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THE NATURAL CONTROL OF ANIMAL POPULATIONS

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A. INTRODUCTION

While an understanding of the processes which regulate the abundance of animal populations is fundamentally important both to applied biology and to ecology in general, it is a subject on which there are very considerable divergences of opinion. These divergences, which have been so much discussed during the past two or three decades, may be attributed to a number of causes: to the common tendency to embrace partial, one-sided explanations instead of seeking a comprehensive viewpoint; to the diverse views engendered by the study of ecologically different groups of animals, or by a too exclusive attention to either the biotic or the physical aspects of ecology; and, besides these outcomes of specialization, to confusion and misunderstanding over the use of certain terms.

But perhaps the major cleavage is that between the upholders of a primarily deductive and of a primarily inductive approach to the subject. The mathematical theories of population interactions, such as the studies of Lotka, Volterra, or Nicholson & Bailey, have led to various conclusions which are sometimes taken as

proven biological facts. These conclusions are the results of deductions from a few simple assumptions. Even when the assumptions are correct as far as they go (and this is not always certain), the conclusions tell us only what would happen in an extremely simple situation immune from the usual environmental disturbances. In relation to natural populations, they should be regarded only as suggestions, though as such they may be an invaluable source of new ideas to be tested in the field.

The important work of Nicholson (1933) resembles the mathematical theories in being primarily deductive in its method. While Nicholson is able to draw on a wide biological knowledge and experience to select and support the premises upon which his theory is founded, and again to relate some of his numerous conclusions to known biological facts, the method remains primarily deductive, and the results cannot be accepted as biological principles until they are shown to correspond with the facts. The views of Smith (1935) resemble Nicholson's in some respects, but the greater part of Smith's argument is

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inductive; a summing-up of biological experience rather than a logical construction based on a few facts, principles or assumptions. Thompson's writings on this subject have been of both types, but he gives predominance to the inductive method of theoretical advance. His papers contain many valuable points, and the general outline of a theory which seems essentially sound, yet is scarcely developed beyond the stage of a few preliminary generalizations. In his paper of 1939 there is a critical survey of much of the literature, including a discussion of the methods and status of the deductive theories.

Of course, there is no clear boundary between inductive and deductive theory, and most authors make considerable use of both methods. In so far as the two types are distinct, both are necessary to the development of the subject, and only harm can be done by failure to recognize both the importance and the limitations of the mathematical type of theory. The inductive approach is the one which comes more naturally to students of a subject which is still largely descriptive. There is a great deal to be done in summing up and generalizing ecological knowledge in a form suitable for application in field investigations, so that both aspects of the subject may flourish as they cannot do separately.

The method of this paper is primarily inductive. I have attempted to give a general account and analysis of natural control in the light of the facts available and the theories that have been put forward to account for them. The point is not novelty, nor a complete review of the literature, but an attempt to provide a more complete and coherent theory than has been available, and to clarify certain issues which have been confused. I hope most readers will find something of interest in the result. To make the major ideas plain, I have excluded many minor points; and no doubt have missed many which might have been included. The discussion is developed with reference primarily, though not exclusively, to entomological data and theories. But I believe the principles outlined apply to most types of animal populations and to those of many micro-organisms.

Natural control will be taken to mean that regulation of the numbers of a natural population which keeps them within the limits of a more or less clearly definable though often very wide range of abundance. The simplest and most straightforward view of variations in abundance is that populations tend to increase when conditions are favourable, and to decrease when they are unfavourable. However, it is usual to regard animals as striving (or at least tending) to increase in numbers, but as being kept below certain limits by the resistance of the environment (Chapman, 1928, 1931), by their own limitations and the failure of the environment to satisfy their needs (Thompson,

1929c, 1939), by biotic control factors or by physical control factors (various authors), by intra-specific competition and natural enemies (Nicholson, 1933), or by density-dependent factors (Smith, 1935).

Control will be discussed in several different ways corresponding to different levels of organization. The first is the consideration of the *factors* responsible for control, for example, certain animals, plants, or features of the physical environment such as protective niches or temperature. In this approach, the environment, and the population's own activities, are divided into distinct elements which are regarded primarily as acting separately upon the population, though interdependent action is not necessarily ignored. Secondly, a better integrated approach is the consideration of working relationships or *processes* such as competition, parasitism, and density dependence. Thirdly, instead of analysing control in terms of factors or processes we shall sometimes consider it as a complete phenomenon, and this of course involves the consideration of *population variations* (this term will always be used in the sense of numerical or density variation only). Finally, control will also be considered as a part of the complex web of relationships which is a feature of the ecological entity comprising the population and its total biotic and physical environment (the *ecosystem*, to use the term suggested by Tansley, 1935).

It will be seen that the paper is divided into primary sections, A, B, etc., some of these being divided into secondary sections such as B₁, B₂, etc. In each secondary section the discussion is confined predominantly to one or other of the above-mentioned levels.

The plan of the paper may be summarized as follows: In section B a brief review of theories of control is given, progressing somewhat irregularly from factor theories to those with a more comprehensive approach. Section C is an attempt to outline a theory of control which is a synthesis and development of certain familiar generalizations; for convenience of presentation, the order of the secondary sections does not follow the series of organizational levels—C₁, C₄ and C₅ deal with population variations, while C₂ considers the whole ecosystem, and C₃ is an analysis chiefly on the level of processes. Section D deals with certain points, some of them less well established, which are placed here in order to leave the main section C clear of too many secondary issues. The trend in this section is from analysis by factors (D₁) to the level of population variations (D₂–D₄) and thence to the most comprehensive viewpoint (D₅).

For the purposes of analysis and discussion, certain terms are newly defined or given a more precise meaning than usual. While I have tried to avoid misleading usages, it may assist readers to have the

following reference list, showing the pages where the terms are defined or explained. Those not in inverted commas are employed in a sense well established in the literature. Terms used in one place only are not included in the list.

	PAGE
balance	26
biocoen	10
'capacity'	14
carrying capacity	5
(inter-)compensation	19
competition	15
'concurrent'*	13
'conservation'	20
density-dependent	4, 11
density-independent	4, 11
'density relationships'	13
ecosystem	2, 10
equilibrium	26
factor	2
'favourable'	11
'functional'*	16
'inverse'*	13
'limitation'	17
'numerical'*	16
overpopulation	5
'performance'	14
'release'	21
'restricted variation'	9
'supply factors'	12
'suppression'	19
'threshold phenomena'	10, 11
undercrowding	11
'unfavourable'	11
'variation(s)'	2

* Types of density relationships.

The term *population* as used here means a number of organisms of the same species forming a more or less frequently interconnected group, separated more or less clearly from other groups of the species.

B. THEORIES OF CONTROL

In this section, the theories of control that are of most interest at the present day are briefly reviewed. Comments on many important points are postponed to later sections, though some are taken up directly here. The selection, classification and the relative prominence given to the various theories have inevitably been somewhat arbitrary, and in this matter I must ask the indulgence of readers and authors.

A fuller discussion of the theories of the German biologists mentioned has been published by Schwerdtfeger (1941), and Thompson (1939) has discussed the theories put forward by British, French and American entomologists.

Among the theories of control, there is an historical trend from earlier theories which sought to explain control upon a comparatively narrow basis, to later

theories which are more comprehensive. There is a very general tendency among the earlier (and some more recent) theories to emphasize the importance of the physical environment in control, while underestimating the importance of the biotic factors, or vice versa.

B 1. EARLY 'BIOTIC' THEORIES

Of the two viewpoints mentioned above, the one more in keeping with the Darwinian trend of biology was that of the predominant importance of the biotic factors. Escherich (1914, 1924), for example, held that control of insect populations is due primarily to natural enemies, especially parasites, and that outbreaks are due to an unbalance brought about by the effects of weather conditions or food supply upon the host or its enemies (cf. Howard & Fiske, 1911).

Others, such as Friederichs (1927), recognized the complexity of the relationships between a population and its biotic environment. Control was attributed primarily, not to parasites only, but to the whole 'biocoenotic complex'.

B 2. THE COMPETITION THEORY

The work of Nicholson (1933) is related to the earlier parasite theories, inasmuch as it is predominantly a biotic theory of control. Nicholson's paper comprises (a) a general theory of control, and (b) a theory of the interactions between populations of enemies and those of their hosts or prey, and a study of the oscillations which are deduced to arise from these interactions. Confining our attention to (a) we may refer to the relevant parts of Nicholson's summary (p. 176):

'The densities of animal populations are known to bear a relation to the environmental conditions to which they are subject, and the existence of this relation shows that populations must be in a state of balance with their environments. For balance, it is essential that the action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way. Examination of the competition to which animals are subject shows that it is generally competition between animals when seeking the things they require for existence, or competition between natural enemies that hunt for them.'

Detailed investigation of the question of competition between searching animals shows that, whether the animals are controlled by competition for food, or for suitable places in which to live, or by the competition of their natural enemies, there is for each species a particular density, referred to as the "steady density", at which balance exists. The value of this steady density depends upon the properties of the species, the properties of the species with which it

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interacts, the nature of this interaction, and the properties of the environment.

'Competition always tends to cause animals to reach, and to maintain, their steady densities. Factors, such as climate and most kinds of animal behaviour, whose action is uninfluenced by the densities of animals, cannot themselves determine population densities, but they may have an important influence on the values at which competition maintains these densities.'

Various points mentioned in Nicholson's paper suggest the outlines of a broader view, obscured, however, by the too exclusive emphasis on biotic relationships. Thus it is noted that competition is the result of environmental limitations, though most emphasis is placed on the competition and very little on the environment. The modifying effects of climate and other factors on the results of competition are recognized. It is mentioned that competition may force surplus animals into unsuitable parts of the environment, where they are destroyed by the physical factors (pp. 139, 173; cf. Thompson, 1929*c*).

These points were given much stronger emphasis by Smith (1935) in his theory of the control of insect populations. While this had certain affinities with the competition theory, there were some important differences from Nicholson. Smith emphasized the distinction which had already been discerned by Howard & Fiske (1911) and Thompson (1928) between *density-dependent* mortality factors, which destroy a percentage that increases as the density increases, and *density-independent* mortality factors, whose effect is not related to population density. He considered the density-independent factors to be mainly climatic, while density-dependent factors included natural enemies, disease organisms, and also the supply of food, space, protective niches, etc., when these are limited, 'since they cause competition'. In spite of this last clause, he laid as much emphasis on density-dependent factors as agents of control as he did on competition. He allowed an important role to various processes which Nicholson had regarded as only minor items in control. He not only extended the category of density-dependent factors to include the aspect of the physical environment mentioned above, but also recognized that climate 'often operates quantitatively in much the same way that is characteristic of biotic factors, that is, it destroys a percentage which increases with density... It seems most probable that this takes place through the existence of protective niches in the environment which are more or less limited in number. Individuals in excess of this number and which can not therefore attain these niches are destroyed by unfavourable climate...' (Pp. 894-5.)

In short, Smith's paper provides a link between Nicholson's theory and the more comprehensive

theories of control, which are discussed in the last part of this section.

B 3. 'PHYSICAL' THEORIES

The vigorous development from the 1920's onwards of experimental work showing the importance of the influence of temperature and humidity on the rates of development, reproduction, etc., of insects, was naturally reflected in new theories of control. Thus Bodenheimer (1928, 1930, 1931) held that the population density of insects is regulated primarily by the effects of weather conditions on their development and more particularly on their survival. He held that a mortality of 85-90% among the early stages is the rule, and that the later reduction of the survivors by enemies, however striking to the observer, is therefore of minor importance. Janisch (1938, 1939) attributed basic importance rather to the influence of non-optimal weather conditions on the general 'constitution' of the organism, affecting its general performance and vigour. Uvarov (1931), emphasizing the strong influence of climatic conditions upon the rate of development and survival of insects, and the obvious correlation between population fluctuations and changes in the weather, seems to have regarded climatic factors as the major controlling agents. In a more recent attempt to sum up the position, Bodenheimer (1938) concluded that 'under normal conditions climate really controls population density in being responsible for the highest degree of destruction. It is, as a rule, the main factor as long as the saturation point of environmental capacity has not yet been approached. This is the normal condition for most animals and even for the longer span of life of species which are inclined to outbreaks.' On the other hand, he adds, biotic factors are important chiefly when a population has approached the environmental capacity, for only density-dependent factors can be relied on to reduce the numbers; but the special stress laid on parasites was unjustified.

These concessions made by Bodenheimer were scarcely such as to satisfy many of the critics of his theories. Schwerdtfeger (1941) points out that while they stimulated many useful new lines of investigation, the weather theories are fundamentally unsound. There is ample evidence that the high rate of mortality due directly to weather conditions, as claimed by Bodenheimer, is not at all general. But the fundamental weakness of these theories, in Schwerdtfeger's view, is the failure to grasp the close and many-sided dependence of a population upon the biocoenotic complex. The most damaging criticism, however, is that made by Nicholson (1933), that these theories fail to explain how physical factors, however important as causes of variation, could possibly regulate populations.

B4. THEORIES OF PERIODIC FLUCTUATION

(a) *Overpopulation theories*

Certain theories intended primarily to explain periodic fluctuations in numbers have an important bearing on natural control. A number of these are based on the general idea that some populations in favourable environments are able to increase in density over a period of years until a level is reached at which 'overpopulation phenomena' develop; these phenomena appear more or less suddenly and reduce the population to a low level. They then relax or disappear and the population goes through another period of increase. These theories relate to particular types of animals and differ as regards the overpopulation phenomena which are supposed to be effective.

(1) Eidmann (1931, 1934), reported that certain forest insects in Germany, in favourable areas, exhibit a gradual increase followed by a rapid fall in numbers, every 10–12 years. He concluded that the decline is due to 'overpopulation phenomena', such as overcrowding, damage to the environment, reduced fecundity, increased susceptibility to diseases, food shortage, and the increase of enemies (Eidmann, 1937). Schwerdtfeger (1941) showed that relatively few populations of the insects concerned show regular fluctuations, and that the reversal of increase (in one species and place) tends to occur at very different levels, often far below the density usually associated with the idea of overcrowding. He concluded that this theory can apply only in a very limited way, and that its chief value is in drawing attention to the importance of overpopulation phenomena as an item in a larger complex of controlling processes.

(2) Dymond (1947) put forward a theory to explain the periodic fluctuations of certain mammals and birds in Canada. In Dymond's words: 'Briefly the theory here offered to account for the periodicity in the fluctuations of the populations of lemmings, hares, voles, grouse, etc., is that the biotic potential of these animals is definitely greater than the normal resistance of the environment in which they live. In other words they are endowed with too high a reproductive capacity and it is the monotony or relative uniformity of the Arctic and far northern environment that accounts for the regularity with which they increase to the unstable level of numbers which brings about the periodic decline.' As to the causes of the decline: 'In the case of dense populations there appears to be a race between disease, emigration and starvation as to which is to reduce the numbers, with the decision determined largely by the reaction of the species to crowding.'

(3) Another type of idea, which may be referred to the general category of overpopulation theories, looks to predators as the chief agents of control, but sees

them as becoming really effective only when the 'carrying capacity of cover' in the environment has been exceeded. For a clear account of these ideas, put forward by Kalabukhov (1935) and others, we may quote from Elton (1942, p. 87): 'Kalabukhov points out that as a population of voles or mice or ground squirrels increases, the food supply on the occupied areas will tend to diminish. When food is scarcer the animals move about over larger distances. This greater movement exposes them more to their enemies and so mortality through these predators will be greater. Also, the deaths from accidents may be more frequent. "The more food there is in a given territory, the smaller is the radius of movement of rodents, and the less the possibility of their death from predators" . . . We might add to this (though he does not) the analogous and parallel action of disease: favourable food supply encouraging resistance, reduction of food supply, increased movement promoting the spread of disease organisms with a resulting higher (sometimes catastrophic) mortality.'

'Kalabukhov's theory has in it a flavour of the American idea of the "carrying capacity of cover", widely current now in game-bird population studies. This was crystallized in American research upon the bobwhite quail, which claims that there is a sudden rise in destruction by predators among quail populations that have begun to overflow the normal protective cover. Kalabukhov does not seem to have considered the fact that the food supply of many mouse-like rodents, and especially voles, is their cover, and that eating down the available food, besides causing increased movements, may often automatically expose the animals more to their enemies. This further concept reinforces his own theory.'

While the efficacy of predators as controllers of mammalian and bird populations is very doubtful (Elton, 1942; Errington, 1946), there is no doubt that the 'carrying capacity' or 'threshold of security' relationship is an important element in natural control.

(4) Clarke (1936) attributed the periodic (9–10-year) diminution in numbers of the ruffed grouse in Ontario to disease, caused by a blood protozoan or some other agent, which attacked the young birds at high population density.

In the same area, MacLulich (1937) studied the varying hare, which has a 10-year cycle, and concluded that the crashes of this species are chiefly due to various diseases. But the work of Green and his collaborators, chiefly in Minnesota, seems to establish that the only important cause of the periodic decline is 'shock disease', an idopathic hypoglycaemia which brings about a progressive increase in mortality of the young hares (Green, Larson & Bell, 1939; Green & Evans, 1940).

MacLulich observed: 'Population figures for the northern part of Frontenac county showed that in

times of abundance the hares occupied practically all types of habitat, whereas in times of scarcity they were confined to their favourite habitat.' Concerning the ruffed grouse, Clarke reported: 'The most suitable territories in any given area are occupied every year, less suitable ones only when pressure of increasing populations makes this necessary.'

(5) Besides the concept of overpopulation, most of these theories use this associated idea of 'overflow' from favourable spots into less favourable parts of the environment as the population density increases. The same idea was used by Thompson (1929*c*, 1939) in his theory of the control of insect populations. It was mentioned by Nicholson (1933) in relation to competition, and Smith (1935) noted its significance in enabling climatic factors to operate in a density-dependent manner.

This and other aspects of environmental capacity will be discussed in a later section. The chief point of interest at this stage is that, owing to the heterogeneity of most environments, overpopulation phenomena tend to set in long before the whole area is 'saturated'.

(6) In general, there is no reason why overpopulation phenomena should be regarded as peculiar to populations which fluctuate periodically. In fact, they are known to be widespread and common. But whereas they may possibly supply a complete explanation of the control of certain populations which fluctuate regularly, in general they do not account for the whole process of control. For example, in some cases it is quite clear that predators or parasites successfully control a population at a relatively low level, far below what could reasonably be called overpopulation. As will be seen in later sections, overpopulation phenomena are only one item of a larger category of processes which can contribute to natural control.

(b) Enemy-prey oscillations

The overpopulation theories deal with fluctuations as characteristics of primary, plant-eating animal populations; fluctuations of their predators are regarded as by-products, or reflexions of the primary ones. Another type of theory places equal emphasis on the fluctuations of a population and that of its predator (or parasite), and in fact regards the fluctuation as a result of the interaction of the two populations. This is the mathematically evolved theory, of which variants have been produced by Lotka (1925), Volterra (1926, 1931, etc.), and Nicholson & Bailey (1935) (see also Nicholson, 1933). Assuming a constant physical environment, and an enemy-prey interaction characterized by a very simple behaviour pattern and not interfered with by other species, it is calculated that the two populations should oscillate regularly above and below a mean level of density. The graph of density against time is in the form of the

now familiar wave-like curves, that of the enemy following somewhat later than that of the prey. The precision of these mathematical demonstrations, and the elegant regularity of the results, are achieved by assuming a very simple and regular (or constant) set of conditions, such as we should seldom expect to find in nature. These theories have not the same status as those based more directly on natural phenomena. While they are certainly a source of valuable new suggestions and working hypotheses, their conclusions, as remarked at the outset, cannot be regarded as biological generalizations unless they are proved by observation or experiment under natural or near-natural conditions. A valuable preliminary is to test them in laboratory experiments.

It is a significant fact that, even under highly simplified conditions in the laboratory, the periodic oscillations predicted by the mathematical theories can be demonstrated only with great difficulty. Gause (1934) produced the phenomenon in mixed cultures of *Paramecium* and yeast, but only by careful manipulation of the cultures. He also demonstrated it with *Didinium* and *Paramecium* together, but again only by repeatedly introducing additional individuals of both species. De Bach & Smith (1941) were able to bring about the greater part of a complete cycle with interacting populations of housefly pupae and the parasite *Mormoniella*. There were seven successive 'generations', which were in fact separate 24 hr. experiments under the same conditions except that each experiment after the first was started with a number of parasites equal to the number of puparia parasitized in the previous experiment, and with a number of puparia equal to twice the number escaping parasitization in the previous experiment.

While recognizing the great interest of these experiments and their results, we may note that they seem more akin to the hypothetical situations of the theories than to natural conditions. A wide gap remains to be covered.

It seems probable that the periodic fluctuations of *Tribolium* in cultures are of the same nature as those we have been discussing, but they must be very complicated, for the larvae and adults act as predators upon the eggs, and the larvae are parasitized by the Sporozoan *Adelina* (Chapman, 1928, 1933; Chapman & Whang, 1934; Ford, 1937; Park, Gregg & Luterman, 1941; Park, 1948).

Since periodic oscillation is difficult to produce even under rigidly controlled experimental conditions, it is doubtful whether many oscillations observed in nature can correctly be claimed as examples of it. Any such tendency is likely to be complicated and obscured by the effects of many factors not considered in the theories.

It might be expected that examples of these 'classical' predator-prey oscillations could be found

among the populations of rodents and their predators, discussed by Elton (1942), Dymond (1947) and others. It seems to be generally agreed, however, that the predators 'are seldom a master factor in bringing rodent outbreaks under control' (Elton, 1942, p. 60; see also Errington, 1946). Only if a predator population, whose fluctuations followed those of the prey, also played a dominant role in the reduction of the prey at the periodic crises, should we have good reason to suspect the presence of a relationship like that described in the mathematical theories. If, as held by Dymond, the Arctic environment is steady enough (or barren enough, to mention another possibility) to allow the appearance of regular fluctuations due to overpopulation phenomena, it is reasonable to seek there, if anywhere, for examples of periodicities controlled by predator-prey interaction.

(c) *The meteorological theory*

Elton (1942) has examined a very extensive body of data on rodent populations, and concluded that periodic changes in the physical environment must play some part in causing the fluctuations in numbers, or at least in making them regular (cf. Huntington, 1931; Severtzoff, 1934; Errington, 1945). But however important physical periodicities (seasonal or otherwise) may be in relation to fluctuations of populations, they do not seem to offer an explanation of natural control. The main interest of these phenomena to the present discussion lies in the question, to what extent they account for the periodic population fluctuations which the overpopulation theories were evoked to explain. But even in this respect they are not of great importance here, for the significance of overpopulation phenomena as agents in natural control by no means depends only on the importance or otherwise of these phenomena as causes of periodic fluctuations.

B 5. COMPREHENSIVE THEORIES

The term comprehensive is intended here to apply to theories which do not attribute control predominantly to parasites, competition, or biotic factors, nor on the other hand to physical factors, but rather recognize that all types of factors may be involved, and that relationships which are predominant in some circumstances may be relatively insignificant in others. The case for such a standpoint will be more fully examined later. The theories that are most in keeping with such a broad view (at least in the entomological field) are those of Thompson (1929c, 1939) and Schwerdtfeger (1941).

Thompson's viewpoint may be summarized as follows: Each species has its own characteristics, including specific needs and limitations. Optimal environmental conditions, in which these needs are

(best) satisfied, are approached at relatively few points. The species multiplies in these favourable places, and the surplus animals so produced are forced out into less favourable places, and so on, so that the increase of the population is first retarded and finally stopped. In general, the control thus exercised is due not only to one or two 'controlling factors' which predominate at all times and places, but to the whole complex of environmental factors, biotic and physical, of which different factors are predominant in different situations. Density effects also operate against increase in the favourable situations. Furthermore, the environmental conditions are subject to change and so bring about reductions in density from time to time. Control is generally due mainly to physical factors in the environments less favourable to life, where density is low; biotic factors are important chiefly in physically favourable environments where density is high. The diversity and other characteristics of the physical environment are an essential element in competition and other density-dependent processes.

Thompson does not attempt any pronouncement as to the relative importance of physical and biotic factors to control *in general*, but contents himself with the conclusion that control is due to the whole complex of factors of all types, of which some are predominant in some circumstances, others in others. The idea of 'overflow' from favourable niches was given prominence by Thompson (1929c), and also by Smith (1935), though Nicholson (1933) did not attach special importance to it. The occurrence of this idea in the overpopulation theories has already been noted.

Schwerdtfeger (1941) deals primarily with population variations and their causes rather than with control. He considers in some detail the effects of various factors upon the egg-output and the mortality of insects. His data on forest insects support the conclusion that a large number of factors of all types operate together and in succession, with varying intensity, to bring about the major fluctuations in numbers. The importance of particular factors varies with the species, stage of development, density, time and place.

On the question of control, he accepts, without discussion, the conclusion of Smith (1935) and others regarding the role of density-dependent factors as the regulators of numbers. But he has also another viewpoint on this matter which arises from the consideration of the whole ecological system of which the particular population is a part.

The many factors of significance to the variation of a population he regards as an entity, the *gradocoen*, which is an intricate system comparable to a three-dimensional network (cf. the concept of the *holocoen* put forward by Friederichs, 1930). It includes the population itself. This system tends to achieve and

maintain an internal equilibrium; systems which fail to maintain equilibrium break up and are absorbed by others, or replaced by newly reconstituted systems. Any undue deviation from normal by one of its constituents is opposed by the elasticity and stability of the system. This idea will be examined below.

Meanwhile, we may note that Schwerdtfeger and Thompson agree that in the problem of control we have to do with a complex of factors, not one or a few 'controlling factors'. Schwerdtfeger goes further than Thompson in considering the complex as a system, operating as an entity, and tending to preserve an internal equilibrium. According to Schwerdtfeger, control is due to this equilibrating tendency of the whole system of which the population is a part, but at the same time he accepts the idea that the actual regulators within this system are the density-dependent factors. According to Thompson, the density-dependent processes which bring about control arise from the complex of factors, including both biotic and abiotic types.

Schwerdtfeger's 'gradocoen' is a sort of ecological unit, comprising all the biotic and abiotic elements directly or indirectly of importance to the variation of the population selected for study. It consists of a 'holocene' (Friederichs, 1930) or 'ecosystem' (Tansley, 1935), except that we exclude any elements which seem to be irrelevant for our purpose.

According to Schwerdtfeger, such a system would maintain an internal equilibrium; but as is often the case in biology, the word is used rather loosely here. It is not meant to imply that the population and all the relevant environmental factors are constant, but it means that they are dynamically interrelated in such a way that excessive variation by any of them is checked by other components in the system, or, more correctly, by the elastic inertia and stability of the system as a whole.

Whether or not it is advisable to use the term equilibrium in this way, for our purpose the chief points in this part of Schwerdtfeger's theory are the ideas involved in his view of the interconnectedness and elastic stability of the gradocoen. These will be discussed in the sections immediately following. Of course, the idea that all types of factors form an interdependent system has been approached or adopted by a number of ecologists in works not primarily concerned with control, e.g. Allee (1934a), Eggleton (1939), and Park (1942).

C. ESSENTIALS OF NATURAL CONTROL

C1. VARIATION, CONSTANCY AND CONTROL

The causes of variations in numbers are often obvious enough in a broad way, though precise knowledge has been reached only for a few ecological situations. It is

widely agreed that variations in the physical environment are, directly or indirectly, the major cause of population variations. That is not to say that biotic factors, such as food supply and enemies, do not generally play an important part in bringing about variations; nor that, when the physical environment is relatively constant, they do not come to play the dominant role. But in the great majority of cases, and particularly with insects, it is clear enough that numerical variations primarily reflect changes in the weather. The weather affects populations in many different ways; it can influence the reproductive rate and the mortality rate, the food supply, and the activity of enemies, to say nothing of more indirect and complex relationships. Even variations which seem to be due primarily to a succession of separate generations, as in many insects, may largely reflect favourable and unfavourable periods in the seasonal cycle; and in any case, seasonal climatic factors are responsible for the sorting out of the generations and keeping them separate, for example by killing off all but one particular resistant stage at regular intervals. To discover which aspects of weather are significant in causing variations in numbers, and precisely how they do this, often requires very close knowledge of the habits and habitats of the species concerned.

The range of fluctuation from year to year is very variable. The ratio of the highest to the lowest annual population observed was 32 : 1 for a population of the coccid scale insect *Ceroplastes floridanus* in Palestine, but only 3·8 : 1 for the scale *Parlatoria camelliae* (Bodenheimer, 1938, p. 103), over 33 : 1 for annual larval populations of wheat midges at Rothamsted (Barnes, see Williams, 1947), over 10,000 : 1 for the pupae of the moth *Panolis piniperda* in certain localities in Germany (Schwerdtfeger, 1941, p. 266), and 36 : 1 and 24 : 1 for the Canadian sockeye salmon in two different rivers (Dymond, 1947). By marking and retrapping, Green & Evans (1940) estimated the population of the varying hare on an area in Minnesota; the rates of the highest to the lowest annual population in the cycle of the 1930's was about 10 : 1. Schwerdtfeger (1935) gave data on the variation from year to year in the population density of four species of forest insects in various places in Germany, over the period 1885–1932. The greatest increases recorded are 29-, 41-, 47- and 93-fold respectively; the greatest decreases are 125-, 200-, 250- and over 3000-fold respectively.

The range of fluctuation in numbers within a year is again very variable, even for the same population. Bodenheimer's data from monthly counts of *Ceroplastes* show the ratio of the highest to the lowest monthly count in 1929 was 270 : 1; in 1931 it was only 7 : 1; for *Parlatoria* it was 43 : 1 in 1936, but only 9 : 1 in 1933. Cutler, Crump & Sandon (1922) reported

that the numbers of a species of Protozoa in the soil sometimes varied from a few hundred to 400,000 or more within 24 hr.

Some populations give an impression of steadiness rather than of variability in numbers. None, of course, are perfectly constant, and some degree of variation is always found upon close examination. When a fairly steady level is maintained, it seems generally to be due to self-regulatory action by the population itself in a comparatively stable environment. For example, some of the birds which maintain a territory system tend to occur in the same numbers year after year in the same locality (Nice, 1937; Lack, 1943). Complete annual censuses of the heron population of Cheshire and South Lancashire in 1939–45 gave figures ranging from 68 to 108 % of the 'normal' population total; and this was during a period of relatively 'marked fluctuations' (Alexander, 1946). Populations of *Drosophila*, cultured under constant physical conditions on an adequate food supply, have been reported to rise to a more or less stationary level of abundance (Pearl & Parker, 1922a, b). The data of Bodenheimer (1938), however, show marked oscillations within a limited range of high numbers, and he described this phase of the population's existence as the 'period of oscillations about a stable maximum'. A nearly steady maximum abundance under special culture conditions has also been observed with *Tribolium* (Chapman, 1928), but over long periods the numbers of this beetle pass through marked oscillations (cf. Chapman, 1933; Chapman & Whang, 1934; Ford, 1937; Park *et al.* 1941). This may be attributable mainly to cannibalism by the larvae and adults, and to the Sporozoan *Adelina*, features which are to some extent special, but by no means unique. It appears that certain other beetles, cultured under similarly standardized conditions, also suffer persistent fluctuations in numbers (Park *et al.* 1941; the coefficients of variability were 39 % for *Tribolium*, 35 % for *Gnathocerus cornutus*, and 69 % for *Trogoderma versicolor*. See also Crombie, 1945, 1946). In other words, the 'equilibrium' number is steady only in a loose sense, and a close approximation to absolute steadiness is very difficult to maintain, even under artificial conditions.

It may be that a closer approach to a steady number can be achieved by some animals, but, owing to experimental difficulties and the long time involved, population growth experiments are often abandoned soon after the numbers appear to have reached a maximum. As shown by the above-mentioned experiments with beetles, the apparent constancy may be only a temporary phase, followed by a succession of fluctuations which may be relatively slow. Whatever happens in laboratory cultures, it is obvious that in nature, climatic variations, to say nothing of other important

factors, are likely to upset any tendency towards precise constancy.

Whether we emphasize the steadiness or the variability of populations is largely a matter of our scale of reference. In spite of variations in density, it is very often possible to recognize for a population a characteristic general level or range of density. Some species, in certain environments, usually occur in large numbers, while others usually occur sparsely. This characteristic order of abundance may be quite different for the same species in different environments, and it may change from time to time even for the same population. Nevertheless, it can generally be specified for a given population over a more or less extended period. It may be regarded as an index of the capacity of the environment to support the species concerned, and of the species to maintain high numbers in that environment.

In discussing the variability of populations, Smith (1939; and cf. Chapman, 1931, p. 204) wrote: 'Paradoxically, animal populations are characterized both by their stability and by their incessant change. Some biologists emphasize one of these aspects, some the other. Actually these expressions are both descriptive of animal populations just as much as they are descriptive of the weather, which changes from day to day but which over a longer period of time is very stable. These characterizations of populations are not inconsistent if it is remembered that they are meant in the relative sense only. Population densities therefore have both static and dynamic qualities, the distinction being analogous to that between climate and weather.'

Undoubtedly there are elements both of constancy and of variability. In a precise sense, populations often vary greatly in numbers; in a very broad sense, they may be regarded as fairly constant. But since an alternation between two opposite viewpoints is often inconvenient or confusing, it seems preferable to combine them and to think of populations as undergoing *restricted variation*. This is the state to which populations are confined by the processes of natural control. If there were no control, variation would be unrestricted.

C 2. THE FUNDAMENTAL RELATIONSHIPS IN POPULATION DYNAMICS

To understand the variations in numbers within populations, and the restriction of these variations, we must consider first of all the most general relationships between a population and its surroundings. The total situation comprising a population in its biotic and physical environment is divisible into many components, among which there are many interrelationships of varying significance. Everyone is familiar

with the complexities that appear if we set down a number of components, and draw in the various influences which are known to operate, whether in general or in relation to an actual example. We soon reach an impressive tangle of interrelationships, and the conclusion becomes inescapable, that the population and its whole environment operates as a single complex.

Nevertheless, we can reach more precise knowledge of the processes at work only if we deal with one or a few aspects of this complex at a time, and consider them almost in isolation. There is a natural tendency to forget the complex background from which the objects of study have been abstracted. This gives rise to many optimistic but wrong conclusions. All conclusions drawn from simplified pictures or experiments should be referred back to the natural situation, to find to what extent they remain valid, or can be expected to do so, in the complex conditions which prevail there.

The most realistic view, though not invariably the most useful, is one which embraces the whole complex of population and environment. Tansley (1935) introduced the term *ecosystem* for the system comprising the animals and plants in a given environment, and the physical environment itself. The term *holocoen* seems to have the same meaning (Friederichs, 1930; Schwerdtfeger, 1941) and the idea of an all-inclusive 'super-organismic unity' was discussed by Allee (1934a).

Clements & Shelford (1939) set out to classify the interactions within such a system. They considered the primary set of interactions to be that between physical environment and the entity comprising all the inhabitant plants and animals. This totality of organisms has been called the *biocoen* (Friederichs) or *biome* (Clements). Such a procedure implies, among other things, that the plants and animals are influenced by the physical environment in analogous ways. It seems a very reasonable viewpoint, and in fact the idea of the biome as an entity has gained wide acceptance (Tansley, 1935). (The use of the alternative terms *biotic community* and *complex organism*, and the viewpoints implied, are much more controversial steps, but need not concern us here. It must be noted, however, that the term biome has also been used by some writers to denote a biotic community, or a biotic formation, e.g. Carpenter, 1939.)

In whatever manner we may find it convenient to subdivide the ecosystem, one of the most difficult and least realistic of major divisions is, in some ways, that between a population and its environment. But because such an approach is demanded by long-established traditions of thought, and because it is so familiar, we tend to overlook the serious difficulties it raises.

A major anomaly appears in relation to endoparasites and other organisms living inside the bodies

of animals. If we attempt to make any simple descriptive distinction between the host population and its environment, we are confronted with the question: Are intracellular symbionts, trypanosomes in the blood stream, toxins released by parasites into the blood, etc., to be classed as parts of the host, or of the environment? Any simple spatial distinction between the two is impossible, and any more complicated distinction is very difficult to maintain consistently.

Another serious anomaly arises if we try to think in terms of the population as something tending to increase, and of the environment as something which opposes this increase. This distinction between a striving population and a resistant environment cannot easily be maintained because a part of the restrictive processes (sometimes a major part) arises from activities of the population itself, such as cannibalism, intra-specific competition, spoiling of the environment, etc. In fact, the tendency to increase may be opposed as much by the activities of the population itself as by the environment, though for the most part we are faced with an intricately combined action by population and environment together. Hence any idea that the environment can be clearly distinguished from the population on a functional basis is illusory.

The reason why the population/environment distinction gives rise to such anomalies is that *the population functions in relation to a whole which includes itself*. It is therefore better to think of the population as an integral part of the ecosystem. If we wish to consider the population as an entity in relation to its ecological setting, that setting should be the ecosystem, rather than an imaginary 'ecosystem minus the population', called the environment. This is not to say that the environment concept should not be used, but rather that we should remember its defects and be ready to replace it whenever necessary.

C.3. DENSITY RELATIONSHIPS

(a) Threshold phenomena

As we have noted, the density or numerical status of a population is usually variable, but only within certain limits. The essential feature is that, as density increases, the probability that the trend will be reversed, that the numbers will begin to suffer a decline, becomes greater and greater, until we reach an uppermost level beyond which the population density is never observed to pass. Correspondingly, the proportional rate of increase often declines as population density increases (cf. Allee, 1931, 1934b; Pearl, 1926; and others); such a relationship is of course the basis of the logistic curve and formula for population growth.

These relationships come about in two ways:
(a) through the fact that new and more severely

unfavourable processes come into play at successively higher levels of density, and (b) by an increase in the intensity of action of various individual factors or processes (density-dependent action).

The entry of new types of unfavourable* processes as density increases was pointed out by Howard & Fiske (1911), who concluded, from their work on leaf-eating Lepidoptera, that parasites were the predominant unfavourable factor at moderate densities, disease when the insects had reached a density far beyond the average level, and famine at the very highest levels. MacLagan & Dunn (1935) concluded that natural populations are automatically checked by density effects (such as depression of reproduction by overcrowding) when all the other inhibiting factors have failed. Some of the well-known phenomena of overcrowding, which will be referred to later, appear only above a certain high level of density, though others are merely intensifications of activities which occur at all densities.

On the other hand, certain 'undercrowding' phenomena, such as a reduced reproductive rate because of infrequent encounters between the sexes, occur only *below* a certain level of density. On the whole, this class of unfavourable influence is much less important than the reverse.

Little is known about thresholds of activity for favourable processes, but the truth and importance of the threshold principle in relation to unfavourable influences is obvious enough. A great deal remains to be done, of course, in demonstrating how it works in specific cases, determining the threshold levels, and studying the causes of variation in these levels. The quantitative data now available relate chiefly to the densities at which crowding effects begin to hinder the increase of certain species. Some interesting figures published by Errington (1945) on the rates of increase and of decrease of bobwhite quail populations in relation to density show very clear threshold effects.

(b) Density-independent and density-dependent factors

The distinction between mortality factors whose intensity of action (proportional effect) depends upon the population density, and factors whose action is independent of density, was first drawn by Howard & Fiske (1911), and later by Thompson (1928), Zwölfer (1930), Smith (1935) and others. We shall make this distinction not only among mortality factors, but among all types of factors or processes.

There has been (and still is) a general tendency to identify density-dependent action with biotic factors, and density-independent action with physical factors, although Thompson (1939) pointed out that nature is

* That is, unfavourable to increase or to the maintenance of the present density. 'Favourable' will be used in the opposite sense.

by no means so simple; the extent to which such a classification over-simplifies and distorts the facts will be apparent from the following discussion.

To consider, first, the *density-independent factors*, we may quote from the valuable paper by Smith (1935, p. 890): 'In general, excessive heat or cold, dryness or humidity, wind or rain will destroy the same percentage of insects regardless of whether they are abundant or rare. Intrinsic weaknesses... also belong in this category, as would non-contagious or non-infectious diseases, and malnutrition due to condition, but not quantity, of food.' (The 'intrinsic weaknesses' concerned are postulated as the causes of the high mortality regularly observed among certain insect larvae.) Density-independent factors often vary a great deal in their intensity from time to time, but these variations are independent of the population density, even if there is sometimes an accidental parallelism.

Notwithstanding the above quotation, Smith himself (*loc. cit.*) and Thompson (1929*c*, 1930, 1939) pointed out that climatic and other physical factors are by no means necessarily density-independent in their effects upon the population. This is because they often operate in combination with density-dependent processes. For example, in the event of drought (density-independent), members of a susceptible species may congregate in niches where extra moisture or protection from evaporation enables them to survive. But the proportion able to survive depends on the size of the population. The favourable space may be sufficient for no more than x individuals. Then roughly x individuals will survive whether the original population was $100x$ or $1000x$. This is a picture, though admittedly an over-simplified one, of density-dependent action brought about by the limitations of the environment (Thompson), or by competition (Nicholson, 1933), according to one's viewpoint. For the present purpose, it shows how a 'density-independent factor' may be involved as an essential element in a density-dependent process; for there would have been no such all-important competition or selection by these niches without the drought conditions in the rest of the environment (cf. Thompson, 1939). This is the sort of complication to be expected from the fact that different factors do not act in isolation, but are subject to the dynamics of the whole ecosystem.

The example also emphasizes the point that it is sounder to consider density-dependent or density-independent processes or actions, than to classify factors on this basis. Not that the latter is impossible. Even in the above example, we may say that the physical factors contribute a density-independent component to the total operation.

Another way in which density-independent and density-dependent factors may be involved in

combined action is seen in cases when weather conditions promote the outbreak of disease. Thus according to Eckstein (1939), certain outbreaks of bacterial or fungal disease among cockchafers in Germany are primarily due to the effects of climatic conditions upon the susceptibility of the larvae and the properties of the soil, as well as upon the population density. (A number of analogous examples are treated from a different angle in Section D 1.) It may be noted also that the density dependence of biotic factors may be so slight as to leave them practically density-independent. For example, the attacks of a polyphagous predator upon a particular population may depend on the availability of alternative prey species, and scarcely at all upon the density of the population in question.

A thorough analysis of any situation would probably have to go beyond a simple division into density-independent and density-dependent factors, and consider degrees of density dependence. Nevertheless, the simple distinction is a very valuable working method, as shown, for example, in the investigations of Errington (1945) on the bobwhite quail.

Density-dependent action is exemplified most clearly by certain biotic factors. Howard & Fiske (1911) considered that parasites were the chief density-dependent factors controlling the numbers of insects, and Smith (1935, p. 890) held that 'entomophagous insects would have to be ranked at the head of the list in general, although in certain specific cases infectious and contagious diseases would precede them'. The natural enemies and pathogenic organisms whose density-dependent action is most pronounced are those which depend wholly or mainly upon the population for hosts or prey. Such enemies tend to affect a greater proportion of the population as it becomes denser, since they are able to find victims more easily and furthermore (in many cases) are thereby enabled to increase in greater proportion than the increase of the host or prey (see, for example, Gause (1934) and Smith (1935) on experimental studies of the relationship between the fly *Phormia groenlandica* and its parasite *Mormoniella vitripennis*, and De Bach & Smith (1947) on the relationship between the same parasite and *Musca domestica*).

Another type of density-dependent action (since we do not propose to restrict the term to mortality factors) is that due to *activities* of the population itself. Under crowded conditions, the mutual interference with feeding, mating and oviposition, and the metabolic effects of continual stimulation, tend to reduce the output of fertile eggs, the rate of development, and the longevity of animals. Other unfavourable activities, such as cannibalism and all forms of intraspecific competition, tend to be intensified as density increases (see Chapman, 1928; Stanley, 1932, 1938; Park, 1932, 1933, 1934; Chapman & Baird, 1934;

Crombie, 1943; and others, on cannibalism in *Trifolium*). Mutually aggressive behaviour tends to appear at high densities among mammals, for example lethal fighting occurs in dense laboratory populations of voles (Elton, 1942, p. 205) and is responsible for a high mortality in dense natural populations of muskrats (Errington, 1946, pp. 152-3). Intraspecific aggression appears even at apparently low densities among some of the birds which maintain exclusive territories.

Density-dependent action also arises when some of the things needed by the population are in limited supply. Food-supply, when it is not much greater than the needs of the population, becomes less adequate as the density increases; the denser the population, the smaller is the share of food per individual. This is partly a numerical relationship, and partly due to the reduction of the total food supply by the population. Similarly, space may become a limiting factor as the density increases (cf. Smith, 1935, p. 890). But while the density-dependent effect is brought about by the action of the population in depleting the supply, this could not occur if the supply were much greater than the needs of the population. Hence the limitations of the environment play a part in the process. (It will be convenient to refer to such factors as *supply factors*.)

Finally, a common type of density-dependent action arises from changes brought about in the physical environment by the population itself. They include what is usually called 'conditioning', i.e. contamination of the environment by excretions, secretions, decaying bodies, and carbon dioxide; also changes in the temperature or humidity brought about by the animals. The denser the population, the more marked do such changes become, and any harmful effects on the population are intensified (e.g. Park, 1938). The influence of various animals upon the vegetation, the soil, the aquatic environment, etc., is often considerable, and raises many economic problems. Such modification of the environment is recognized as an important element in ecological succession and related changes (e.g. Fuller, 1934; Hutchinson, 1941). Of course, populations often influence the environment in a way beneficial to themselves. Summarizing this matter in his review of density effects, Hammond (1938, 1939) wrote: 'On the credit side of the ledger, it has been shown that in such diverse forms as protozoa, crustaceans, worms, marine and fresh-water fish, and amphibians the formation of groups may be a protection against toxic substances dissolved in the liquid medium, the presence of noxious solids, extremes of temperature, and other elements of bad environment. Under certain conditions a group of these animals may bring the medium more nearly to optimal conditions or perhaps contribute some important substance to it

and so increase their own rate of growth or reproduction. Increasing population density up to a certain point has been shown to increase the longevity of *Drosophila* and to increase the net rate of reproduction of *Tribolium*.

Modifications of the environment may be favourable up to a point, and then become unfavourable. Oxley & Howe (1944) and Wilson (1946) showed that insect populations in bulk grain cause a persistent rise in temperature. This change is at first favourable and enables the insects to multiply more rapidly. But when the temperature passes beyond the optimal level, conditions become progressively unfavourable, and finally the insects die out or migrate to the surrounding grain.

The prevalence of density-dependent effects arising from mutual interference, and of those due to modification of the environment, has been established by a large body of work, chiefly on insects and micro-organisms. The results and conclusions have been discussed in reviews such as those by Allee (1931, 1934b, 1941), Ford (1937), Hammond (1938, 1939), MacLagan (1941) and Park (1941), and in shorter reviews of special aspects in many research papers.

In the above treatment of density dependence and density independence, emphasis is laid upon them as *processes*, involving the population as well as the factors which act upon it. This procedure differs widely from that adopted by Voûte (1943), who has put forward a scheme of classification of the 'resistance factors' (i.e. unfavourable factors) affecting insect populations. Voûte first divides all resistance factors into two groups: (A) factors which influence all members of a population, physiologically (e.g. temperature); and (B) factors which influence only certain members, 'mechanically' (e.g. parasites, predators). Then each group is subdivided into: (I) factors completely independent of density, (II) factors whose effect on the population depends on its density, and (III, in group B only) factors whose own development, as well as their effect, depends on the population density (e.g. monophagous parasites). Group B I is further subdivided. The result is a complicated scheme, which seems rather arbitrarily constructed, and is difficult to use. It is doubtful whether such a classification justifies itself. The scheme and its attendant terminology may be seen in use in a recent discussion on control (Voûte, 1946).

(c) The form of density relationships

If we wish to make a more precise study of density-dependent processes, we are faced with some uncertainty about the scope of the term. As indicated below, it might be taken to apply broadly to a whole class of processes, or strictly to one particular type.

To avoid confusion, it will be best to use other terms in defining these categories.

The widest reasonable extension of the term density-dependent would cover the whole class of what will now be called *density relationships*, i.e. all relationships which are significantly influenced, directly or indirectly, by the density of the population.

As noted already, a density relationship may operate only above or below a certain threshold level of density. Alternatively, it may be in force at all densities. In either case, within its range of operation, the intensity of action of a density-related process either increases or decreases as the density rises.

Thus we may distinguish between (a) *concurrent* density relationships, in which the intensity of the action rises as density increases, and falls as density decreases, and (b) *inverse* density relationships, in which the intensity of the action falls as density increases, and rises as it decreases. It is important to note that, in making this distinction, we are referring to the intensity of action *per individual* member of the population, or to the *proportional* effect on the population as a whole. A predator species may kill more and more individuals as the population increases, but if it does not kill an increasing *proportion* of the total population, then its action is not concurrent. If the proportion killed decreases as density rises, the action is inverse. (If it remains constant at all densities, or varies independently of density, the action is density-independent.)

The term density-dependent, in the moderately restricted sense implied in earlier pages, is synonymous with the term concurrent; i.e. they both cover the processes associated with typical parasites and predators, disease organisms, cannibalism, competition for space and food, and modification of the environment.

While *inverse processes* seem to play a much less important part in population dynamics than do the concurrent types, they are worthy of some attention. An example of an inverse process is to be seen when there are insufficient encounters between the sexes to provide for prompt mating, or to provide for the frequent recopulations required to secure a maximal egg-output in certain insects such as *Tribolium* (Park, 1932, 1933); the degree of sex isolation is inversely related to density. Again, many birds which feed on a number of insect species do not increase their consumption of any one species as its numbers increase, or at least not in proportion to the increase in numbers (Tothill, 1922). Hence the percentage mortality due to such a factor declines as population density increases (cf. Nicholson, 1933, p. 171; Smith, 1935, p. 889). The same thing happens even with predators or parasites living on the one species exclusively, provided their rate of increase is relatively slow and their individual capacity for attack is sufficiently limited.

Thus Tinbergen (see Hartley, 1947) found that the intensity of predation by hawks on passerine birds was concurrent, within certain limits; but when the prey species was increasing much more rapidly than the predator, the effect of the latter was proportionately smaller, although the prey density was higher (cf. Flanders, 1935).

The action of any unfavourable processes which are inverse will decline as density increases. Together with favourable concurrent processes, their effect is opposed to that of most density-dependent factors.

What can be said concerning the quantitative aspects of relationships between density and the performance* of populations? One of the assumptions on which the logistic law of population growth is based is that the rate of increase is an inverse linear function of the population density (cf. Smith, 1935; Crambie, 1945). The same assumption is made by Volterra (1926). In laboratory populations, such as those of certain insects which have been studied from this point of view, there is sometimes an inverse linear relationship between density and an aspect of performance or some activity which has been measured (Park, 1933; Chapman & Baird, 1934; Stanley, 1941; Crambie, 1943, 1945). But this is far from being a general rule, and many other types of relationship have been found in experiments of this sort. The analysis of these relationships, the fitting of curves to the data, and the interpretation of the results in biological terms form an interesting offshoot of the main problem of natural control.

For natural populations, however, no simple relationships are likely to be traceable, or even to exist, in a precise or constant form. We have to deal with relationships as they appear in variable conditions, and as interdependent parts of dynamic complex. Yet density relationships undoubtedly exist under such conditions, and they have been demonstrated by quantitative data in a few cases. We need many more data of this sort. Of course, there are many difficult problems associated with getting quantitative data, in a form suitable for the purpose, and with analysing them successfully, and the development of this subject depends primarily upon investigators who count such problems among the attractions of the study of natural populations.

(d) *The causes of density dependence*

(i) *Limited capacity of the environment*

The fact that the environment participates in density related actions is obvious enough, for the

* 'Performance' will be used in a broad sense, including both the level of density and the current rate of increase or decrease of a population. Either of these alone, or the rates of development, reproduction or survival, are *aspects* of performance.

majority of density dependent factors are physical or biotic environmental factors. It is also clear that any density relationship is subject to the modifying influence of the rest of the ecosystem; for example, mutual interference in crowded conditions is likely to be greater when the temperature is high.

That this is not the full extent of environmental participation in density relationships follows readily from the foregoing passages. We have seen, for example, that the amount of modification of the environment by a population is density-dependent, and reacts back upon the population accordingly. It may also be noted that the degree of shortage of food is density-dependent, and this applies equally to space or any other supply factor. The density dependence arises both from the automatically reduced share per individual when there are more individuals, and from the action of the population in reducing the total supply. Even in the case of mutual interference due to crowding, the environment plays an essential part by restricting the free expansion of the population.

In fact, a fundamental reason for all the above types of density-dependent actions is the *limited capacity of the environment* to maintain large numbers of the species concerned. The capacity of an environment with regard to a species would be measured by the overall density or total numbers of that species which the environment could support. The capacity of an environment is different with respect to different species, and for any one species it changes with the variations of the environment. It may be reduced or increased by the population itself, as when the total food supply is depleted or the environment favourably modified.

The limiting effect is not imposed suddenly and rigidly at a fixed level of density, but gradually and flexibly and in relation to an upper limit which varies. The controlling factors concerned are density-dependent in their action because the limitations of the environmental capacity affect the population in some degree even when the environment is far from being fully occupied. For example, if space or food supply are limiting factors, the share per individual may be more than sufficient up to a particular level of density, then gradually recede from optimum as density increases, until the absolute minimum necessary for survival is reached. (But there is usually a tendency at suboptimal levels of supply for some individuals to get an adequate share while others do poorly and perhaps fail to get enough for survival.) Some of these effects may be found even at the lowest densities, though most operate only above a certain threshold. All of them tend to operate more intensely as density increases. In other words, the more nearly the capacity limit of the environment with respect to a particular species is approached, the more density-

dependent factors come into operation, and the more intensely do they bear upon the population.

We shall see later how the remaining types of density-dependent action can also be related to the concept of capacity.

There is an obvious relationship between the idea of environmental capacity and the 'carrying capacity' idea of Kalabukhov, Errington and others, and the closely related idea of overflow from favourable niches, stressed by Thompson and by Smith (see section B). Whether or not we accept the hypotheses of all these writers in the precise forms in which they presented them the fact remains that the general principle of which they are examples is fundamental to natural control.

One aspect of capacity, the food supply, links the theory of control with what Lindeman (1942) called the trophic-dynamic aspect of ecology. This is the study of the energy relationships between the successive levels in the 'Eltonian pyramid' or food chain, in which plants constitute the 'primary producers', supplying food to the phytophagous animals ('primary consumers'), which in turn supply food for their enemies, and so on. There is a loss of total available energy as the scale is ascended (cf. Macfadyen, 1948).

(2) *The significance of competition*

Intraspecific competition is a natural activity relationship arising from the limited capacity of the environment—particularly as the density approaches the capacity limit. The term competition commonly includes (a) direct active struggle between individuals or groups; (b) 'a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms' or 'the attempt to secure more than a proportionate share of a limited supply of something, e.g. raw materials, food, space or material for construction' (Clements & Shelford, 1939); and (c) the occupation or consumption by earlier arrivals of something in limited supply, so that late-comers are automatically excluded or deprived.

For our present purposes, the interesting point about competition is that whenever it occurs it is almost inevitably density-dependent. The amount of space, food, etc. available per individual diminishes as the population density rises, and any competition for them becomes more intense. There are no doubt exceptions to this, such as examples of competition of one type being superseded by responses to more urgent requirements at higher density, but these are minor considerations.

Competition is sometimes wasteful, in the sense that fewer individuals survive on a given supply of food (for example) than could be reared upon

it if there were no original overcrowding nor struggle. However, this is only likely to be important in control when food supply is a 'key' controlling factor.

Interspecific competition also plays some part in control. The competitors of a species are those species whose habits resemble its own in one or more respects, i.e. whose needs overlap its own (cf. Crombie, 1947). In competition for a supply of something, the competitor populations are equivalent to extensions of the population studied; individuals of a competitor population are equivalent to a variable number of individuals of the population studied. The presence of competitor species intensifies the density-dependent action of supply factors just as if the density of the population studied were higher than it actually is. Their presence forces down both the upper and the lower limits of its range of variation. They represent a reduction in the effective capacity of the environment.

Special importance has been attached to the process of competition by some writers on control, especially Nicholson (1933), who regarded it as the essential element, without which natural control could not be maintained. However, Nicholson used the word in a much broader sense than is usual; e.g. (p. 140) 'Many organisms alter the chemical and physical nature of their environment, and, generally, the increase in density of such organisms causes the character of the environment to become progressively less suitable for themselves. This clearly is a form of competition....', and again (p. 135) 'If the severity of its action against an average individual increases as the density of animals increases, the decreased chance of survival, or of producing offspring, is clearly brought about by the presence of more individuals of the same species in the vicinity. This can only mean that the decreased chance of survival is due to increased competition of some kind.' The second passage contains the key to Nicholson's idea of competition: it is essentially a statistical conception. What he means is not competition as understood by most biologists, but a broader and more generalized relationship, covering all cases in which the presence of other individuals leads to a decreased chance of survival or a reduced rate of increase, per individual. It is, in fact, any unfavourable density-dependent relationship.

(3) *The density-dependent influence of natural enemies*

As noted earlier, a natural enemy is density-dependent in its action on the host population because it finds hosts (or prey) more readily when they are dense. Of course, if the host population is doubled but the enemy takes less than twice the former number of victims, then its action is not density-dependent;

the density relationship is not concurrent, but inverse (cf. p. 13). To be density-dependent, the enemy must take a greater proportion of the population as the host density increases.

In other words, to be density-dependent, the enemy must respond to changes in the numbers of the host (cf. Nicholson, 1933; Varley, 1947). The nature of this response is commonly twofold. First, there must be a *functional* response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly. A frequent, but not invariable result of this is an increase in the numbers of the enemy (a *numerical* influence), due to an increased rate of survival or of reproduction, or both; this may or may not be sufficient to produce an increase in the *proportion* of enemies to the increasing hosts.* The numerical relationship is most important when the enemy develops rapidly and passes through several generations to each generation of the host, as do many parasitic insects (Flanders, 1947).

Many natural enemies concentrate in places where the host or prey is dense, thereby showing a more emphatic density dependence than would otherwise be possible. This resembles a functional response when the movement takes place within the environmental limits, but is more like a numerical response when there is immigration of enemies. Richards (1940) wrote that the parasites of the small white butterfly (*Pieris rapae*) 'show a tendency to congregate in the areas where the host is most numerous. This may have a buffer effect on the population, hindering both complete extinction and too rapid multiplication of the host'. If so, it is a reinforcement of the buffer effect characteristic of all density-dependent enemies, whether they congregate or not, and characteristic, in fact, of density-dependent processes of all sorts.

It will be recalled that Nicholson (1933) distinguished clearly between control by enemies and the other types of control, which he attributed to intra-specific competition. Control by enemies, he pointed out, depends on intraspecific 'competition' among individual enemies in searching for victims, or, as he repeated in more clearly statistical terms, on the readiness with which the enemies can find the hosts. Again, it must be remarked that many of the relationships which make the action of enemies density-dependent cannot be described as competition in the usual sense. For example, in the case of pathogenic micro-organisms, there is an increase in the frequency of contacts between host individuals as host density

* Varley (1947) proposed to distinguish parasites and predators from other density-dependent factors by calling them *delayed density-dependent factors*. But there is no essential delay in the *functional* response of enemies to changes in host density.

rises, i.e. an improvement in the supply of hosts. The micro-organisms are thereby distributed more readily from host to host, and so tend to increase in relative numbers. Here there is no question of active competition nor of active seeking for hosts. The micro-organisms simply take advantage of the improved capacity of their environment to support their rapid multiplication. Even a virus can react in this way. Yet we have a genuinely density-dependent relationship.

As with the other types of density-dependent factors, we may relate the density-dependent influence of natural enemies to the limited capacity of their environment. Like other populations, that of an enemy species is limited by the capacity of its environment. In this environment the population of the host or prey is an important element. The host population density determines to some extent how readily the enemy can find the victims necessary for its survival and success. Hence inevitably the host density influences the intensity of the enemy's attack upon the host population.

(4) Density dependence and capacity: Conclusions

The limitation of populations is a result of the limited capacities of environments. The effects of limited capacity operate even when the density is considerably below the capacity limit, but becomes stronger as density increases.

The ways in which the density dependence of different types of factors is related to environmental capacity may be summarized as follows:

(1) The type of density-dependent effect in which capacity seems to play the least part is *mutual interference*. Yet this is due to crowding, arising from the fact that the amount of space in which conditions are suitable, is limited. Obviously, the interference will increase as density rises. It may be regarded as competition for supply factors.

(2) Other density-dependent factors clearly depend, not on density alone, but on the relationship between abundance and capacity. The total *supply* of food or space is an aspect of capacity. The amount available per individual depends both on the density and on the total supply. A reduction in this aspect of capacity, without change in numbers, or an increase in numbers without any change in capacity, would have the same general effect—an intensification of the density-dependent action.

In the above types of density dependence, we have a simple combined action by the population and the environment together. In the following sorts of density dependence, there are two distinguishable aspects, first a density-related effect of the population on the environment, and secondly a correspondingly density-related action of the environment back upon

the population. The density relationship may be regarded as being reflected back to the population from the environment.)

(3) *Enemies*: If an enemy is sufficiently dependent on the population as a supply factor, its success in finding hosts or prey will vary according to the population density, and further, if it is sufficiently responsive to such variations, the proportion of the population attacked will increase concurrently with density. Thus the effect of host density on the enemy is reflected as the density-dependent effect of the enemy on the host. But this is possible only if the population is to some extent needed by the enemy for its maintenance, only if the limited supply of this species is (for the enemy) one of the more pressing aspects of the limited capacity of the environment. In other words, the host or prey is a density-dependent supply factor for the enemy (cf. Varley, 1947).

(4) *Modification of the environment by the population*: Unfavourable modification represents a reduction in one or more aspects of environmental capacity, the extent of the reduction increasing concurrently with density. The result is an increase in the intensity of the relevant density-dependent actions.

Favourable modification represents an increase in environmental capacity concurrent with density. Such action is opposed to that of the other density-dependent factors.

In addition to these density-dependent relationships, the presence of *competitor species* reduces the effective capacity of the environment for the population concerned. We shall see later (p. 18) that the presence of alternative hosts or prey for its dependent enemies may have a similar effect.

C4. PHASES OF CONTROL

So far we have referred to natural control as a single process, the result of density-dependent actions. The present section considers its major component elements, and the part played by density-related processes in each of them.

(a) Limitation

The chief effect of the density-related processes which bring about control, particularly of their property of intensifying as the population density increases, is to 'head off' each rise in density and bring it to a halt. Indeed, since the complex of forces is in a state of continual activity, and for other reasons to be examined shortly, the reversal of an increase often comes rather abruptly. Generally, the higher the density, the more likely is a rising trend to be soon reversed. Thus there is an upper limit, however vague and variable it may be, to the density of each population. The whole process by which

populations are 'kept down' may be referred to as *limitation*.

Perhaps the simplest examples of limitation are those in which a population appears to limit itself. This is often due to unfavourable effects of the population upon the environment, a type of phenomenon to which reference has been made earlier. In some cases, a single unfavourable effect alone seems to be immediately responsible for limitation. Thus McKenzie (1943) found that a species of the scale insect *Matsucoccus* on *Pinus ponderosa* had very few enemies, the limiting factor being mortality due to the killing of the branches by the insects themselves as the local density increased.

Unfavourable influences usually affect the rate of development and reproduction, as well as increasing the mortality rate. Because many populations which maintain a very high reproductive rate seldom reach correspondingly high densities, it is widely considered that mortality is by far the more important of the two (cf. Smith, 1935, p. 881). Darwin (1859) remarked that the relative abundance of species of birds or of insects seemed not to be correlated with the number of eggs laid. Nevertheless, a change in the reproductive output of a particular species may have a considerable effect on its density, as in the case of the short-eared owl, cited by Elton (1927, p. 141). Thus changes in the influences affecting reproduction may often be important (cf. Boyce, 1946, on *Tribolium*). Some outbreaks of pests seem to be due largely to this cause.

The density level at which a factor can limit a population is a feature of some practical importance. As pointed out by Smith (1939; and cf. Nicholson, 1933): 'A parasite... in order to be effective must have the ability to find and destroy the surplus progeny of its host at a low host density, whereas an ineffective parasite can accomplish the same thing, but only at a high density.... For this reason the searching ability of the parasite becomes a matter of prime importance, far outranking its reproductive capacity, since the latter is usually, if not always, more than ample.' The elements which affect the power of host discovery by parasitic Hymenoptera were discussed by Flanders (1947). The following paragraph from his paper notes an interesting development of the above point:

'Muir (Williams, 1931) states that: "Theoretically, other things being equal, a predator should be more valuable than a parasite, because the latter only kills a single host or a small number of the host, but a predator generally destroys a large number during its life." Paradoxically, as pointed out by Smith (1937), it is this fact that makes the predator less efficient than the parasite as a control factor. Other things being equal, the most effective species of natural enemy is one that requires the least amount of food for

individual development.' This is supported by the fact, noted by Flanders, that in most groups of insect pests, parasites have been more important than predators in biological control. Other papers dealing with the relative effectiveness of insect parasites and predators are those by Thompson (1929a) and Ulliyett (1938).

As always, we must bear in mind that there are usually many factors simultaneously active, and that each of them modifies the action or the results of others. For example, animals succumb more readily to disease if their food is deficient, and more readily in some physical conditions than in others. The capacity for reproduction and survival depends upon the physical environment as well as on the inherent qualities of the species. Moreover, a combination of two or more factors may produce a limiting action which they could not exert singly.

As is well known, the mode of control tends to change during the development of an animal, some factors having different effects upon successive developmental stages (cf. Holdaway, 1932), some operating only at an early stage of growth, others only at a later stage (cf. Bodenheimer, 1938; Thompson, 1939; Schwerdtfeger, 1941). For this reason, among others, the importance of a control factor cannot be correctly estimated simply from the numbers of animals killed by it, nor from the percentage killed. The assessment of the real control value of two or more factors operating successively is a special problem which has been studied by Thompson (1928), Bremer (1929) and Bess (1945). Thompson and Bremer assess the contribution of the separate factors towards reducing the population to the level of the previous adult generation. Thompson calculates the 'indispensable mortality', i.e. the percentage reduction due to a factor over and above that which it is calculated the other factors would have produced without it (cf. Parsons & Ulliyett, 1936). Bess estimates for each factor the proportion by which it reduces the surviving population. He points out that in one generation of a fecund species, a kill of 5% of the original population may be unimportant if only 50% have been killed by other factors, but very important if 90% have previously been killed. Although the later factors may kill only a small proportion of the original population, yet, if their density dependence is sufficiently marked, they may play a decisive role in regulating the population density from generation to generation. Nicholson (1933, p. 136) went so far as to write: 'If an attempt be made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed upon the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced, and how readily they are influenced, by changes in the density of animals.' While the second sentence is the kernel of the matter, a study of the

proportions killed by these factors under various circumstances is the chief means available for discovering their degree of density dependence. Analogous considerations apply to density-dependent factors which are not mortality factors.

An important development in this field is the experimental attack upon the problem by Smith & De Bach, working with citrus scale insects and their parasites. One of their methods is to exclude parasites from sections of the scale population by means of organdie sleeves (Smith & De Bach, 1942). The other is to eliminate insect parasites or predators in certain plots by application of selective insecticides (De Bach, 1946). In either case, the comparison of the densities with and without enemies provides a valuable index of the effectiveness of the enemies.

Different factors do not necessarily work in co-operation. For example, if natural enemies keep the population density at a moderately low level, other influences such as food- or space-shortage or disease may not come into operation. In this way the population may be saved from the more drastic reduction it would probably suffer if these factors became operative. Or again, a physical change which reduces the population may operate even more effectively against an enemy. Varley (1947, p. 179) has given numerical examples showing how the destruction of insects, some of which have been parasitized, may lead ultimately to an increase in their numbers, because of the greater effect of the mortality upon the parasite species (cf. Nicholson, 1933, p. 151). Taylor (1937) described a striking example of how one enemy may indirectly prevent effective control by others: in Fiji, the coconut leaf-mining beetle, *Promecotheca reichei*, was normally kept under economic control by indigenous parasites; but when the mite *Pediculoides ventricosus* appeared in Fiji, it periodically eliminated all but one of the developmental stages of the beetle; under these conditions the native parasites, needing 'multiple-stage' populations of their host for continuous multiplication, were no longer able to control the beetle, which then became a serious pest.

A population may be affected in the same way by the presence of alternative hosts or prey for its enemies as it is by competitor species. Suppose a controlling enemy is capable of keeping the total population of its hosts or prey about a certain level. Then if another species provides (say), half the enemy's requirements, the population studied will be only half as abundant as it would be in the absence of the alternative host or prey—at least this will be so if the enemy is the only controlling factor acting at such levels of density.* Many related questions, such as what may be ex-

* But if the enemy, because of ample alternative hosts or prey, comes to be no longer significantly dependent on this particular species, the action of the enemy upon it will cease to be density-dependent.

pected to happen when there are several competitor enemies, what is the effect of hyperparasites or predators of an enemy, and so on, were considered by Nicholson (1933) and, in a more formal mathematical way, by Nicholson & Bailey (1935). While predictions of this type are likely to be upset in the complex conditions of nature, they suggest useful hypotheses for the investigation of natural populations (cf. Varley, 1947).

The relative effectiveness of a single enemy species as against two or more is a question of some economic importance. While instructive general discussions and theoretical studies are available (Thompson, 1923, 1929*b*; Smith, 1929; Volterra, 1926, 1931, etc.; Nicholson, 1933; Nicholson & Bailey, 1935), no simple comprehensive answer is possible. The evidence from theoretical considerations and from practical experience suggests that the use of several enemy species together is often the better course (e.g. Clark, 1934). Smith pointed out that control by several enemies tends to be more reliable than that due to a single enemy, for any failure of one of them tends to be compensated by an increased effectiveness of the others, in response to the higher host density.

The compensation principle, which applies very generally, is an expression of the fact that if one limiting factor fails, others are called into play by the higher density, while if the numbers are unduly reduced, density-dependent factors operate less severely. The significance of such 'intercompensation' in the control of vertebrate populations has been discussed by Errington (1946). Its importance in connexion with insect populations has often been remarked (e.g. Nicholson, 1927; Thompson, 1928; Bremer, 1929), and is most obvious in cases where a succession of control factors is known to operate. Compensation is obviously important in the practical control of pests, and in relation to the maximum 'catch' which can be taken from a population without detriment to the subsequent yield, as in fisheries.

Limitation is often complicated by seasonal changes. In climates with a marked seasonal cycle, the factors limiting a population are likely to be different at different times of the year. The effective limitation may even be confined to a few months in each year; but it cannot be assumed that the elimination of the bulk of the population represents the essential part of the process. As has been mentioned above, the final small losses may have decisive importance.

If in one season or generation there is a failure of the normal limiting processes, there will be an unusually dense population in the following season or generation. This often provokes limiting processes of corresponding severity.

(b) Suppression

We must now consider the existence of a time lag in density dependence. As population density increases, the intensity of action of a limiting factor responds by a progressive intensification. This response is not necessarily instantaneous; its promptness varies according to the type of factor and the type of population. The intensity of overcrowding effects may approximately correspond to the density at the time; but the intensity of the effects of a natural enemy may correspond less to the current host density than to the host density a generation (of the enemy) earlier. As we saw above, the first response of a density-dependent predator or insect parasite to increased host density is functional, i.e. there is a more or less immediate increase in the intensity of attack by each individual enemy. This is likely to be followed later by a rise in the numbers of the enemy, due to increased survival and reproduction rates in the presence of a more easily found supply of hosts or prey. So long as host density continues to rise, the fact that part of the response is delayed does not fundamentally affect the relationship or its results. But when the host increase ceases, the effects of this delay may be of great importance, as will be shown below.

If there is little or no delay in response by the limiting factors, and there is an adequate food supply and steady physical conditions, a population may reach the limiting density and maintain itself near that level for some time. But if there is a delay of (say) a week in the response of one of the limiting factors, then, when the density increase comes to a stop, the intensification of the action of this factor will tend to go on for another week. While it may not reach the intensity it would have reached in that week if host increase had continued, it will certainly exceed the value it had when the host increase was brought to a standstill. Hence it will bring about a decline in density (cf. Nicholson, 1933, p. 161). Furthermore, the same delay in response which occurred during host increase will tend to continue during host decrease, but the intensity will be continually *above* the value corresponding to the current host density, instead of below it.

The forced decline in density caused by this excess intensity may be called *suppression*.

Sometimes the forced decline may go on until the population is exterminated as, for example, in the 'relaxation fluctuations' studied by Gause (1934), in which a prey population in the presence of a predator population goes through a cycle of increase, decline and extinction. But other factors may intervene to prevent this. For example, in some of his experiments with *Didinium* preying on *Paramecium*, Gause was able to prevent the complete extinction of the prey by providing some protective cover.

The natural control of animal populations

Suppression by enemies is also countered to some degree by density effects among the enemies. For example, Flanders (1935), Salt (1936) and De Bach & Smith (1947) have shown that insect parasites suffer a reduction in their reproduction rate at high density. This would seldom have important effects on the density relationship between parasite and host while the host density is high; but if enemies rapidly reduce a host population and then become concentrated at high density on the surviving groups, the enemies may suffer any of the usual effects of overcrowding in full degree, particularly of course a shortage of food or hosts. Special mention may be made of superparasitism. Flanders (1947) wrote: 'So efficient is the searching capacity of the individual hymenopteron that the survival of many species appears dependent on the fact that the searching activities of the individuals of a population are unco-ordinated. Overlapping and duplication of individual action (superparasitism) tend to preclude the general extermination of the host (when not general, extermination is temporary) and thus insure a continuity of hosts available for oviposition'. Ulliyett (1945) found that when the numbers of the parasite *Microbracon* were unduly high in relation to those of its host (*Ephestia* larvae), the numbers of parasites were reduced by superparasitism.

These hindrances in the way of suppression by enemies tend to prevent a persistence of the excess intensity and of the corresponding decline in density. A more general counter-effect to suppression of all sorts is the relaxation,* as density falls, of the totality of density-dependent actions, leaving a larger and larger gap to be filled by the excess intensity if suppression is to go on. Only if the excess intensity is particularly great and persistent can the density be forced down to a level approaching zero.

The above type of suppression, arising from the delayed response of a factor to the density, may be produced by predators, parasites or pathogenic organisms.

There is another sort of suppression which affects aggressors rather than their victims. When the food supply (plants or prey) is readily accessible, but limited, the intensity of food shortage increases relatively suddenly and rapidly as the supply approaches exhaustion. What remains is hopelessly inadequate for the size of the population, which therefore becomes reduced, more often by indirect effects of food-shortage than by actually starving to death; but meanwhile the animals search very intensively and consume all the remaining food which can be found. Thus the supply of food has no opportunity of increasing until the population feeding upon it is reduced to a very low level. Under stable environmental condi-

tions, there might possibly be a balance between a growing food supply and a steady population consuming, so to speak, all the interest and none of the capital of the food supply. But such a balance would be very easily upset, and generally a much less precise relationship prevails.

A similar type of suppression affects populations which contaminate their environment. Generally, the contamination during a period of increase is not only due to the current or recent population (although that would be sufficient to produce an intensifying effect), but also persists and accumulates from the past. This persistence, in addition to the results of any delayed effects (e.g. of decomposition) causes a forced reduction of the density as in the earlier examples.

This type of suppression occurs whenever something required by the population is in limited supply, provided other factors allow the population to increase to a high enough density, and provided the food, space etc., is at least temporarily destroyed, occupied or vitiated when used.

(c) Conservation

It has been mentioned that in some cases the suppression of a population may tend to persist until it is nearly exterminated. Moreover, powerful density-independent factors, if sufficiently persistent, may also tend to kill the whole population. Finally, factors inversely related to density operate more severely as the density decreases.

That populations are not more commonly exterminated by these forces is due chiefly to the relaxation of density-related influences as the density declines. Other factors tending to save populations from extinction include the presence of a few protective refuges, the occurrence of superparasitism and of overcrowding effects among enemies (all of these have been mentioned already) and such processes as selection and adaptation. These diverse factors or processes produce a result which is in a sense the opposite of limitation, and which may be referred to as *conservation*.

The relaxation of density-dependent forces at low density applies not only to factors which figure prominently in limitation, but to all influences. Hence, any tendency of suppression to exterminate a population is generally offset, at a more or less reduced level of density, by the relaxation of other density-dependent forces. For example, the effects of contamination of the environment may be partly offset by the ability of the animals to move about more freely, or by the reduction of disease, as the density diminishes. The relaxation takes many forms. For example, animals are less easily found by natural enemies when their density is low. For this and other reasons, an enemy may reduce the density of its host to a certain level and then be unable to effect any

* 'Relaxation', as used here, refers simply to a decline in the intensity of action of a factor upon the population, and no connexion with 'relaxation fluctuation' is implied.

further reduction (cf. Muir, 1931, on the *critical point of parasitism*). Again, when the density of a population declines, there is less competition for the more favourable niches in the environment, so that all the survivors may find room in the places giving maximum protection from physical rigours.

The last point involves one aspect of the important part played by the heterogeneity of most environments. This heterogeneity helps to ensure that, whatever the general conditions, some part at least of the environment will be able to offer protection and refuge for some of the population.

If the greater part of a population is killed by unfavourable physical conditions, the survivors (unless their success is entirely due to their being in protected situations) will on the average be those which are more resistant to such conditions. Hence, unless the survivors are weakened by continued exposure, it will be more difficult for the unfavourable conditions to exterminate the population than it was to reduce it. It may also happen that individuals which survive long enough may become better acclimatized or adapted.

Another way in which many populations are saved from extinction is through the existence of dormant or otherwise resistant or protected forms, such as overwintering eggs, cysts, pupae, or other hibernating or aestivating stages.

Sometimes a population will temporarily change its habits under severe stress, e.g. it may change its diet for a time while its normal food is scarce (cf. Elton, 1927). Dugmore reported that after a severe reduction of the African buffalo by rinderpest, the remnants of the population in the Sudan changed from diurnal to nocturnal feeding habits, retiring to cover during the day; later reports indicate a return to its former habits after more than 20 years of population increase (Elton, 1927).

To summarize the aspects of conservation, there is a strong tendency for the last remnants of a reduced population to survive the unfavourable conditions; this is due to one or usually more of the following factors, and perhaps to others as well: (a) the heterogeneity of the environment and the existence of a few specially favourable refuges, (b) isolation and the consequent tendency to escape enemies and disease, (c) the occurrence of superparasitism (by parasitic insects) and overcrowding effects among enemies as host numbers fall, (d) some other aspect of the relaxation of unfavourable influences which accompanies a fall in density, (e) immunity, (f) acclimatization, (g) selection, (h) the existence of a specially resistant stage in the life history, or (i) a self-protective change in behaviour.

(d) Release

It is well known that when a population is severely reduced, any predators, parasites or disease organisms

which are more or less wholly dependent on the population concerned tend to be even more severely reduced. One or more of these enemy species may be of major importance in the control of the population. This relaxation of controlling influences is the normal accompaniment to falling density.

But sometimes, and in spite of the processes of conservation which apply to the populations of enemies and victims alike, an important enemy may be locally exterminated. Then the subsequent increase of the host population is likely to be both faster and more sustained than usual, until other factors effect control at a higher level. Or the missing enemy may reappear by immigration, and belatedly set about the process of overtaking and controlling the swelling host population. What is more common is something intermediate between this and the normal relaxation of controls. For example, predators, parasites or disease may be reduced to a few nuclei at low density, so that the host population can often increase again for a time before the normal relationships with these control factors are re-established.

Again, if food supply is normally an important control factor, the extra food which accumulates during a period of low density may allow a rapid subsequent increase to unusually high numbers.

In general, a great reduction in density tends to disorganize natural control, and sometimes a population temporarily escapes more or less completely from one or several of its important controlling agents; this allows it to increase more rapidly than is usually possible for it, at a given level of density, and may allow it to reach a higher density than usual. This phenomenon may be referred to as *release*. The clearest examples of release are to be observed in populations whose control is normally dominated by one or two 'key' factors; in other types of control it is less likely to be important, because of compensatory action by other factors.

(e) Fluctuations inherent in control

It is interesting to note that two of the aspects of control are such as to promote fluctuations. Suppression promotes downward fluctuations from high density; release promotes upward fluctuations from low density. Of course, in a normally variable environment, even limitation and conservation lead to reversals in the trend of density rather than to steady numbers. Suppression and release are due to more purely biotic forces which may sometimes reinforce and sometimes cancel the more or less irregular fluctuations due to weather, etc.

There is some tendency for release to follow suppression, and vice versa. The existence of a very high density exposes a population to the risk of some suppressive process coming into operation. If this process persists, and forces the numbers down to a

very low level, the likelihood then arises that some parts at least of the population will be temporarily released from the usual controls, and it may reach very high numbers again before being overtaken by control.

An apparent example of suppression following partial release has been observed in the pine moth *Bupalus piniarius*. The fluctuations of this species in a pure stand of its host tree were described by Engel (1942). Under these conditions its natural enemies are less numerous than usual, so that the moth can increase rapidly and reach unusually high densities. But when the enemies finally do overtake it, they cause an unusually rapid reduction in the numbers of the moth.

Reporting observations on a quite different animal, the bank vole, Evans (1942) wrote: 'The population "survival" from a period of high density to one of low density appeared to be greater in those habitats which had normally maintained a low population density. It is suggested that habitats which will maintain only low densities may be essential to the ultimate survival of a species.' In other words, where the density is never very high, the catastrophic effects of violent suppression are avoided.

It is difficult to estimate how far these tendencies are extended towards a series of continuous oscillations in density. Under most conditions, any such tendency would probably be lost among the many other influences at work, such as the effects of weather changes, and all the intercompensatory forces characteristic of normally complex biocoenoses. The question is further discussed in section D 4.

C 5. THE LEVEL OF ABUNDANCE

So far we have discussed the controlling processes by means of which a population is kept within a certain range of density. While it has been convenient and useful to consider control in this restricted sense, most biologists would take a broader view, and think of the natural control of a population as including the determination of the general level of abundance to which the population is confined by the regulating processes. Control in this broader sense may be thought of as a phenomenon separable into the three parts: (a) the regulating processes, which we have discussed above, (b) the determination of the level of density, and (c) the determination of the general level of abundance, which may be defined only after a population has been observed over a period of time. These three sets of processes are not really distinct; each includes a good deal of the other. This is particularly true of (b) and (c), for the general level of abundance is no more than the actual density over a period, and it must be determined in the same way (or succession of ways). But neither is (a) really distinct

from (b) and (c). Thus, although we have so far concentrated upon the controlling processes, this has involved us, for example, in a consideration of environmental capacity. The conclusion we reached may be re-stated in this form; that a population is as big (numerically) as the capacity of the ecosystem allows. Rather more fully: the density of a population is determined by the capacity of the ecosystem to maintain large numbers of the species, and large numbers of its density-dependent enemies. We have also noted some of the factors which determine the level below which a population is limited.

In fact, for a given species in a given environment, it is quite clear that it is the controlling processes which determine the abundance of the population. But in general, we must not take for granted either the characteristics of the species or those of the environment. Then the abundance of a population depends, first, on its own specific characteristics and capabilities, and, secondly, on the general suitability of the environment for the species concerned, i.e. upon physical conditions, and on the quality of the food, as they affect the rates of reproduction and survival. Thirdly, it depends on the amount of space, food, etc., available. Fourthly, it depends on the prevalence and efficiency, or otherwise, of enemies, competitors and diseases. In short, the level of abundance depends on all the major elements in the complete ecosystem.

Many biologists would say that in general one major element, namely climate, tends to play the predominant role in the determination of abundance. According to the nature of the species, there are some types of climates in which it can be abundant when other conditions are favourable, and other types in which it can seldom or never be abundant. The physical conditions in some environments are quite different from the general meteorological conditions, yet are still related to them in a broad way; even the vegetation, which considerably influences the physical conditions as well as dominating the environment in other respects, is itself determined in a general way by climatic influences.

Be this as it may, the abundance of a population depends on all the major aspects of the general environment. More immediately, it is determined by those aspects of the environment which are predominant in control. The *precise* level of density at any time depends on all this and upon many temporary and 'chance' circumstances in the ecosystem at the time.

The question, whether the controlling processes or the environmental background is generally more important in the determination of abundance, is meaningless. And in relation to particular cases, it has meaning only when major parts of the ecosystem are taken for granted. Given a particular population and its general environment (not the immediate control factors) we

may say the control factors determine the level of abundance—as has been shown in practice with various insect pests. But in general we have also to recognize the validity of the complementary proposition: given a population and its immediate control factors, the level of density is determined by the general environment. In fact, all three elements—the population with its specific characteristics, the general environment, and the control factors—together determine the level of density, and while it is convenient in studying actual cases to take one or two of them for granted, the conclusions so reached must not be expected to apply in general.

Consider, for example, a population whose density is apparently determined by parasites. In his interesting account of the natural control of the knapweed gall-fly *Urophora jaceana*, on a site near Cambridge, Varley (1947) provides data showing the effect of the chalcid parasite *Eurytoma curta* on the density level of the fly. Apart from a number of modifying factors whose action is studied, the general effect of climate, for example, is taken for granted. This is natural and inevitable. But Varley makes the generalization: 'Where other factors permit its survival it is the controlling factors which mainly determine whether a species shall be rare or common'. This is correct only if it refers to the immediate or direct determinants of abundance.

The viewpoint of this section is somewhat similar to that of Nicholson (1933, p. 172) on the subject, inasmuch as Nicholson holds that the controlling processes are the immediate determinants of density, the physical environment being the ultimate determinant; for the physical environment influences the controlling processes, besides determining which controlling agents shall be present. Smith (1935) seems to consider the determination of density as part of the regulating processes, except in extreme cases of a shift in the general level, as in outbreaks of a pest. It is partly for this reason that Smith lays more emphasis upon the importance of climatic factors in regulation.

The theory that the size of a population depends on the resultant of the push of 'biotic potential' against 'environmental resistance' is based on a sound idea, but its development by Chapman (1928, 1931) is open to many objections, some of which were referred to by Nicholson (1933) and Thompson (1939). One of its faults is the term environmental resistance, which ignores the important fact that populations to some extent control themselves. The resistance comes from the whole ecosystem, not only the environment. This theory deals essentially with the resultant resistance, measured in terms of the performance of the population. It says nothing about the relative contributions of the interacting elements to the final resultant, though it suggests ways of assessing them.

The immediate determinants of the abundance of

a population are not necessarily the same in all parts of its environment. Frequently it is held at a low density over the greater part of the environment, because of exposure to enemies or because tolerable physical conditions exist only in a few niches. But in the more favourable parts it may reach a high density, and be controlled by different enemies, or by exhaustion of food supplies, or overcrowding, or some other factors not operative elsewhere.

On the whole, then, it seems there is no certain basis in present knowledge for any very simple generalization about the determinants of the level of density, except that the immediate determinants are the control factors and the ultimate determinants are all the chief elements of the ecosystem. In particular cases, on the other hand, it is sometimes found that parasites, food shortage, or some other one or two factors, are responsible for setting the general level considerably below that which would otherwise prevail. For example, Hardy (1938) considered the reason for the greater abundance of the diamond-back moth (*Plutella maculipennis*) in New Zealand than in England was the low rate of parasitism in New Zealand, and suggested the introduction of further parasites. This was done and has apparently been very effective in reducing the pest (Anon. 1946). Or (what may be the same thing) a favourable change in a particular factor may allow a considerable rise in density; thus Criddle (1930) reported that maxima in sharptailed grouse populations were due primarily to the periodic abundance of food provided by grasshopper outbreaks.

For particular groups of animals, such as a class of vertebrates, an ecological type of insects, etc., it is possible to establish generalizations of the sort reached by Errington (1946). From his study of predation among vertebrates, he concludes that for birds and mammals 'predation looks ineffective as a limiting factor to the extent that intraspecific self-limiting mechanisms basically determine the population levels maintained by the prey'. In other words, of the environmental determinants the non-predatory elements are the important ones. Even such a general statement is very useful. Generalizations may also be made about particular regions, such as the statement that in general the level of density of populations is relatively low in the tropics, perhaps because of the intense struggle against enemies and competitors (Hesse, Allee & Schmidt, 1937, p. 404).

D. SOME SPECIAL QUESTIONS

In this part of the paper we shall consider several themes which, although important and interesting, are not essential to the conception of control developed in the previous part. Some points of this sort have been dealt with in earlier pages, because it would

have been inconvenient to separate them from the themes discussed there.

D I. THE RELATIVE IMPORTANCE OF DIFFERENT FACTORS IN CONTROL

There has been a good deal of discussion for many years as to the relative importance of different factors in control, particularly as to whether biotic factors are more important than physical factors, and vice versa.

In general, the performance of a population depends both on its inherent qualities and on the nature of the environment, and it would be pointless to claim that either is more important than the other. If biotic factors include the inherent characteristics of the population, or its modes of reaction to the environment, we cannot assess their importance relative to that of the physical environment. But can we compare the importance, to control in general, of physical and biotic environmental factors?

Taking a broad view, we see that the physical factors provide the environmental climate which influences very considerably the general vigour, the rate of development, the powers of survival and the general level of metabolism and activity of a population. Further, they play the major role in determining whether or not a given species can exist at a particular place, and often in determining the general level of density. This is borne out, for example, by the fact that it has been possible to map the areas of distribution and of mass development of various insects, using meteorological and physiological data; such maps correspond reasonably well with the actual occurrence of the species concerned, in those parts of the world to which they have penetrated (e.g. Cook, 1925; Bremer, 1929; MacLagan, 1932; Zwölfer, 1935; Davidson, 1934; Ulliyett, 1936). By comparison, the biotic factors often play a secondary role: even although they may sometimes bring about the extermination of a population, they cannot operate unless the physical conditions are suitable for the existence of the species concerned. Furthermore, biotic factors are always subject to the influence of physical conditions, while the reverse is true only in certain cases (cf. Thompson, 1929c). In this sense, the physical factors are of primary importance, the biotic factors secondary.

But if we consider the controlling processes, i.e. the more direct or immediate determinants of density, we are at once impressed with the great importance of the biotic element. A population's own activities play such an important part in its control, and natural enemies are so often important, that we are tempted to rank the living elements as predominant over the physical background. Yet, as we have seen earlier, the general environment enters into all the density-relationships which are responsible for control.

To look at this matter in another way, it is clear that factors do not act independently upon a population. They are parts of a complex system and subject to the influence of the whole. This means, among other things, that the influence of a factor upon a population depends upon other factors. Although this is generally recognized, very few authors seem to have realized its full implications. It applies with special force to the question under discussion, because—to mention only the most striking feature—the action of biotic factors is often influenced decisively by physical conditions.

The effects of a physical change upon the physiological processes of different species are usually unequal and sometimes opposite (and the physical limits for survival are often different for associated species). In many cases these differences have been shown to play an important role in determining the outcome of the population interaction of an animal with a parasite or predator. Such facts have been known for many years, but their significance seems to have been generally underestimated in theoretical discussions.

A number of examples in which the effect of parasites, predators or diseases on insect populations is dependent upon temperature, humidity, or both, were cited by Uvarov (1931, pp. 152–5) and Payne (1934), and others were described by Ulliyett (1938) and Pruthi (1940). Ross (1908) stated that the numbers of malarial parasites in man or birds increased with a rise in the external temperature. Ahmad & Ullah (1939) showed that the relative success of the bollworm *Earias fabia* and its parasite *Microbracon lefroyi* were very different under different physical conditions. 'It is well known that the development of aphid parasites is so relatively slow during cool weather that aphid populations often increase enormously before they are controlled biologically' (Flanders, 1947). Holdaway (1932) showed that the cannibalistic limitation of its own species by *Tribolium* was affected by humidity. Beauchamp & Ulliyett (1932) showed that the outcome of competition between pairs of species of planarians depended in some cases on the temperature, in other cases on the joint influence of temperature and the rate of flow of the water in which they lived. Hutchinson (1941) discussed some examples showing the important part played by physical conditions in determining which of two or more competing species of micro-organisms become dominant. Ball, Reeves, Boyden & Stone (1935), in an ecological study of the celery leaf tier, *Phlyctaenia rubigalis*, in Florida, 'worked out an extremely complicated biological complex involving 2 host plants for leaf tiers, 3 parasites, several birds, 2 diseases, and a number of predators, all intimately associated in an unstable balance largely influenced by temperature factors.... A fluctuation of 1° or 2° from the normal mean temperature of the 3 winter months... was found to make

the difference between serious infestation and no commercial injury. This almost hair-trigger reaction was the result of a number of interacting factors, the most important being the time required to mature a celery crop as compared with the time required to mature a brood of worms.' It has been found (Solomon, 1946) that populations of the grain mite *Tyroglyphus farinae* in English granaries tend to be severely reduced each summer by the predatory mite *Cheyletus eruditus*, whereas this predator is quite ineffective in the winter. Both species survive the seasonal changes of physical conditions, but their interaction is fundamentally affected.

Failure of an enemy in certain environments is not always due to retardation of its rate of increase relative to that of the host, or to reduced activity; certain physical conditions may bring about a lack of correspondence between generations or emergence of host and enemy. According to Baker & Jones (1934) such disharmony of life cycles has been an important factor in reducing the effectiveness of the parasite *Exeristes robator* in the control of the corn borer, *Pyrausta nubilalis*, in parts of North America. Richards (1940) states that the life cycle of the parasite *Apanteles glomeratus* is ill-attuned to that of its principal host under English climatic conditions, since a third generation tends to emerge in the autumn, generally in the absence of any corresponding third brood of its main host, the larva of *Pieris brassicae*. The natural control of certain gall midges is strongly influenced by the effect of weather conditions on the rates of development and times of emergence of their parasites, and on the condition of their host plants, in relation to the time of emergence of the midges (Barnes, 1935, 1940).

There is another difficulty in assessing the relative importance of biotic and physical factors in general. In particular cases, our impression of the relative importance of different factors depends a great deal on the relative amounts of variation of each factor, and particularly on the amount of their divergence from the optimum. If physical conditions are steady and favourable, biotic factors may appear to be all-important (cf. MacLagan & Dunn, 1935; Ford, 1937), but if physical conditions are very variable or extreme, biotic factors may seem to be of minor significance. Thompson (1929c) concluded that physical control is most effective in regions such as the polar zones, deserts, and other barren places, where physical conditions are unfavourable to life, and least effective in places like tropical rain forests, favourable to life; the importance of biotic factors varies in an inverse manner (cf. section D 5). It must also be borne in mind that the degree of sensitivity to adverse conditions, particularly to physical conditions, may differ a great deal as between species. Some are vulnerable, others hardy; some are strongly

influenced by small changes, others seem relatively indifferent to large deviations from the optimum.

It is often possible to pick out one or two 'key' controlling factors, which are chiefly responsible for setting a limit to the density of a species in the areas where it is common. For example, Salt (1932) showed that the enormous potential increase of the sheep maggot fly, *Lucilia sericata*, is offset chiefly by the restricted supply of suitable food for the larvae. The abundance of the lucerne flea, *Smynthurus viridis*, depends mainly upon moisture and temperature (MacLagan, 1932; Davidson, 1934), and that of the mite *Tyroglyphus farinae* on moisture (Solomon, 1946). The work on the celery leaf tier reveals temperature as a key factor in the control of this moth (p. 24). Discussing fresh-water animals, Eggleton (1939) wrote: 'for the bottom dwellers, the character of the substratum on and in which they live is usually of such paramount importance that its effects may completely outweigh the influence of other powerful factors. In the swiftly flowing streams which we are considering this factor vies for first place in influencing the benthos with the ever-present stream characteristic, current....' It should be recognized, however, that such statements apply only to situations in which the other important elements are relatively stable and favourable. Any important part of the whole complex which is outstandingly variable or unfavourable is likely to act as a 'key' controlling factor (cf. Allee & Park, 1939).

Of course, what is termed a 'factor' is largely a matter of convenience, and can usually be analysed into a number of separate elements if its operation is closely studied. Thus 'moisture', as it affects *Smynthurus*, includes soil moisture content (determined by climate, soil type, topography, etc.) and the humidity and evaporating power of the air (Davidson, 1934).

Finally, the question of the relative importance of factors is subject to the difficulties arising from cases of inextricably combined action by two or more factors. For example, suppose a change in physical conditions destroys the local food supply of a population and so causes it to move into another area where, on an inadequate diet, it is unable to escape from a predator species which thus exterminates it. Which is the more important, physical change, food shortage, or predator?

To summarize, it is difficult to say in general whether physical or biotic environmental factors should be considered more important in control, for both are fundamentally involved. But it is often possible to make such a decision with reference to a specified situation. In particular situations, even a single factor, either biotic or physical, may be recognizable as dominating the control of a population. But there is always the difficulty that factors are not

completely distinct from and independent of the ecosystem as a whole.

D 2. BALANCE OF POPULATIONS

The common idea that populations exist in a state of balance or equilibrium is closely connected with natural control. Unfortunately, there has been a great deal of confusion and inconsistency both as to the meaning of the term and the nature of the phenomena it has been applied to. We shall now consider under what circumstances it is appropriate to apply it to populations.

The term is of course borrowed from physics. A body is said to be in (static) *equilibrium* when it is at rest, or has a uniform velocity. The forces acting upon such a body are in *dynamic equilibrium*, i.e. their resultant is zero. An object or system is in *stable equilibrium* insofar as it can return to its former position or state after displacement.

(a) Correct application of the term 'balance'

Since biological phenomena involve a higher level of organization than physical phenomena, physical terms and ideas apply to them only by analogy. But when such analogies are used, they should be carefully and logically developed, for if they are treated more loosely than need be, confusion is inevitable.

If we are to apply the idea of equilibrium logically to population density, it would seem that a population should be regarded as approaching equilibrium insofar as it approximates to a steady density. This is presumably the conception which Elton (1930) had in mind when he stressed the unbalance or disequilibrium of natural populations. Attempting to generalize the dynamics of the matter, Chapman (1928, 1931) held that the biotic potential ('the inherent property of an organism...to increase in numbers') tends to maintain a state of balance with the resistance of the environment; balance is reached when these two forces are equal, and the population remains steady. Lotka (1925) discussed biological equilibria, and pointed out the proper use of the term as a description of an unvarying state. He remarked that, strictly, a biological equilibrium such as that of a constant population is not true equilibrium, since its steady state is maintained by a continual expenditure of free energy, but he thought it justifiable to neglect this point.

As is well known, populations which approximate to a steady density will return to this level after the density has been artificially raised or lowered. In other words, population equilibrium is stable.

(b) The views of Nicholson and of Smith

Nicholson (1933) used the term balance in a very different way from that which has been indicated

above. He maintained that since the density of a population is related to environmental conditions, changing when they change, the population must be in a state of balance.* If the general environmental conditions are constant, competition keeps the population to a constant density, and a state of stationary balance prevails. Comparing the state of a varying population with that of a free balloon, Nicholson (p. 133) wrote: 'The balloon is continually in a state of tending towards a position of stationary balance, but continues to rise and fall because the position of stationary balance is changing all the time.' In terms of population density, the population is tending all the time to come into equilibrium with the prevailing environmental conditions, but these conditions are continually changing, so drawing the population towards a continually changing equilibrium level.

This use of the term equilibrium is open to serious objections. In the first place, even if we agree that each population continually tends to come to an equilibrium level, it only *tends* to do so, i.e. at the most, it has a *tendency* towards equilibrium. But, says Nicholson, this level towards which the density tends is continually changing. Therefore it is not an *equilibrium* level towards which the population tends. In short, Nicholson's use of the idea of equilibrium seems quite inappropriate, and bound to create confusion.

Yet another viewpoint is that adopted by Smith (1935), who regarded population balance as synonymous with a very roughly steady state, and interpreted all normal fluctuations in density as deviations from a fixed average. He wrote (p. 878), 'there is brought about a kind of equilibrium which, by physical analogy, must be referred to as "stable" as contrasted with equilibria of the unstable or neutral types. This is due to the fact that any tendency of the density to depart in either direction from the average modifies the environmental forces acting on the density in such a way as to restore it to the average. Even extreme oscillation, therefore, does not destroy the equilibrium. Oscillations are the resultant of the forces which adjust the numbers of individuals of a species to the capacity of the environment in which the species happens to exist. This is the characteristic of populations which is referred to by that much misused term "balance of nature".' However, 'temporary displacement of the equilibrium position occurs when a species which is ordinarily of little or no consequence appears in enormous numbers...' (p. 879).

This seems an extremely loose application of the term equilibrium. If we consider that all or most

* Thompson (1939) considered that Nicholson here identified balance with the cause-effect relationship between environment and population, and that he used the term balance in two different senses.

populations are usually in stable equilibrium, it is difficult to avoid the conclusion that most natural phenomena are in the same state. It is necessary to add that Smith is by no means alone in his use of the idea that insect populations exist in a state of equilibrium which is broken only at times of outbreaks (see, e.g. Schwerdtfeger, 1934; Graham, 1939; Voûte, 1946). But it may be that economic entomologists tend to lay more stress than is theoretically justifiable on the difference between the variability of 'normal' and outbreaking populations.

(c) *Dynamic equilibrium*

Reference must be made to the idea, widespread among biologists, that while *static* equilibrium involves constancy, a population which varies in response to environmental changes is still in *dynamic equilibrium*. But dynamic equilibrium usually refers to the balance of the *forces* operating upon a body or within a system which is in static equilibrium. The appropriate application of this to population density is, therefore, that dynamic equilibrium is a condition in which the various forces or influences affecting the abundance of a population are balanced, i.e. their resultant is zero, and the population density is constant. If we apply the term balance very loosely then the dynamic balance involved is equally loose; but in no way does the addition of the epithet 'dynamic' make a loose application of the term balance more appropriate.*

(d) *Balance between populations*

If two species living together in the same environment each maintain an approximately constant density, and each influences the density of the other in some degree, so that each is somewhat reduced, though not eliminated, by the presence of the other, then we may speak of a balance between the two populations. Some apparent examples of such a relationship are seen in laboratory experiments with micro-organisms (Gause, 1934) and insects (Crombie, 1945). It could scarcely occur in a varying environment.

Certainly, pairs of populations in a natural biocoen often vary dependently. For example, the variations in the numbers of a predator may bear a continuous

Another term, *kinetic* equilibrium, is used in physics for the state of *any* moving body, the equilibrium being that between the force of inertia of the body and the forces which give it acceleration (d'Alembert's Principle). The term dynamic is occasionally applied specifically to such equilibrium, but this is unusual. In any case, this sort of equilibrium is shared by all bodies or systems which are neither at rest nor moving with uniform velocity. Hence it is not particularly useful to apply the term in this sense to populations.

relationship to those of a particular prey population. But such relationships are usually neither simple or precise enough to make the idea of a balance between the populations appropriate; linked or dependent variation would be a better description.

Lotka (1925) made the point that slowly changing populations which bear an approximately constant relationship to each other, so that they may be regarded as mutually equivalent, may reasonably be said to form a *moving* equilibrium. In his chapter 21, he applied this term to the system comprising the American populations of man, swine, cattle and sheep, which, over several successive decades, increased in roughly equal proportion, governed by the increasing size of the human population. Lotka applied the idea of moving equilibrium only to systems which change very slowly in relation to the time required to restore equilibrium.

In her study of the effect of environmental conditions on the success or failure of the parasite *Microbracon* in controlling the Mediterranean flour moth, Payne (1934) made great use of the phrase 'host-parasite balance'. The analogy implied is with a loaded weighing balance, which tips to one side or the other in a state of *imbalance*. However, since the intention is quite clear, no confusion arises in this case.

(e) *Conclusions*

First, to summarize: the application of the physical term equilibrium or balance to a population at constant density involves an appropriate and reasonable analogy. The term is not appropriate to normally variable populations, even if they are regarded as tending towards a varying equilibrium level, or as (very roughly) fluctuating about a fixed mean level. Nor should the epithet 'dynamic' be used as if to indicate that only a loose sort of equilibrium is involved. A state of balance between two or more populations may be said to exist if each is approximately constant at a level of density determined partly by the others.

Perhaps the most practical conclusion to draw is that in view of the confusion arising from the loose application of the term equilibrium, biologists should take care to avoid using it inappropriately; other terms should be used to describe the state of populations varying in density; and finally, whenever the term equilibrium or balance is used in biology, it is advisable to state fully and clearly which forces are involved, and in what the state of balance is considered to consist.

D 3. THE MODE OF VARIATION IN ABUNDANCE

The question of balance is closely related to the way in which population variations are conceived; so indeed is the whole question of natural control, and it

is inevitable that the mode of variation should have been touched upon several times already in this discussion. In the previous section, Nicholson's idea, that density tends towards, or fluctuates about, an equilibrium level which varies, was discussed in reference to the concept of balance.

Nicholson (1933) seems to have introduced this idea of variation for the immediate purpose of separating (*a*) the fluctuations of a population about the 'steady density' (the temporary equilibrium position) from (*b*) the changes in numbers due to alterations in the level of the 'steady density' itself. The fluctuations (*a*) are supposed to be due primarily to interactions with enemy populations, while the changes in level (*b*) are due ultimately to the physical environment; the validity of this distinction depends partly upon whether or not it is considered possible to sort out the two kinds of fluctuations. Nicholson's ultimate object was apparently to provide a basis in biological theory for mathematical deductions about population interactions, in which the environment is first assumed to be constant and later introduced as a modifying element. The distinction is of course very difficult to maintain in practice, although Varley (1947) has recently made a beginning in the application of these ideas to a practical problem. It is also interesting to note the parallel with the ecological system of Clements & Shelford (1939); they postulate a primary level of interaction between the living elements of the ecosystem and the physical environment, and a secondary set of interactions between the organisms.

Such a distinction between two types of agents is justified if it is found useful in dealing with mathematical or practical problems. But it does not follow that population dynamics must be viewed exclusively or even predominantly from this angle. I have taken the view that for the purposes of a general theory of control, it is not the most useful line of approach.

We have also referred earlier to the concept that populations simply fluctuate more or less regularly about a mean level of density. Smith (1935, p. 878) writes: 'The general picture of the population changes of a species may... be represented as a series of more or less periodic fluctuations of varying intensity about an average density.' This is close to the idea, criticized by Uvarov (1931, p. 161), that variations in population density can be compared to the swinging of a pendulum from side to side of the mid-line. It also has affinities with the mathematical theories of enemy-prey interactions in a constant environment, which envisage the populations concerned as undergoing regular oscillations.

This is much too regular a picture to be generally applicable. Natural populations, on the whole, fluctuate much more violently and erratically, responding not only to changes in associated populations, but to the irregular variations of the physical en-

vironment. Many populations fluctuate chiefly within a low range of density, with occasional outbreaks; if we draw in the mean density level on a population graph covering a long-enough period, it is above the level of most of the fluctuations. If these fluctuations are related to any mean value, it must be to a lower, temporary one, which is superseded each time there is an outbreak. This is the view Smith adopts. But this is only a special case of a more general difficulty. Many other population curves do not give the least impression that the fluctuations are related to the mean value. Movements towards the mean are often reversed before it is reached. Furthermore, while the idea of fluctuation about a mean may seem realistic when the fluctuations are small compared with the mean value, it is scarcely appropriate to cases in which the 'deviations' are almost as great as the mean value, still less so when some of them are many times greater (cf. Thompson, 1939; Bodenheimer, 1938).

The idea of more or less regular fluctuations about a mean is linked with the conception that each deviation from the average produces forces which cause a return to the average. Certainly, as we have seen, high or low densities do tend to produce conditions causing a return to intermediate numbers, or sometimes to the opposite extreme. But Smith, as in the passage quoted on p. 26, held that 'any tendency of the density to depart in either direction from the average modifies the environmental forces acting on the density in such a way as to restore it to the average'.

To this we must object that there are forces tending to reduce the population even when the density is low, and forces tending to increase the numbers even when they are high. Only, the more extreme a variation becomes, the more is one set of forces strengthened, and the other weakened, until finally the point is reached where the trend of increase or decrease is reversed. When and where the reversal occurs will depend, not on the relation between the present density and the average density, but on the current condition of many varying factors in the ecosystem. Many of these factors are irregular in their variation, yet only within certain limits. Similarly, the density variation of the population will probably be irregular, but only within certain limits, often within the range of a recognizable general level of density. In short, its variation is restricted, it is subject to natural control.

D 4. DO CONTROLLING PROCESSES CAUSE PERIODIC FLUCTUATIONS?

An explanation of the way in which enemies or food shortage might cause population oscillations was offered as long ago as 1863 by Herbert Spencer in *First Principles*, and a partly speculative example

from populations of Lepidoptera was described by L. O. Howard in 1897 (both quoted by Lotka, 1925). Modern ideas on periodic fluctuations have been considerably influenced by the concept of 'classical oscillations' developed in the mathematical theories of enemy-prey interaction.

When Gause (1934) set out to reproduce 'classical oscillations' experimentally, he found that the natural tendency of the micro-organisms he used was towards 'relaxation oscillations', in which the predator steadily killed all the prey and then died out itself. It was only by carefully manipulating the experiments, or systematically adding to the populations, that he was able to produce cyclic fluctuations. It was easier, by providing a refuge for the prey, to produce a sort of incomplete relaxation oscillation in which some of the prey survived the dying out of the predator and then increased freely.

It may seem, as indeed it is, a long step from these highly artificial experiments to the 10-year cycle in natural populations of the varying hare. Nevertheless, we have seen that MacLulich (1937) considered the fluctuations of the hare populations he studied to be examples of relaxation oscillations of the modified type in which a refuge is available—in this case a means of survival for the 'enemy' (disease organisms) as well as for the prey. While later work (Green *et al.* 1939) suggests that the disease responsible for the decline of the hare populations may be physiological and not infectious, MacLulich's theory at least serves to draw attention to the fact that a series of incomplete relaxation oscillations might be indistinguishable from genuine 'classical oscillations'.

By whatever name we call them, the type of oscillations envisaged by the overpopulation theories of Eidmann, Dymond, Kalabukhov, Clarke and others (see section B 4) come into the same general category as the 'relaxation oscillations' of Gause's experiments. The consequences of overpopulation tend to destroy all the animals, but a few survive in protective 'refuges'.

When the crash of a population is apparently due to a particular enemy or disease, the survival of a few nuclei of these appears to be a regular phenomenon.

The recovery of the fluctuating population may be regarded as a reaction to the further reduction of enemies or disease because of the low density of the host, or in some cases perhaps to the development of immunity, and often to changes in weather, etc. After a crash due to food shortage, the food organisms will similarly benefit from the low density of the population, and will normally recover and so make another increase possible. Persistent ill-effects of over-crowding disappear after a period at low density. These matters were discussed in section C 4, where we noted a general tendency towards population fluctuations both upwards from low densities and

downwards from high ones. As we have seen, this is not confined to interacting populations, but may arise in a population which temporarily uses or spoils its physical environment.

The question, whether we should expect any of these phenomena to produce *regular* oscillations in nature, is a difficult one. It depends on our estimate of the constancy (or regularity) of environments. In this connexion, two general observations seem significant. First, the periodic fluctuations of natural populations are not precisely regular; indeed, in many cases the existence of an element of regularity can be established only with difficulty and over a long period of years. Secondly, most of the populations whose fluctuations are the most strikingly regular live in the far north, where the environment may be regarded as unusually uniform (Dymond), and unusually barren, with a relatively small number of species (on the latter point compare section D 5).

But it must be recalled that we have discussed only the processes of obvious importance in control. We have neglected the alternative explanation of these periodicities, namely that the regular fluctuations, or some of them, may be caused or regulated largely by climatic periodicities, as suggested by Elton and others. The problem of assessing the relative importance of these two types of causes of periodicity is beyond the scope of this discussion.

What we can conclude here is that there is a general tendency to population fluctuations which would tend to be regular in a sufficiently regular environment. This arises, like control itself, from other sources besides the enemy-prey interactions of the mathematical theories. They are different in origin from the irregular fluctuations commonly arising directly or indirectly from the vagaries of the weather and from other sources, but of course the two types of variation merge together.

D 5. REDUCED VARIABILITY IN COMPLEX ECOSYSTEMS

Voué (1946) has brought together a great deal of evidence, chiefly from the literature on European forest entomology, in support of the conclusion that outbreaks of forest insect pests are more common in homogeneous woods than in mixed forests. He discusses the reasons for this in terms of his own views on control. Planted woods and some natural forests consist predominantly of one or a few species of tree, with, correspondingly, an undergrowth poor in species, and a relatively poor variety of phytophagous insects. The result is a reduction in the birds and other general predators. This 'faunistic impoverishment' tends to allow outbreaks of insect pests. On the other hand, in mixed virgin forests, particularly in the tropics, the great variety of plants supports a

considerable number of species of phytophagous insects, which form a manifold and dependable food supply upon which a relatively large number of general predators can maintain themselves. The presence of these adaptable enemies tends to prevent outbreaks of pests. Woods in which the trees are mostly of the same age are said to be particularly prone to the development of insect outbreaks, because they tend to reach a stage of maturity at which the leaves are wilting and especially susceptible, all at about the same time.

Graham (1939) also put forward the generalization that certain types of insect outbreaks principally occur in woods where one species of tree predominates.

Similarly, Engel (1942), whose observations on *Bupalus piniarius* were mentioned earlier, concluded that the enemies of this moth are normally less numerous in pure stands of the host tree than in mixed (multi-specific) stands, because no alternative hosts are available to them in the pure stands. Hence *Bupalus* can increase rapidly and reach high densities in the pure stands before being controlled by the enemies. But when the turning-point is reached, the subsequent decline is more rapid than in the mixed stands.

Again, on the basis of observations in eastern Sumatra, Schneider (1939) considered that in the natural forest each species of plant is attacked by a complex of insects, each of which is controlled by polyphagous enemies; but if a species of plant is grown in pure culture, only a few insect species and their enemies can live on it; such a biocoenosis is more labile than a natural one, and serious outbreaks of phytophagous species occur.

In a broad way, there is a geographical zonation of degrees of ecological complexity. The fact that terrestrial life tends to be less abundant and varied as one moves from tropical forest to temperate regions and thence to polar and other barren regions is widely recognized. Combining this point with that of the preceding paragraphs, we should expect a corresponding trend from smaller to greater variability in the densities of populations. There is evidence to support this conclusion. For example, one of the generalizations made by Graham (1939) was that periodic outbreaks of forest insects are more common in temperate than in tropical forests. Periodic fluctuations of populations are most common and marked towards the arctic regions; they are perhaps least evident in tropical forests, but this point seems to have been little studied. A suggestion well in line with this is that a characteristic of the far northern areas which leads to periodic fluctuations in the numbers of animals is their barrenness, their easily exhaustible food resources (Huntington, 1931).

It should be noted that there is a general tendency

for population densities of most species in the tropical forests to be relatively low, perhaps as the result of a more intense struggle against enemies and competitors (Hesse *et al.* 1937, ch. 20). The lower density would mean smaller and less noticeable fluctuations in an absolute sense; but the proportional fluctuations are probably also smaller, because of the greater complexity of the biocoenoses. Another characteristic of tropical populations noted by Hesse *et al.* is that successive generations follow each other in more rapid succession in the warmer climate, and the different developmental stages commonly occur simultaneously. To whatever extent these circumstances make for reduced variability, as suggested by Bremer (1929), they must be added to the other forces opposing large fluctuations of tropical forest populations.

Of course, all this must be interpreted very flexibly and generally, and other factors besides biotic complexity should be considered, especially differences in the variability of climates. Voûte (1946) attached some importance to the idea that an irregular climate might disturb the 'balance' of a population sufficiently to lead to an outbreak.

Other aspects of the physical environment may also have an important influence on the variability of populations. For example, in a very heterogeneous physical environment, there is more likely to be a continual supply of favourable micro-habitats, however changeable the general conditions may be; on the other hand, only a certain fraction of such an environment is likely to be favourable at any one time; these circumstances would be likely to operate against any tendency to extreme variation in the density of a population. The indirect results of physical heterogeneity are likely to be more important than any direct effects. For example, patchiness in the distribution of plants, and hence also of many animals, is to a considerable extent a reflexion of differences in the soil, water supply, etc.

As Thompson (1929c) pointed out, the relative importance of physical to biotic factors is greatest in the barren places of the earth, and least in places like the tropical forests, where physical conditions tend to be uniformly favourable and life most abundant.

To sum up, there is considerable evidence that in the more complex biocoenoses, i.e. those with the greater numbers of interacting species, the variability of the populations tends to be less pronounced. A complex biocoenosis has many resources for compensatory action. The natural control of a population within it is many-sided, resilient and unlikely to break down. Since a varied physical environment is also likely to damp down population fluctuations, and since physical variety tends to be reflected in the plant cover and the dependent animals, the above conclusion should not be restricted to the biocoenosis. In short, population

variability tends to be inversely related to the degree of complexity of the ecosystem.

E. SUMMARY

A. This paper attempts to clarify the subject by giving a systematic account of the processes considered to be involved in the natural control of animal populations.

B. First, a brief survey is made of the chief types of theories offering an explanation of natural control. The earlier theories looked to natural enemies as the main agents of control. Somewhat later theories gave predominance to physical factors. Control has been attributed exclusively to competition, including competition between natural enemies, or, more broadly, to density-dependent mortality. Among theories of periodic fluctuations, many ascribe control to some aspect of overpopulation of the environment, while mathematical theories envisage control due primarily to natural enemies. Certain 'comprehensive' theories lay emphasis on the complexity and essential interconnectedness of the population-environment system, and hold that the particular causes of control vary with the circumstances.

C. The elements of natural control are outlined as follows:

C1. The numerical variation of populations is often considerable and yet is kept within certain limits.

C2. A population and the items of its environment form a closely interconnected complex or ecosystem. The relationships of a population are with the whole ecosystem (which includes itself) rather than with the environment only.

C3. The distinction between density-dependent and density-independent action is discussed, with examples; it by no means corresponds to the division between biotic and physical factors. Density-dependent action is defined as that which intensifies (per individual) as population density increases, and relaxes as density falls; it is the chief agent of control. Some processes are inversely related to density.

Control of a population is a result of the limited capacity of the ecosystem with respect to that species or with respect to its enemies or both. The limiting influence begins to operate at densities far below the capacity limit, intensifying as this limit is approached; this is the basis of most kinds of density dependence (the other kinds are modifications of environmental capacity, the degree of modification naturally depending on density). An enemy is density-dependent in its action on a host (or prey) population if it attacks a greater proportion as the host density increases. The enemy will do this if it is capable, and if the supply of the host is a limiting factor in the enemy's environment.

The presence of competitor species, and sometimes

that of alternative hosts or prey for the enemies of a population, tends to intensify the action of the control factors involved.

C4. Four phases of control are distinguished: *limitation*, which sets a variable upper limit; *conservation*, which tends to prevent extreme reduction; *suppression*, or a forced decline from high density; and *release*, a temporary escape from normal control after a severe reduction. Each is brought about by characteristic density relationships. Suppression and release promote fluctuations.

C5. The level of abundance depends ultimately on all the major elements of the ecosystem, although the density-related, controlling factors are the immediate determinants. Only in regard to particular types of situations, or of animals, can more precise statements be made.

D. Some related matters are also discussed:

D1. The possibility that either physical or biotic factors may be primarily responsible for control in general is examined. Decisions can be reached only about particular types of situations.

D2. Some of the ways in which the term 'balance' or 'equilibrium' has been applied to population relationships are checked against its physical meaning. It is generally inappropriate to any except nearly constant populations, and this applies equally to 'dynamic equilibrium'. To prevent confusion, the above terms should not be used in biology without full explanation of the meaning intended.

D3. Although population variation is restricted, the view that density generally fluctuates about a mean value, and the related idea that deviations from this mean set up a tendency to return to it, are oversimplifications. The idea that density tends towards a *varying* level raises the practical difficulty of distinguishing the two sets of variations, but may be useful.

D4. The laboratory demonstration of the 'classical' oscillations predicted by the mathematical theories has so far proved very difficult. Instead, 'relaxation oscillations', in which the predator population kills all the prey and then dies out, have tended to appear. When 'refuges' are available, as in nature, remnants of each population normally survive such crashes, and may increase again. In very regular environments, a succession of these cycles might be maintained; in more general terms, a repeated cycle of suppression and release (see C4) might occur. But this is speculative, and perhaps other causes are more important in producing periodic cycles in nature.

D5. There is evidence that animal populations fluctuate less violently in very complex ecosystems, for example in tropical forests, than in woods poorer in plant and animal species, and that the most violent fluctuations tend to occur among the animals in plantations of one species, or in barren places like the

far north. Also, irregularities in the physical environment (but not in climate), by increasing the complexity of the ecosystem, probably reduce the numerical variability of populations.

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ADDENDUM

Among the papers I had not seen when this discussion was written, one of special importance is Ulliyett's treatise (1947). Special attention is paid to the density-dependence of the mortality factors.

There is a rather full discussion of general principles bearing on the natural control of *Plutella*, with some interesting conclusions about artificial control measures.