PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Introductory Remarks

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These proceedings, like the meeting from which they sprang, bring together two topics of long-standing interest to ecologists: the regulation of individual species and the relative abundance of different species in a community. Indeed, the explicit quest for understanding population regulation can be traced to Gilbert White who, in 1778, queried why year after year there were always eight pairs of swifts in Selbourne. In view of the amount of study which has already been expended on these topics, one may ask 'what is new?' As is clear from this symposium, we are now more in a position to achieve a synthesis of these two topics. Another difference from the situation of some 40 years ago is the fact that plants are now being considered alongside animals and we are gaining new insights from their study.

Coming to more recent history, from about 1920 until 1970 the emphasis was on the dynamics of single- and two-species population interactions. Several models were produced, of which the Lotka–Volterra and Nicholson–Bailey models have been the most enduring. Quite properly, ecologists searched for meaningful field tests of the theories which underlay these models. Such tests involved the measurement of populations in the field, to constructing precise life tables. This work was most straightforward in certain insects, where discrete generations imposed by the seasonal cycle enabled the complexities of overlapping generations and the problems of the determination of the precise age of an individual to be circumvented. Some of the leading work of that time was undertaken in Australia by Davidson & Andrewartha, in Canada by R. F. Morris and his colleagues, and in the United Kingdom by O. W. Richards, N. Waloff at Silwood Park and by G. C. Varley in Oxford. Many techniques were developed for enumerating populations and for analysing them, among the best known being key factor analysis. This technique was devised to detect the stage at which variations in survival contributed most to generation-to-generation fluctuations in population size. As modified by Varley and Gradwell, the technique could also be used in the search for regulating factors, but there were many complications. Some of these factors were statistical arising from a lack of independence of data, but others were because of the sheer mechanical labour of analysing complicated sets of data when all one had at one's disposal were hand-turned calculators, a situation that it is hard to envisage today.

As this work progressed, two further insights added to the complications, though at the same time refocusing our questions in a more constructive way. The first concerns a recognition that we are seldom dealing with individual, isolated populations. Varley always stressed that he chose the winter moth for his investigations because the flightless females ensured that he was handling an isolated population. At the same time as he was undertaking this work, I was involved in studies on the fritfly (*Oscinella frit*). This is a pest species and its study was a necessary condition of my employment. I quickly found that the population in any area was by no means isolated: not only did it change its location every generation (and there were generally three generations in a year) but frequently the adults would move over many miles every few days. Virtually all I was able to say about the meta-population was that the total mass over England and Wales on a warm day in late summer would be well over 200 t! This underlines some of the basic ideas that had led Andrewartha and Birch to entitle their iconoclastic work '*The distribution and abundance of animals*'. As this book shows, the patchiness of nature and the dispersal and interplay of local populations within the mosaic of the environment are today recognized as central topics in ecology.

Underlying much of the early work on population change in the field was the belief that this change could be simply analysed to show whether or not there were regulatory mechanisms at work. However, theoretical advances in the 1970s (in which R. M. May played an important part) have shown that even simple regulatory mechanisms can, under certain conditions, give rise to apparently random fluctuations which in fact are deterministic 'chaos'. This is particularly true when there are time delays and strong nonlinearities, as probably often occur in populations. This theoretical understanding shows that much of the debate at the famous Cold Spring Harbor Conference in 1957 was based on a false premise. The superficial behaviour of a population over time be it steady, cyclic or fluctuating, does not, of itself, tell us a lot about the fundamental dynamical mechanisms: erratic fluctuations may be caused by unpredictable and density-independent environmental events, or they may equally well be caused by strong density-dependence.

The structure of this volume follows in many ways the development of the subject. This is entirely logical; it is important to build our present view of ecology on the fundamental understanding of simple population interactions. On this edifice, we can then turn to the wider view of communities, including genetic variation, as well as the variation in time as reflected through the fossil record.

With environmental problems dominating the news, it is particularly important for ecologists to ask 'where are we now?' and 'what is needed next?' Looking back to my own career in 1950, the justification for ecological research came largely under two headings. First, there was what was then known as 'economic zoology', namely pest control or the harvesting of economically important animals (fish and fur-bearers). Such work was widespread in Australia, Canada and the United States. Secondly, and much less extensive, there was pure research, curiosity about our natural world. Today the situation is entirely different. Human impact on the environment is widely recognized and we stand on the threshold, 'if not somewhat beyond the threshold', of a global environmental change. Many resources are being made available for measurements of the physical environment, but I would suggest that it may well be easier, indeed more appropriate, to detect the integrated impact of such environmental changes through biological indicators. For this we need long-term and comprehensive studies: base line studies. We need to monitor our populations, to observe how they change. It is indeed ironic that just as we are embarking upon this great, unintended experiment with nature of human-induced change in the global climate, long-term studies in Britain which will provide basic information, such as the Rothamsted Insect Survey and fundamental taxonomy, are under tighter constraints than at any time during the past few decades, while abundant resources are available for study of distant worlds (i.e. astronomy) and for the physical conditions of our own world. Those funding biological work need to consider these parallels and to recognize both the need (that is, the understanding and recognition of environmental change) and the opportunity presented by this unique event, at a time when novel and 'high-tech' instrumentation is available to help with the required data. Against this background, the exciting developments in ecology that are reported in this symposium are especially important in helping us to gain fuller and much needed understanding of the world in which we live!

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