

Prefaces

Preface to fourth edition

My coauthor for the Third Edition, and the original author of *Ecological Methods*, Sir Richard Southwood FRS, known to his many colleagues and friends as Dick, died on 26th October 2005. For those interested in reading about his long and highly distinguished career his Wikipedia page http://en.wikipedia.org/wiki/Richard_Southwood will direct you to obituaries and his Royal Society biographical memoir. Dick was a wonderful man to work with and a fine head of department. While achieving senior academic positions at an unusually young age, he retained an open and pleasant manner, a love of natural history, and remained accessible to the most junior members of staff, all of whose names he would invariably know. When he was head of the Department of Zoology at Imperial College and I was a first-year undergraduate, I was astonished that he knew the name of every undergraduate in his department.

I was keen to revise *Ecological Methods* in part to honour Dick's memory, but also because, I feel, the book still serves a useful purpose acting as an ecologist's handbook of methods and sources of information. While The Web now gives ecologists, even in isolated spots, access to a huge amount of information it can be difficult to glean the full range of possibilities for experimental approaches, sources of information and sampling gears. The old problem of how to design a successful sampling scheme and build samplers remains with us.

The trends in ecological research that we noted in the Preface to the Third Edition have continued at an accelerating pace. Computation and data handling has advanced greatly, and the present edition includes many references to R, the computing language and environment for statistical analysis and graphics. The dramatic growth in R packages for ecologists, all of which are offered free of charge, is one of the most important developments since the publication of the Third Edition. I have included many examples of R code in the present edition. Electronic developments in radar, sonar, remote sensing satellites, miniature tags, geographical positioning, movement detectors, lights, digital cameras, mobile phones and batteries have all greatly increased the opportunities for data acquisition. These advances, combined with novel biochemical techniques such as species detection from amplified DNA fragments, are creating tremendous opportunities for ecological research. We now have tools and resources that would have seemed incredible to a 1950s or 1960s ecologist. Yet, many of the techniques we use are still based on the ideas developed and refined between 1930 and 1980. Indeed, some of our sampling methods would have been familiar to our hunter-gatherer ancestors. One of my aims has been to maintain continuity with this great body of earlier knowledge. In part, this is because earlier papers are able to describe techniques and equipment in far more detail than is normal today. But, it is also the case

that our predecessors often had great insight, and in many cases we can re-apply their ideas using our superior electronics and data handling to good effect. It is heartening to note that as journals have fully digitised their back numbers, many earlier papers are being regularly cited.

Early ecologists suffered from a lack of long-term time series. With each passing decade datasets are becoming larger and the opportunities for more detailed analysis of temporal dynamics increases. In addition, remote sensing and large-scale observation, as undertaken in particular by bird and butterfly watchers, has greatly extended the opportunity for spatial analysis. Recent concerns about species loss, habitat destruction and fragmentation, and the effects of climate change are dependent on the collection and analysis of temporally and spatially extensive data sets. The collection and handling of these data and the computation of indices of change, species richness and diversity are important fields which continue to develop.

Dick Southwood is still included as an author of *Ecological Methods* Fourth Edition because there are still many parts of the book which were originally authored by him and have been little changed. However, I answer for the inadequacies of the present edition. Finally, I would like to express my gratitude to all my colleagues, including Clive Hambler and Anne Magurran in particular, who have directed me to interesting work and techniques for inclusion. This edition has been much improved by the careful and accurate work of the copyeditor, Mr William Down. The book would have many irritating errors without his thoughtful attention to detail. A considerable task for a book of this size and complexity.

Peter Henderson
Lymington, February 2015

Preface to third edition

We have been encouraged to prepare this third edition by the continuing use of the earlier editions. In doing so we have been struck by contrast between the advances in some areas, especially data handling, and the enduring value of various other techniques. Ecology has continued its advance into the popular and political domain, though far from everything that has gained the 'eco-' prefix falls within our purview. The underlying paradigm of ecology has however shifted. In particular the concept of the metapopulation is now recognised as central to the understanding of the distribution and abundance of animals and its exploration aided by the accessibility of numerous data sets, often with large temporal or spatial scales. The availability of molecular techniques has encouraged the consideration of genetic and phylogenetic aspects and has permitted the growth of quantitative comparative analyses described by P.H. Harvey and M.D. Pagel (1991) *The Comparative Method in Evolutionary Biology* (Oxford).

The extent to which we have felt that revision was necessary has varied greatly in different parts of the book. Where there has been little change in the method, we have retained the early references. We have done this on the bases that journal editors formerly permitted more detailed description of methods, that these papers will not

be located by computer searches and that these pioneers continue to deserve credit. Other portions have required considerable modification; we have deleted one chapter (12) and added a new one (15), as well as reorganising the structure in some places. Although the primary focus remains on insects, which are in terms of species the dominant animals, we have taken the opportunity to explicitly expand the coverage to all major macroscopic groups.

The widespread availability of high capacity PCs, with software packages and access to the internet, has totally changed the speed and ease of handling (and sometimes accessing) data. We have therefore given references to some relevant software packages and web sites, whilst eliminating many descriptions of time consuming graphical methods. However, we believe that the advice given in the preface to the second edition is even more applicable today. The researcher, who relies entirely on the output of a computer, is in danger of drawing false conclusions and overlooking possible insights. It is essential to understand the features of the data (are there any outliers?), the assumptions of the methods, the biological basis of the analysis and to acquire a feel for the capabilities and responses of the species under study.

The interpretation of 'ecological methods' remains as described in the Preface to the First Edition, namely those methods peculiar to ecologists, either in their origin or in modification. Just as the measurement of physical factors, using the methods of the physical sciences, has always been outside the book's scope, so are the methods of molecular biology. These are described in a number of works such as *Molecular markers for population ecology* (1998), *Ecology* 79, 359–425, edited by A.A. Snow and P.G. Parker.

We are most grateful to many ecologists who sent comments on the second edition. In particular generous help has been given by Drs C. Henderson, D.J. Rogers, A.E. Magurran, W.D. Hamilton, G.R.W. Wint and Mr C. Hambler.

T. R. E. Southwood

P. A. Henderson

Oxford, October 1998

Preface to second edition

In the twelve years since the First Edition was prepared there have been remarkable developments in ecology. The subject has changed its lay image, from a rather recondite branch of biology, to something that is widely considered 'good', but only vaguely understood. The public's focus on environmental problems and the insights into these that ecology can provide are a great challenge to ecologists to develop their subject: they need to be able to provide reliable quantitative inputs for the management of the biosphere. The enormous volume of work that it has been necessary to review for this edition is evidence of the extent to which ecologists are seeking to meet this challenge.

I believe that the theme of the first edition, the need for precise measurement and critical analysis, is equally valid today; although many recent studies show levels of sophistication that were beyond my wildest hopes when I embarked on the preparation of the first edition. In his review of the first edition Dr R.R. Sokal was kind enough

to say it was an 'unusual book' for it covered both traps and mathematical formulae, topics that were usually of interest to different people. This, I am glad to say, is now no longer generally true. The computer and the electronic calculator have revolutionised the handling of ecological data, but neither can make a 'silk purse' of sound insight, out of a 'sow's ear' of unreliable raw data or confused analytical procedure. More than ever the ecologist needs to keep his biological assumptions in mind and remember the value of preliminary simple graphical analysis as a means of recognising new patterns and gaining fresh insights.

It has been a gratifying, though exhausting, experience preparing the new edition! Progress has been so rapid in several areas that some chapters have been completely or largely rewritten (e.g. 11, 12, 13), whilst most have large new sections. It has been necessary to be highly selective in the additions to the bibliographies, even so there are nearly a thousand new entries and only a few older references could be deleted. I hope that, with the advent of *Ecological Abstracts*, the selective nature of the bibliographies will not handicap workers. As the mathematical side of ecology has grown, so have the problems of notation and it is now quite impossible (without extending far beyond the roman and greek alphabets!) to retain a unique notation throughout. Apart from widespread and generally accepted symbols, I have merely aimed to be consistent within a section.

I am most grateful to many ecologists who have helped me in this revision by sending me reprints of their papers or notes on difficulties and errors in the first edition. Detailed criticism, advice and help, including access to unpublished work has been generously given by M.H. Birley, P.F.L. Boreham, M.J.W. Cock, G.R. Conway, M.P. Hassell, R.M. May, A. Milne, S. McNeill, G. Murdie, G.A. Norton, S. Parry, P.M. Reader, G. Seber, N.E.A. Scopes, L.R. Taylor, R.A.J. Taylor, T.W. Tinsley, J.M. Webster, R.G. Wiegert and I.J. Wyatt. I am deeply indebted to them, and to others, especially Margaret Clements and my wife, who have assisted with patience and forbearance in the essential tasks associated with the preparation of the manuscript of the new edition.

T. R. E. Southwood
Imperial College
Silwood Park, Ascot.
October 1977

Preface to first edition

This volume aims to provide a handbook of ecological methods pertinent for the study of animals. Emphasis is placed on those most relevant to work on insects and other non-microscopic invertebrates of terrestrial and aquatic environments, but it is believed that the principles and general techniques will be found of value in studies on vertebrates and marine animals.

The term ecology is now widely used in the field of social, as well as biological, science; whilst the subject of ecology, covering as it does the relationship of the organism

to its environment, has many facets. It is, in fact, true to say that the ecologist may have need of recourse to almost all of the methods of the biologist and many of those of the physical scientist: the measurement of the physical factors of the environment may be a particularly important part of an ecologist's work and he will refer to books such as R.B. Platt & J.E. Griffiths' (1964) *Environmental Measurement and Interpretation*.

There are, however, certain methods that are peculiar to the ecologist, those concerning the central themes of his subject, the measurement, description and analysis of both the population and the community. These are *ecological* methods (as opposed to 'methods for ecologists' which would need to cover everything from laboratory workshop practice to information theory); they are the topic of this book. During the 10 years that I have been giving advanced and elementary courses on ecological methods at Imperial College, London, and at various Field Centres, the number and range of techniques available to the ecologist have increased enormously. It has been the comments of past students on the utility of these courses in helping to overcome the difficulties of coping with the scattered and growing literature that have encouraged me to attempt the present compilation. I am grateful to many former students for their criticisms and comments, as I am to the members of classes I was privileged to teach at the University of California, Berkeley, and at the Escuela Nacional de Agricultura, Mexico, whilst writing this book.

Although the general principles of most methods are of wide application, the study of a particular animal in a particular habitat may require certain special modifications. It is clearly impossible to cover all variants and therefore the reader is urged to consult the original papers that appear relevant to his problem. I am grateful to my publishers for agreeing to the publication of the extensive bibliographies, it is hoped that these will provide many leads on specific problems; they are, however, by no means exhaustive.

The present book is designed to be of use to those who teach the practical aspects of animal ecology in schools, training colleges and universities; insects, being numerically the dominant component of the macrofauna of terrestrial and many aquatic habitats, almost invariably come to the forefront of ecological field work. This volume is intended as an aid to all who need to measure and compare populations and communities of animals, not only for the research ecologist, but also for the conservationist and the economic entomologist. Population measurement is as necessary in the assessment of the effects of a pesticide and in the determination of the need for control measures, as it is in intensive ecological studies. It is frequently pointed out that ecological theories have outstripped facts about animal populations and I trust that it is not too presumptuous of me to hope that this collection of methods may encourage more precise studies and more critical analysis of the assembled data so that, in the words of O.W. Richards, we may have 'more light and less heat', in our discussions.

The topics have been arranged on a functional basis, that is, according to the type of information given by a particular method. As a result some techniques are discussed in several places, e.g. radiotracers will be found under marking methods for absolute population estimates (chapter 3), the measurement of predation and dispersal (chapter 9) and the construction of energy budgets (chapter 14). By its very nature ecology cannot be divided into rigid compartments, but frequent crossreferences in the text, together

with the detailed contents list and index, should enable the reader to find the information he needs. The sequence of chapters parallels, to a large extent, the succession of operations in a piece of intensive research.

It is a pleasure to express my great indebtedness to colleagues who have read and criticised various chapters in draft: Dr N.H. Anderson (ch. 6), Dr R.E. Blackith (ch. 2 & 13), Dr J.P. Dempster (ch. 1, 2 & 3), Mr G.R. Gradwell (ch. 10), Dr C.S. Holling (ch. 12), Mr S. Hubbell (ch. 14), Dr C.B. Huffaker (ch. 2), Dr G.M. Jolly, (section II of ch. 3), Dr C.T. Lewis, (section I of ch. 3), Dr R.F. Morris (ch. 10), Dr O.H. Paris (ch. 9 & 14), Mr L.R. Taylor (ch. 2 & 4), Professor G.C. Varley (ch. 10) and Dr N. Waloff (ch. 1, 2 & 10); frequently these colleagues have also made available unpublished material; they are of course in no way responsible for the views I have expressed or any errors. For access to 'in press' manuscripts, for unpublished data and for advice on specific points I am grateful to: Drs J.R. Anderson, R. Craig and D.J. Cross, Mr R.J. Dalleske, Drs W. Danthanarayana, H.V. Daly, E.A.G. Duffey, P.J.M. Greenslade, M.P. Hassell, P.H. Leslie, J. MacLeod, C.O. Mohr, W.W. Murdoch and F. Sonleitner, Mr W.O. Steel, Drs A.J. Thorsteinson, R.L. Usinger, H.F. van Emden, E.G. White, D.L. Wood and E.C. Young. Ecologists in all parts of the world have greatly helped by sending me reprints of their papers. I have been extremely fortunate too in the assistance I have received in translating; Mrs M. Van Emden has generously made extensive translations of works in German, and with other languages I have been helped by Dr F. Baranyovits (Hungarian), Dr T. Bilewicz-Pawinska (Polish), Mr Guro Kuno (Japanese), Dr P. Stys (Czechoslovakian) and Dr N. Waloff (Russian).

Much of the manuscript was prepared whilst I held a visiting professorship in the Department of Entomology and Parasitology of the University of California, Berkeley; I am indebted to the Chairman of that Department, Dr Ray F. Smith, for his interest and the many kindnesses and facilities extended to me and to the Head of my own Department, Professor O.W. Richards, F.R.S., for his support and advice. I wish to thank Mrs M.P. Candey and Mrs C.A. Lunn for assisting me greatly in the tedious tasks of preparing the bibliographies and checking the manuscript. My wife has encouraged me throughout and helped in many ways, including typing the manuscript.

T.R.E. Southwood
London, October 1965