability of the environment until it falls to the threshold value, when further growth is made impossible.

When considering the influence of requisites upon the distribution or densities of populations, it is generally necessary to specify the particular properties

of the requisites which are important under the prevailing conditions. For example, the properties "density", "rate of generation", "quality", and "accessibility" of food all individually influence population survival and density. Properties of requisites, and also those of the animals themselves, which have discrete influences upon populations are here referred to as *density factors*. The limitation of spatial distribution which such factors exercise can be regarded as the imposition of extreme density limitation in the areas from which they exclude the animals. Inimical factors (such as adverse temperatures, or the density or activity of a particular natural enemy) are regarded as qualifying attributes of the requisite "favourable space". When animals or plants are attacked by natural enemies, they are themselves requisites, and their density or availability are factors which may influence the densities of their natural enemies.

When we are concerned with the immediate influence of the environment upon populations it is usually most convenient to regard this as explicable in terms of the effects produced by such density factors. On the other hand, when dealing with the longer range effects produced by the interaction between populations and their environments, it is necessary to specify the requisites of which the density factors are attributes, for (as will be shown later) the patterns of population change and maintenance are greatly influenced by other attributes of the requisites, such as their inherent qualities of transience, persistence, temporary existence, and multiplication.

In order to make clear the effects environmental factors may have upon populations, it is necessary to distinguish between several categories of requisites and factors. An *unresponsive requisite* or factor is one which remains unaltered in spite of any change in the population considered. For example, the prevailing climatic conditions are quite unaffected by any change in the densities of most kinds of animals. A *responsive requisite* or factor, on the other hand, is affected by change in population density, as when the increasing amount of food used by animals in a growing population causes a progressive reduction in the amount remaining unused at any moment. If the quantity or quality of the requisite is not only affected in this way by density change, but in turn modifies its influence upon population change, the requisite is *reactive*. It does not necessarily follow that an induced change in a requisite will change the influence of the requisite upon the population. For example, if the population is limited by the action of natural enemies at a level far below that permitted by the food supply, an increase in density produces a response in the food supply but no reaction by it; for, although population growth undoubtedly does cause greater depletion of food, this has no effect upon the population, food being still available to individuals in excess of requirements. Such responsive requisites, in common with all unresponsive requisites, are *non-reactive requisites*.

When population densities are far below the capacity of the environment it sometimes happens that population growth causes the properties of a requisite to become more favourable, so inducing still further growth. Influences

which augment change in this way are *density disturbing factors*. For example, the trampling down of shrubs and old grass by herbivores in a sparsely occupied environment may increase the amount of palatable grass subsequently available to the population or, if the population is reduced below a certain critical density, trampling may be insufficient even to keep clear the then available amount of pasture, so that this decreases progressively with time. Invariably such augmentative reaction to density change is replaced by density governing reaction as the population approaches the capacity of the environment.

It is more usual for reaction to oppose change in density; for increase in population must sooner or later lead to significant reduction in the quantity, quality, or accessibility of one or more requisites, and this inevitably slows down growth and eventually precludes any further growth. The properties of requisites which react in this way are *density governing factors*, for it is their reaction to density change which holds population densities in relation to environmental conditions.

Non-reactive requisites, whether responsive or unresponsive, are incapable of bringing about such adjustment. For example, food which remains in excess, and favourable climatic conditions which remain unaltered by population growth clearly cannot check progressive growth. The quality of the food or the temperature prevailing, however, may have an important effect upon the level at which a population is adjusted by governing factors; for these factors may alter the properties of the animals (such as their activity, viability, and reproductive powers), or those of the governing requisites (such as the quality or rate of supply of food) and, as will shortly be shown, governing reaction adjusts population densities in relation to such properties. It may be said, then, that non-reactive factors may play a part in laying down the rules which are enforced by the governing factors, such non-reactive factors being referred to as *purely density legislative*. It should be noted that density governing factors are also density legislative, for it is the amount and quality of the governing requisite which determine the size of the population which can be borne under the prevailing conditions when limiting depletion is reached.

In brief, governing factors are the primary determinants of population densities, both in their governing and their legislative capacities; whereas non-reactive factors modify these densities by influencing the properties of the animals, and also those of the governing factors. Thus, as governing and legislative factors together determine population densities, they may be referred to collectively as *density regulating factors*, for the verb "to regulate" commonly has the two component meanings of rule making and rule enforcement —although it sometimes signifies rule making only.

The interrelationship of these density factors which are properties of requisites is shown diagrammatically in Figure 1. One factor shown there has not been discussed, as it is not strictly speaking a density factor. A *density inactive factor* is a property of a requisite which does not affect density, although it is essential for the existence of animals. Thus the supply of sea-water does

not influence the number of marine animals which can live in unit volume, but there must be such a supply if the animals are to exist, and its extent places an extreme limit upon their possible distribution. Similarly, the supply of oxygen for terrestrial animals commonly does not vary significantly, and so, although absolutely essential for most animals, it does not influence their densities.
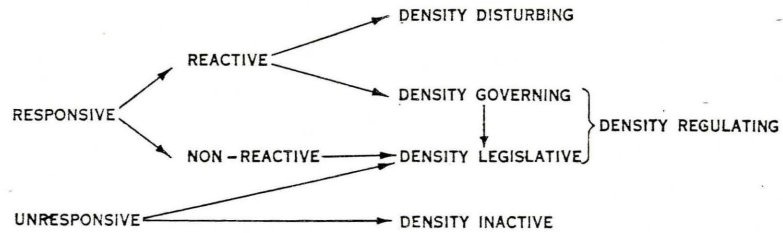

Fig. 1.—Classification of requisites and of their properties in relation to their response to density change and to the influence they have upon population density.

It sometimes happens that factors which do not themselves respond to density change act as the tools or *instruments of destruction* used by true reactive factors. Thus increasing density, instead of causing increasing mortality or decreasing natality in such ways as the depletion of the food supply or of the amount of favourable space still unoccupied, may cause a greater proportion of the animals to move into parts of the environment intrinsically less favourable than those they would occupy by preference. Clearly the underlying mechanism of this increasing exposure to destructive influences is competition for food or favourable places; but the immediate cause of destruction may be unfavourable temperature, or attack by general predators which could not reach the animals in their preferred habitat. In such situations it is confusing to speak of such destructive agencies as "density dependent factors", as has been done by several authors (see Solomon 1949) when arguing that climatic factors may directly control population densities. Clearly the "density dependent factor" is the availability of food or favoured places, whereas the adverse climatic factors merely destroy such individuals as the dispersive effects of competition expose to their influence.

It has long been realized by many biologists that the observed general relation between population densities and environmental conditions could only be brought about by reactive factors which permit populations to grow when at relatively low densities, and oppose growth when the densities become relatively high. Various terms have been proposed for such reactive factors, the one in general use in recent years being *density dependent factor*. This appears to have given rise to some confusion, for it implies any significant environmental element or quality which is influenced by density, and thus might be taken to have the meaning given the term "density responsive factor" here. The term is often used in this loose sense; so, to avoid misunderstanding, it is necessary to replace it by a term which signifies the characteristic effect of such

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factors upon density, rather than the effect of density upon them (which is an attribute of other kinds of factors as well). "Controlling factor" (Nicholson 1927, 1933) conveys the correct idea, but unfortunately may lead to confusion when discussing population problems related to the control of pests, for in this context "to control" has the meaning "to modify the control so that the density of the pest is reduced to a point at which the economic damage caused is negligible" (Nicholson 1933). The term "density governing factor" has therefore been substituted, but its meaning is precisely that of "density dependent factor" according to definition (Smith 1935).

"*Density independent factor*" is still less apt, for its significant characteristic is not that it is uninfluenced by density but that, even though it may respond to density change, its effect upon density remains unaltered. "Non-reactive factor" has therefore been substituted, this term including both unresponsive and non-reactive responsive factors.

III. Some Experimental Evidence Concerning Population Regulation

It is easiest to appreciate how populations accommodate themselves to the varying conditions of their environments by examining what happens to populations of a given species when maintained under widely differing experimental conditions.

(*a*) *Intraspecific Competition*

The experiments upon which Figure 2 is based were briefly described in a previous article (Nicholson 1948) as follows:

"A number of glass tubes, each containing one gramme of homogenized bullock's brain as food, were used, and in each of these a different number of freshly hatched *L. cuprina* larvae was placed. Such series of cultures were replicated many times. The number of emerging adults was then plotted against the number of larvae from which they had been derived. It was found that with progressively increasing densities of larvae, mortality at first increased only slowly, but the size of pupae and of adults fell progressively. However, this kind of compensation for increasing competition for food cannot continue indefinitely. A point was soon reached beyond which mortality increased rapidly with larval density and the number of adults produced per gramme of medium fell progressively with further increase in larval density.

"These relations are shown clearly in the accompanying figure. In this particular example, eggs laid at intervals of two hours over an eight-hour period were used, each of the five batches of eggs contributing equally to the numbers of larvae used in any one culture tube. A curve with the same general characteristics was obtained when there was no appreciable age distribution, all the eggs being laid within a period of one hour, the only important difference being that the descending part of the curve was much steeper."

These experiments demonstrated the important part played by the wide scatter in the properties of animals upon the reaction of populations to depletion of their requisites. Examination of the cultures showed that even when no

individuals were given special advantages there were very great differences in the rates at which the individuals grew, so that when the food was exhausted some individuals were comparatively large and some small. These differences were accentuated when (as in Fig. 2) some individuals were given the special advantage of having access to the food earlier than others. The result of this was that the number of larvae reaching a sufficient size to produce viable pupae when the food was exhausted fell progressively with larval density. Were there no such scatter of properties and opportunities, increasing density would produce no mortality until the point was passed at which the amount of food obtained by each individual fell below that necessary for the production of viable pupae; at this and all higher densities there would be no survival.
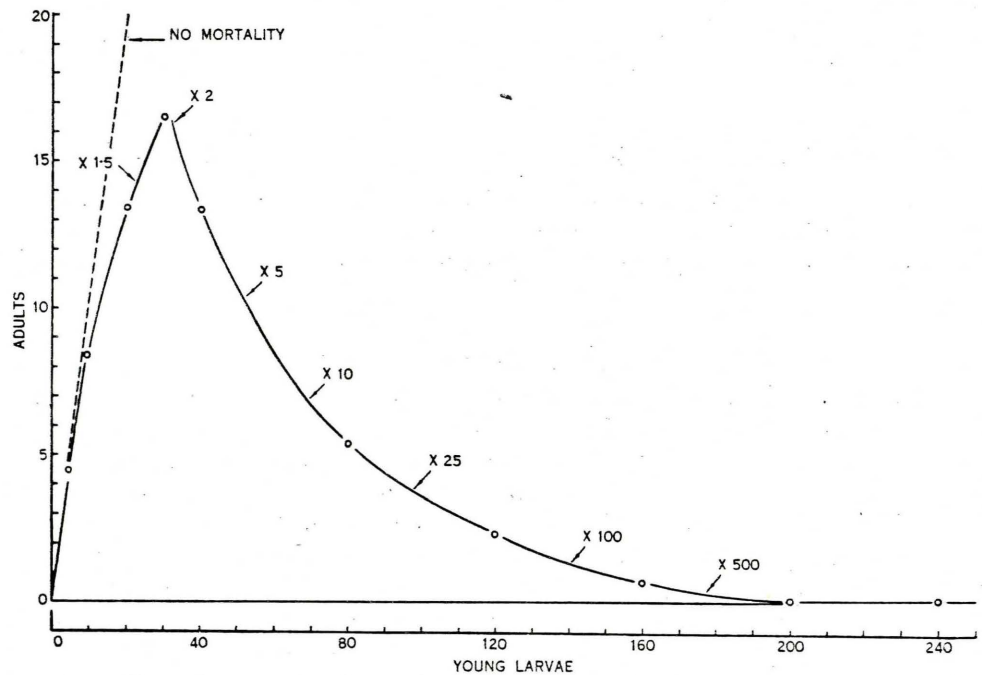

Fig. 2.—Effect of competition for food amongst larvae of *Lucilia cuprina* upon the number of adults produced (see text).

Figure 2 shows that, above a certain critical density, further increase in larval density causes not only an increase in the percentage mortality but also an actual reduction in the number of adults produced from the gramme of food consumed. This is because increasing quantities of food are consumed by the increasing number of larvae which fail to mature. Starting at a low density, then, the tendency is for a population to grow progressively so long as a surplus of offspring survives. Further growth is rendered impossible when the percentage of offspring destroyed by competition equals the percentage which is surplus to that necessary for the replacement of mature animals as they die. Consequently, the greater the power of increase (i.e. the ratio of offspring to parents in the absence of competition effects) the smaller is the number of adults produced from a given quantity of food at equilibrium. This

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is clearly shown in Figure 2, in which the points indicated by numbers pre-
ceded by the multiplication sign show the equilibrium levels of larvae and
adults at each power of increase represented by these numbers. Inspection
shows that any departure of density from the equilibrium level for any given
power of increase (which is assumed to remain constant) leads to an oscilla-
tion about this level; unless the power of increase is less than 2 (in the example
given), when an asymptotic approach to this level results (see Nicholson 1948).

However, whether the population oscillates or not, the reactive influence
of competition causes populations to be adjusted at or about the levels repre-
sented by their equilibrium densities. Consequently, if some adverse environ-
mental factor causes a reduction of the birth-rate or the destruction of some
of the surplus offspring produced, this lowers the power of increase of the
animals and so increases the number of adults produced.

The important part played by the wide scatter of the properties of animals
and those of their environments in population dynamics cannot be over-
emphasized. On the one hand it permits populations to adjust themselves to
their changing environments in the way just described, and so strongly influ-
ences both densities and patterns of population change; and on the other it
permits populations to persist under conditions far more adverse than could
be withstood if all individuals had only the average properties and opportunities,
and if no parts of the environment were more tolerable than others. The greater
the surplus of offspring produced, and the wider the scatter of the properties
and opportunities of the individuals, the greater is the ability of the population
to accommodate itself to adverse conditions.

Experiments such as that graphically represented in Figure 2 illustrate the
fact that when any requisite is in short supply, the individual animals get as
much of it as they can, and so reduce the amount available to other individuals.
It is this reactive lessening of the favourability of the environment which pre-
vents the indefinite growth of populations, and holds population densities in
general relation to the prevailing conditions. This state of reciprocal interfer-
ence which occurs when animals having similar needs live together and which
influences their success is here called *competition*. This use of the term has
been criticized (e.g. Dobzhansky 1950) on the ground that the word "competi-
tion" has an emotional content and implies the taking of active steps against
competitors. In this restricted sense the word would be applicable only to the
actions of some of the higher animals; but such restriction of meaning is un-
warranted, as it commonly does not apply in ordinary usage. For example, in
art competitions the competitors are not expected to take action directly against
one another—each simply paints as well as he can and the prize goes to the
one who does best. The derivation of competition (*com*: together; *petere*: to
seek) also indicates its appropriateness in the present context. It should also
be noted that the sense in which "competition" is used here conforms exactly
with normal usage in plant ecology.

It is necessary to distinguish between two kinds of competition, as they
produce different effects upon the patterns of population growth and mainten-
ance. *Scramble* is the kind of competition exhibited by a crowd of boys striv-
ing to secure broadcast sweets, and is illustrated by the competition of *L.*

cuprina larvae already described. Its characteristic is that success is commonly incomplete, so that some, and at times all, of the requisite secured by the competing animals takes no part in sustaining the population, being dissipated by individuals which obtain insufficient for survival. With *contest,* on the other hand, the individuals may be said to compete for prizes (such as a host individual, or an amount of favourable space an individual can arrogate to itself) which each provides as much of the requisite as an individual needs to enable it to reach maturity, or provides fully for the development of one or more of its offspring. Thus the individuals are either fully successful, or unsuccessful; and the whole amount of the requisite obtained collectively by the animals is used effectively and without wastage in maintaining the population.

(b) Mechanism of Balance

The foregoing considerations, and the experiments they are based upon, show how competition may be expected to influence populations. In order to test the conclusions reached many cultures of the Australian sheep blowfly, *Lucilia cuprina* Wied., have been maintained, each under a different set of conditions. The essential feature of such cultures is that the populations are left to develop and maintain themselves without interference—the only action taken, apart from keeping daily records, being the maintenance of the conditions decided upon at the beginning of the experiment, including the provision of a continuous supply of those requisites the insects expend. Only brief reference can be made here to some of these experiments.

Figure 3 illustrates the population changes which took place in a population maintained under as nearly constant conditions as possible. The culture room was held at 25°C, water and sugar for the adults, and also larval food (to which the adults did not have access), being provided in excess of requirements at all times. The governing requisite was ground liver, which was available to the adults alone, and each day 0.5 g of this was placed in the breeding cage. In common with the other experiments referred to in graphs and tables here, the initial parts of the culture are not recorded in Figure 3 because they are not pertinent to the present discussion.

The outstanding characteristic of this culture was the maintenance of violent and fairly regular oscillation in the density of the adult population. The reason for this is simple. It will be observed that significant egg generation occurred only when the adult population was very low. At higher densities competition amongst the adults for the ground liver was so severe that few or no individuals secured sufficient to enable them to develop eggs. Normal mortality, therefore, caused the population to dwindle until the consequent reduced severity of competition permitted some individuals to secure adequate liver and so to lay eggs. As it takes more than 2 weeks for the eggs so generated to give rise to new adults, the population continued to dwindle for this period, during which many more eggs were generated, for competition amongst the adults for ground liver continued to slacken. The eggs then generated in due time gave rise to

new adults, which led to a rapid increase in the adult population, and the resultant overcrowding caused virtual cessation of egg production. A new cycle of oscillation then began.
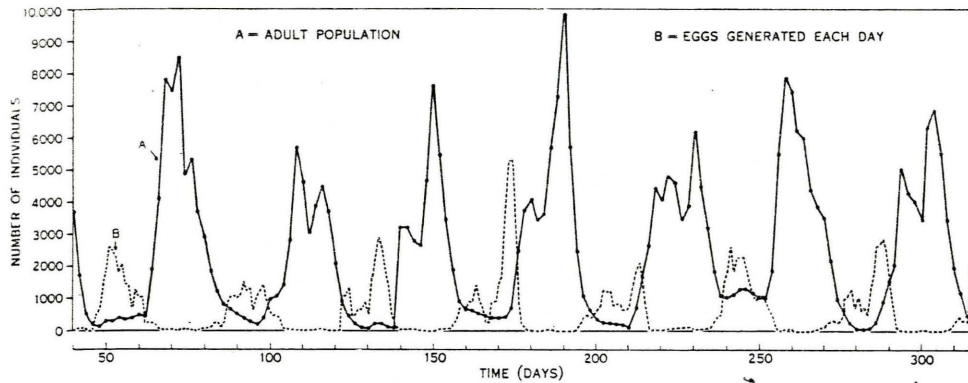

Fig. 3.—A population of *Lucilia cuprina* governed by the daily supply of 0.5 g of ground liver for the adults. *A* is the observed adult population; and in *B* the number of eggs generated each day is plotted at times 2 days before they were actually laid, this being the time taken in development after the intake of adequate food. (The lack of a clear inverse relation between the various low adult densities and the number of eggs produced is due to the fact that adults are mostly senile as the adult minima are approached, near the minima many are newly emerged and incapable of laying eggs, and subsequently highly fertile young individuals dominate.)

If increased acquisition of food were to cause fully mature adults to come into being immediately (instead of merely initiating the subsequent production of eggs and the still later development of adults) this prompt reaction would cause the system to be non-oscillatory. This is because reaction would cause the population first to approach, and then to maintain the *equilibrium density* of the species under the prevailing conditions, this being the density at which production of offspring precisely compensates for the loss of adults by death; for any departure from this level would immediately bring compensating reaction into play, and this would cease as soon as the equilibrium density was attained again. This, then, is the balancing mechanism which holds population density in general relation to the prevailing conditions; and the system of balance is often highly oscillatory, simply because animals commonly take a significant time to grow up, so causing a time lag between stimulus and reaction. During this lag period the stimulus continues to generate more and more reaction, and this continues to come into operation for a similar lag period after reaction has removed the stimulus.

If such violent oscillation as is shown in Figure 3 were observed in nature, one might well conclude either that there must be some periodic element in the environment underlying it or, alternatively (as the maxima are some hundreds of times as great as the minima) that population density is unrelated to the constant environmental conditions. However, not only do we know that there

was no external periodic influence under the conditions of culture, but also we have observed in detail the mechanism which causes the oscillation. As to the suspicion that the general density level has no relation to the environment, this is shown to be untrue by comparison with other experiments. The culture illustrated by Figure 3 was supplied with 0.5 g of ground liver per day and the average density of adults was found to be 2520. In another culture in which all conditions were precisely the same, except that only 0.1 g of liver was provided per day for the adults, the average density of adults was 527. Thus, in spite of the violence of the oscillations produced in both cultures, the average density was almost precisely proportional to the supply of the governing requisite.
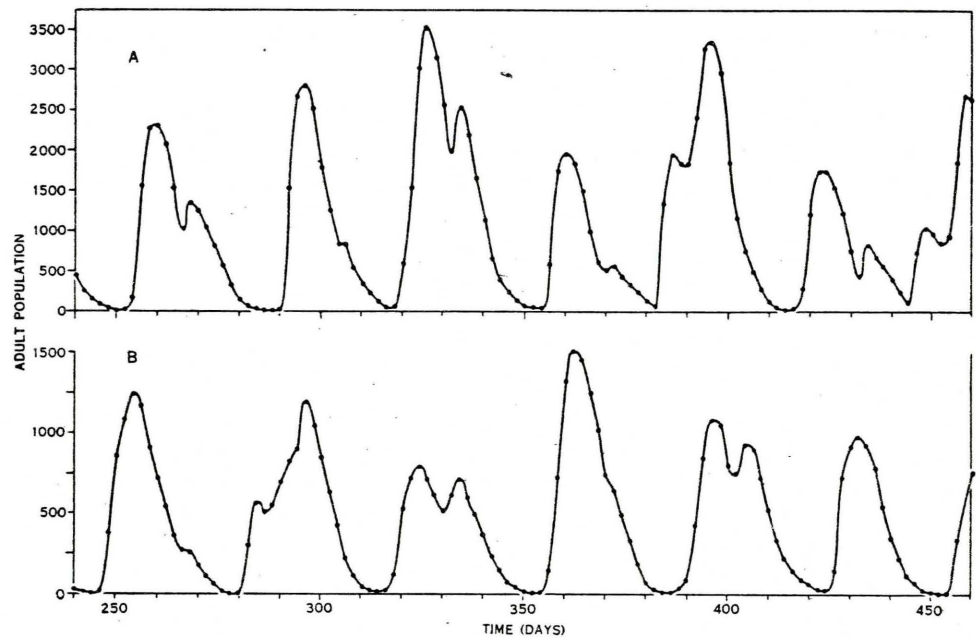
Fig. 4.—Adult populations of *Lucilia cuprina* governed by the supply of meat for the larvae— excess ground liver, water, and sugar being supplied for the adults. In A 50 g of larval food, and in B only 25 g, was supplied. Note that the vertical scale in A is only half that in B.

This point is further illustrated by Figure 4, but in these cultures (which were run concurrently), the adults always had excess ground liver available, whereas the daily supply of larval food was restricted to 50 g of meat in A and 25 g in B. To simplify comparison B has been drawn to double the vertical scale used in A. It will be seen that the form, violence, and period of the oscillations in the two cultures are essentially the same, and that the average density of B is approximately half that of A; that is to say, the average densities are proportional to the supply of larval food, which is the governing requisite.

These examples illustrate what is meant by the balance of populations (see Nicholson 1933). Some biologists have expressed the opinion that the term is

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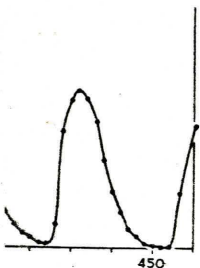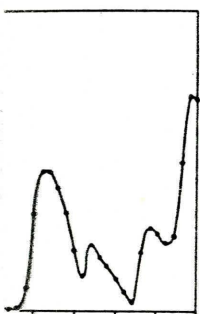ble the vertical
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inappropriate (e.g. Solomon 1949), but this appears to be due to an unjustified belief that "balance" and "equilibrium" are synonymous. The ordinary usage of the word "balance" implies controlled movement, or at least potential movement, about a position of true equilibrium. Think, for instance, about the balancing feats one sees on the stage or at a circus: always the mechanism is expertly controlled corrective movement which opposes each departure from the position of equilibrium. *Balance* refers to the state of a system capable of effective compensatory reaction to the disturbing forces which operate upon it, such reaction maintaining the system in being. It is the exceedingly important state of compensatory reaction upon which populations, in common with ships on stormy seas, depend for their continued existence.

(c) Automatic Adjustment to External Stresses

Not only can governing reaction hold populations in a state of balance at levels associated with the supply of a requisite, such as food, but within very wide limits it can adjust populations to withstand the effects of adverse environmental factors. Many experimental examples of this have been given elsewhere (Nicholson 1954). To illustrate the mechanism of compensation some details are given in Tables 1 and 2 of another pair of cultures. In these 50 g of meat were placed in each culture every day, both larvae and adults being dependent upon this. Thus the culture conditions were essentially the same as in the experiment described elsewhere (Nicholson 1950), the oscillations in A being similar to those there illustrated. In A there was no imposed destruction, whereas in B 50 per cent. of all adults present in the cage were destroyed every second day by bisecting the interior of the cage with a guillotine-like partition, and allowing the adults in one half of the cage to die. It will be seen that this resulted in the destruction of 79 per cent. ($100 \times 337/426$) of all adults produced (this exceeds 50 per cent. because many adults were exposed to destruction several times). However, not only was there this great destruction, but the age composition of adults was greatly altered—the population naturally consisting dominantly of young individuals. So, as adults do not begin to lay eggs until they are at least 2 days old, this destruction greatly reduced the mean birth-rate, in addition to shortening the mean adult life span (Table 2), and both these factors contributed to the reduction of the coefficient of fertility (that is, the number of offspring produced on the average by an individual during its lifetime, both males and females being included when calculating the average, just as with birth-rates). In spite of this great destruction of adults and reduction of fertility, the average population of adults was virtually the same in B as in A, in which there was no imposed destruction (Table 1).

Actually this reduction of the coefficient of fertility in B was part of the compensation for imposed destruction, for more adults had to exist in order to produce sufficient eggs to cause any given degree of larval competition. In addition, columns a and b in Table 1 show that further compensation was due to an increased rate of production of adults in B from the smaller number of

eggs laid, compared with A. This clearly was due to lessened larval competition, the mechanism being that illustrated in Figure 2.

TABLE 1

AVERAGES OF OBSERVED QUANTITIES IN TWO CULTURES OF *LUCILIA CUPRINA*, IN WHICH THE POPULATIONS WERE GOVERNED BY THE COMPETITION OF BOTH LARVAE AND ADULTS FOR 50 g OF MEAT SUPPLIED DAILY OVER PERIODS EXCEEDING 7 MONTHS

Situation	Larvae Hatched per Day a	Adults Emerged per Day b	Adults Destroyed per Day c	Natural Deaths of Adults per Day d	Mean Adult Population e
A—No imposed destruction	4287	220	0	220	1498
B—50% adults destroyed every second day	2248	426	337	88	1456

In all environments tolerable to a population, the position is automatically reached at which the number of individuals dying, whether from natural causes or imposed destruction, in any long period equals the number produced in the same period. That this actually happens is shown by the data in Table 1 (columns b, c, and d), and also in the tables given elsewhere (Nicholson 1954)

TABLE 2

CHARACTERISTICS OF THE POPULATIONS DERIVED FROM THE DATA IN TABLE 1, USING THE EQUATIONS AT THE TOP OF THE COLUMNS

Situation	Total Mortality Due to			Mean Adult Life Span $i = e/b$	Mean Birth-rate $j = a/e$	Mean Coefficient of Fertility $k = a/b = ij$
	Larval Competition $f = \dfrac{100(a-b)}{a}$	Imposed Destruction $g = \dfrac{100c}{a}$	Natural Deaths of Adults $h = \dfrac{100d}{a}$			
A	94·9%	0	5·1%	6·8	2·9	19·5
B	81·5%	14·7%	3·8%	3·4	1·6	5·4

concerning many populations of *L. cuprina* subject to greatly varying conditions, including heavy destruction and conditions which seriously affect birth-rate. The agreement between recorded average figures for natality and mortality is always very close. This at first sight seems surprising, having observed in many populations the violence of the oscillations which have their origin in great inequalities of natality and mortality; but it follows from first principles

that such agreement must exist in any population which neither increases nor decreases its general level over long periods.

It is evident from these considerations that imposed destruction (within the limits of tolerance of a population) does not add to mortality, except as an immediate and transient effect; for mortality due to reactive factors is correspondingly and automatically reduced until only the surplus of offspring is destroyed, just as it was before the new destructive factor operated. Thus Table 2 shows that the imposed destruction of 79 per cent. of adults led to a readjustment of mortality distribution such that this destruction became 14.7 per cent. of all individuals—place being made for this by a reduction of 13.4 per cent. in the mortality due to larval competition for food, and of 1.3 per cent. in that due to senility (see columns f and h, Table 2). The key effect of destruction in this example was the reduction of the birth-rate, due to the changed age composition of the adult population. Because of this the adult population in B, although approximately equal to that in A, produced only about half the number of eggs per day, so lessening larval competition and leading to a daily emergence of about twice as many adults as were produced in A. Although 79 per cent. of these were destroyed sooner or later by the imposed factor, they all contributed for a time to the adult population recorded; but this was not double that in A simply because the average life span of the individuals was reduced to half. In this example, then, compensation for destruction was partly due to a reactive change in fertility, and partly to reactive change in the intensity of competition which led to a modification of the mortality distribution (see Table 2), the total mortality remaining at 100 per cent., just as it was without any imposed destruction.

In the cultures (Nicholson 1954) in which different percentages of adults were destroyed at emergence, the imposed destruction naturally did not have any direct effect upon the age composition of the adult population. In cultures in which populations were limited by larval food, therefore, the necessary compensatory reduction of larval competition could only be produced by a reduction of the adult population, for the reproductive rate was independent of density, the adults always having excess food available. This is what happened, but it was found that the reduction of the adult population was far less than the percentage of imposed destruction—the destruction of 99 per cent. of the emerging adults, for example, causing a reduction of the average adult population to about one-tenth, instead of to one-hundredth, of the population free from imposed destruction. This was because the lessened larval competition (due to the reduction of the adult population, and so also of the number of eggs laid) caused far more individuals to reach the pupal stage, as is strikingly illustrated by Figure 5.

On the other hand, in another series of cultures (identical to the foregoing except that adult food, instead of larval food, was the governing requisite) compensation was produced wholly by reactive changes in fertility. Without imposed destruction, adult competition for the limited supply of ground liver adjusted the fertility coefficient at 1.1. The coefficient of fertility was not

unity in this instance simply because there was a mortality, due to unknown causes, of about 8 per cent. amongst developing individuals, which was apparently independent of density. With increasing percentages of destruction of the emerging adults, this coefficient increased correspondingly, being, for example, 10.8 with 90 per cent. destruction. Such compensation is due to the fact that destruction reduces the number of adults surviving and so lessens the competition amongst them. Consequently, as the adults individually obtain more ground liver, on the average, than before, they lay more eggs; and governing reaction causes the adult population always to tend towards the level at which just sufficient surplus eggs are laid to compensate for the imposed destruction. As in the previous examples, the reduction of the population was not proportional to imposed destruction—90 per cent. destruction, for example, only reducing the adult population to about one-third.
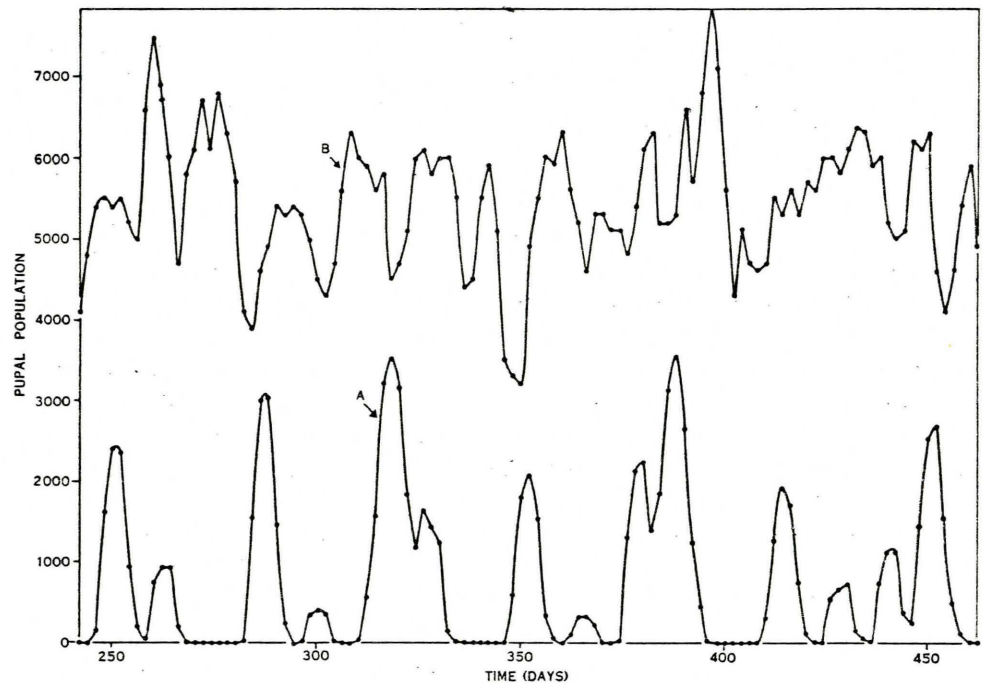
Fig. 5.—A, the population of viable pupae in the same *L. cuprina* culture as *A* in Figure 4; *B*, the population of viable pupae in a concurrent culture similar in all respects to *A* except that 99 per cent. of the adults emerging each day were destroyed.

The foregoing examples show that populations can adjust themselves to even very heavy destruction, and that such destruction induces reaction which always tends to counter its direct effects. This it does by increasing the density of the age-group immediately preceding the one subject to destruction, and this in turn induces further reactions which either increase or decrease the densities of other age-groups, according to the circumstances. This is in conformity

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with conclusions reached elsewhere (Nicholson 1933, C.9* and C.18; Nicholson and Bailey 1935, C.16, C.17, C.18, C.31, and C.32) concerning the effect of introducing a new destructive factor (possibly another species of parasite) when the density of the host species is governed by specific parasites.

Populations not only adjust themselves to destructive factors, but also to any other change in the favourability of the environment—provided this does not exceed the generally very wide limits of tolerance of the species. Thus in a series of cultures governed by larval food supply, the average life span of the adults was made different by supplying each culture with an excess of a sugar solution at a concentration differing from those of the solutions used in the others. Sugar has an important effect upon the longevity of adults (at least in crowded cultures) and the sugar intake of the adults was limited by their capacity to take up liquid. The life span was found to decrease markedly with reduction in the concentration of the solutions. The effects were similar to those produced when the adult life span was shortened by direct destruction (see Table 1)—the adult population increasing a little, and the rate of emergence of adults increasing considerably, as the sugar content of the solutions and the life span of the adults decreased.

In another experiment, in which larval food was the governing requisite, the adults were given a poor oviposition site. This reduced the birth-rate to about one-third, and the consequent reduction of larval competition raised the adult population to 1667, compared with 1252 in an otherwise similar culture in which the oviposition site was good.

(d) Complementary Governing Factors

When new responsive factors are introduced they strongly tend either to displace the original governing factors, reducing these to the status of purely legislative factors, or to operate themselves as purely legislative factors. The new and old responsive factors can operate together as *complementary governing factors* only if each produces a significant effect upon the population when responding to the same density change. That is to say, both factors must react significantly to a similar range of densities.

This is very clearly illustrated by the series of population experiments with *L. cuprina* already referred to. The readily controllable variables were the supply of food for the larvae, and of ground liver, water, and sugar for the adults. In most of the experiments one of these depletable materials was selected as the governing requisite, and it was supplied at a constant rate sufficient to maintain a population within the capacity of the breeding cage. The others were supplied in excess of the requirements of the insects at all times, and so were purely legislative factors; for, although most noticeably responsive

* The words "lower" and "higher" are incorrectly placed in Conclusion 9, as the arguments accompanying it show. C.9 should read "According to whether a destructive environmental factor operates before, after, or at the same time as a given parasite species, both the initial and final steady densities of the host species are respectively higher than, lower than, or the same as they would be if the parasites were alone responsible for destroying the surplus hosts."
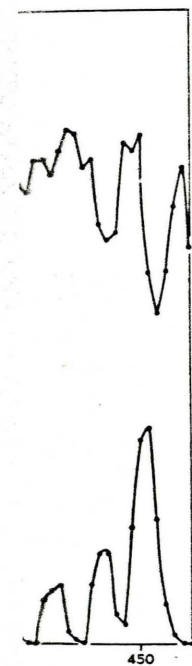
to density, the variation in the amount remaining unused had no significant effect upon the competing individuals, being always in excess of requirements.

In a few experiments the supply of each of two of these requisites was so adjusted to that of the other that there was significant depletion of both at the same general level of population, and so each played a governing role. For example, as it appeared that at the average density of a population governed by a daily supply of 50 g of larval food the adults needed only about 0.5 g of sugar, only this quantity of sugar was supplied per day, ground liver and water being maintained in excess—whereas all three adult requisites were in excess in the control culture. The experimental and control cultures were each supplied with 50 g of larval food per day. The average population level was very little affected by the reduction in the sugar supply, but reaction was more efficient, for the peaks of the oscillations were greatly reduced owing to the much shortened life span of the adults (due to sugar deficiency) when the population exceeded the average level. In another example (Nicholson 1954) the daily supply of ground liver for the adults was limited to 1 g, sugar and water being provided in excess, and the larval food was supplied at 50 g per day. The consequent great increase in adult competition and the resultant great reduction in oviposition (and so also in larval competition) increased the average adult population to 4042, compared with 1252 in an otherwise similar culture in which unlimited ground liver was supplied to the adults.

In another experiment new density governing destruction was imposed by destroying all but five of the emerging individuals each day—which naturally means that the percentage destroyed increased with density. Although this reduced the adult population from 1252 to 63, it increased the daily emergence of adults from 157 to 774. This evidently approaches a limiting situation, however, for only 33.7 per cent. of the pre-imaginal individuals died, and there is reason to believe that the coefficient of fertility, which proved to be 233.5, is near the extreme capacity of *L. cuprina*. That is to say, competition was reduced to very low levels in both the larval and adult populations. Therefore, if the permitted emergence of flies were reduced further, there could be little compensatory reaction; and so the population size of all age-groups would then tend to be directly proportional to the number of flies permitted to emerge. This shows how a new reactive factor may completely take over governing functions from another.

(e) General Implications of Experimental Results

It is thus seen that whenever a population is subjected to adverse factors which either increase the chance of destruction of the animals or interfere with their production of offspring, reaction causes a relaxation of the intensity of competition and by so doing it compensates for the disturbing effects of such factors. When the governing requisite is food such relaxation of competition reduces the wastage of matter taken up by the population; for with adults a greater proportion is used for the production of offspring, and with larvae less is used up by larvae which obtain quantities inadequate to enable them to

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reach maturity. Population density is therefore not simply a function of the available amount of food, or even of the amount of food some other kind of governing factor permits the population to use, but is markedly influenced by the wastage of food commonly caused by competition; and it is competition for some limiting depletable requisite which regulates density by determining how much food a population is permitted to use and how much of this it wastes.

In brief, governing reaction does not merely operate to oppose any departures of a population from its equilibrium density, but also enables populations to adjust themselves to withstand very great environmental stresses (particularly when their inherent reproductive capacity is high), and to maintain themselves in a state of balance under widely different environmental conditions. Moreover, the reduction in density which adverse factors produce as a primary effect is always opposed by compensatory reaction, being lessened, or even converted into an increase in density, when the population adjusts itself to the continued operation of the adverse factor.

IV. Theoretical Consideration of Population Regulation in Simple Situations

It has now been shown that populations of one particular type, exemplified by those of *L. cuprina*, both react to the environment and cause reactions in the environment in such a way that their densities are automatically adjusted in relation to the prevailing conditions. As will shortly be shown, however, there are many other kinds of population systems; so, very briefly, we will consider their known characteristics in order to determine whether populations of other kinds can also reach a state of balance with their environments. But first it is necessary to define certain important properties of animals and of their environments which have an important bearing upon this problem.

An individual animal clearly has only a limited field of action. The size of this is determined partly by properties of the species and partly by properties of the particular requisite concerned—such properties as the rate of movement of the animals, the distance at which they can perceive the presence of the requisite, their efficiency in obtaining this requisite when perceived, the conspicuousness or concealment of the requisite, protective qualities which oppose destruction by the animals, and movement of the requisite sought which influences the likelihood of contact with, or escape from, the animals. The joint effects of such properties upon the efficiency of animals in obtaining a particular requisite can be allowed for by defining the *procurement field* of the species, for the given requisite under the given conditions, as the maximum amount of space an average individual can exhaust of the given requisite in unit time when there are no new accessions of the requisite to the environment. When, as is generally assumed in the following discussions, the requisite is generated continuously, exhaustion clearly does not occur; but, when stimulated to their maximum efforts by scarcity of the requisite, the animals explore their procurement fields effectively, either by moving about or reaching out to obtain the requisite or, alternatively, by making use of movement which

brings particles of the requisite into their ambit. Thus the procurement field is a measure of the maximum effective field of action of an average individual in a unit of time, and so of the intrinsic efficiency of animals in satisfying a particular need under prevailing conditions. The "area of discovery" (Nicholson 1933; Nicholson and Bailey 1935) of an entomophagous parasite is its procurement field measured as the area effectively explored by an individual during its lifetime.

For the existence of a species it is clearly necessary that there should be a sufficient quantity of each requisite in the space of the appropriate procurement field to supply at least the minimum needs of an individual. This minimum tolerable quantity is the *maintenance quantum* of the given requisite for the species living under the prevailing conditions. When this quantity is available to an average individual, it is just sufficient to maintain the individuals and permit them to produce sufficient offspring to replace those that die. It is influenced, not only by the needs of the animals and the qualities of the given requisite, but also by the abundance and qualities of the other requisites present. This is because the use of these requisites may influence the metabolic processes of the animals and so alter the amount of the given requisite needed. Although its value is so influenced, the maintenance quantum is an important requirement of individuals of a given species which can be specified quantitatively under any given set of conditions.

It should be noted that the word "quantum" is here used in its ordinary sense of "required or desired or allowed amount; as much as suffices" (O.E.D.). The idea of invariability associated with this word by physicists must not be transferred to the word in its present context. On the contrary, it must be recognized not only that its value varies with environmental conditions, but also that its value represents an average of the varied amounts of the given requisite obtained by different individuals in unit time when living under equilibrium conditions.

Requisites of a species which are continuously generated do not accumulate indefinitely in the absence of this species; for accumulation is always opposed by a process of attrition, due to such things as the action of other animals, deterioration caused by physical factors, or decay. Accumulation is arrested when the intensity of attrition counterbalances that of generation. If this limited accumulation of a requisite is such that there is less than the maintenance quantum in the procurement field of the given species, this species clearly cannot maintain itself in the given environment; but if it is such that there is exactly the maintenance quantum in the space of the procurement field, the species is just barely able to exist at an indefinitely low density—for any higher density would augment the attrition, so reducing the amount in a procurement field below the maintenance quantum. This minimum density of the requisite which will permit a species to persist is the *threshold density* of the given requisite for the species under prevailing conditions.

If accumulation of a requisite in the absence of the given species exceeds the threshold density, the introduction of this species will be followed by popu-

lation growth, for the animals at first obtain more than their maintenance quanta. By so doing they deplete the requisite until, when it reaches the threshold density, further growth becomes impossible, provided that reaction takes effect immediately. But if, as commonly happens, there is some delay before reaction affects the population, growth continues for a time, so reducing the requisite below its threshold density, and this in turn inevitably causes a subsequent decrease in the population, as has already been shown in the experiments with *L. cuprina*. Thus reaction causes the requisite and the population to approach, or to oscillate about, their respective *equilibrium densities*—that of the requisite being the threshold density under the prevailing conditions, and that of the population being the density at which the animals use the requisite at the rate it becomes available.

For convenience in the discussion which follows of relatively simple situations, it will be assumed that some property of only one requisite functions as a governing factor in each. This seems likely to be generally true, for, as the rate of production of each requisite is commonly purely a property of the environment, it is improbable that two or more requisites should be produced by chance at such relative rates that they are depleted to near their threshold densities by the same density of animals. So, at equilibrium, all requisites are likely to remain in excess, except the one which is first reduced to its threshold density by a growing population; for no matter how abundant the other requisites may remain, the limiting effect of this one requisite prevents the maintenance of any higher density.

(a) Populations at Equilibrium

Initially attention will be confined to populations which consist of individuals which all have the same requirements and live in constant environments —the offspring, and also the governing requisite, being generated continuously at a constant rate. That is to say, we shall confine attention to very simple animals, such as certain protozoa which do not change their properties as they grow, and, when more complex animals are considered, we shall make the reasonable assumption that the governing factor affects only one developmental stage or age-group, such as the larvae, or the adults.

For equilibrium of the animals, an average individual must obtain its maintenance quantum of the governing requisite in unit time. This is possible only if the equilibrium density (G_E) of the governing requisite is such that there is one maintenance quantum (q) in the procurement field (i) of an individual. So

$$G_E = q/i. \quad .. \quad .. \quad .. \quad .. \quad (1)$$

It is necessary for equilibrium of the governing requisite that it should be used at the rate it is generated, in order to prevent its subsequent accumulation or depletion. Commonly a fraction (l) of this requisite is lost to the population, being destroyed by competitive factors; so for equilibrium the amount (lg) of the governing requisite destroyed by these factors, together with the amount ($N_E q$) used by the animals, must equal the amount (g) of the govern-

ing requisite generated in unit time. So $lg + N_E q = g$, and therefore the equilibrium density (N_E) of the animals is

$$N_E = (g - lg)/q. \qquad .. \qquad .. \qquad .. \quad (2)$$

It is implicit in equations (**1**) and (**2**) that there is no induced mortality, and that depletion of the governing requisite has reduced the reproduction of the animals to the replacement rate. It often happens, however, (as with L. cuprina) that animals reproduce at more than the replacement rate even at equilibrium, the surplus offspring produced being destroyed before they can themselves reproduce. These surplus individuals waste a fraction (w) of the governing requisite, in the sense that this fraction is rendered unavailable to those individuals which maintain the population by maturing and reproducing. The effect of this upon the equilibrium density (N_E) of mature animals is clearly

$$N_E = (g - lg - wg)/q. .. \qquad .. \qquad .. \quad (3)$$

As the amount of the requisite so wasted tends to vary directly with the magnitude of the surplus of individuals produced, the greater the reproductive rate the lower tends to be the density of animals permitted to mature.

When predators have prey as the governing requisite they tend to limit this to the threshold density, which is also the equilibrium density of the requisite (G_E), as do animals of any other kind. By so doing they limit the rate of generation (g) of the prey to bG_E at equilibrium, where b is the birthrate of the prey. This in turn limits the density (N_E) of the predators, for equation (**2**) becomes

$$N_E = (b - lb)G_E/q. \qquad .. \qquad .. \qquad .. \quad (4)$$

It is clear from equation (**4**) that the predator density (N_E) is independent of the number of prey individuals required for the maintenance and replacement of the predator individuals, for the value of G_E is proportional to that of q (see equation (**1**)).

Substituting q/i for G_E (equation (**1**)), equation (**4**) becomes

$$N_E = (b - lb)/i, \qquad .. \qquad .. \qquad .. \quad (5)$$

which shows that the greater the efficiency (i) of the predators, the lower is their density. That is to say, the predators reduce the rate of generation of their prey to meet their minimum needs, which are satisfied by a low density (G_E) of prey when their procurement fields (i) are large, and in consequence their own density (N_E) is correspondingly low, being limited to that which can be supported by this low density of prey.

It will be noted that equations (**4**) and (**5**) are simply interpretations of equation (**2**). Even without such interpretation equation (**2**) represents the necessary conditions for the equilibrium of natural enemies; but as the rate of generation (g) of the governing requisite (the prey) is a function of the birthrate and of the density of the prey, and as the latter is also a function of the efficiency of the enemies, terms representing these properties are included in

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expressions which define *g*, and these are substituted for *g* in equation (**2**). This permits the components of *g* to be studied and their separate influences upon population density to be determined in this situation. Examination of other situations lacking the extreme simplicity of those described directly by equations (**1**), (**2**), and (**3**) has indicated that any equilibrium situation can similarly be represented by substituting for one or more of the original terms in these basic equations expressions and new terms which define the original terms.

When the animals considered constitute the governing requisite of natural enemies, equation (**1**) shows that their equilibrium density (G_E) is determined by the properties *q* and *i* of these enemies; and when the animals govern themselves by inducing reactions in a governing requisite, equations (**2**) and (**3**) show that their equilibrium density (N_E) is determined by the values of *g* and *l* (which primarily represent properties of the environment) and those of *q* and *w* (which represent intrinsic properties). Thus *g, l, q, w,* and *i* are the *primary parameters of population density,* for it has been found that the influence of any other significant factor upon equilibrium density can be represented in the basic equations (**1**), (**2**), and (**3**) by the change it produces in the value of one or more of these parameters, or by the substitution of interpretative expressions or terms, as in equations (**4**) and (**5**). A more detailed analysis along these lines will be published later.

(*b*) Population Growth and Maintenance in Simple Situations

Attention is restricted in this section to populations limited by the reaction of one requisite only, and living in environments which remain constant except in so far as they are influenced by the actions of the animals.

In an environment which remains constantly favourable a population grows unchecked, the population density (N) increasing in time *t* to $Ne^{(b-d)t}$, the rate of growth at any moment being

$$dN/dt = (b-d)N. \quad .. \quad .. \quad .. \quad (6)$$

Here e is the base for natural logarithms, and the coefficients of birth and death (*b* and *d*) have values appropriate to the stable age distribution which occurs in any population multiplying without check (Lotka 1925), and so equation (**6**) is true whether the animals are born virtually mature or take an appreciable time to develop to maturity.

However, the environment of a growing population cannot remain constantly favourable indefinitely, for animals progressively deplete some of the things essential for their existence, so ultimately lowering the favourability of the environment to the limit of tolerance. Inevitably it is such environmental reaction to density which limits populations, for animals can exist only when the environment is favourable, and their populations then grow until at least one requisite is reduced to the threshold of favourability, when further growth is impossible. Such reaction of the environment which opposes density change

impresses different patterns of population growth and maintenance according to the kind of reaction and the qualities of the reacting requisite, as shown in the accompanying chart (Fig. 6). A primary division is made into *density triggered reaction,* i.e. reaction to density change which remains negligible until the population reaches some critical density, when opposing reaction operates with great violence; and into *density conditioned reaction,* i.e. opposing reaction which progressively increases in intensity with density. The latter is further subdivided in the way shown in Figure 6.

These categories of reaction will be dealt with in turn, subdivisions being made within each according to certain qualities of the reactive requisites. *Persistent requisites* are those which are not expended when used, and invariably consist of some form of favourable space which becomes available again
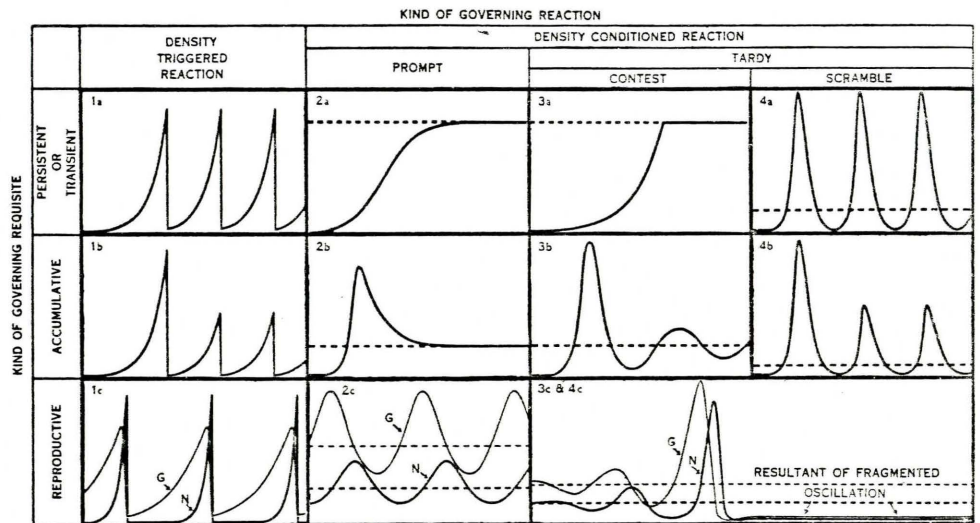
Fig. 6.—These graphs illustrate what are considered to be the characteristic (but not invariable) patterns of population change in the situations indicated. In categories 3 and 4 they represent the densities of mature animals alone. The horizontal broken lines represent the equilibrium densities of the organisms. *N* indicates populations of natural enemies, and *G* those of prey (the governing requisite).

when vacated. *Transient requisites* disappear quickly if not used, and so cannot accumulate; the best example is sunlight — a dominantly important, though transient, requisite for most plants. *Accumulative requisites* when unused remain in the environment for a significant period before disappearing. *Reproductive requisites* do not merely accumulate but multiply when unused. Surprisingly, persistent and transient requisites give rise to the same patterns of population change. This is because a transient requisite (such as a food material which rapidly becomes unavailable if not used promptly) can be regarded simply as a quality of favourable space. It is a quality which determines the population density the space can support, for there is neither accu-

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mulation nor multiplication of the requisite to influence this capacity in relation to the recent past history of the animals and their environments.

The classification of basic population systems used in the chart (Fig. 6) is by no means the only possible one, but it is used to illustrate the effects produced by those factors which appear to dominate population regulation. Naturally other factors may influence these patterns, which are described only in their simplest form. Moreover, the systems tend to intergrade, and sometimes population regulation combines the features of more than one of them.
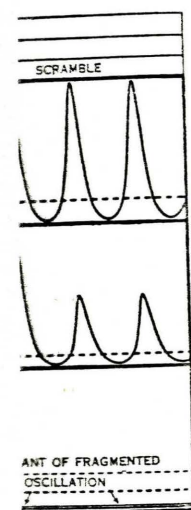
(i) *Density Triggered Reaction.*—It may happen that a population is permitted to grow unchecked until it reaches some critical density at which violent opposing reaction is triggered, so reducing the population to a very low level. The low density of the population then causes reaction to be relaxed, so once more permitting unchecked growth. Such *relaxation oscillation* is thus described by equation (6) if a limit is placed to the permissible value of *N*, and a term is introduced representing the population reduction which takes place whenever this limit is reached. Because of the stable age distribution which occurs in populations when multiplying unchecked, the lag due to the time spent in development by higher animals does not influence the character of relaxation oscillations, except possibly for a short time after the minima.

Relaxation oscillation appears unusual amongst animals and it is doubtful if it ever occurs in the simple form described, for generally conditioned governing reaction plays a part during some phases of growth at least. This is certainly true of the best known examples, namely plague locusts and lemmings. However, these frequently multiply with little check until they reach the critical density at which the majority of individuals migrate in mass away from the favourable regions in which they have developed. Here the requisite is favourable space, and reaction is triggered when it becomes critically crowded and so unfavourable. The consequent relaxation oscillations are represented schematically by 1*a* in Figure 6.

When animals invade a favourable environment in which an expendable requisite has accumulated, they tend strongly to multiply without check until virtually all of this requisite has been removed, when the population necessarily crashes. The requisite then begins to accumulate again, so permitting the population later to multiply from the low level to which it was reduced, so producing a succession of relaxation oscillations which may be expected to be smaller than the initial one produced in the previously uninhabited environment (1*b* in Fig. 6). However, density conditioned governing reaction generally plays some part, at least in the region of the maxima, so causing an approximation to some one of the other *b* systems in the chart.

Relaxation reaction may be produced at times by interaction between two kinds of organisms. For example, certain kinds of moths commonly appear to multiply without check until, when their caterpillars are excessively abundant, there is a devastating outbreak of bacterial disease, which apparently could not make headway previously because of inability to spread in less dense popula-

tions. Assuming this explanation, the course of events is shown schematically in 1c (Fig. 6), G representing the victim species and N the disease organism.

(ii) *Prompt Density Conditioned Reaction.*—In its simplest form this is described by the Verhulst-Pearl logistic equation (Pearl 1926), which in its differential form (Gause 1934) is

$$dN/dt = N (K - N)b/K, \qquad .. \qquad .. \qquad (7)$$

where K is the capacity of the environment in units representing places for individual organisms, and b is the coefficient of multiplication of the organisms when free from any effects of crowding.

Extreme promptness of reaction is represented by this equation. Thus, not only are the organisms assumed to multiply at a rate proportional to the still unused fraction $((K - N)/K)$ of the environmental capacity remaining *at that moment,* but the organisms exercise their full influence upon interaction *from the moment they are born*—for the rate of population change is a function of N, differences of properties associated with the ages of individuals being neglected. The main reason for giving further consideration to such remarkable hypothetical organisms is that they have been used to represent animals in some well-known theories of population dynamics which need to be placed in true perspective. However, such considerations may have some bearing upon the dynamics of simple microorganisms which multiply by binary fission, for these have properties approximating to those of the hypothetical organisms; and in addition, they reveal the characteristics of certain fundamental types of interaction when uncomplicated by the effects of developmental lag.

A primary assumption in the logistic equation is that there is a fixed capacity (K) of the environment for organisms of the given kind, such that when these organisms have multiplied to their limit they subsequently remain constantly at their maximum density. It should be particularly noted that this is a postulate in the equation, and not a conclusion. Clearly, therefore, the governing requisite is favourable space, for no other kind of requisite can be used up to a limiting degree and yet retained for use by the organisms. The capacity may, however, be determined by some transient requisite (such as sunlight required by simple algae) which, being continuously generated, gives a constant favourable quality to the space. The situation is that represented by 2a in Figure 6.

Another primary assumption is that the rate of multiplication of the organisms at any moment is proportional to $(K - N)/K$, that is to the fraction of favourable space remaining unutilized at that moment. This means that the logistic equation can apply only to special situations in which the rate of population growth is Nb when N is indefinitely small, and is less than this when N increases even slightly. This is an untenable assumption unless application of the logistic equation is expressly restricted to such situations; for it implies that the values of b and K have a particular relation, whereas b and K are determined by independent factors and so may have any relative values according

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to the circumstances. This simplifying assumption was presumably adopted to avoid discontinuity in the equation; for if K exceeds the density at which the organisms can barely find all they need to multiply at the maximum rate permitted by their intrinsic properties (represented by b) they will multiply exponentially (equation (6)) until such time as the favourability of space becomes sufficiently reduced to slow down the rate of multiplication.

It is clear from equation (7) that, as b/K is a constant, the assumption has been made that the rate of population change is proportional to the product of N and $K - N$. This shows that N and $K - N$ are not mere numbers, but densities, for it is reasonable to expect the number of contacts promoting multiplication to vary directly with the number of organisms (N) per unit volume and the quantity ($K - N$) of unutilized favourable space per unit volume. On the other hand, with the same number of organisms of a given kind and the same quantity of unutilized favourable space in environments of different sizes, the number of contacts in unit time would inevitably be greater in the smaller environments than in the larger ones.

Because of the postulated relation between the values of b and K already referred to, b/K in the logistic equation represents the fraction of the available space effectively explored by an individual organism in unit time. Consequently, we may put $b/K = i$, i being the *coefficient of interaction*, defined as the procurement field of the organisms measured in the small unit of time used when defining rates of population change. Like b/K, i is a constant, being unaffected by population change.

The logistic equation (7) may therefore be rewritten in the notation adopted here as

$$dN/dt = iNG, \qquad \qquad \qquad (8)$$

for the quantity ($K - N$) of unutilized favourable space per unit volume is the density (G) of the governing requisite.

However, unlike equation (7), this equation does not show the dependence of the number of "still vacant places" upon N; but, as any increase in N causes a corresponding decrease in G, this is shown by

$$dG/dt = - iNG. \qquad \qquad \qquad (9)$$

As the sum of N and G is always the same (K), the greatest rate of change must take place when $N = G$, i.e. when $N = K/2$. With progressive departure of N and G from equality, the rate of change asymptotically approaches zero, so leading to a symmetrical and sigmoid growth curve ($2a$ in Fig. 6).

However, only when the density of animals reaches the level at which there is significant interference between individuals (that is, when iNG is not greater than bN) do equations (7), (8), and (9) begin to apply; but as this generally happens when N is far below $K/2$, the form of the growth curve is but little affected by this factor.

When the governing requisite of the hypothetical organisms is something, such as food, which is expended when used, the population change during any

given moment is equivalent to the amount of the requisite obtained less the amount used for maintenance during that moment.   That is,

$$dN/dt = iNG - qN, \qquad .. \qquad .. \qquad .. \quad (10)$$

where the density (G) of the requisite is expressed in unit quantities each sufficient to produce an additional organism when obtained by an individual which has already satisfied its maintenance requirements, and the maintenance coefficient (q) is expressed in the same units and represents the maintenance quantum of the requisite in a very small unit of time.   Similarly, assuming a constant rate of generation (g) of the governing requisite (also expressed in the same units) the change in density of the requisite during the given moment is equal to the amount produced less the amount used by the organisms.   That is,

$$dG/dt = g - iNG. \qquad .. \qquad .. \qquad .. \quad (11)$$

To make a first approximation to real situations it is necessary to introduce a term into equations (10) and (11) (as with the logistic equation) to represent exponential growth at population densities below the level at which effects of crowding are significant, and also a term to represent the average time of natural persistence of unused particles of the requisite.   The graph 2b in Figure 6 was calculated using equations embodying these corrections, but its general form can readily be accounted for verbally.   Equilibrium is clearly attained when the amount of the requisite used purely for maintenance equals the amount generated, that is, when $qN = g$; but in a previously unoccupied environment there is considerable accumulation of the durable requisite, so initially a growing population greatly overshoots the equilibrium density by using up this accumulation.   Subsequently it falls towards it, owing to the depletion of the requisite, either asymptotically or, under certain circumstances, it may execute damped oscillations about this level.   Growth approximates the form of the logistic curve only near the limiting situations in which accumulation of the requisite in the absence of organisms is barely above the threshold level for the population (so restricting population density to negligible proportions), or in which the persistence of the requisite is so short that it is virtually transient, so that competition is dominantly for favourable space, as in equations (8) and (9).

Organisms (such as yeasts) which enter a resting state when the environment approaches the limit of favourability often maintain for long periods the maximum population attained by using up an accumulated durable requisite; but it is illogical to argue from the experimental demonstration of such prolonged existence in a quiescent state (Pearl 1926; Gause 1934) that normal active animals should also maintain constant populations when they reach their maxima.

To examine the interaction of organisms with requisites which reproduce, we will assume that these consist of similar hypothetical organisms; that when a predator (having already satisfied its full maintenance requirements) con-

tacts n prey organisms it undergoes fission, so producing one additional organism; and that the prey has a coefficient of multiplication b. Expressing G and q as numbers of prey (the governing requisite), equations (**10**) and (**11**) then become

$$dN/dt = (iNG - qN)/n, \qquad .. \qquad .. \qquad .. \quad (\mathbf{12})$$
$$dG/dt = bG - iNG. \qquad .. \qquad .. \qquad .. \quad (\mathbf{13})$$

These equations show that for equilibrium $iG = q$, and $b = iN$; so that $G_E = q/i$, and $N_E = b/i$.

Equation (**12**) shows that when G exceeds this equilibrium value the number of prey eaten exceeds the number used in maintenance, and so N must rise; and if it is below this value N must fall. Similarly equation (**13**) shows that if N is above or below its equilibrium value G must respectively fall or rise. Thus when the changing population of either one of the animals passes from above to below its equilibrium value, or vice versa, this reverses the direction of change induced in the other population. Thus a system of *coupled oscillation* is produced ($2c$ in Fig. 6), oscillation being due to a linkage between the two changing populations, and not to the operation of lag reactions. In the simple situation examined, the oscillations are found to be sustained at a constant amplitude dependent upon the degree of initial displacement of density.

In form (but not in all the factors involved) equations (**12**) and (**13**) are identical with the basic equations of predator-prey interaction independently developed by Lotka (1925) and Volterra (1931). The assumption of immediate reaction limits even approximate application of the Lotka-Volterra equations to the simplest microorganisms. Their failure to allow for the use of some of the prey for the maintenance of the predators surprisingly does not lead to results differing in character from those derivable from equations (**12**) and (**13**). This is because a coefficient of predator death is used in place of q (equation (**12**)), which also represents an expenditure of material proportional to predator density—but the assumption of a constant inherent death rate is inadmissible when applied to microorganisms which multiply by fission. It is the neglect of the inevitable change in age composition as populations increase and decrease which limits even the approximate application of the Lotka-Volterra equations (and also of equations (**12**) and (**13**)) to exceptionally simple microorganisms, for individuals of these alone amongst animals undergo no important change in properties with age.

Gause (1934), using cultures of *Paramecium* feeding on yeasts, obtained oscillations closely corresponding to the Lotka-Volterra equations. On the other hand, when he used *Didinium* as predator and *Paramecium* as prey, his cultures quickly came to an end, due to the complete destruction of the prey. His figures clearly show that this was due to the unjustifiably small size of the microcosms he used (0.5 ml of liquid medium); for the introduction of only three individuals of *Didinium* into a rapidly growing culture of *Paramecium* was followed immediately by a steep fall in the numbers of the latter, so clearly

showing that even three *Didinium* in 0.5 ml of medium must be far above the equilibrium density of this predator. Consequently, cultures of *Didinium* in such minute microcosms would be required to be represented by fractions of an individual as the minima were approached, in order to conform with the equations. That is to say, these experiments did not conform to the conditions necessary for the equations to apply, for these equations represent the statistical effects of the interaction of large numbers of individuals operating in adequate space. Unlike equations (**12**) and (**13**), the Lotka-Volterra equations do not explicitly present space as an essential parameter. The fact that it is implicit to them appears to have been overlooked by Gause when designing his experiments. As to the experiments using much larger microcosms (to which Gause makes passing reference) it would appear that these were initially loaded with such a high density of organisms that vast numbers of *Didinium* individuals, supported by the prey they had already eaten, were still present when *Paramecium* was reduced to a low density, so leading to the complete elimination of *Paramecium*. The result might have been very different had the initial densities of the organisms been low or the available space much greater.

On the basis of these experiments Gause (1934, p. 128) concluded that "in *Paramecium* and *Didinium* the periodic oscillations in the numbers of the predators and of the prey are not a property of the predator-prey interaction itself, as the mathematicians suspected, but apparently occur as a result of constant interferences from without in the development of this interaction." This holds only for the minute microcosms he used. On present evidence it would appear that it was not the mathematics but the experiments which were at fault, for these did not reproduce the conditions postulated in the Lotka-Volterra equations. Gause's experiments with *Paramecium* feeding on yeasts apparently did reproduce these conditions and gave results broadly consistent with the mathematical expectation.

(iii) *Tardy Density Conditioned Reaction (Contest)*.—Some time always elapses between the event which leads to the birth of an animal and the beginning of significant competition by that animal with other individuals for the necessities of life, this being most marked with the higher animals. It is generally difficult to represent such developmental lag in sufficiently precise terms for mathematical examination, but its effects can be deduced readily by verbal argument, and by the study of experimental and natural populations.

Initially we will confine attention to animals exhibiting developmental lag which *contest* for their requisites; that is to say, an individual either obtains as much of the governing requisite as it needs for survival and reproduction or, being unsuccessful, relinquishes the requisite to its successful competitors. Thus with contest all of the governing requisite collectively secured by animals is used effectively in maintaining the population.

If the requisite consists of a fixed quantity of available space, the situation is most easily represented by plants competing for sunlit space. When a plant species invades a new and favourable area, population growth is at first exponential, the population consisting dominantly of young individuals. By the time

crowding significantly impedes further population increase, the number of indi-
viduals greatly exceeds the number of mature plants the space can accommo-
date, for the space requirements of young plants are small. Subsequently there
is a fall in density as the more powerful, or more fortunate, maturing individuals
displace their neighbours, until equilibrium is reached when the only space
available to young individuals is that vacated by the dead. Thus the growth
pattern of the total population should resemble graph 2b (Fig. 6), whereas
that of mature individuals is represented schematically by graph 3a, for their
density progressively increases with little check until they completely fill the
available space. Populations of animals with sessile or territorial habits may
have similar growth patterns.

If the requisite consists of expendable but durable objects these, being
generated at a constant rate, inevitably accumulate in an unoccupied region, so
leading to an exceptionally high density of animals shortly after introduction.
Subsequently reactive changes in the density of the requisite, always tend to
cause the population to approach its equilibrium density; but, as the effects
of this reaction always lag for the time taken in development, density change
is not arrested when this level is reached, but continues beyond it, thus leading
to *lag oscillation* (3b in Fig. 6). This situation is of doubtful importance, for
animals seldom contest for non-persistent objects other than prey.

Volterra (1931) discussed the effects of substituting lag reactions ("actions
héréditaires") for the immediate reactions assumed in the basic part of his study
of the interaction of predators and prey, but the biological meaning of his
conclusions is obscure. He retains the assumption that increase in predators
and decrease in prey are directly proportional to the number of contacts
between them.   Thus his primary assumptions were essentially the same as
those of Nicholson (1933) and Nicholson and Bailey (1935) (although his
mathematical models were quite different), for the only kinds of predators and
prey which approximate to his premises are lethal "parasites" of the insect
type and their "hosts." When such a "parasite" lays an egg it provides its off-
spring with all it needs for full development, and usually some mechanism
reserves the attacked "host" for the exclusive use of the parasite larva. Com-
petition is therefore of the contest type. For this reason, and the additional
fact that entomophagous parasites commonly develop large numbers of eggs,
we can assume (as a first approximation) that the number of hosts destroyed
and the number of parasite offspring produced are proportional to the number
of contacts between parasites and unparasitized hosts, so making mathematical
analysis simpler than with other types of predators and prey. In this system
oscillations are produced which are due to both coupling and lag effects. In
simple situations such *coupled-lag oscillations* (3c, Fig. 6) were shown by
Nicholson and Bailey to increase in amplitude with time.

Such systems of growing oscillation are inevitably self-destructive, for
limitless growth in amplitude is clearly impossible. The depletion of some
requisite by the hosts when they reach high densities may prevent the peaks of
the host oscillations from rising above a certain density, so converting the

system into one of sustained oscillation. If this does not happen the distribution of the population inevitably becomes discontinuous when the minima become very low, for individual families of animals must often be widely separated. If the descendants of each family do not disperse readily they form an isolated group which interacts independently with any parasites associated with it, and so a system of *fragmented oscillations* is created (Nicholson 1933, 1947; Nicholson and Bailey 1935). At any moment some groups of individuals are growing unchecked while others are in process of extinction by parasites, and migration of both hosts and parasites into unoccupied areas takes place all the time, so giving rise to new centres of oscillation. Such fragmented and changing distribution of hosts at a very low average density appears to be characteristic of control by really effective parasites (Nicholson 1947).

Varley (1947, p. 181) has claimed that "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 with amplitude." This is an overstatement, for the examination of numerical models has shown that oscillations grow in amplitude with time even when a considerable fraction of the surviving animals live in protected situations. In fact, it was found necessary to assume quite low powers of increase of the hosts, and the protection of the greater part of the fraction of hosts required to survive for population maintenance, before the postulated damping could be obtained—and if more than this fraction is so protected the parasites naturally cease to be capable of governing host density.

If some host individuals are more difficult to find than others, i.e. if the area of discovery (the procurement field) of the parasites is greater for some hosts than for others, the proportion of "difficult" to "easy" hosts in the population naturally increases with increased destruction. Although this tends to lessen the rate of growth of successive oscillations, numerical examples have indicated that only when the area of discovery for the "easy" hosts is many times as great as that for the "difficult," and when the power of increase is low, is it possible to convert the system into one of damped oscillation. Thus the tendency for populations of interacting parasites and hosts to exhibit growing oscillations is very great, and the erratic and ever-changing fragmented distribution of many insects, notably sessile ones, strongly suggests that population systems which are basically of the growing oscillation type (3c, Fig. 6) are common in nature (Nicholson 1947).

(iv) *Tardy Density Conditioned Reaction* (*Scramble*).—The characteristic of "scramble" is that success is commonly incomplete, so that some, and at times all, of the requisite secured by the competing animals takes no part in sustaining the population, being dissipated by individuals which obtain insufficient for survival.

Examples of populations governed by the depletion of a requisite for which they scramble are the cultures of *L. cuprina* already referred to (see Figs. 3, 4, and 5), and details of the governing mechanism have been given. Reaction is of the right kind to compensate for overcrowding, but, owing to the time taken for the offspring to develop, the effects of the high mortality or low

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natality caused at high densities continue for some time after the population has reached its equilibrium density. Thus lag oscillations are produced and these are more violent than in situation 3b (Fig. 6), for high densities do not merely cause great depletion of the requisite but also great wastage. If the intrinsic birth-rate is very low an asymptotic approach to the limiting density is probable (Nicholson 1948).

Schematic representations of such lag oscillations are shown in Figure 6 for animals governed by transient requisites (4a) and by accumulative requisites (4b), the only important difference being an accentuation of the violence of oscillation due to effects of intermittent requisite accumulation in system 4b, particularly initially.

The mathematical models created for predators of the protozoan (Lotka 1925; Volterra 1931) and entomophagous parasite (Nicholson and Bailey 1935) types and their prey do not apply directly to predators which scramble for their prey (such as birds of prey and carnivores), for the assumed direct relation between the number of contacts and the number of predator offspring produced is not even a reasonable approximation to reality. However, from the character of the interaction with prey one would expect oscillation of the coupled-lag type (3c, Fig. 6); and that this sometimes occurs is strongly suggested by the fact that fragmented distribution of *Icerya purchasi* in California, and of *Opuntia inermis* in Australia, was observed to result from the introduction respectively of *Rhodolia cardinalis* and of *Cactoblastis cactorum* (Nicholson 1947). The fact that such fragmented oscillation is unusual in populations of the higher animals strongly suggests that vertebrate predators are seldom the primary governing factors of their prey. Often they appear to be little more than the destructive instruments of some governing requisite—as when the depletion of food or of favourable space weakens the prey or drives them from their refuges, so permitting them to be attacked by predators, which they would otherwise escape (Nicholson 1947).

V. POPULATION REGULATION IN COMPLEX SITUATIONS

(a) Climatic Influences

For ease of analysis attention has so far been restricted to populations living under constant conditions—constant except insofar as they are affected by the actions of the animals themselves, or by the influence of a newly intro-duced factor under consideration. Such constancy of conditions is seldom approached in nature. For example, there is commonly a wide variation of climatic conditions with the seasons, and of climatic conditions in different parts of the range of any given species.

It has often been claimed that climate is dominantly responsible for the regulation of populations. This is probably true if "regulation" is used in the rule-making sense alone, for climatic conditions not only have a great direct influence upon the well-being of animals, but they are ultimately largely respon-sible for determining the composition of the communities in which they live.

In other words, climate may greatly influence the values of the primary density parameters, and by so doing affect the level at which governing factors adjust the densities of populations. On the other hand, climatic conditions are unaffected by any changes in the densities of the animals subject to them; and so, being unable to react to density change, they cannot govern populations, although they may have a profound legislative influence upon population densities.

It sometimes happens, however, that the densities of animals are governed by reactions of microclimates. For example, some insect pests of stored grain limit their densities by raising the prevailing temperature or humidity to barely tolerable levels.

To show why climate cannot govern population densities, let us assume that all other factors in the environment are also non-reactive. If, then, all conditions are favourable to animals of a given kind, their population will grow without check, and so, in any long period of time, the animals will increase to indefinitely large numbers. This is true even though the permitted rate of geometrical increase is very low, and irrespective of whether the environment remains constant or fluctuates violently about this average favourable level. Conversely, if the conditions are unfavourable, however slightly, the population must tend towards extinction in any long period of time. Even if the degree of favourability were maintained at the minimum, so just permitting the bare replacement of animals as they die, the absolute density would be independent of the environment, being simply the initial density in a constant environment, or fluctuating about this density in a fluctuating environment. In fact, in all three situations the absolute density at any moment would be merely a function of the initial density and of the subsequent history of increase and decrease in relation to the varying favourability of the environment. Change in density would be related to change in favourability; but absolute density would be independent of the conditions prevailing at any moment.

The fact that population levels are observed to be related to the climatic favourability of environments has often been claimed to show that the climate itself determines population levels. This view is untenable, for it is evident from the considerations just presented that the existence of this relation proves that there must be some governing mechanism in the environments which climate can influence in order to produce it; for climate itself merely permits population increase or causes decrease, according to its favourability or otherwise.

Although true equilibrium is impossible under fluctuating conditions, there is at each moment a density level which, if it were attained by the population, and if the environmental conditions prevailing at that moment were to persist, would cause the environmental forces opposing density change, including those induced by the population, to exactly counterbalance the properties of the population favouring multiplication. Consequently, it can be said that the level of equilibrium density fluctuates in association with environmental fluctuations, through the effects these have upon the properties of animals and those of their requisites. Reactions tending to cause increase or decrease are produced respectively when a population is below or above the equilibrium density appropriate to the conditions prevailing at each moment. Consequently, reaction

holds populations in leash to the ever-changing levels of their equilibrium densities. Although such influences as developmental lag, and the coupling of prey populations with those of their predators, may cause oscillations of internal origin, reaction forces such oscillations to take place about the equilibrium levels which change with the changing environment.

The situation is complicated by the fact that any marked climatic changes produce very noticeable direct effects upon population densities. In addition, any periodic change of climate tends to impose its period upon oscillations of internal origin, or to cause such oscillations to have a harmonic relation to periodic climatic changes. For example, if the natural period of oscillation under constant conditions were more than 1½ and less than 2½ years, there is reason to believe that seasonal influences would cause peaks of abundance to occur regularly every 2 years. This is because the phase of growth is likely to be prolonged when conditions are very unfavourable, whereas if this phase coincides with very favourable conditions it would be passed through quickly; so there is a strong tendency for the increasing and decreasing phases of oscillation to coincide in time with external conditions which favour them, provided these external influences are powerful.

General considerations and the examination of numerical examples have indicated that, although the period of climatic oscillation may be imposed upon oscillations of internal origin, the violence of population change is likely to be much greater than that which would be produced by, say, seasonal change alone. That is to say, the actual variation in population density tends to be much greater than the variation in its equilibrium level (Nicholson 1933, C.73, C.74, C.75, and Fig. 11). Thus reaction between populations and their governing requisites is probably largely responsible for the violence of population fluctuations in nature; but, because these fluctuations strongly tend to coincide in time with environmental changes in favourability, there is a natural tendency to conclude that population densities are wholly determined by the varying physical environment. The very existence of oscillation of internal origin is masked by synchronization with periodic external changes.

If the fluctuating conditions are definitely unfavourable at times, a population progressively decreases during those times, but at the intermittent favourable periods the population tends to adjust itself to the prevailing conditions. This determines the density at the beginning of each unfavourable period and therefore also the general level from which the population falls during these periods. Density governance is merely relaxed from time to time and subsequently resumed, and it remains the influence which adjusts population densities in relation to environmental favourability.

In spite of their inability to govern population densities, climatic factors have an influence of outstanding importance upon populations, but their influence is purely legislative. This influence can be represented in the basic equations by appropriate changes in the values of one or more of the primary parameters.

With field populations the analysis of such influences is greatly complicated by the fact that an environmental change may do more than alter the

values of the primary parameters, for it may also cause the attribute of being in shortest supply to be transferred from one depletable requisite to another. Consequently, the same species population may be governed by the depletion or impairment of different requisites at different times in the same place, or in different parts of its distribution area at the same time. These complexities do not affect the validity of the equilibrium equations, for no matter what may be the identity of the governing requisite, the appropriate values of g, q, w, l, and i together represent the collective influence of the environmental and intrinsic factors on equilibrium densities—but with fluctuating conditions, the identity of the governing requisite represented by these parameters may change from time to time.

(b) Edaphic Influences

Although the nature of the soil and the characteristics of the land surface seldom directly affect animal populations, they do so indirectly by profoundly influencing the composition of the plant communities in different places. This frequently leads to a mosaic of widely varying environments within which the habitat of a given species exists only in widely separated patches. Most species are well adapted to cope with such fragmentation of their habitats. They have a more or less defined dispersal stage, during which they readily move out of their true habitats, sometimes to great distances, and they also have the ability to recognize favourable situations when they are encountered. These adaptations are particularly significant when conditions which contribute to an animal's habitat are ephemeral, and when different life-stages occupy different habitats, for species lacking these properties would often be unable to find some of the favourable parts of the region in which they occur.

The unfavourable environments which animals encounter when they stray from their proper habitat commonly do not menace the animals, for generally they merely lack some particular requisite, such as food or oviposition sites. Consequently the adaptations just mentioned enable animals to occupy fully all favourable sites, and the fragmentation of their habitats has little effect upon their well-being. The populations are governed by density reactions within these favourable sites, these being the only places in which competition is significant. This is true whether the unsuccessful animals remain within the true habitats or disperse into the surrounding unfavourable country. In the second situation the cause of death or of inability to produce offspring may appear to be the unfavourability of the conditions to which the animals are subject. but this is only a secondary effect of the competition within favourable sites which forced out the unsuccessful animals.

Thompson (1939, p. 338) claimed that "the discontinuity and variability in habitats, produced by the physical factors both in time and in space, is undoubtedly the primary extrinsic factor of natural control". In support of this conclusion he asserted that when an organism "increases in numbers it necessarily spreads, both in space and time. As it spreads it moves to points outside its optimum environment, when its rate of multiplication immediately diminishes". However, more critical examination shows that multiplication throughout the

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occupied area cannot be reduced in this way to the bare replacement rate, as is necessary for population limitation.

As Thompson's arguments imply that the spread of organisms is unaffected either by the degree of favourability of the environment or by population density, it is clear that he postulates random movement of the constituent organisms. In these circumstances, populations could not spread appreciably beyond the border zone of minimum favourability, the characteristic of which is that the fraction of organisms born there which is lost by random movement into the neighbouring unfavourable areas equals the fraction of organisms which is surplus. In all less favourable areas the organisms would multiply less rapidly and so could not maintain their numbers (the rate of diffusion by hypothesis being a constant). On the other hand, in all more favourable zones the rate of multiplication would be greater, and so the fraction of offspring lost by diffusion from them would be less than the surplus produced. The resultant growth of the population in such areas would be augmented by diffusion into them of some of the offspring born in neighbouring favourable areas. That is to say, the population would grow without check in all favourable areas other than those on the border line of favourability. Inevitably overcrowding would soon occur throughout most of the occupied area, so leading to limitation by competition.

Similar arguments apply to the spread of populations in time, and they are well illustrated by the numerical example Thompson (1939, p. 339) used in an attempt to show that the spread of a population causes a progressive fall in the rate of multiplication. Thompson terminated the examination of this example at the second generation, but when it is continued into subsequent generations it at once becomes clear that the population within the favourable period continues to multiply at a rate exceeding that of geometrical increase, and that the fate of the animals occurring during the unfavourable period has no influence upon this rate of increase.

The reason for the great difference between the diffusion patterns of inanimate objects, such as gas molecules, and those of organisms is that the latter have finite lives. The new organisms which continue the diffusion after others die necessarily begin their operations within the favourable areas in which they were born. This inevitably restricts the ultimate distribution of the population to the favourable areas plus a surrounding unfavourable zone, no part of which is at a greater distance from some favourable area than that which can be traversed by an individual during its lifetime. Consequently, spread into unfavourable areas is definitely restricted by the distribution of favourable conditions, and it cannot continue to increase progressively so long as more than the replacement number of offspring is produced by the organisms, as Thompson postulated.

(c) Biotic Influences

Animals which are directly dependent upon plants may govern the densities of their food plants, and so also their own densities; but more often they are governed by other factors at densities which cause them to have little, if any,

influence upon the densities of their food plants. Plants influence animals not
only by providing them directly or indirectly with food, but also by determining
in large measure the composition of the communities in which they live, by
satisfying special requirements, such as nesting sites and refuges, and by provid-
ing favourable microclimates.

Animals are influenced by other animals in many different ways. The den-
sities of some are directly influenced by those of the animals they are dependent
upon, whereas they have little or no influence upon the densities of their bene-
factors. Examples are epizoic, coprophagous, and commensal animals, and
benign parasites. A few are symbiotic and so tend to increase the densities of
their partners. More often animals adversely affect animals of other species.
Pathogenic organisms and predators (including "parasites" of the entomophagous
kind) destroy their hosts or prey, and by so doing may limit their own popu-
lations as well as those of the animals upon which they are dependent. As
has already been shown, there is a strong tendency for such interaction to lead
to periodic oscillations in density. When the predators attack several species
of prey and the prey species are attacked by several species of predator, the
periodic oscillations in density each pair of interacting species tends to produce
inevitably interfere, sometimes opposing and sometimes assisting one another.
In this way erratic and aperiodic oscillation in density is likely to be produced,
and to be made still more complex by the influence of varying climatic
conditions.

Under natural conditions populations are not only subjected to the disturb-
ing influence of fluctuating climatic factors and of various destructive agencies,
but they have to exist together with populations of other animals which require
some at least of the same requisites. Now, for the contemporaneous existence
of several different species in the same place, each species must possess some
advantage over all the others with respect to some one, or group, of depletable
requisites, and in addition be able to tolerate the depletion of other requisites
which is caused by competing species (Nicholson 1933, C.2). The reason for
this is that each species must govern the density of at least one such requisite
in order to govern itself, so excluding the possibility of any other species govern-
ing (and so being governed by) the reaction of the same requisite. It will be
observed that this conclusion defines the necessary conditions which determine
whether two or more species can live together or not, in contrast to "Gause's
hypothesis" which, according to Lack (1947) is that "two species with similar
ecology cannot live together" (see Gilbert, Reynoldson, and Hobart 1952).

Implicit to this conclusion are the important qualifications that all the
species are restricted to the area within which they compete, and that environ-
mental conditions are constant throughout this area. This is often not true,
for environmental conditions change from place to place, often within very small
areas, and it may well happen that each of the competing species has an advan-
tage over all the others in certain parts of the region in which they occur. If
there were no diffusion of the populations, each species would exclude the
others from those parts of the region in which it is most potent. Normally,
however, there is such diffusion, and consequently intermingling of populations

of different species with similar requirements should be a permanent situation, in parts of the environment at least. This is because the tendency for each species to displace the others from the places in which it is most potent is continually countered by immigration of new individuals of the other species from those parts of the environment in which they in their turn are most potent.

It is evident that fluctuations and oscillations in abundance of different species living together should often interfere with one another, this being most marked when two or more species influence the abundance or availability of a common requisite, or the density of a polyphagous natural enemy. The oscillations of internal origin should sometimes oppose and sometimes augment one another, so causing irregularity in the time of occurrence and in the magnitude of the peaks of abundance of any one species. Seasonal changes should still tend to impose their period upon the populations, but the effects of interference would be to cause many apparently erratic changes in the populations unrelated to any external change.

It should be noted that, although some factors act merely as the instruments of destruction employed by some governing factor, they are generally legislative factors and may produce important effects upon density levels. For example, many vertebrate predators seem capable of attacking only those prey individuals which are weakened by dearth of food or by age, or which have been forced by population pressure to leave the refuge of their natural habitats. At first sight it might appear that in this situation the predators merely destroy individuals which are already doomed to death from other causes, and that consequently they should produce no significant effect upon the density of their prey. This is far from true, for it is notable that such destruction tends to limit the prey population at near the highest level their pasture can support. Were it not for the destruction of semi-starved prey by the predators, populations of herbivorous animals would reduce their food to extreme scarcity, so leading to a fragmented distribution of both herbivores and their food plants at very low average densities (Fig. 6, situation 4c).

This raises a very important question. Almost all kinds of plants are attacked by one or more species of animals, and animals tend to reduce their food supplies to the threshold density at which they can barely find enough food to maintain themselves and to produce sufficient offspring to replace them at death. With most kinds of herbivorous animals this would lead to an extremely sparse distribution of their food plants—yet observation indicates that terrestrial plants succeed in occupying fully practically every site in which conditions are suitable for plant growth. The question is, how can these apparently contradictory conclusions be reconciled?

Sometimes herbivorous animals do limit their densities by reducing their host plants to such scarcity that they have great difficulty in finding them, as happened as a result of the introduction of *Cactoblastis cactorum* into Australia to attack *Opuntia* spp. (Dodd 1936) and of the introduction of *Liothrips urichi* into Fiji to attack *Clidemia hirta* (Simmonds 1937). It is possible that such fragmented distribution of plants caused by the action of their enemies (notably insects) is far commoner than is realized, for the influence of the enemies

is inconspicuous when balance exists and both insects and their host plants are scarce and widely scattered. However, it is quite evident that this situation is not general, and that usually animals are prevented by other factors from directly limiting their food supplies. One mechanism is the destruction of weakened herbivores by natural enemies, in the way already referred to, which prevents the eating out of pastures and causes the herbivores to maintain populations near the maximum density the pastures could possibly support. Insect enemies of plants, on the other hand, appear generally to be reduced by their own enemies to the threshold level for these, which commonly means that their effect upon plants is not very significant. Probably many factors other than the availability of their food plants and the attack of natural enemies limit the populations of some plant-eating animals, but there seems very little doubt that the major influence which prevents animals reducing vegetation on the earth to extreme sparseness is the attack of phytophagous animals by enemies of their own.

(d) Population Balance

In spite of the violence and complexity of population changes produced by the interaction of different systems of population oscillation of internal origin and the influence of climatic changes upon these, it is clear that the underlying mechanism is one of balance. The densities (N) of populations and those (G) of their governing requisites are counterposed, and any change in these quantities (whether produced by the environment or by the action of the population itself) sets up reactions which tend to cause approach to a condition of equilibrium.

The balance a population maintains in spite of the varying conditions in its environment can be likened to that of an equestrienne dancing on the back of a horse cantering round a circus ring: her movement is partly due to her own action and partly to that of the horse, and she remains poised upon the horse's back by expertly adjusted compensatory reactions to all the disturbances which tend to cause her to fall. The persistence of populations in their ever-changing environments, and their maintenance of degrees of abundance in general conformity with the changing conditions, are wholly dependent upon compensatory reaction to external forces.

The conclusion that populations govern themselves by inducing the environmental resistance which limits their densities in relation to prevailing conditions is the antithesis of Chapman's (1931) theory of "biotic potential," which postulates that resistance is purely a characteristic of the environment, and that the properties of organisms are adjusted to this, presumably by the process of evolution. Even if such precise adjustment of properties were produced, it could not adjust population densities in relation to environmental conditions, for the properties of the animals would then be in a state of equilibrium with those of their environment at any density (Nicholson 1927, 1933).

If populations were dependent upon such qualitative adjustment of their properties to those of their environments, pest control would be far easier than it has proved to be. It would merely be necessary to apply a control measure to reduce the pest population to, say, 1 per cent., and then, without any further

action, population density at any subsequent time would be only 1 per cent. of what it would otherwise have been! In fact, pest control by chemical means has demonstrated conclusively and on a vast scale that the rate of growth of populations is influenced by their densities. When no measures are taken to control pests which are well established, their populations are never in a continuous state of progressive growth. After the first application of insecticides, however, the pest populations invariably begin to grow very rapidly from the low levels to which they have been reduced, and they soon reach densities which make it imperative to apply insecticides once more. This process must be repeated at intervals in order to maintain control of the pests. Evidently the factors which previously checked population growth have automatically relaxed their influence.

(e) Economic Control of Pests

When considering the imposition of new destructive factors upon populations living in simple situations, it was shown that the populations automatically accommodate themselves to the new situations, provided the destructive factors continue to operate. When a state of balance is re-established after the introduction of a destructive factor the total mortality is adjusted to 100 per cent., just as it was when the destructive factor did not operate, for density reactive factors relax their action to make place for the destruction caused by the new factor. In doing this they cause more individuals to reach the life stage of the animals affected by the new factor (Table 1). Consequently, when balance is re-established, the number of animals in the stage surviving destruction is greater than it was when the new factor first operated (although less than before the destructive factor operated), and the density of animals at some other stages may even be increased, as has been shown.

That new destructive factors do not add to mortality in the long run, but merely change the distribution of mortality, and that reaction always tends to counteract the immediate effects upon density produced by such factors, are facts which must be taken into account seriously when considering problems of pest control. They probably in part account for the common experience that control measures often do not maintain the effectiveness obtained when they were first tried. It is important to recognize, however, that in the examples upon which these conclusions were based the governing function was exercised by the same factor before and after the introduction of the destructive factor. There is good reason to believe that when control measures are effective this is because they have taken over the governing function, and have reduced the original governing factors to purely legislative status. Such displacement of the original governing system has its dangers, for any relaxation of the control measures is likely to lead to a serious outbreak of the pest which is likely to reach a density far above that which existed before control was applied. Developmental lag permits this to occur before the original governing factors react sufficiently to check population growth and subsequently to re-establish the original state of balance.

Similarly it seems improbable that introduced natural enemies can exercise effective control of a pest unless they take over the governing function; and, as has already been mentioned, they are most likely to be effective if their interaction establishes a system of growing oscillations which leads to fragmented distribution of both natural enemy and prey. The establishment of such systems is frequently prevented by an imperfect correspondence in time or in space between the occurrence of enemies and their prey. For example, the seasonal period during which insect parasites of a given species hunt for their hosts may not completely coincide with the period during which their hosts are in a suitable stage to attack, so that hosts which reach the vulnerable stage during certain periods are completely free from attack. This leads to outbreaks of hosts at certain times of the year, which are terminated after the parasites come into action. The immunity to attack of part of the host population reduces the average efficiency of the parasites in finding hosts. As this is equivalent to reducing the value of the procurement field (i), this leads to an increase in the densities of both parasites and hosts (see equations (**4**) and (**5**)). Such imperfect correspondence between the time or place of operation of a parasite and the time or place at which the vulnerable stage of the host exists is probably one of the most important causes of inefficient control by parasites. It may well lead to such high densities of the hosts that these cease to be governed by the parasite—the governing function being taken over by some other factor (such as the food supply of the host), and the parasite density becoming a purely legislative factor.

(f) Natural Selection

It is generally agreed that natural selection has played a very important part in the development of the highly organized communities which make such complete use of the inhabitable parts of the land surface, and it should be noted that balance due to density governance is an important part of the mechanism of natural selection. It tends to hold the intensity of reaction at the level which just counteracts the innate ability of a population to grow. This induced intensity, being adjusted to the average properties of the individuals, is insufficient to prevent the growth in numbers of individuals with advantageous properties, whereas it is too powerful to permit the other individuals to maintain their numbers. As individuals of the favoured kind increase in numbers, the intensity of reaction progressively increases towards the value which counterbalances their properties, so slowing down their own rate of multiplication and accelerating the displacement of individuals to the original less potent kind, which are therefore forced to extinction (Nicholson 1927, 1933).

A point of considerable interest revealed by the present study of the mechanics of population regulation is that natural selection does not necessarily favour the success of the species, in the sense of increasing its abundance. For example, if within the population of an entomophagous parasite there were some individuals which were more efficient than the remainder in finding hosts they would unquestionably find more hosts and so have more offspring. Consequently their descendants would progressively displace those of the less efficient individuals. But increased efficiency means that the procurement field (i

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is relatively large, and it will be seen from equation (5) that the selection of this advantageous property reduces the equilibrium density of the parasites possessing it. Similarly, equations (1) and (4) taken together show that if because some individuals required fewer prey for maintenance and replacement (q is reduced) they and their descendants displaced the others, the equilibrium density of the predators would remain unchanged by the selection of this advantageous property: and equation (3) shows that the selection of the offspring of individuals with a greater than average reproductive capacity (which would be inevitable if other properties remained unaltered) would reduce the equilibrium density of mature animals, for the increased surplus of offspring produced would cause a greater wastage of food by those individuals which are prevented from maturing (w increased).

These considerations confirm the conclusions reached elsewhere (Nicholson 1927) that natural selection preserves individuals with advantageous properties without reference to the success of the species, and that the elimination of individuals which do not possess these advantageous properties is due to automatic intensification of environmental reaction resulting from the changed properties of the population which selection has caused.

It should be noted that the selection of advantageous properties in one species may cause it to deplete some requisite it shares with another to below the threshold density for the competing species, which it therefore displaces. So, natural selection continually tends to disturb population balance by improving the properties of competing species, instead of producing balance, as it is often supposed to do.

On the other hand, the improved properties selected may enable a species to extend its geographical or ecological range, or to break up into daughter species if the selective influences are different in different parts of its range. Thus the properties of animals, and also the compositions of the communities to which they belong, are largely resultants of the selective influence of density governance when operating over long periods; and this in turn has an important influence upon features of the physical environment, such as microclimates.

(g) Population Dynamics

In brief, by providing a mechanism which causes well-adapted organisms to be completely displaced by those with even slightly better adaptation, the self-governing reactions of populations in large measure determine the properties of organisms and those of the communities to which they belong; and in addition, they adjust the densities of populations in relation to these properties and those of the physical environment. As the considerations given in the earlier parts of this article show that the underlying mechanism of self-governing reaction almost always is competition, there can be little doubt that competition is the major force which regulates the amount of matter and associated energy taken up from the environment by communities of organisms, and which also determines the course which this takes through populations of different species before being returned to the inorganic environment.

VI. Critical Review of Evidence and its Interpretation

(a) The Place of Thought in Research

The foregoing discourse begins with the statement of certain facts cf common knowledge which are so well established as to be incontrovertible. The implications of these facts are examined in relation first to very simple situations, and then to progressively more complex ones, and eventually general conclusions are reached concerning population growth and maintenance under natural conditions. Although much use is made throughout of further evidence derived from observations and experiments, the method of investigation is essentially deductive reasoning. The approach is thus the same as that used in earlier articles (Nicholson 1933; Nicholson and Bailey 1935); so, as this has been seriously criticized by certain biologists, notably Thompson (1939) and Ullyett (1953), it is necessary to examine its validity.

In particular Thompson and Ullyett criticize the deductive use of mathematics in investigations of population problems—an approach which they consider unsound. Epitomizing his views Thompson (1948) said, "It is a mistake to imagine that by any mathematical subterfuges, we can dispense with direct contact with nature. Observation and experiment must remain the basic elements of entomological science." Taking it at its face value, no biologist would deny the evident truth of this assertion; but it contains the unjustifiable implication that when mathematics have been used for the study of population problems the postulates used have not been based upon ascertained fact. This is not true of most mathematical investigations—although there are a few notable exceptions. The omission of thought as one of "the basic elements of entomological science" is probably not due to this element being taken for granted (as might be argued), but rather to the fact that its supreme importance is all too frequently ignored by biologists working in this field. The common and reiterated insistence upon the paramount importance of observation and experiment, and the deprecation of "theorizing" (which seems to be the fashionable word for any deliberate and sustained thought) indicates a gross misunderstanding of scientific method. There appears to be a widespread idea that the facts of nature can be revealed by observation and experiment alone, so avoiding both the pitfalls and labour of thought; and the history of the investigation of the problems presented by populations certainly supports this surmise. Misconceptions upon this subject appear sufficiently widespread to justify a brief discussion of the relation between observation, experimentation, and thought.

The course of any sound investigation can be represented diagrammatically as follows:

Investigation necessarily begins in the mind and (in the natural sciences at least) the first step is to find what actually happens in nature. Initially this

generally consists of reviewing pertinent data already collected, and then making new observations to check, and to add to, the facts already known. Not only is thought necessary in the selection of the field to be studied, but also in the selection of the kind of observations to be made; for, no matter how complete one may attempt to make the observations, only a chosen few of the things that occur and happen are in fact recorded. In this way additional information is gathered which on consideration suggests lines for further investigation. Whether this takes the form of a more intensive study of the facts already gathered, or of further observation, or of experiment, depends upon one's assessment of the situation. In general, one should first extract all possible information from the available data to obtain the maximum guidance for further observation and experimentation; and one should make observations in the field, in preference to laboratory experiments, when these can provide the information sought—for facts so revealed can be seen in their proper context. The observational method, however, has serious limitations, for the things observed and recorded are commonly the resultants of the interaction of many factors whose separate influences cannot readily be disentangled. Many different interpretations of the observations may be possible. The observer may fail to recognize some of the possibilities, and there is a strong tendency for him to attribute the cause of the things he observes to some particular influence which he happens to be studying, or which he subconsciously prefers. Statistical analysis may help to disentangle the roles of the various influences; but often the only way to do so is to maintain most of the variables constant in laboratory experiments, so enabling one to study the effects produced by the various influences acting singly, or in small manageable groups. The precise results so obtained can be used to elucidate field observations, or to formulate new hypotheses worth testing. The experimental method has the further advantage that it is concerned with the characteristics of mechanisms and with the effects they produce under given conditions, and so the conclusions reached can be applied to populations of animals of any kind which are influenced by the same mechanisms.

Thus a necessary condition for investigation is a continual interplay between thought and observation or experimentation, which leads eventually to understanding. In any sound investigation thought must occupy a central and dominating position. It must be honest and accurate, and disciplined in the highest degree. It must precede and follow each active step in observation and experiment; and when an understanding of the immediate problem has been achieved, the discipline of thought must be studiously maintained, for much confusion has been caused in biology by extrapolating sound conclusions to fields in which the basic considerations upon which they were based do not apply.

As mathematics is an exceptionally powerful tool of thought, this method should be used wherever it is applicable. It is true that it does no more than reveal clearly relations which are implicit in the postulates used, but it commonly does this with greater precision than any other form of thought, and it often reveals things which would remain hidden without its aid. The truth of the conclusions reached is necessarily dependent upon that of the postulates. Consequently if field observations give results at variance with mathematically

derived conclusions, the error does not lie with the mathematics, but must be due to the postulates being inapplicable to the situations studied. It is therefore critically important to base the postulates upon facts so firmly established by observation and experiment as to be unquestionably true. However, much progress can often be made by using terms in the equations which are only first approximations, as, for example, by assuming a particular relation between population density and the intensity of environmental reaction which is known to be at least approximately true for some animals. The results so obtained form useful guiding hypotheses for further investigation. The mathematical method is not an alternative to observation and experiment but is necessarily a supplement.

(b) Critical Review of Some Population Theories

Although I agree heartily with the view that there is an urgent need for more intensive observation and experiment in order to acquire knowledge of populations and of the mechanisms which control them, and although no one could be more critical of the use of "theorizing" (in the sense of loose and ill-founded conjecture) as a means of reaching understanding, a study of the investigations of population problems which have so far been carried out has forced me to the conclusion that the greatest present need is for greater clarity of thought, not only in the formulation of hypotheses and theories, but also in the collection and interpretation of data.

In general biologists are prepared to expend almost unlimited time and labour in the collection of data; but only too often they give surprisingly little thought to the questions of what kinds of data need to be collected to throw light upon the problem under investigation, and of the true implications of the data when they are collected. For example, certain investigators have expended great effort in determining the percentage destruction caused by each of a number of factors which influence populations of a given animal and (confusing their hasty conclusion with ascertained fact) have claimed that the particular factor which causes greatest destruction is dominantly responsible for the limitation of population density. A little thought along the lines given in earlier parts of this article would have shown that no direct relation between percentage destruction and population density can be expected, and that therefore, not only is the conclusion unjustified, but so also is the collection of data of this kind when seeking the real cause of population limitation. Other examples which have already been considered in detail are the naïve deductions of many biologists that, because population densities often have a clear relation to the prevailing climate, therefore climate controls population densities, and the oversight by Gause of the essential space component of the Volterra equations which caused him to design inappropriate experiments to test the validity of these equations, and therefore to reach an erroneous conclusion.

Although the commonest source of error in population theory has been unjustifiable inference from often inappropriate data, it has occasionally been due to "theorizing" with little or no basis of ascertained fact. Thus Chapman based his well-known theory of population regulation wholly upon a supposed analogy

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between the resistance of environments to population growth, and the resistance of conductors to electric currents, as represented by Ohm's law. He brought forward no biological evidence, but contended that "the ratio of the number of organisms which should be present because of the inherent ability of organisms to reproduce themselves (the biotic potential) and the number which are present may be considered as the measure of the resistance of the environment" (Chapman 1931, p. 196). This analogy would be justifiable only if it were true that in a given environment density varied directly with "biotic potential", for the basis of Ohm's law is that electrical current in a given conductor varies directly with electrical potential. But this is not true, for it has already been shown that there is no constant relation between population density and "the inherent ability of organisms to reproduce", and that sometimes, notably in the experiments with *Lucilia* (see Fig. 2), there is an inverse relation between these quantities.

Thompson's mathematical investigations of the interaction of entomophagous parasites and their hosts (which he recapitulates in his 1939 article) are little better based. His primary assumption is not merely that each female parasite can lay a certain definite number of eggs, but that it does lay this number, so long as any hosts remain in the environment. It is not surprising, therefore, that he concludes that a parasite population can never overtake the host population (which is assumed to be free from any check other than the action of the parasites) unless its reproductive rate is greater than that of the hosts, and that in this situation the overtaking of the host population is inevitably followed immediately by the extermination of both hosts and parasites. These conclusions are clearly as unreal as is his primary postulate, which completely ignores the fact that the chance of a parasite finding sufficient hosts in which to lay its eggs must become small when the host density becomes very low.

It appears that Verhulst, Pearl, Lotka, Volterra, and Nicholson each independently chose the same factor as being of primary importance in population regulation, and Bailey based his mathematical investigation upon the postulates provided by Nicholson. This factor is the progressive decrease in the favourability of the environment which is associated with progressive increase in population density. Essentially the same simplifying assumptions were made by each of these investigators about the relation between such growth-opposing reaction and population density. Further postulates, implicit in the terms used, limit the application of the Verhulst-Pearl equations to competition of very simple microorganisms for favourable space, and the application of the Lotka-Volterra equations to simple microorganisms interacting as predators and prey. These limitations were not appreciated even by the authors themselves, and the attempt made by many biologists to use these equations to describe the growth and regulation of populations of higher animals has led to much misunderstanding.

A deplorable example of the misapplication of equations is the fitting of logistic curves to the data provided by growing populations of some of the higher animals. Thus Pearl (1926) succeeded in fitting logistic curves to growing populations of many different kinds. If he had claimed that the

equations upon which these curves were based were merely convenient descriptions of the observed growth of the populations, one could not take exception to the procedure. Unfortunately, he went further and claimed that his success in curve-fitting showed "that populations grow in size according to the same mathematical law that individual animals and plants follow in the growth of their bodies in size" (Pearl 1926, p. 208). Examination shows that he did not hesitate to introduce new terms into his equations when they would not otherwise fit the data under examination. In this way he described the growth of the population of Sweden during the last 300 years by a logistic equation, in spite of the fact that during the period 1700 to about 1860 the percentage increase of the population per decade became progressively larger, in contrast to the characteristic progressive diminution with time of the rate of multiplication of cells in organisms, or of populations of microorganisms, to which the original logistic equation applied. Such curve fitting gives spurious relations.

The fact that the Nicholson-Bailey equations take into account the lag effects which are caused by the time taken by animals in development makes them applicable to certain of the higher animals, but their application was from the first explicitly restricted to predators of the entomophagous "parasite" type and their "hosts". Equations (1), (2), and (3) in the present article describe the equilibrium conditions for any kind of animal, and they can be modified by dividing the terms into their components to describe more precisely the equilibrium conditions for any particular kind of animal, as has been done for predators in equations (4) and (5). From these it is easy to derive equations describing growth and maintenance in populations of very simple microorganisms, as has been done in equations (7)-(13); but, because of development lag and the difficulties this introduces, such as complex changes in the age composition of populations, it is far more difficult to derive equations describing the growth and maintenance of populations of higher animals. Nicholson and Bailey (1935) have done so for the special case of predators which contest for their prey; but populations of animals which scramble for their governing requisites are far more difficult to represent mathematically.

Thus most of the well-known mathematical theories of population regulation are complementary, and each represents a different group of population systems. They fall quite naturally into the general scheme of classification developed in this article (see Fig. 6).

This brief review of population theories shows that much of the present confusion in the subject has been due to insufficient attention being given to the correct interpretation of data, and to a tendency to extend valid conclusions into fields in which the considerations upon which they were based do not apply. The question naturally arises as to whether or not this is also true of the present investigation.

(c) Basis and Validity of Conclusions in Present Investigation

In the following discussion the primary considerations upon which the present investigation was based are restated, and the validity of the conclusions reached is assessed.

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All biologists are aware that populations are influenced by many and varied factors, but an underlying orderliness is equally evident. The necessary first step in the investigation, therefore, was to classify the various types of factors according to their influence upon populations, and to define and study those pertinent facts about animals and their populations which are axiomatic, or so well established by generations of observers as to be unquestionably true. Of these the following established facts seemed to me to be most significant and to provide the basis for an understanding of population dynamics:

(1) All animals have an innate ability to reproduce and to multiply under favourable conditions.

(2) The favourability or otherwise of the environment for a given species determines whether its population is permitted to grow or is caused to decrease.

(3) As every animal born must die, and can die only once, a population cannot persist for long periods in any given environment unless the birth-rate and death-rate are virtually equal (when each is averaged over a representative period); for if numbers of births and of deaths remained appreciably different the population would decrease or increase geometrically, so either directly falling to extinction, or causing its own extinction by overwhelming its environment, in a comparatively short time.

(4) As populations grow, the constituent animals use up more and more of the limited available quantities of depletable requisites (such as food and favourable space), and increasing density often intensifies the action of inimical factors (for example, by increasing the densities of any natural enemies dependent upon the animals concerned, or by increasing the concentration of harmful metabolites).

(5) Because animals produce such effects upon their environments, growing populations progressively reduce the favourability of some factors, whereas decreasing populations permit favourability to recover. Such compensatory reaction inevitably governs population densities at levels related to the properties of the animals and those of their environments.

(6) Consequently, when operating in association with density governing factors, non-reactive factors (such as climate) may have a profound influence upon density, for many non-reactive factors influence either the properties of animals or environmental favourability.

(7) Operating by themselves, however, non-reactive factors cannot determine population densities for, if sufficiently favourable, they permit indefinite multiplication or, if not, they cause populations to dwindle to extinction. On the other hand, they inevitably limit distribution to those areas within which they are favourable.

These basic considerations are of general application, being quite independent of the nature and of the complexity or otherwise of the situations in which the animals live. They are simply statements of well-established knowledge,

and of implications which follow so directly from this knowledge as to be incontrovertible. It follows directly from these considerations that populations should exist in a state of balance in all favourable environments and that (except where some non-reactive factor causes the environment to be only barely favourable) density-controlled compensatory reaction enables populations to adjust themselves to severe external stresses, and so to remain in being. The observed facts that populations of the same species are maintained in many widely different environments without progressive change in density, and that they are not reduced to extinction when a new destructive factor is imposed, confirm these conclusions and show that balance cannot be due to a precise adjustment of the intrinsic properties of the animals to those of their environments.

After establishing these broad generalizations, further consideration showed that there are certain well-established facts which can be used to make other generalizations within more restricted fields. Density governing reaction is primarily dependent upon only two things—the characteristics of the population and those of its governing requisite, or group of requisites. All other pertinent factors produce their effects by modifying these characteristics. Analysis showed that requisites react upon population density in different ways according to whether they are favourable space, expendable things such as non-living food, or other organisms used as food; and that four distinctive types of reaction by populations to changes in availability of governing requisites can be recognized. Different combinations of kinds of governing requisites and of kinds of population reaction thus constitute the 12 situations graphically shown in Figure 6. From knowledge of the characteristics of the animals and of their governing requisites, it was found possible to deduce the characteristic pattern of population growth and maintenance in each situation.

Although the facts upon which such generalizations were based have been well established by the experience of generations of biologists, no one would be content to accept the conclusions unreservedly without checking them by observation and experiment. All observations of natural populations and all experiments with laboratory populations known to me are consistent with the conclusions reached in this article, and many provide clear evidence supporting them—although it is true that the interpretations some investigators have placed upon their observations and experimental results are inconsistent with these conclusions. Most such observations and experiments have been inconclusive, for when investigators lack the guidance of a particular theory, it is almost inevitable that some observations having a crucial bearing upon that theory fail to be made, or to be recorded. Moreover, in order to check the correctness of a theory, it is not only necessary to find whether a population behaves in the way predicted, but also whether the underlying mechanism is that described by the theory. As already indicated, it is commonly difficult to identify mechanisms with certainty by field observation and, in general, little attempt has been made to analyse the influences of the different variables in the comparatively few laboratory populations that have been studied.

It was for this reason that an intensive study of laboratory populations of *Lucilia cuprina* was undertaken (Nicholson 1954). The pertinent results of

some of these experiments have been briefly mentioned earlier in this article. In each experiment some one particular variable was singled out for study, the others being maintained constant—or the interaction of two, and sometimes three, variables was studied. Some biologists consider that the artificial conditions under which such populations are held make the results inapplicable to natural populations. This is untrue, for the factors studied are those known to influence natural populations, and an essential part of such experiments is the study of the interaction of such factors.

On the basis of the theory deduced from the general considerations already given, it was found possible to predict that *Lucilia* populations should behave in certain definite ways which should vary according to the particular conditions to which they are subjected. In all experiments the populations held under these defined conditions conformed to the predictions with gratifying precision, and the mechanism governing population growth and maintenance was revealed in detail and found to conform to that postulated. Not only did the results conform to the predictions made about animals which scramble for a consumable governing requisite (notably the maintenance by animals with a high birthrate of violent and sustained periodic oscillations in density in a constant environment) but they also confirmed the general conclusions which it has been predicted should apply to any kind of population existing in a favourable environment. They clearly showed that populations limit themselves by progressively reducing the favourability of the environment as they grow, so maintaining themselves in a condition of balance with their environments; that on the average the number of births equals the number of deaths, imposed destruction not increasing mortality but merely causing a redistribution of mortality amongst the lethal factors; and that compensatory reaction enables them to accommodate themselves to even very severe environmental stresses.

(d) Basis and Validity of Conclusions in Earlier Investigations by Nicholson and Bailey

It is noteworthy that the investigations of Nicholson (1933) and of Nicholson and Bailey (1935), which dominantly dealt with the interaction of entomophagous parasites and their hosts (situation 3c in Fig. 6), apart from leading to special conclusions relating only to parasites and hosts (notably the production of oscillations in density which grow in amplitude with time), also led to the same general conclusions. This provides supplementary evidence about the soundness of these investigations, which were based upon considerations of well-established facts concerning factors known to influence natural populations of parasites and hosts. Until such time as they can be adequately checked by observation and experiment, the special conclusions reached can only be regarded as reasonable hypotheses, although they are far more soundly based than most opinions about the effects of interaction between entomophagous parasites and their hosts. Already there is much circumstantial evidence from field observations which supports some of these hypotheses. The experiment of de Bach and Smith (1941) in which pupae of *Musca domestica* were parasitized by *Mormoniella vitripennis* gives some support to the conclusion that

interacting populations of hosts and parasites produce oscillations which grow in amplitude with time, although the experiment was unfortunately concluded before crucial results could be obtained. Probably the most important feature of this experiment is the close correspondence between the observed and the calculated densities of the hosts and parasites in each of the seven generations studied, which shows that with *Mormoniella*, at least, the postulate of random searching corresponds closely to the behaviour of the parasite.

Thompson (1939) bases most of his criticism of the investigations and conclusions of Nicholson (1933) and of Nicholson and Bailey (1935) upon his belief that this concept of random searching is unsound. Like Ullyett (1953) he places much stress upon the indisputable fact that individuals of many species search in ways which are far from random, but both authors ignore the statement of Nicholson (1933, p. 141) that "if individuals, or groups of individuals, search independently of one another, the searching within the *population* is unorganized, and therefore random. Systematic searching by individuals improves the efficiency of the individuals, but otherwise the character of the searching within a population remains unaltered." Only when the searching of individuals is systematically influenced by the activities of others does searching by the population as a whole become non-random, as when the individuals lay claim to territories. Consequently, random searching is a reasonable primary postulate when applied to entomophagous parasites. It should be noted that, in essentials, it is the same simplifying hypothesis as that used by Verhulst, Pearl, Lotka, and Volterra in their equations, which, stated in general terms, is that the chance of an individual obtaining a sufficient quantity of the governing requisite to enable it to produce one offspring varies directly with the density of the requisite at each given moment. This clearly is only a first approximation, but it must often be closely approached in fact. "Random searching" is simply a convenient term with which to refer to the underlying mechanism of this probability relation, at least with such animals as entomophagous parasites. It is interesting to note that Thompson (1924), following the example of Fiske (1910), used essentially the same probability relation when discussing the problem of superparasitism, but his unfortunate failure to use it also in his investigations of interaction between parasites and hosts made these quite unreal.

Both Thompson and Ullyett appear to hold the view that the conclusions of Nicholson and Bailey are completely dependent upon the assumption of random searching. This view is incorrect for, as has already been mentioned, even great departures from the condition of random searching may not prevent successive oscillations in density from growing in amplitude, as when the parasites are unable to search in a significant fraction of the environment. However, it is the part played by compensatory reaction to density change which these authors seem most loath to accept. The qualitative features of Nicholson and Bailey's conclusions concerning this are quite independent of the truth or otherwise of the concept of random searching. Without stating the precise relation between density and intensity of environmental reaction, essentially the same conclusions concerning the effects produced upon populations by density governed reaction to environmental change have been derived from the well-

established fact that growing populations inevitably and progressively deplete some requisites, and they are confirmed by the experiments with *Lucilia* populations in which the relation between density and the success of the individuals is very different from that which is represented by the probability of random contacts. The concept of random searching applies only to certain kinds of animals; and, although it may represent part of the mechanism of compensatory reaction to density, it is not an essential part of this mechanism.

Ullyett (1953, p. 83) stated, "the possession of life endows the organism with one of its main characteristics, namely, that 'something extra' which is not found in inorganic nature." He also stresses the inherent plasticity of organisms, and the multiplicity of causes of mortality which even individually are not constants. He argued that because of these considerations mathematics is inherently inapplicable to the study of living organisms. This is a surprising claim when one considers the notable success of actuaries in dealing mathematically with the probability of events in human populations, events which are determined by a multiplicity of causes, including the plastic behaviour of man who is generally considered to possess "that something extra" in greater degree than any other organism. The mathematics used to describe populations always deals with the probability of certain occurrences amongst large numbers of individuals, and does not assume precise and invariable behaviour of the individuals. For the preliminary study of a problem it is often convenient to assume that particular properties or influences are constants, but this is not a necessary assumption. If it is known that these properties or influences vary in an orderly way, terms can be introduced to represent this particular orderliness; and it should be noted that even choice and free will in man are known to produce orderly influences upon events, provided the number of men exercising these abilities is very large.

(e) The Collection and Interpretation of Evidence: Summary

The foregoing considerations show clearly that, in order to obtain a knowledge of populations and of the mechanisms which regulate them, we must be prepared to use all means available to us for ascertaining and interpreting facts, for each has special virtues and limitations. Extensive observation has provided us with some general knowledge which has proved invaluable in enabling us to ascertain the general features and characteristics of populations. Intensive observation of particular populations provides us with special information about these populations, and enables us to determine in a general way what factors are influencing them—but commonly it is difficult to disentangle the influences of the individual factors. Laboratory experiment enables us to separate these factors physically and to determine their separate influences, and with further experiments we can determine the effects produced by these factors upon one another, so ultimately enabling us to interpret intelligently what we observe in the field.

Observations and experiments, however, do not themselves provide answers to our problems. It is necessary to devote at least as much care and energy to their design and interpretation as to the collection of data. The history of population investigations shows that their weakness has been mainly due to the

inadequate use of rigorous thought; and the main source of error with theories and hypotheses has been a lack of a clear appreciation of the fact that conclusions reached can logically be applied only to situations which conform to the postulates upon which they were based.

Mathematics, being a particularly powerful tool of thought, should be employed wherever it is appropriate, but its limitations must be recognized. It is true that no equation could conceivably be produced which takes into account explicitly all factors known to influence populations; but this does not mean that mathematics is therefore useless when dealing with problems of natural populations, as some biologists appear to believe. However, there is no need to make equations as complex as this for, although the number of kinds of factors known to influence populations is very great, only a few of these significantly influence any given natural population. Moreover, it is often possible to represent the collective influence of a large number of factors by a single term, for in ultimate analysis all factors affect populations by influencing the birthrate and longevity of the animals, or the availability and quality of the governing requisites, or the magnitude of the maintenance quanta of the governing requisites for the animals under the prevailing conditions. Consequently, knowing the kinds of effects the various factors produce upon the properties of the animals and those of their environment, it is possible to determine the kinds of effects which will be produced upon the population by any change in one or more of the factors by using relatively simple equations, as has been done earlier in this article. Mathematics thus provides a ready means of determining how populations may be influenced by given environmental conditions, which is generally all we want to know; but, if a truly quantitative representation of a population is required, a precise quantitative study of all the factors in the environment and of their individual influences upon the properties of the animals must necessarily be made.

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