INTRODUCTION

The study of Population Dynamics is central to the science of Ecology and is fundamental to many applied problems in agriculture and conservation, but it is a subject that has been plagued by controversy for over 50 years. The arguments have mainly concerned the ways in which natural populations are stabilised and the role of density-dependent processes in this stabilisation. At times, these arguments have been so acrimonious that many people have been deterred from entering the debate, thus reducing the progress that has been made.

One of the problems, in the past, has been a lack of precision in the terminology used, so that arguments have been caused by misunderstandings in what people mean by terms such as regulation, equilibrium, and stability. At the same time, real differences in opinion have sometimes been ignored on the grounds that they are simply semantic, whilst other workers have met criticisms of their views by then redefining terms, thus shifting the 'goal posts'. Over the years, many researchers have come to think that continuation of the debate is futile, and have withdrawn into their own field-based or theoretical studies without concerning themselves with generalisation of their findings. As a result, a gap has developed between theory and practice, and too few studies have been made which test the basic concepts underlying population theory. Future progress depends on bridging this gap, and this Symposium was aimed at being a step along that road.

With these problems in mind, we took the unusual action of trying to agree definitions of the more important terms with the contributors to the Symposium, before the meeting started. All contributors had the opportunity to discuss these definitions and agreed that if they needed to deviate from them, they would say why this was necessary and then give their own definitions. We may not finish up agreeing with one another, but we can try to ensure that differences are real, and not simply the result of loose terminology.

Undoubtedly, if Population Ecology was starting today as a new scientific discipline, we could find more acceptable definitions for many of these terms. Thus it would be preferable sometimes to replace old deterministic definitions with stochastic ones. However, although usage of some terms has tended to change over the years, wherever possible, we have tried to keep their original meanings. This both safeguards the priority of the originator of an idea, and of its critics, and reduces misunderstandings when reviewing old and new literature. Inevitably, agreement has required some compromises, but the outcome of these deliberations is seen in the list of definitions on page - .

Three terms require special comment, namely regulation, limitation and stability. These terms make use of words that are in regular English usage and so care is required to ensure that they are used only within the more limited definitions required in Ecology. All three terms are needed in order to distinguish between different concepts of population control. Population stability is used to describe a relative constancy in population size; the population showing no trend, and population fluctuations being in a narrower range than expected from random variation. No mechanism is implied by the use of the term, as increased stability can result from many kinds of process, which may or may not be related to population density. In contrast, regulation and limitation both refer to increased stability brought about by density-dependent processes. Regulation describes the return of a population to a theoretical equilibrium density, whereas limitation describes the reduction in population growth as density approaches the carrying capacity of the environment. These two views of how density-dependent processes are likely to determine population size are very different. Regulation requires a feed-back of density on population growth, so that any deviation (up or down) of population size away from the equilibrium density is countered by an increase or decrease in mortality, reproduction or dispersal. Population limitation results from an increased resistance to population growth as density approaches the ceiling set by available resources. Unlike regulation, limitation operates only at relatively high densities and its effect can only be downwards; it can not affect the probability of extinction at low densities. It is important to recognise that both the equilibrium and the ceiling are dynamic, in that they may change from generation to generation in response to environmental variation.

In planning the programme for this Symposium, we tried to include speakers whose views reflect the full range of opinions on how natural populations are stabilised. Whilst these speakers will stress their differences in opinion, many of these views may not be mutually exclusive. We are still not in a position where we can be certain that all populations of all insect species are stabilised in the same way. All ecologists rightly aspire to producing a generalised theory, akin to say, the theory of evolution, but we are still some way away from this; perhaps not surprisingly, in view of the huge array of life styles adopted by insects. More progress may be made if we are a bit less dogmatic in our approach than our predecessors were.

Since the last Symposium of the Society on Insect Abundance in 1967 (Southwood, 1968), computers have become readily available to researchers, and we now have a larger number of long-term data sets for analysis. As a result, theoretical studies have expanded enormously. Perhaps the most important recent theoretical development has been the recognition that different species may have very different population structures. In particular, the concept of metapopulations has brought some of the ideas of island biogeography into population ecology. Metapopulations are assemblages of local populations inhabiting discrete habitat patches and connected by migration. Local populations have a substantial risk of extinction, so that metapopulations persist regionally in a balance between local extinctions and recolonisations. Obviously the scale over which a metapopulation can exist depends on the mobility of the species, and ideally, we need to know this when planning a field population study. Unfortunately, the majority of past studies do not provide information to enable one to judge the integrity of the population being studied. This would not matter if immigration and emigration, to and from the population were quantified, but few researchers have attempted this. Ilkka Hanski will discuss the importance of scale in insect population dynamics in Chapter 1.

Although population theories have been elaborated and extended, the basic arguments about the processes causing population stability and persistence that were voiced in 1967 are still with us today. In 1967, there were three main hypotheses to explain the observed relative stability of insect populations, namely those generally associated with the names of Andrewartha & Birch (1954), Nicholson (1954), and Milne(1957), and recent developments of their ideas are covered in Chapters 2, 3 and 4 by Piet den Boer, Mike Hassell and Jack Dempster, respectively.

The arguments that have occupied our science for so long really rest on a hierarchy of basic questions, and we suggest that you bear these in mind when reading this book. Firstly, how important are density-dependent processes in governing the extent of fluctuations in population size, and the persistence of populations? Secondly, if they are important, how are these density-dependent processes likely to act? Do they provide a mechanism for regulating populations around a theoretical equilibrium density, and if so, can both intraspecific competition and predation act in this way? Alternatively, is competition the only process capable of consistently acting in a density-dependent manner, and is it capable of regulating a population about an equilibrium density, or simply of limiting the upward growth of populations?

Related to all these questions is how different trophic levels interact with one another. In 1960, Hairston et al published a paper in which they proposed that plants, decomposers and carnivores are all limited by their food resources (ie, by the trophic level below), whilst herbivore populations are kept below the limits of their food by predators (ie, by the trophic level above). No doubt they were greatly influenced by the superficial impression of an abundance of plant food, given by a predominantly green world, but their views met widespread acceptance amongst ecologists. Obviously, if these views are correct, they suggest that population limitation might be more common in all plants, decomposers and carnivores, but not in herbivores. Several of our contributors will refer to this question of top-down versus bottom-up control of populations, and Charles Godfray and Bill Murdoch and their colleagues, deal specifically with top-down effects of natural enemies on their prey populations in Chapters 6 and 7. Are such effects density- dependent and can they regulate prey populations? Also, are natural enemies of any greater importance in the population dynamics of herbivores than at other trophic levels?

Changes in the 'quality' of individuals with changing population density has long been recognised in some types of insect. Some are brought about by physiological and behavioural changes resulting from competition, but others are the result of genetic changes from differential survival of genotypes with changing density. This topic of density-dependent changes in the quality of individuals is covered in Chapter 8 by Simon Leather and Caroline Awmack, and we are especially grateful to them for taking on this task at very short notice.

The potential importance of density dependence has greatly influenced the thinking of ecologists over the years, so much so that many have concentrated on simply attempting to detect density dependence in population data, on the assumption that density dependence can be equated with regulation. Detection of density dependence in population data is actually not as straightforward as was at one time thought. In 1967, correlation techniques were being used, but a battery of alternative methods are now available and these are discussed in Chapter 5 by Peter Rothery.

At the time of our last Symposium, population studies tended to be aimed at developing life tables covering all developmental stages of the study insect, and then using k-factor analysis (Morris, 1959; Varley and Gradwell, 1960) to investigate the roles of separate factors in accounting for population size. The life-table approach proved valuable in identifying the cause of density-dependent factors, and the stage of the life cycle at which they were operating, but as we shall see, the detection of density dependence is simply a first step in identifying processes that might regulate or limit population size. We then need to determine whether they are actually capable of affecting population change from one generation to the next.

The life-table approach was particularly useful in identifying the impacts of mortality factors on population size, but it was far less useful in studying the impacts of those processes affecting recruitment. More recent studies have largely corrected this imbalance, and contributors to this book give several examples in which variations in fecundity are largely responsible for changes in numbers from one year to the next. Adult behaviour, particularly at the time of egg laying, can play a dominant role in determining the use of resources and interactions with other organisms, by their offspring. Modern population theory has to take cognizance of such behavioural traits.

So much for theoretical considerations. The second half of this book concentrates on 'case studies'. These have been grouped into three main themes. The first considers the extent to which we can generalise about the population dynamics of closely related taxa. Repeatedly during this Symposium we have heard how populations of individual species are constrained by their phylogenies - their life styles, specific food or climatic requirements, evolved interactions with other organisms, etc. One might expect, then, to find patterns in the population dynamics of closely related taxa, as indeed has been found in previous reviews of the population dynamics of particular insect groups (eg, Dempster, 1963, 1983; Price et al, 1995). Tony Dixon and Pavel Kindlmann review the population dynamics of tree-living Aphididae in Chapter 9, whilst Nigel Straw, and Jeremy Thomas and his colleagues similarly review the Tephritidae and the genus Maculinea (Lycaenidae), in Chapters 10 and 11, respectively. If we cannot generalise about the population dynamics of these closely related taxa, there is little hope of doing so, more broadly across the Insecta, or indeed, across the Animal Kingdom.

Next, we have two chapters comparing the dynamics of the populations of two well-worked species in different geographical locations, namely, the cinnabar moth, Tyria jacobaeae (Eddy van der Meijden, Mike Crawley and Roger Nisbet, Chapter 12) and the winter moth, Operophthera brumata (Jens Roland, Chapter 13). Are the same processes operating on their populations in different locations, or do different environments impose fundamental differences on their population dynamics?

Then, we have four contributions covering the population dynamics of less well known groups of insects. Peter Price and his colleagues describe their long-term studies of gall-forming sawflies in Chapter 14 ; Ian McLean reports on research on a gall-forming psyllid (Chapter 15); Takayuki Ohgushi describes his long-term study of an herbivorous ladybird (Coccinellidae) (Chapter 16); and finally, we have the only paper considering the population dynamics of a general predator, when Ola Finke describes her work on a dragonfly community in Chapter 17.

It is disappointing how few studies have been made of the population dynamics of predators and parasitoids. The latter, in particular, are such a diverse and successful group of insects, that they form a major gap in our coverage. There are very few studies of populations of phytophagous insects that have not considered insect parasitoids, but research has concentrated on their impacts on their prey populations, rather than on their own population dynamics.

Nevertheless, we think that we have put together an exciting set of contributions, covering a wide range of insect species. To be honest, we did not expect to get a meeting of minds between holders of different views, but we do hope that readers of this book will receive a clear picture of where the subject stands today, and will be stimulated into thinking about what research is required to bridge the gap between theory and practice.

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