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Edited by J. B. CRAGG

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J. B. CRAGG

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Advances in

ECOLOGICAL RESEARCH

VOLUME 2

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Preface

The main aim of *Advances in Ecological Research*, as was pointed out in the preface to Volume 1, is ". . . to present comprehensive accounts of selected topics of ecological research in such a way that biologists with a general interest in ecology as well as specialists in ecology, can obtain a balanced picture of what is taking place".

Mr. M. E. Solomon's review of processes involved in the natural control of insects will certainly not be the last word in this very controversial field of study. In taking the insects as his basic material and utilizing information from other groups of animals, he has presented a personal viewpoint of this branch of population dynamics. This should help the general ecologist who cannot hope to keep up with the vast literature and provide workers in population dynamics with many points for discussion and development. In the first number of *Advances*, Professor M. E. D. Poore gave an account of his approach to the analysis and description of plant communities. His discussion of classification was of value to animal as well as to plant ecologists. In this number Dr. Joyce Lambert and Mr. M. B. Dale have looked at the classification of plant communities in a different way and they challenge some of the views expressed by Professor Poore. Their paper, in discussing methods of analysing phytosociological data, gives readers a chance of assessing the value of computers in this branch of ecology. Now that the International Biological Programme is taking shape, the information and discussion in Dr. Gorham's and Dr. Bray's paper will provide a valuable starting point for those who will soon be engaged in studying the production of terrestrial communities as part of an international effort. Finally Professor J. Heslop-Harrison's extensive review of genecology provides the ecologist not familiar with the extensive links between genetics and plant ecology, with a broad perspective of the subject and presents a challenge to the animal ecologist.

It was originally planned that *Advances in Ecological Research* should appear every two years. However, sufficient contributions of high quality are coming forward to justify annual volumes.

September, 1964 J. B. CRAGG

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Analysis of Processes Involved in the Natural Control of Insects

M. E. SOLOMON

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I. INTRODUCTION

A short title may cover a wide field. The title of this article is by no means long enough to show precisely what I propose to deal with and which topics will be omitted. The word insects does duty for terrestrial insects and mites. Birds and small mammals appear only in the role of predators upon insects. The emphasis will be on the results of practical studies of population dynamics, especially in the field, on the sorts of data that are needed for the study of natural control, and on their elementary analysis. I shall not deal with statistical methods, nor developments in mathematical modelling, nor the methods of sampling and counting animals. I shall touch only incidentally on philosophical questions such as whether the numbers of animals are regulated or not, and consider instead how to assess the degree of regulation. However, this cannot be done effectively unless there is understanding between writer and reader as to what is meant by this term and certain others. To make these matters clear, I have included explanations of terms and a simple framework of ideas about natural control, which I hope will show the bearing of the topics discussed upon the central problem of how the numbers of animals are regulated.

In the last few years a good deal of new information has become available through studies of insect and mite populations in the field and in small-scale experiments. At the same time, new or newly adapted methods of analysing population dynamics have been introduced and put to work on the results of these investigations. The most notable body of new data and methods comes from studies of forest insects in England (by Varley and Gradwell), the Netherlands (by Klomp and his colleagues) and particularly in Canada. I shall make frequent reference to the recently published account, by Dr R. F. Morris and his colleagues of the Green River Project, on the spruce budworm in the fir and spruce forests of New Brunswick. This project is remarkable for the concentration of manpower over an extended period, for the broad approach to what is a major economic problem, and for the amount of attention devoted to problems of measurement, analysis and mathematical formulation. Other data I have found very instructive include those of Richards and Waloff (1961) on the broom beetle and those of Holling on predation.

The new data are particularly welcome to students of insect population dynamics, since their thinking has generally suffered from an insufficient basis of ascertained fact. The information that has been available has been mainly derived from laboratory experiments, from biological and chemical control undertakings in partly or completely unnatural circumstances, from the simpler examples of regulation in the field, or from investigations that did not go far enough, or not in the right directions, to uncover the regulatory processes. There has been a special shortage of facts about the more difficult, but widely typical, populations that are members of complex communities and subject to manifold influences. The work on forest insects is now providing more data of this sort. It would be valuable, from this point of view, if more of the original observations on the spruce budworm were published. The report (Morris, ed. 1963) presents the relationships found, in impressive completeness, but includes very little of the observational data.

At this stage the problems of how to set about analysing the dynamics

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of populations, and the elementary biological thinking that should guide us in these matters, are of prime importance. The questions involved include the following, which I propose to discuss in later pages. How can the roles played by different factors and sorts of factors in natural control be estimated? How can the presence of regulation be detected, and how measured? How is the effect of a mortality factor changed when it is preceded or followed by other mortalities of various types? In what ways is the action of predators and insect parasites related to the density of the prey? Can different aspects of this action be considered separately?

Methods of attacking these questions will be illustrated as far as possible by use of published data from field investigations, but in some cases by means of hypothetical examples. My aim will be to deal with the methods and examples in their simplest forms. Simple procedures based on elementary ideas are not only easily assimilated; their implications are relatively clear, and they are amenable to development in various directions to meet the needs of particular investigations. I shall not deal with some of the more sophisticated methods and models which forego some or all of these advantages in the interests of specialization for a particular set of circumstances. This does not imply any depreciation of the making of mathematical models, an important aspect of population dynamics which has recently undergone vigorous development, as may be seen from the papers of Watt (1961, 1962), Holling (1962) and others. I agree with Watt's view that in the study of insect populations, as already in fisheries research, this sort of theory is likely soon to become a major means of advance, the more so to the extent that the models are kept in touch with field data, and field investigations are organized in such a way as to use and test the models. But the present article will deal rather with the elements from which complex models may be constructed.

Theories of natural control involve assumptions that must be tested by observation or experiment if the theories are to be seriously employed. This aspect of the relationship between theory and practice emerges explicitly in Section VI, in connection with the influence of predators and parasites upon insect populations.

Thus the article concentrates on a few aspects of a wide subject, and refers to other aspects only briefly or not at all. Within the chosen topics, selection has often been necessary, and sometimes inescapably arbitrary.

II. CONCEPTS AND TERMS

We must begin with the truism that the numbers of animals in natural populations are limited — strikingly so in view of the high rates of reproduction that many species can achieve under favourable conditions. Whatever processes are responsible for this restriction are referred to collectively as natural control. Franz (1962) has suggested the alternative term limitation. If a more formal statement is necessary, natural control can be defined as the process(es) keeping the numbers of animals, in a population not controlled by man, within the limits of fluctuation observed over a sufficiently representative period (cf. Solomon, 1957, p. 132, also Stern *et al.*, 1959, p. 87).

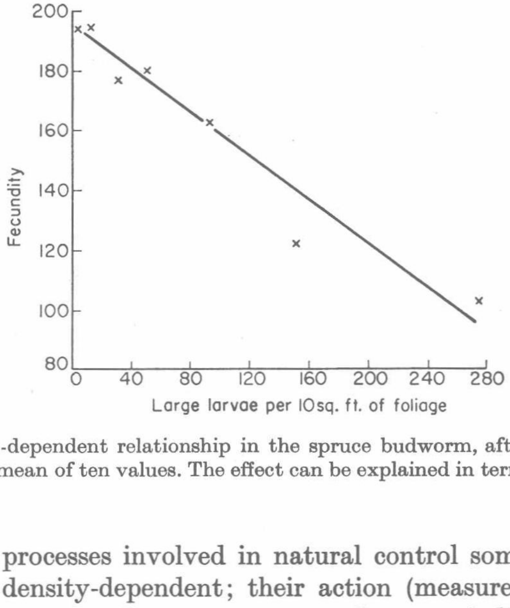

FIG. 1. A density-dependent relationship in the spruce budworm, after Miller (1963a). Each point is the mean of ten values. The effect can be explained in terms of food supply or starvation.

Among the processes involved in natural control some can be distinguished as density-dependent; their action (measured proportionately, as percent mortality or as mean effect per individual of the population) becomes increasingly adverse when density rises, and decreasingly so when density falls (Fig. 1, and cf. Figs. 9A, 14, 15, 16). This relationship between adverse action and density may show itself promptly, as in some forms of competition, or in a lagging reaction, as in the case of an increase of parasites or predators following an increase in the hosts or prey (Fig. 3).

Because the proportionate adverse action of density-dependent processes declines when density falls, as well as intensifying when density rises, such processes tend to curtail fluctuations, whether upwards or downwards, that go beyond the average or normal levels of abundance. Nicholson (1933) regarded them as acting in a compensatory way against any departure from an equilibrium level which continually changes. The restriction of *increases* in density in this way is an active process; the curtailment of downward fluctuations is not —

it is simply an effect of the relaxation of the active process. The principle of this action is the same as that of the governor on an engine; it is the cybernetic principle of negative feed-back. Thus it can be said that

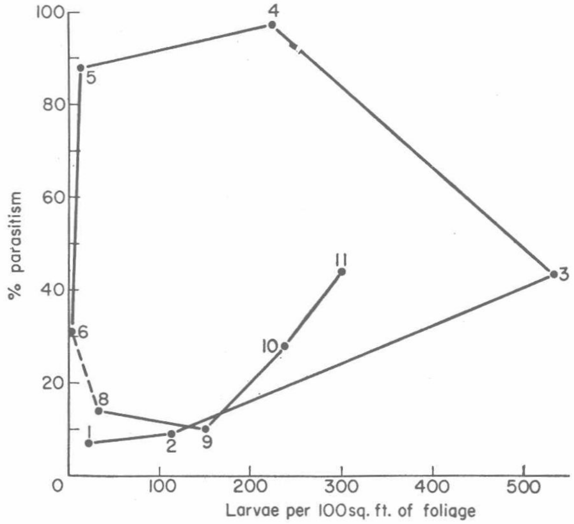

FIG. 2. Graph of data tabulated by Morris (1959) for larval population density and % parasitism of the black-headed budworm, *Acleris variana* (Fern.) (Tortricidae) by a complex of Ichneumoid and Tachinid parasites, in successive generations in a stand of conifers in northern New Brunswick.

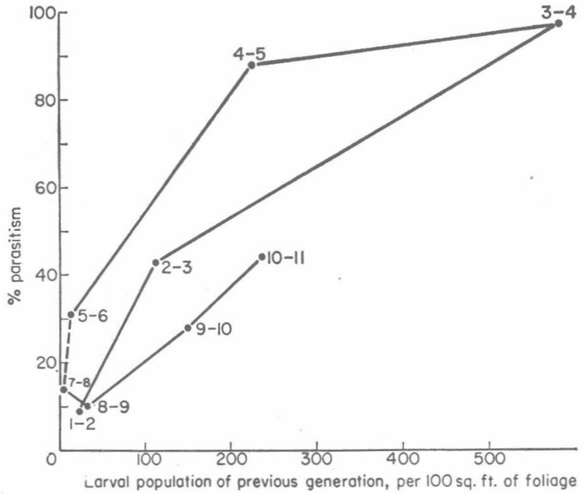

FIG. 3. The same data as Fig. 2, but current % parasitism graphed against host population density in the previous generation, showing (delayed) density-dependent relationship.

density-dependent processes tend to regulate abundance or population density, and I restrict the use of the term regulation to this process (cf. Nicholson, 1954b, density regulating factors). If an increase of population is stopped by some process other than a density-dependent one, this may for the time being constitute an aspect of natural control as defined above, but I do not call it regulation.

In an earlier paper (Solomon, 1949) I equated natural control and regulation, but the general tendency has been away from this strict interpretation of natural control, and I have since used the more inclusive definition. In practice, regulation cannot be studied adequately without reference to the wider aspects of population dynamics, for anything that happens to a population, and anything that it does, may have an effect on its regulation.

Regulation can be imposed by all types of density-dependent processes: by the action of predators, parasites, or pathogens, by intra-specific competition for various requisites including food, shelters and nesting-sites, and by mutual interference or agression which can also be interpreted as an aspect of competition for space or resources. Competition may lead to losses by emigration. In animals that have a social organization, regulation through competition may be mediated by restrictions imposed by the population upon its members.

Density-dependent processes are distinguished from inverse processes, which operate in the opposite sense, i.e. their adverse action becomes proportionately weaker as density rises, or intensifies as density falls. For example, in a sparse population reproduction may be hindered by the infrequency of encounters between the sexes; or, as density increases the proportion parasitized may decline (Fig. 4, and cf. Figs. 9A and 17). Many natural enemies behave as inverse factors under certain environmental conditions, or when the ratio of enemies to prey is low. This is a consequence of their limited capacity for attack. The significance of this feature was first emphasized by Thompson (1939, and earlier). Examples will be cited in Section V.

The action of density-independent processes is not significantly dependent upon population density.

A little more should be said about the differences between prompt and lagging density-dependence. Intra-specific competition generally seems to be promptly density-dependent, and so, at times, does the influence of predators. But in a common type of parasite-host interaction, part of the response of the parasites to an increase in host density is to increase in abundance, which cannot be done promptly. The parasites commonly fail to increase for a time even after the host increase from a low density has been resumed. The result of this delay, as Varley (1953) has pointed out, is that in parts of the parasite-host

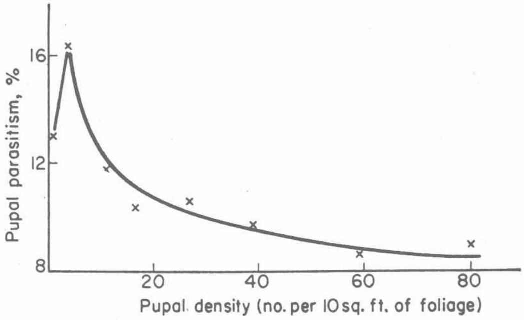

FIG. 4. A predominantly inverse density relationship in the influence of parasites upon the spruce budworm. (From Miller, 1963b.)

oscillation the parasite acts like an inverse factor, at other times like a promptly density-dependent one. While the differences between lagging and prompt density-dependence are often important, they both tend in practice towards regulation, oscillatory in the one case, plain in the other; and both are likely to be rather irregular in most natural environments. The more rapidly the parasite can develop and reproduce compared with the host, the more closely is its action likely to approximate to that of a promptly density-dependent factor. Also some predators and insect parasites can react at once to a rise in prey density by attacking at a proportionately higher rate, in which case this part of their response is promptly density-dependent (Solomon, 1949). Some lagging density-dependent processes do not arise from natural enemies, but from damage to the environment, or, as in one recorded instance (Wallace, 1962), from a toxic effect of feeding on dead bodies.

Taken as a group, natural enemies cannot be classified as all promptly density-dependent, all lagging density-dependent, nor as inverse factors, nor as density-independent. Their action is varied, and affords examples of all of these relationships except perhaps the last. A classification of types of action or types of density relationship is one thing, a descriptive classification of factors (weather factors, parasites, etc.) is another, and the two cannot be fitted neatly together. Certain correspondences occur, not in accordance with firm rules but rather as tendencies, subject to various qualifications and exceptions.

In discussing the influences acting upon a population we may refer to any element in the situation, e.g. predators, competitors, predation or competition, as a factor. At the same time, predation and competition are processes, and may be studied as such. If we are concerned with the way in which the effect of a process or factor varies with the population density, we are studying a relationship, of a type that may be distinguished as a density relationship. Thus, if we find that a population suffers a density-dependent mortality, and identify a predatory population as the cause of this, the predators or their predation constitute a density-dependent factor, the predation is a density-dependent process, and the process can be regarded as the expression of a density-dependent relationship. The use of these different terms need imply no more than choosing the words appropriate to the context.

The term population, as I use it in this paper, simply means any group of animals, usually of one species, that can conveniently be considered as a unit. For the present purposes we may assume that all individuals of the same species and of a particular stage of development are equivalent, although in practice it is desirable, when possible, to take account of differences in age and genetics. In practice, males and females may sometimes be differently involved in density relationships. When different developmental stages occur together, one should take account of the numbers of each stage separately.

III. THREE TYPES OF PROCESSES INFLUENCING ABUNDANCE

On an elementary and fundamental level one can make a three-fold classification of the processes involved in natural control. The three categories are (*a*) regulation by density-dependent processes, (*b*) modification of the regulatory processes, and (*c*) imposition of changes in abundance independently of population density. The use of these simple distinctions is convenient in thinking about population dynamics on the theoretical level and in analysing field observations. The following paragraphs are intended to establish this classification for the purposes of the succeeding discussions.

A. REGULATION BY DENSITY-DEPENDENT PROCESSES

The simpler aspects of regulatory action are the immediate effects of increases or decreases in density, e.g. in intensifying or alleviating competition.

When there are significant lagging effects the picture is more complicated, for lagging or persistent effects tend to give rise to oscillations. For example, it sometimes happens that predators, parasites and phytophagous animals do not immediately relax their attack on the supply of food if this becomes over-taxed, but rather exploit it more intensively; then their numbers are belatedly reduced by shortage of food; the consequent relaxation of attack allows the food to increase again; the consumers, owing to such delays as the time required for growth and reproduction, at first increase rather slowly, and only later come again to dominate the food supply.

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