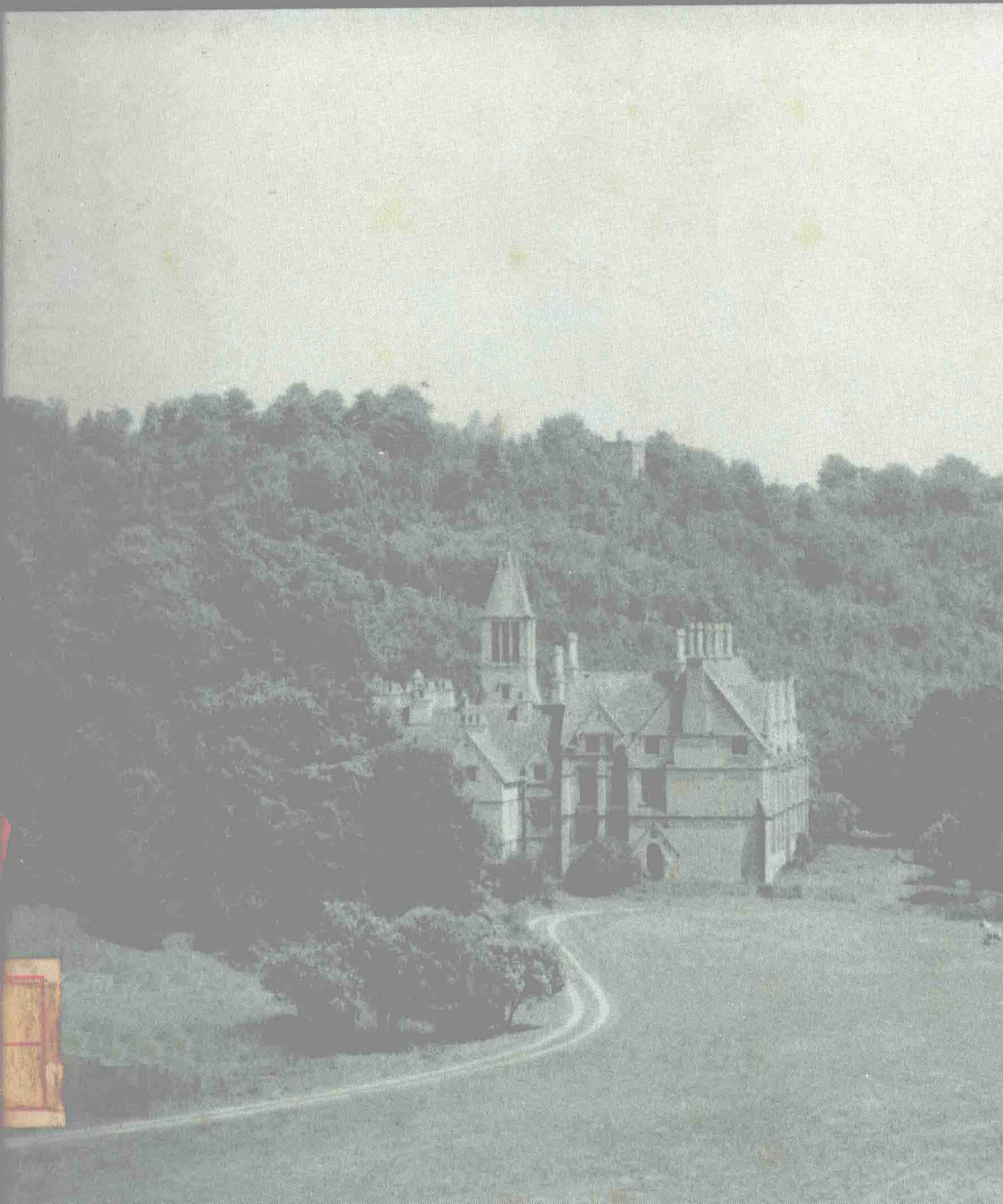
Case studies in population biology

edited by L. M. Cook



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Preface

There are between 1.5 and 15 million living species of plants and animals. The generation of diversity is a central process of evolution, but the reasons for it are imperfectly understood. Botany and zoology are concerned with the study of living systems at all levels from macromolecule to communities of species, a manifold approach which is necessary before we can hope to unravel a general picture of evolution. Population and evolutionary studies have been a feature of the zoology departments of Manchester and Liverpool Universities for many years. Emphasis has been placed on the need to relate theoretical models to real situations and teaching commitments to research. Field courses are an excellent way of combining both requirements, and they play a prominent role at Manchester and Liverpool.

This book presents a series of studies linked by the following common characters. They originate from observations made on field courses held at Woodchester Park Field Centre, Gloucestershire, UK; they are designed to investigate the factors determining numbers within species and coexistence between species of animals; and they are concerned with the problem of the extent to which theoretical models can be related to natural populations. The following pages present some data, provide some answers, and in so doing, give an account of the methodology of aspects of ecological field studies.

The contributions also record the influence of J. Gordon Blower on the development of ecological field studies in Manchester. It would not be his nature to wish his name to appear on every page, but his influence, pervades the book. His part has been to create the course at Woodchester Park (and earlier at other centres) and modestly but persistently to question the assumptions of population ecology in an effort to get the answers right. He will be remembered for this by generations of students. At a time when increasing emphasis seems to be placed on self-promotion and the acquisition of research grants, it is a pleasure to recognise the influence of a different type of approach. For Gordon Blower, satisfaction and self-confidence have been derived

from a single-mined respect for the subject. This book is dedicated to him and to that aproach, following his retirement from formal teaching in September 1982.

The courses could not have run so successfully without the whole-hearted cooperation of Mr and Mrs A.R. Kelly. We thank them for the facilities they have provided at the Field Centre, both for the courses themselves and for research throughout the year. We are grateful to the people of Nympsfield for their welcome over seventeen years. A notable characteristic of the Manchester Zoology course has been the contribution of Richard Abbott. We thank him for his technical and logistic skills and for many liaison activities, always performed with a light touch.

L. M. Cook

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Introduction

This book could be seen as an account of the population biology of a very few animal species in a limited area in south-west England. From another point view, it is also an account of how university research develops out of, and contributes to, university teaching. This is a theme frequently developed by university lecturers in justification of the apparently ambiguous role of a university; we hope that we have provided here a practical example of how teaching and research are mutually related. A third view of this book might be that it is an examination of a very important topic in population biology, namely, how one defines a population. We trust that this third view, at least, justifies the book.

Three separate threads have combined to produce the research described here. One is the educational background alluded to above; these studies developed out of field courses run for second-year zoology students at Manchester University. A second thread is the ecological and geographical background, providing appropriate animals in sufficient abundance for study. A third thread is the historical one, providing an appropriate base, a field centre, which we have been privileged to use for 17 years, enabling us also to observe changes in animal populations over that time span. These three threads will be elaborated further in this chapter.

Educational background

The Department of Zoology, University of Manchester, has run field courses in population biology each year since 1953. Initially, they were run at various locations in the Lake District, but, after interludes of one year each at Swansea (1965) and Snowdonia (1966), the courses have taken place at Woodchester Park in Gloucestershire since 1967.

The course lasts for two weeks, and in nearly every year has been held in the last week or so of June and the first week of July.

Initiating the course, establishing its content and its format, were among the most important contributions made by J. Gordon Blower to the academic life of Manchester's Department of Zoology. To outsiders, he is probably best known as a millipede specialist, author of the Linnean Society's Synopsis for that group (Blower, 1958, 1985). To us, his colleagues, he is formally Reader in Ecology (appointed in 1959, having served previously as a demonstrator from 1948 and as a lecturer from 1951), and informally the best teacher of undergraduates amongst us; several generations of students would, we know, concur with that judgement.

Among the other contributors to this volume, R.R. Askew, L.M. Cook and D.W. Yalden are also members of staff in the Department of Zoology at Manchester, and have attended the field courses at Woodchester Park in practically every year from 1967 onwards. Dr M.V. Hounsome was originally a postgraduate student in the department, and since 1974 has been Keeper of Zoology at Manchester Museum; he has attended the field courses, specifically to organise bird-ringing activities, since 1971.

One direct consequence of the use by Manchester of Woodchester Park has been that other universities have become aware of the suitability of the site for their own field courses. In some cases, this has arisen because Manchester postgraduates or staff have taken up appointments in other universities. Notable among these was the late Dr J.A. Bishop, a member of staff at Manchester in 1967–1968, who moved to Liverpool University's Department of Zoology in 1968 and started a tradition of use of Woodchester Park which continues to the present. Professor A.J. Cain was concerned with establishing Woodchester Park as a venue for field courses both during his time at Manchester (1963–1968) and then from Liverpool. Two of the present contributors, R.J. White and J.S. Bradley, became involved as postgraduates of Liverpool Department of Zoology. Of the other contributors, W.I. Montgomery was an undergraduate student and then a postgraduate at Manchester. Dr R.R. Baker, a member of staff at Manchester since 1974, actually became acquainted with Woodchester Park initially as a demonstrator at Newcastle upon Tyne Zoology Department through field courses introduced by another ex-Manchester postgraduate, Dr B. Shorrocks.

Run originally for students of Honours Zoology only, the courses have been duplicated for Biology students. The first course for them was organised in 1975 by R.R. Baker, and has run every year since then, usually in the fortnight following the zoology course. Thus we have, for more recent years, a month of information on some populations, notably birds and mammals.

The main emphasis of the Manchester field courses has been estimation of the size of animal populations. As Gordon Blower remarked in his introduction to the report of the first Woodchester Park field course in 1967, 'The most important characters of an animal population are the number of individuals and the age structure of these.' In most years, the first class exercise has been to examine the population of earthworms. Various sites around the Field Centre have been used, not always the same sites every year nor, in detail, the same procedures. Formalin extraction has always been the principal method, though in some years we have also attempted comparison with potassium permanganate used (like formalin) as a repellant, and with hand sampling. After this, the class has split into a number of groups, each studying the population of a very mobile group of animals by mark, release, recapture procedures. The traditional animals for teaching these techniques to zoology students in Britain have been grasshoppers, and these we too have studied in almost every year. We have also extended the techniques to populations of moths, damselflies, butterflies, small mammals and small birds in most years, and have on occasion applied them, either in class exercises or in individual student projects, to such diverse animals as the bug *Calocoris sexguttatus*, ants, wolf spiders, ladybirds, ground beetles, and even earthworms.

We had several reasons for selecting the topic of population estimation for such concentrated attention. It is essential in most practical and theoretical studies in animal ecology to have some idea of population size; in some studies (estimating levels of predation, for example), the absolute population size may be required, whereas in others a relative index may suffice (for example, when estimating selection pressures on different phenotypes). As an educational tool, we have found that approaching the study of animals through estimation techniques focuses the attention of students on the biological problems involved. The techniques of mark, release, recapture could perfectly well be taught using beads in a laboratory, or even taxis at an urban railway station (Bishop & Bradley, 1972), but the biological problems posed by, for instance, trap shyness and trap addiction, territoriality, migration and 'mortality' (whether real or statistical — loss of marks at ecdysis, for instance) are problems that force themselves on the students' attention.

Much of our effort on the field courses has been concerned with teaching the mathematical procedures, and much student effort has been expended in getting them correct. This led to the production of a student handbook (Blower *et al.*, 1981) summarising this aspect of our courses. Computer programs have recently taken the tedium from this part of the work. The question of the best statistical procedure to use remains an important one for discussion on the courses, and there is a

difficult balance between what is efficient statistically and what is biologically practical. One recurrent theme in discussion, however, has been 'What *is* a population?'; this will be elaborated further in this volume. Students are frequently mystified but intrigued to spend five or six days studying a group of animals and then to realise, as they analyse their results, that they don't actually know how to define the population on which they have been working. The problem scarcely arises with grasshoppers or small mammals, which are perceived to be contained within some arbitrary grid or quadrat under study. It is most acute with birds and, especially, moths, which are highly mobile animals that are sampled only at one or a few points in a large 'home range', the points at which mist nets or moth traps are operated.

Some of the chapters that follow are directly concerned with this problem. Chapter 4, discussing the bird population of Woodchester Park over 13 years, derives directly from the field courses. The other chapters all concern animals that have been studied on field courses but have been pursued further by postgraduate students working over a three-year period for their doctorates.

Geographical and ecological setting

We could not have continued to visit Woodchester Park for so many years, and the postgraduate studies could certainly not have been concluded successfully, unless a suitable range of populations, of adequate size for study, had been assured. Other field-course sites which we have on occasion used have not attracted such constant attention, nor produced such intensive studies, suggesting that there is something a little special about Woodchester Park. If there is, then it stems from its geographical and ecological setting.

Geographically, Woodchester Park occupies a deep eastward-opening valley in the Cotswold Hills. It lies in the county of Gloucestershire, in vice-county 34 of the Watsonian system, and in the National Grid square SO 80; the buildings of the Field Centre, 'the Cottage', are at SO 812013. The valley opens near the small town of Nailsworth, 4 km away. Stroud is 6 km away to the north-east of the Field Centre; the nearest large towns are Gloucester (18 km N), Cheltenham (27 km NE) and Bristol (37 km SW) (Fig. 1.1). Most of the Park lies in the parish of Woodchester (Woodchester village is just 3 km north of Nailsworth), but the parishes of Nailsworth, King's Stanley and Nympsfield also impinge upon it. The Park is roughly 4 km long from east to west, approximately 1 km across at its widest from north to south, and has a map area of about 250 ha. In altitude it ranges from 213 m (700 ft) in the west to 75 m (250 ft) in the east. The

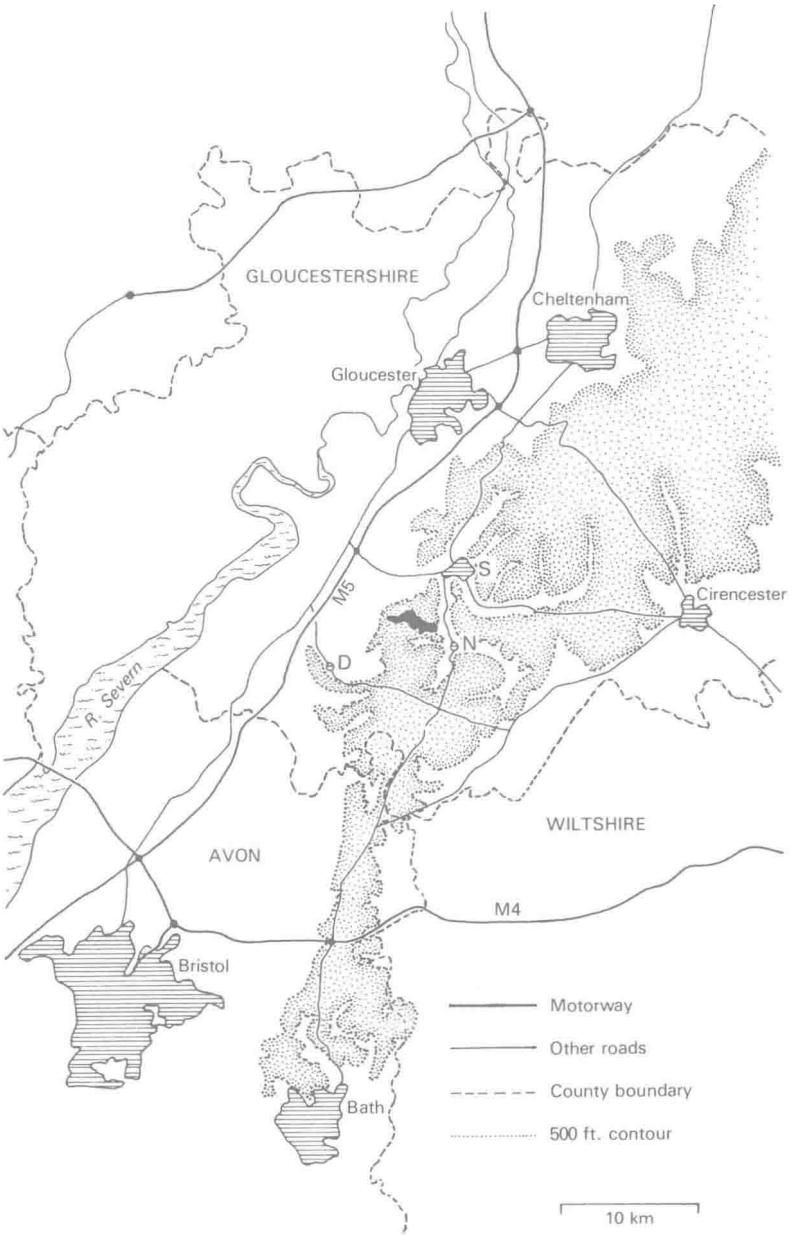

Fig. 1.1 Woodchester Park: regional setting. Woodchester Park (shaded black) occupies a valley which opens eastwards near Nailsworth (N), with Stroud (S) to the north and Dursley (D) to the south. (Based upon the Ordnance Survey Map with the permission of the Controller of Her Majesty's Stationery Office, Crown Copyright reserved.)

Fig. 1.2 Woodchester Park: local setting. Woodchester Park occupies part of three parishes, King's Stanley (K.S.), Nympsfield (N.) and Woodchester itself (W.). (Based upon the Ordnance Survey Map with the permission of the Controller of Her Majesty's Stationery Office, Crown Copyright reserved.)

valley is steep sided, incised into a plateau which is, all around, at an altitude of 150–230 m (Fig. 1.2).

This geography reflects very directly the geology of the area. The Park lies entirely on rocks of Jurassic age, notably the Inferior Oolite, a hard erosion-resistant limestone responsible for much of the scenic, as well as architectural, attraction of the Cotswold Hills. In the bottom of the valley, the Park rests on the Marlstone Rock Bed, an impervious clayey limestone which is frequently, as in the Park, the marker for a line of springs (Cave, 1977). Above this lies a bed of bright yellow sand, the Cotteswold Sands, about 30 m thick, and, in the valley, the usual site of badger setts. On top of the sands lie the limestones of the Lower and Upper Inferior Oolites, approximately 42 m thick, constituting the hard surface for the plateau in this region, and the summit of the scarp slope of the Cotswolds just a kilometre or less to the west and north of the Park (Fig. 1.3). In particular, Selsley Common, just north of the valley on the scarp slope and formed from the Upper Inferior Oolite, is important to us as a site where grasshopper population studies (see Chapter 3) and our class exercises on both grasshoppers and butterflies take place.

Climatically, Woodchester Park is in the relatively mild south west of Britain. The meteorological station at Cheltenham records a mean annual temperature of 10°C, with a mean daily maximum of 14°C and a mean daily minimum of 6.2°C; annual total rainfall has averaged (1916–1950) 69.3 cm (27.3 in). More significant for us than the long-term averages has been the variation in weather from year to year, since this has very marked repercussions on the fauna available to study on the field course each year.

We remember such extremes as the drought of summer 1976, and the long, hot spell that year which started during our field course, or the cool, wet spring of 1977 which resulted in us finding no adult grasshoppers, no Yellow Underwing moths, and too few butterflies to study.

Superimposed on this geographical and geological setting is an ecological setting which in part reflects the natural fauna and flora of the region, but even more the historical and agricultural history of the area. There are nine chambered tombs and tumuli within a 5 km radius on the surrounding plateau (notably 'Hetty Peglar's Tump', 2.5 km away to the south west), indicating that late Neolithic/Beaker Age people were well established in the area by 3000 BC. There are also two hill forts, presumably of Iron Age, at Uley Hill and Ring Hill, 3.5 km to the south, and 8 km to the north, respectively. Human occupation of the area in Roman times is also well attested by archaeological remains, notably the villa with its famous mosaic at Woodchester itself (Sheils, 1976). The former presence of Anglo-Saxon

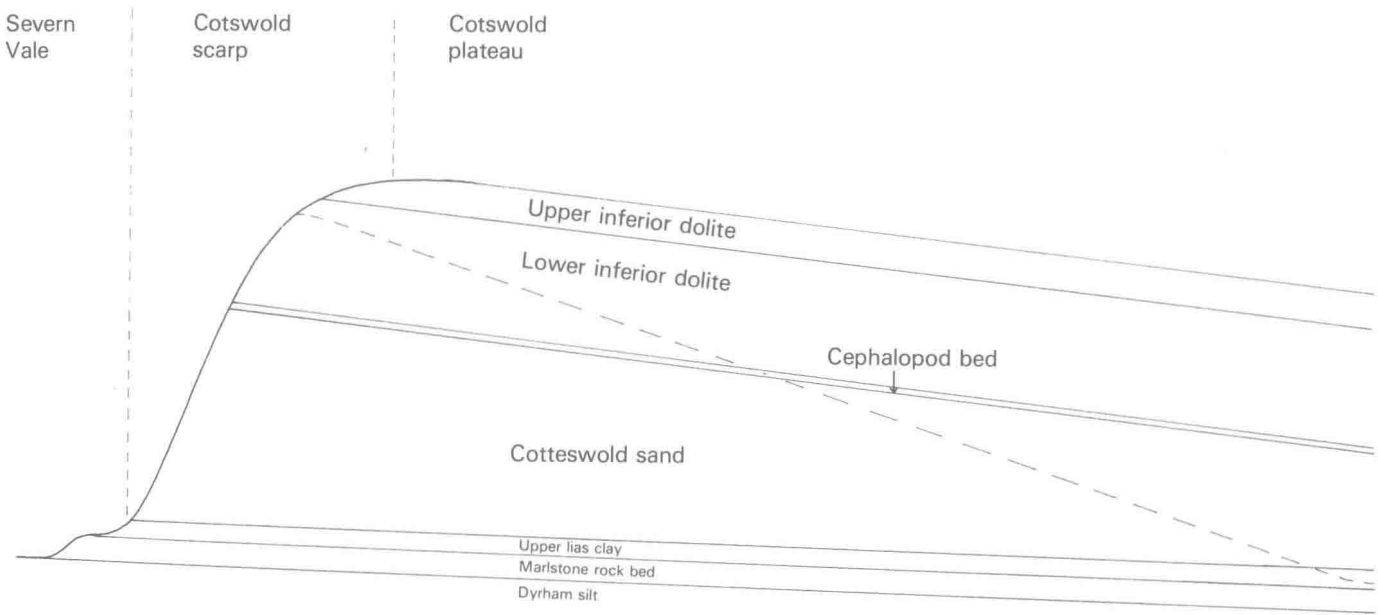

Fig. 1.3 Woodchester Park: geological setting. A schematic geological section through the Cotswold Scarp in the vicinity of Woodchester Park. The depths of the named strata are drawn roughly in proportion.

settlers is indicated less by archaeological remains than by their place names, which we still, in essence, use: Nailsworth (Naegl's enclosure), Woodchester (the Roman camp or settlement in the wood), Nympsfield (Nymed's field) and King's Stanley (stony clearing), the principal parishes, are essentially Old English names (Smith, 1964*a*, *b*), as are those of other local features. In the Domesday Book of AD 1086, Woodchester, Nympsfield and (King's) Stanley are recorded as manors, and they have a well-documented existence since then. (Nailsworth is exceptional, in that it developed as a non-conformist settlement from the seventeenth century onwards at the 'corner' of Horsley, Minchinhampton and Avening parishes and was created as a parish in 1892 (Herbert & Sheils, 1976).)

The human population of this area of Gloucestershire has probably always had a modest density, and this has undoubtedly contributed to the survival of some of the interesting patches of habitat in the area. At the time of the Domesday survey, AD 1086, the Cotswold plateau held three or four plough teams and six to seven recorded people per square mile (Darby & Terret, 1954). This was about the average density for the English Midlands generally, with parts of Leicestershire and Nottinghamshire more densely populated but Staffordshire, Shropshire and northern Warwickshire more sparsely occupied; it implies that the valleys, at least, were well farmed. King's Stanley had 18 men listed, and Woodchester had 16 villagers and 12 smallholders. At the start of the modern censuses, Nympsfield had 523 citizens in 1801, and 532 in 1811, but the population dropped steadily through the nineteenth century to only 216 people in 1901 (Minchin, 1907). There has been some modest increase this century, however, and 398 people were recorded at the 1971 census. In Woodchester, the population has been more stable, averaging 882 (range 816 (1861) to 974 (1871)) during the nineteenth century; in 1971, it was 820.

A park is recorded as early as 1311, but it was greatly enlarged by enclosure, absorbing open field and common land in Woodchester parish and overlapping into neighbouring parishes, in the early seventeenth century. In the early eighteenth century, it was described as the largest park in the county, with a boundary 7 miles in circumference. Spring Park, as it was often called, was later landscaped, perhaps by John Spyers who made a survey of it in 1782. The ownership of the manor, subsequently the park itself, is well documented from AD 1199 onwards. It belonged to the Ducie family from 1631 to 1846, when it was sold to William Leigh. He demolished the manor house, and started on the construction of a new house, the Mansion; meanwhile he lived in the Cottage which is now the Field Centre. The Mansion was, in fact, never completed, though it still stands as an imposing piece of architecture (Verey, 1969). The majority of the

park is currently managed as a private forestry venture (Sheils, 1976).

One ecologically important feature which is clear from the historical records is the continuity of woodland in the area. In Woodchester parish, woodland is recorded in documents as early as AD 716, and wood sales were economically important in the fifteenth and sixteenth centuries. Nisbet & Vellacott (1907) quote Rudge (1807): '. . . the most extensive (beech woods) are . . . the magnificent woods at Spring Park, and on Frocester and Stanley Hills, belonging to Lord Ducie.' In King's Stanley, Domesday records woodland 1 × 1½ leagues in extent; subsequent records mention 80 acres of woodland in 1295, 161 acres in 1322, and 148 acres of 30- to 40-year-old beech in 1568 (Herbert, 1972). Although woodland history is not quite so well documented in Woodchester and Nympsfield, it seems certain that some of the steep slopes in the park have been continuously covered in woodland, albeit well-managed and exploited woodland. The preponderance of Beech (*Fagus sylvatica*) certainly reflects human management of the woodland (Thorley, 1981) rather than, as was once thought, the persistence of 'ancient beech woods', but the patches of deciduous woodland, which include Field Maple (*Acer campestre*), Gean (*Prunus avium*), and Yew (*Taxus baccata*), may well be relics of ancient woodland.

The history of open grassland habitats locally is less clear. By analogy with elsewhere in southern Britain, one may suppose that the limestone plateau was cleared of forest in or by late Neolithic times, say 4000 years ago. Probably areas of herb-rich limestone grassland, such as the lower slopes of Selsley Common, have had a continuous history of grazing since that time. We know that attempts to enclose Selsley were made, and successfully resisted, in 1831 and 1852; earlier, in 1766, its area was estimated at 150 acres. Common rights of grazing are still exercised, from May to October each year, under the control of the grazing committee of the parish council (Herbert, 1972). However, the upper, level part of the common was ploughed under the wartime emergency agricultural powers, and 40 years later that part of the common still has a herb-poor pasture, dominated by Ryegrass (*Lolium perenne*), which contrasts sharply with the herb-rich grassland on the slopes.

Within the park, most of the limestone grassland, and much of the deciduous woodland, has been replaced by conifer plantations (see Fig. 1.4). These are mostly of larch (*Larix* sp.), but include also cypresses (*Thuja*) and spruce (*Picea*); there are also some plantations of hybrid poplar (*Populus* × *euramericana*). Three meadows remain in the valley bottom, and small remnants of limestone grassland persist, notably at 'Inchbrook Meadow' to the east, just outside the park gates, and at the top of the valley to the west. The valley bottom contains