MICROCLIMATIC FACTORS IN AVIAN BREEDING PATTERNS:

IMPLICATIONS FOR WOODLAND NATURE RESERVE DESIGN.

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Thesis submitted for the degree of Ph.D. in the University of Leicester.

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ABSTRACT.

MICROCLIMATIC FACTORS IN AVIAN BREEDING PATTERNS: IMPLICATIONS FOR WOODLAND NATURE RESERVE DESIGN.

by

GRIFFITH JOHN WARRILOW

Temporal variation in the first day of egg-laying of the Blue Tit within a deciduous woodland is accounted for by the small but significant spatial differences in microclimate, particularly temperatures. The warmer areas, which are confined to the southern half of the wood, are also characterised by larger clutch sizes and greater survival of nestlings into the local population.

Furthermore, examination of the total breeding avifauna of this wood shows densities to be highest in the warmer areas and particularly along the south-facing edge zones.

Investigation of 16 woodlands (range 0.01-14.9 ha) shows that bird species richness increases with increasing woodland area but that there is an inverse relationship between breeding bird density and woodland size. However, the total species number and breeding density of 14 small woods are markedly higher than those of a single large wood of roughly equal size. These differences are accounted for by the high proportion of edge zone within a group a small woodlands (86%) compared with the single larger wood (24%). The clear importance of small woodland patches to the total avifauna of East Leicestershire, and presumably other parts of lowland England, is stressed.

The proportion of edge zone is influenced by woodland size, shape, internal structure (including the presence of rides and clearings), slope and aspect. Combinations of these factors can result in edge zone depth being considerably increased in a woodland.

The importance of the edge zone to maximising species numbers is described in relation to various strategies of woodland nature reserve conservation. One such strategy advocates that species numbers and breeding densities in a very large wood can be enhanced by careful attention to management proposals such as ride-widening, tree-thinning and coppicing. The influence of these findings on future large-scale planting is also discussed.

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The Nest Record Scheme at Billesdon Coplow was operated by Mr. D.G. Kirton, who also built the nest-boxes. His assistance in the field was of great value.

Land-owners were most co-operative in providing me with unrestricted access to the study woodlands. Janet and Arthur Bridgwood, at Billesdon Coplow, deserve special mention in this respect. They permitted DGK and I to erect 90 nest-boxes, 2 weather stations and 35 sucrose screens in their wood. Other helpful land-owners were Mr. T.G.M. Brooks (Wistow), Mr. J.F. Goddard (Wistow), The Quorn Hunt (Botany Bay), Sir Henry Tate (Owston), Mr R. Wright (Loddington Reddish).

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PART I

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THE INFLUENCE OF MICROCLIMATE ON BLUE TIT BREEDING SEASONS

CHAPTER 1

GENERAL INTRODUCTION.

1) Aims of the Study.

The aims of this thesis are:

- i) to examine the factors responsible for determining the breeding success of the Blue Tit Parus caeruleus¹ in woodland patches. Particular emphasis is placed on the spatial variation of microclimate within woodland and how this relates to the start of egg-laying and subsequent fledging success for this species.
- ii) to establish which factors are responsible for local microclimatic differences in woodland and to show how these vary as woodland plot characteristics such as size, shape, slope and aspect change.
- iii) to investigate whether variations in the density of breeding birds within a range of woodland patches are explained by these microclimatic differences.
- iv) to examine the extent to which area, shape and spatial pattern of woodland patches influence bird breeding densities and total species numbers.
- v) to investigate possible avian conservation strategies for woodland in the light of the results of this study.

East Leicestershire was selected as a suitable area in which to study these topics for several reasons. First, the area contains numerous woodland patches of varying size, slope, shape and isolation. The O.S. 1:25,000 sheets SK60/70 and SP69/79 (see map enclosed in back cover pocket), which cover the study region, show about 406 of these woodlands. Despite the intensification of arable farming in Leicestershire since the Second World War, they have persisted in

¹All scientific names of fauna and flora are given in Appendix 2.

the landscape through their long traditional association with fox-hunting, many of them being maintained as fox coverts. Secondly, many of these woodlands are of a type commonly found throughout lowland England, namely semi-natural mixed deciduous woodland with occasional admixtures of exotic species such as sycamore, larch, etc. They are therefore typical of a much wider area of Britain than just East Leicestershire. Thirdly, study sites had to be easily accessible in order to facilitate the disjunctive nature of sampling of a part-time study of this type when much of the fieldwork would have to be undertaken in evenings and at weekends. Fourthly, it was an important consideration woodlands should fulfil the basic requirement of being undisturbed by the general public, thus permitting specialised meteorological equipment to be left safely for long periods. Lack of persistent human activity is also important when breeding bird populations are to be regularly monitored. A limited attempt to control a few corvid species is made by land owners in some study woodlands, but this effort is extremely irregular, usually conducted in non-breeding periods and has no apparent effect on the rest of the breeding avifauna. Its impact on the presence of some corvids, however, is described in Chapter 10. Most woodlands in East Leicestershire, and all the study sites, are privately owned and have no public access.

There has been a long history of woodland reduction in Great Britain, the story of which has been well covered in several standard textbooks, e.g. Tansley (1949), Rackham (1980), Peterken (1981). Today little natural or semi-natural woodland remains. Only about 7.6% of Britain has a forest cover and only about 1.5% is covered by semi-natural broad-leaved woodland which, it is agreed, possesses the richest avifauna (see, for instance, Simms 1971, Ratcliffe 1977, Fuller 1982). This reduction and fragmentation of our forest cover poses serious problems for the preservation of several species of flora and fauna. It is against this background that the present study should be viewed. Moreover, there are two potential future land use strategies which provide a context for this study, namely the effect on the avifauna of (a) the continued fragmentation of woodland and (b) an increase in woodland area brought about by, for instance, the Set-aside Scheme proposals.

Similar studies to this one are few in number. A general survey of bird species numbers in British woods led Moore & Hooper (1975) to conclude that nature reserves should be as large as possible to maintain the maximum species richness. After examining the effect of forest fragmentation on birds in Maryland (USA)(latitude 39°N), Whitcomb *et al.* (1981) also were clear that reserves should be "hundreds or even thousands of hectares" in extent (p.190). Galli

et al. (1976) and Askins et al. (1987) also examined species-area relationships, New Jersey (USA)(40°N) and Connecticut (USA)(42°N) respectively, and in reached the same conclusion. In addition, two of these studies (Moore & 1975, Galli al. 1976) attempted to specify Hooper el minimum area requirements for individual species. None of them, however, reported whether the total species number of several smaller woods is greater than that of a single large wood of equivalent area.

One study alone, that by Ford (1987) in Oxfordshire (52°N), has examined this aspect in detail. In finding that many more species can be supported by several smaller plots than a single large woodland of equal area, he suggests that the preservation of several small woods could be offered as an alternative conservation strategy to the single large woodland. This is tentatively ascribed to a greater proportion of the 'edge zone', with its associated denser vegetation, in smaller plots. The term 'edge zone' as used here refers to the ecotonal zone along the perimeter of a woodland patch which possesses distinctive dynamics, vegetational structure and species composition. (A more detailed description of the edge zone is presented in Chapter 8).

Ford (1987) comments briefly on the negative relationship found between woodland area and bird breeding density, a feature noted by other researchers. It merits stressing here that, to date, Ford's study represents the only detailed investigation of species-area relationships of woodland avifaunas in Britain. Further, it should be pointed out that virtually all the research conducted for this thesis was undertaken prior to (and therefore without knowledge of) the recent publication of Ford's work; my fieldwork period running from April 1980 - June 1988.

This present study also examines species-area relationships and bird breeding densities for a range of woodlands similar to those in Ford's study. The general location of the study woodlands are shown on the O.S. 1:25,000 map extract located in the back cover pocket.

For this thesis, site selection is based on more rigorous specifications than in other species-area studies. First, of the 18 study woodlands² (range 0.01-110.7 ha), fourteen (range 0.01-2.2 ha) are closely grouped within a 2000 m x 1000 m rectangle at Wistow (centred on O.S. grid reference 644960;

²The plates follow Chapter 6.

Plate 1). These woodland patches were selected to provide a total area (8.8 ha) roughly equal to the size of each of two other study woodlands, Billesdon Coplow (11.4 ha; G.R. 710045; Plate 6) and Botany Bay Fox Covert (14.9 ha; G.R. 705046; Plate 6). This would facilitate comparisons to be made between their respective species compositions and breeding densities. The total bird population of all 14 woodland patches was censused. Secondly, particular care was taken to include, within the Wistow group of woodlands, a wide variety of patch shapes and sizes. Thirdly, the two largest study woodlands for which total bird populations were also surveyed, Billesdon Coplow and Botany Bay Fox Covert, were selected to provide, within adjacent sites of roughly equal areas, contrasting perimeter shapes and a wide range of slopes with different aspects. Whilst canopy cover is continuous in Billesdon Coplow that of Botany Bay is broken occasionally by broad rides and clearings. Fourthly, a total of six control plots (each of 4 ha) were chosen within the core or interior zones of two considerably larger woodlands. Of these, four were sited in Owston Big Wood (110.7 ha; G.R. 790065; Plate 19) and two in Loddington Reddish (36.2 ha; G.R. 776022; Plate 17). These control plots would enable 'interior' species to be identified and their breeding densities to be established. In addition to the 6 plots situated in the interior zone, a further two control plots (4 ha each) were sited along the southern margin of Loddington Reddish to monitor bird species richness and breeding density of the edge zone of a large woodland.

Furthermore, this study investigates in more detail than hitherto the principal factors responsible for spatial variations in breeding densities, and particularly the influence of the edge zone on the breeding avifauna. Proposals for conservation strategies are based on the results from these findings. Though birds are sometimes quoted as the best biological indicators of environmental change (e.g. Blondel 1983), brief consideration is also given in this study to the implications of the results herein to other fauna.

Fieldwork was mostly restricted to intensive sampling during the period March-July each year. The main fieldwork activities for this study may be briefly listed as follows:

- i) monitoring first dates of egg-laying in Blue Tit at Billesdon Coplow, 1980-1987.
- ii) detailed examination of microclimate at two weather stations in Billesdon Coplow, March-June 1983 and 1984.
- iii) determination of mean monthly temperatures using sucrose solution sensors, Billesdon Coplow, January-June 1984 and

1985.

- iv) preliminary investigation of breeding bird populations in selected woodlands, April-June 1985.
- v) vegetational mapping of trees with characteristics indicative of being within the woodland edge, Billesdon Coplow, 1986.
- vi) complete census of breeding bird populations in all 16 study woodlands and 8 control sites, April-June 1987.

2) Methods

Full details on specific methods of study are provided at appropriate points in the chapters that follow and in certain appendices. Only a broad outline is now given in this introductory review.

For the microclimatic studies, fine detail was essential since, for example, differences of a degree or less in temperature have been shown to be important in some aspects of avian ecology. The availability of thermistors, solarimeters, omni-directional sensitive cup anemometers and miniaturised automatic data-loggers now permits such approaches where the 'disturbance factor' can be greatly reduced.

As will be later described in Chapter 4, the published literature on the practical application of the sucrose inversion method provided limited assistance. For this reason, the data gathered at Billesdon Coplow by this method between January-June 1984 are insufficiently validated to be included in the thesis. Only those from the following year are presented.

Total breeding bird populations of the 16 study woodlands were censused using the standard mapping method (Enemar 1959, IBCC 1969). Those of the 8 control sites were determined by the point count method (Blondel *et al.* 1970). A detailed description of these methods is given in Appendix 3.

When examining woodland patches attention was given to the assessment of the 'edge' characteristics so that the edge zone and interior zone of each example could be determined.

3) The Arrangement of the Thesis.

The thesis is arranged in two parts, each sub-divided into chapters. Part I begins with a general introduction to the thesis and to the area of study. It presents a detailed investigation of woodland microclimate at one particular site and shows how this influences the breeding season and survival of the Blue Tit.

From the more detailed approach of a single site in Part I the study is then broadened in Part II to consider the influence of microclimate on the breeding avifauna of several woodlands. In particular, spatial differences in breeding densities are examined within both small and larger woodland plots, and these are related to patch size and shape.

Each part has its own review of the literature and discussion section. The thesis ends with a general discussion, where the findings of the previous chapters are brought together as a framework for exploring the implications of the study for avian conservation strategies, and the summary and general conclusions.

The area under study is covered by O.S. 1:25,000 maps SK 60/70, Leicester (East), and SP 69/79, Kibworth. Six-figure grid references are cited after relevant place-names. Those given for woodlands identify the approximate centre (e.g. Billesdon Coplow, G.R. 710045).

Heights and other measurements are in the metric system.

The level of significance used in all statistical tests in this thesis are presented as follows:

P<0.05 as * P<0.01 as ** P<0.001 as ***

Whilst it is recognised that the term 'patch' may refer to a wide variety of altered habitats within a matrix (see, for example, Forman & Godron 1986), unless stated otherwise, use of the word 'patch' in this thesis is taken to mean a woodland patch.

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In references to plants, the nomenclature followed is that of Clapham, Tutin & Warburg (1981); for birds, the systematic list of Voous (1973, 1977a, 1977b) is followed.

The Appendices contain all tables and figures (in Appendix 1), technical details and other material whose inclusion in the main body of the text would, in the author's opinion, interrupt the flow of the arguments presented.

All the figures presented in the thesis have been drawn by the author.

CHAPTER 2

DESCRIPTION OF THE STUDY SITES

Introduction.

A total of eighteen woodlands were selected in East Leicestershire for study. The fragmented nature of the woodland in this part of the county is clearly apparent from the O.S. map extract (back cover pocket). Overall, only 2.9% of Leicestershire has woodland cover (I. Evans, pers comm), making it the third least wooded county in Britain.

The study woodlands extend from the Wistow Estates in the south-west to the Owston woods in the north-east, a distance of approximately 20 km. In the region of Wistow the landscape is almost flat and lies at an altitude of about 90m O.D. (Fig. 2.1(map 3)).¹ From here, the land in East Leicestershire rises steadily towards the north-east where it becomes progressively more undulating as the higher ground is dissected by several small streams. The ridge upon which the western part of Owston Big Wood stands represents, at over 210m O.D., the highest elevation in any study woodland (Fig. 2.1(map 2)).

The study woodlands are situated mainly on Clays of the Upper, Middle or Lower Lias or on calcareous Boulder Clay. In general, these soils are poorly drained and waterlogging is common particularly along rides frequented by horseriders where the surface readily becomes poached. Several of the woods are drawn regularly by the local fox-hunts.

A range of woodland sizes was included, from 0.01ha to 110.7 ha. The following criteria were used in selecting woodlands for study:

- i) presence of mature trees over the entire site forming a closed canopy, or nearly so;
- ii) trees of predominantly or exclusively broadleaved species; particularly pedunculate oak, beech, ash, maple, or sycamore;

¹All figures are presented in Appendix 1.

- iii) widespread, but not necessarily continuous, field and scrub layers;
- iv) the presence of a mature woodland edge;
- v) surrounded by altered habitat, usually farmland, thereby functioning as a habitat island;
- vi) no areas of large-scale clear-felling, burning, or planting within the woods immediately prior to or during the study period;
- vii) a variety of woodland patch shapes with different orientation;
- viii) a variety of topographical gradients should be present in, at least, some woods;
- ix) each showing varying isolation from other wooded patches;
- x) all situated on similar soils.

One particular aim of this study is to establish whether the total species richness and breeding bird density of a cluster of smaller fragmented woodlands differ from those of a single larger wood of equivalent area. In order to investigate this pattern 14 smaller woods, varying in size from 0.01-2.2 ha (total area, 8.8 ha) were chosen on the Wistow Estates. The total species number and breeding bird densities here were compared with those recorded at Billesdon Coplow (11.4 ha) and also at Botany Bay Fox Covert (14.9 ha).

Site descriptions were compiled from ground surveys (made in 1987/88), published data (where available) and vertical aerial photographs (taken in 1969/70).

The vegetation stand types used by Peterken (1981) were adopted for the description of the semi-natural woodlands: Botany Bay Fox Covert, Loddington Reddish and Owston Big Wood. However, being more recently planted and not conforming to these types, the other study woodlands were not classified by this method. Instead more general descriptions are provided. To assist with these accounts the categories defined by Elton (1966) were also adopted as follows:

i)	ground layer	<0.15 m,
ii)	field layer	0.15-2.0 m,
iii)	scrub layer	2.0-6.0 m,
iv)	woodland layer	>6.0 m.

However, it must be pointed out that the vegetation forming the ground layer is believed to have limited importance in terms of woodland avifauna since few species are ground nesters or feeders and so is usually omitted from the following site descriptions.

1) Wistow Estates.

A total of 14 woodlands were selected around Wistow Church $(52^{\circ}34'N 1^{\circ}03'W;$ Plates 1-3) which, alone, represents the remains of the former village of Wistow, deserted in Medieval times. The woodlands (W1-W14) are situated within a rectangular area approximately 2000 m east-west and 1000 m north-south. They vary in area from 0.01 ha to 2.2 ha; all but two patches are less than 1.0 ha in extent (Plates 2 and 5). Many exhibit a linear shape (Plates 1, 3 and 4), through being planted along the sides of the Grand Union Canal when this section was under construction in about 1797. Details of individual woodlands, including size and shape, are presented in Table 2.1.²

The broad flood-plain of the River Sence dominates the landscape here (Plate 3) and slopes imperceptably towards the west. The land is slightly higher to the north of the Grand Union Canal and to the south of Wistow Church. The Wistow study woodlands lie between an altitude of 84-98 m O.D. (Fig. 2.1(map 3)).

The principal species of the woodland layer and the scrub or field layers for each Wistow woodland patch are listed in Table 2.1. In summary, pedunculate oak was the most widespread species in these patches, forming the main woodland layer in 8 of them. Two woods each were composed of ash, horse-chestnut and Lombardy poplar. Beech, sycamore, Scots pine and alder were also quite widespread, being recorded in another 4 woods, although at low densities. A few isolated examples of elm, lime, crack willow, aspen and walnut were also noted and further emphasise the wide range of tree species present in the Wistow study woodlands. Hawthorn was the most widespread plant of the scrub layer, being dominant in 9 patches; blackthorn or box formed this habitat layer in three more woodlands.

Table 2.1 gives details of the habitats adjoining each wood which, in general terms, lie within an intensively agricultural landscape. Four of the study woodlands are connected directly by hedgerows to neighbouring patches. The presence of aquatic habitats (with streams, the River Sence and Grand Union Canal), a suburban-type garden and parkland (scattered trees set in grassland) further increase the habitat diversity of this region.

²All tables are presented in Appendix 1.

2) Billesdon Coplow.

Billesdon Coplow (52°38'N, 0°57'W; Plates 6-12) is situated on a knoll which forms a western outlier of the Liassic Marlstone escarpment in East Leicestershire (Plates 6 and 7a). It covers an area of 11.4 ha and is approximately 400 metres square. The highest point is roughly in the centre of the wood (Fig. 2.2a; Plate 7b). The northern half is characterised by gentle slopes (maximum gradient, 5°) towards the north-west, north-east and east; the southern half has steeper slopes (maximum gradient, 13°) that change in aspect from west through south to south-east. The wood lies between an altitude of 168-201 m O.D.. There is no surface drainage in Billesdon Coplow.

In view of Billesdon Coplow being the site of much specialised microclimatic and bird population research, it is appropriate to provide a more detailed description of the vegetation than for the other woodlands.

There are many distinct vegetational zones within the wood (Fig. 2.2b), each dominated by a single tree species as follows: beech on and around the crown of the hill (Plates 8 and 9); pedunculate oak along the northern, western and southern margins (Plate 10); sycamore in the south-eastern sector (Plate 11); and larch in the north-east (Plate 12). Adjacent to this larch plantation is a small area of Norwegian spruce. Small, but less important, additional details to these principal areas are shown in Figure 2.2b. Further species present at low density, and having no clear distribution pattern, are horse-chestnut, sweet chestnut and Scots pine. Bramble forms a widespread but discontinuous field layer throughout much of the wood but this gives way to a low rhododendron scrub in the south-eastern corner (Plate 11). The main species of the scrub layer, hawthorn, is thinly distributed over the whole site.

Billesdon Coplow is surrounded by farmland which is predominantly permanent pasture (Plates 6 and 7). There are just two hedgerows which physically adjoin the wood but neither is directly connected to a neighbouring patch. However, lying close-by, but separated by the main Leicester-Tilton on the Hill road, is Botany Bay Fox Covert. The perimeters of the two woods are off-set and do not immediately face each other. Adjacent to both woodlands is an area (2 ha) of parkland ecotone (open canopy woodland with grassland) (Plate 6) which, owing to the absence of field and scrub layers, did not meet the criteria used for woodland selection in this study. Thus it was excluded from the breeding bird surveys.

3) Botany Bay Fox Covert.

Botany Bay Fox Covert $(52^{\circ}38'N, 0^{\circ}58'W;$ Plates 6, 13-16) has an area of 14.9 ha and is roughly star-shaped with three vertices. The maximum diameter is about 600 m. It lies at an altitude of 154-172 m O.D. with the land sloping gently westwards from the eastern woodland margin (Fig. 2.1(map 1)). A few minor streams drain the wood and all flow westwards to the River Soar.

The wood is uniformly composed of the 'wet ash-maple' stand type (Plates 13 and 14) but there is also a thin scattering of pedunculate oak, sycamore and Scots pine trees throughout. The main species of the field and scrub layers are bramble and hawthorn respectively (Plate 14).

Three small areas of about 30-50 m diameter each were clear-felled during the mid-1970s (Plate 15) and, today, still have an open canopy. The field and scrub layers are especially well developed in these clearings. The importance to avian breeding patterns of the open canopy here and along the main ride of the wood (Plate 16) is discussed in Chapter 9.

Botany Bay Fox Covert stands in an agricultural landscape of mixed farming (Plate 6). Four hedgerows adjoin the wood but none is connected directly to a neighbouring wood.

4) Loddington Reddish.

Loddington Reddish (52°37'N, 0°52'W; Plates 17 and 18), with an area of 36.2 ha and approximately 700 m square, is one of the largest woodlands in East Leicestershire. It represents a small remnant of the former Norman hunting preserve called Leighfield Forest which covered much of East Leicestershire (Evans 1979).

The wood is situated on the gently sloping SW-facing valley side of the Eye Brook (Fig. 2.1(map 4); Plate 18) and lies between 125-172 m O.D.. A few small streams drain the wood into the Eye Brook, which forms a tributary of the River Welland.

Loddington Reddish is almost uniformly composed of the 'typical wet ash-maple' stand type. However, there are a very few small areas containing other stand types including 'invasive elm' and 'acid pedunculate oak-hazel-ash'. Some scattered alder, horse chestnut, sycamore and Scots pine trees were also noted. Hazel is found along the banks of the streams.

In order to investigate the 'interior' breeding bird population of this large wood, sample populations provided by two control plots, each of 4 ha, were monitored (Fig. 2.3a). The siting and measurement of these, and other, control plots (in Owston Big Wood, see below) are described, more appropriately, in Chapter 8. Two further plots were located along the SW-facing margin of Loddington Reddish so as to include areas of the edge zone and its associated avifauna.

In view of the uniformity of the vegetation throughout the wood, it follows that the composition of each control plot closely parallels that of the wood as a whole. However, in addition to the dominant ash and maple, a few Scots pine (in control plot A) and pedunculate oak trees (in all four plots) were identified. Ash in these plots is mainly old coppice or regrowth.

The field and scrub layers form a dense, and frequently impenetrable, vegetational zone and are dominated by bramble and hawthorn respectively.

Loddington Reddish lies in an agricultural landscape, with extensive fields of pasture to the east and south (Plate 17) and with arable elsewhere (Plate 18). Removal of hedgerows in recent years results in just 3 adjoining the wood. None connects directly with neighbouring patches despite the high density of woodlands in this region (Plate 17).

5) Owston Big Wood.

Owston Big Wood is the larger of two woods which comprise the Owston Woods (52°39'N 0°50'W; Plate 19). With a total area of 141.9 ha, together they form the largest ancient woodland in Leicestershire (Jeeves 1985). They also represent the largest remaining fragment of Leighfield Forest, the former Norman hunting preserve (Candlish 1977). Owston Big Wood (110.7 ha) is separated from Little Owston Wood (31.2 ha) by an unclassified road (Plate 19).

Owston Wood remains Big one of the few woodlands in East Leicestershire for which some detailed historical documentation exists. The account which follows is based mainly on work by Jeeves (1985) but with additional information from Candlish (1977).

The present Owston Woods may be the site of continuous forest cover since the post-glacial climatic amelioration some 8,000 years ago. Clearance of woodland on these higher parts of East Leicestershire may have taken place later than elsewhere in the county owing to the difficulty of cultivating the heavy clay soils here.

The earliest documentation for the woods appears in 1086 A.D. in the Domesday Book. Evidence that its area and shape then were probably very similar to, if not the same as, the existing shape is provided by the remains of a wide bank and ditch around much of the present perimeter. The function of this structure, constructed in early Medieval times, was to prevent stock entering the woods and causing damage to the trees. Confirmation that the present shape was in existance in 1814 is provided by the First Edition of the One-inch Ordnance Survey map.

Coppice management had been practiced in Owston woods since Medieval times but was allowed to lapse early in the 20th century. Since the cessation of coppicing the wood has reverted to high forest. It seems that the composition of the wood, in the late 19th century, was uniformly mixed broad-leaves/conifers in roughly equal proportions but, through large-scale felling and clearing, few conifers remained by the late 1920s. As stated above, some further clearing and subsequent planting of conifers took place between 1959-1967, but this was restricted to the western part.

As bird populations were only monitored in Owston Big Wood the following details relate to this wood alone.

The long axis of the wood is orientated east-west along a prominent ridge (Fig. 2.1(map 2)). From the highest point (213 m O.D.), close to the western end of the wood, the ridge gently declines eastwards to about 160 m at the eastern margin. Most of the wood is situated on the northern side of the ridge where the gradients are gently inclined northwards or north-eastwards. A few small streams, here forming headwaters of the River Welland, drain these slopes. Despite the small size of the streams, some valleys are relatively deeply incised into the surface deposits. Locally, these emphasise the undulating nature of the landscape in the woods. In contrast, the southern side of the ridge is characterised by steep slopes which are confined, within the wood, to the south-western corner. There is no surface drainage on these gradients.

Adopting the classification of semi-natural stand types proposed by Peterken

(1981), Jeeves (1986) identified 7 types in Owston Big Wood. The most widespread was 'acid pedunculate oak-hazel-ash' woodland. Smaller, but still important, areas of 'wet ash-wych elm' and 'invasive elm' stand types were Mature sycamore and beech, though nowhere identified. abundant, were widespread. The deeper valley floors held some alder. Many small areas in the western half of the wood (visible in the vertical aerial photograph, Plate 19) were partially cleared and subsequently replanted between 1960-67 with exotic particularly Corsican pine and Western red cedar (Candlish 1977). species. Overall, plant species richness is higher in Owston Big Wood than in any other East Leicestershire woodland (Jeeves 1986).

As in Loddington Reddish, 4 control plots, each of 4 ha., were established in Owston Big Wood to monitor the species richness and breeding bird density of the interior zone. These plots were sited at intervals along the main (E-W) central ride (Fig. 2.3b). The morphology and vegetation of these 4 control plots may be described as follows:

- i) control plot A: situated in the western part of the wood on the ridge crest, which slopes gently towards the south-east. Owing 1970's to the clearance of some broadleaves in the and subsequent replanting with conifers (as described above), this plot contains a higher proportion of evergreens than the other control plots. However, it is included in the survey as being representative of much of the western part of the wood. Elsewhere are found ash, maple and some sallow. Since there has been no recent thinning of the vegetation the present woodland is very dense.
- ii) control plot B: sited close to the centre of the wood on the north-facing slope. Alder grows along a waterlogged valley floor near the northern boundary of the plot. Elsewhere, the canopy is composed mainly of the 'pedunculate oak-hazel-ash' stand type with some smaller areas of conifers.
- control plot C: also situated on a north-facing slope towards the iii) eastern end of the wood. Canopy composition is less uniform than in the other plots at this wood. Approximately equal proportions of 4 stand types were identified, namely 'wet elm', 'acid pedunculate oak-hazel-ash', 'acid ash-wych birch-ash-lime' and 'invasive elm'. A row of Western red

cedars line one side of the main ride.

iv) control plot D (Plate 20): situated on a north-facing slope close to the eastern end of the wood. Mostly of the 'acid pedunculate oak-hazel-ash' stand type with small areas of 'plateau alderwood' and 'wet ash-wych elm'.

In all four control plots, the impenetrable field layer was composed predominantly of bramble with an admixture of honeysuckle, dog rose and trailing rose. The scrub layer, which was less continuous, comprised hazel with scattered hawthorn and willow. Both the structure and species composition of the field and scrub layers were uniform, not just in the four control plots, but throughout the entire wood.

Full details of the mapping method used to determine the bird populations in the control plots at Owston Big Wood and Loddington Reddish are presented in Appendix 3. Other details, including the measurement of the plots and times and dates of field visits, are given in Chapter 8 and Appendix 4.

Except for Little Owston Wood to the east, Owston Big Wood is surrounded by farmland with arable mostly to the north and pasture to the south (Plate 19).

A total of 17 hedgerows adjoin Owston Big Wood, but none is connected directly to a neighbouring wood.

The degree of isolation of all woods (including those with control plots) was assessed in terms of distance to neighbouring woods and extent of hedgerow connectivity and these results are discussed in Chapter 10.

Geology and Soils.

The woodland sites chosen for study were all situated on relatively uniform soils, thus fulfilling one of the criteria previously cited (on p.2.2) as a requirement for inclusion. The soils are mostly derived from Lower Jurassic rocks which form the surface topography of East Leicestershire. There are, however, extensive superficial deposits of Chalky Boulder Clay which conceal these rocks. In addition, some valley floors have substantial alluvial deposits.

The Lower Jurassic sequence in East Leicestershire is:

/

Upper	Lias	-	Clays (mainly)
Middle	Lias	-	Marlstone Rock Bed
		-	Middle Lias Clays (and some Sands)
Lower	Lias	-	Clays (with Ferruginous Limestones)
			(Ford 1972)

The altitude of each woodland determines its relative position within this geological sequence and therefore the main rock types present at each site. Thus in general terms this means that the woodland on the highest ground, Owston Big Wood, is situated predominantly on the Upper Lias, with Billesdon Coplow and Loddington Reddish, at lower elevation, on the Mid Lias series and Botany Bay Fox Covert and the Wistow woodlands, at even lower altitude, on Lower Lias rocks.

Here follows a more detailed description of the geology and soils of each study site:

1) Wistow Estates.

The study woodlands at Wistow are all situated on Lower Lias Clays and Limestones. However, these rocks are almost completely covered by alluvium in the flood plain of the River Sence and by Chalky Boulder Clay elsewhere. Thus all woodlands, with a single exception, lie on soils derived from one of these two surface deposits. This one wood, W9, is situated on a small exposure of the Lower Lias rocks (Plate 3). The woods situated on alluvium are W5, W6, W7, W8, and the eastern end of W14 (Fig. 2.1(map 3)). All other woodlands stand on glacial drift cover which here forms slightly higher ground away from the valley floor.

2) Billesdon Coplow.

The crown of the knoll (above the 200 m contour) is capped with a layer of the Mid Lias Marlstone Rock Bed. Elsewhere in the wood, the soils are derived from the Mid Lias Clays and Sands. There is one very small exposure of Lower Lias Clays and Limestones which just penetrates the extreme south-eastern corner.

3) Botany Bay Fox Covert.

The Mid Lias series, which dominate Billesdon Coplow, extend a short distance into Botany Bay Fox Covert as far west as the 170 m contour line (Fig. 2.1(map 1)). The rest of the woodland, which lies below this altitude, stands entirely on the Clays and Limestones of the Lower Lias.

4) Loddington Reddish.

With the exception of one small area above the 150 m contour, Loddington Reddish is situated entirely on soils derived from Clays and Sands of the Mid Lias series. The upper slopes of the wood, however, are partly on Upper Lias Clays and partly on a spur composed of the Marlstone Rock Bed (Mid Lias). A section of this spur is overlain by glacial sands and gravels.

All four control plots are situated on the Mid Lias Clays and Sands.

5) Owston Big Wood.

The ridge upon which Owston Big Wood stands is composed entirely of Upper Lias Clays. However, these rocks are not everywhere exposed within the woodland having been extensively overlain by Chalky Boulder Clay. Indeed the Clays of the Upper Lias reach the surface only on the steep south-facing slopes (in the SW corner) and along a deeply-incised E-W orientated valley on the northern flank of the ridge. One small area of glacial sand and gravel outcrops near the southern perimeter of the wood.

All four control plots are situated on Boulder Clay but (B) and (C) each have a small area of Upper Lias Clay present.

CHAPTER 3.

FACTORS INFLUENCING THE BREEDING SUCCESS OF THE BLUE TIT: A REVIEW OF THE LITERATURE.

The number of studies on breeding success that refer just to the Blue Tit are limited. More commonly, studies cover the Great Tit alone or, to a lesser extent, both the Great and Blue Tit. As the Great Tit is very closely related taxonomically to the Blue Tit (Voous 1977b), and, as other authors have combined together their study of the two species in their researches, the following review examines the results of the findings of both species. However, it is appreciated that some of the findings relating to the Great Tit may not be fully applicable to the Blue Tit.

The cyclical synchronization of breeding in birds is controlled by environmental stimuli (Lofts & Murton 1973). In most mid- or northern-latitude species this is a response to proximate factors, of which the most important is the seasonal change in daylength (Murton & Westwood 1977). This photoperiodism is manifested in the secreting of gonadotrophic hormones (follicle stimulating hormone and luteinizing hormone) from the pituitary gland, which initiate and regulate the development of ova and sperms. Through the synthesis of steroid hormones, they are involved also in the development of accessory (the sperm ducts and oviducts) and secondary (plumage colour, song and breeding behaviour) sexual characters. The photoperiodic regulation of the breeding cycles in the Great Tit has been demonstrated through gonadal development induced by increased daylength (Suomailainen 1937).

However, the photoperiodic response mechanism alone cannot explain consistent differences in mean laying between different parts of the same habitat or between adjoining habitats, a feature commonly noted in tit breeding studies (Lack 1955, Perrins 1979, Dhondt *et al.* 1984).

In order to form eggs the laying female requires a food intake surplus to that needed for the maintenance of existance metabolism (Royama 1966, Perrins 1970). Royama (1966) has estimated that this could amount to 40% more food for some species. The greatest demands are met by small birds with large clutches, including Blue Tit, where the clutch may represent, occasionally, up to 150% of the female's body weight (Perrins 1970). For the female Blue Tit in

the pre-laying period, the nutritional requirements are met by feeding mainly on the larvae of *Diptera*, *Hemiptera* and *Lepidoptera* (Betts 1955), all protein-rich sources. Food is described as the ultimate factor in determining the start of laying (Kluyver 1952).

Smaller female Blue Tits will require less food for basal metabolism than larger ones. Consequently, any surplus food can be utilised to form eggs earlier and this has been offered as the explanation why lighter females tend to breed earlier (Jones 1973, Perrins 1979).

The timing of breeding in Great and Blue Tits is known to vary each year so that the main nestling period coincides with peak caterpillar abundance (Gibb 1950), upon which the young are fed. Factors responsible for this yearly shift of caterpillar abundance are unclear but it appears to be a response to mean air temperatures in the spring (Perrins 1979).

Though there are problems in conclusively showing that food availability alone determines laying date, the importance of food for egg formation is clear. This is well demonstrated by the seasonal decline in clutch size in Great and Blue Tits as food progressively diminishes for the female (Lack 1966, Perrins 1979). Furthermore, the survival of nestlings tends to decline through the season. Again this may be a result of the peak caterpillar abundance, upon which the young are primarily fed, having already passed. Clearly, breeding success in the Blue Tit, which lays just one clutch of eggs each year (that is, is single-brooded), is heightened if laying is earlier rather than later in the season.

To examine the extent to which food availability is a major factor in determining first-egg-date, empirical studies involving artificial feeding have been undertaken (e.g. Kluyver 1951, Jones 1973), but Perrins (1979) believes their results to be inconclusive. However, Källander (1974) was able to demonstrate that Great Tits did breed a few days earlier in an area of woodland where artificial feeding was maintained. This led him to speculate whether laying date was controlled by the food being ingested or, indirectly, through the food acting as a visual stimulus.

In Oxfordshire (52°N), Perrins (1979) has noted that tits consistently breed a day or two earlier in lower-lying, south-facing woodland and also along the woodland edge. Uncertain of the factors causing these patterns, he surmised that light and warmth might be greater here. He also suggested, but offered no

supporting data, that higher urban temperatures may cause Great Tits to lay earlier in gardens than in woods nearby; a feature noted in several studies (Kluyver 1951, Lack 1955, 1958, Perrins 1965). However, this pattern was not true for Blue Tit in the same habitats (Perrins 1965). Unfortunately, Perrins (1979) creates some confusion over his findings. On p.169 he states "Great Tits, but not Blue Tits, in gardens lay a few days earlier than those in nearby woodland..." and later (p.178), "As shown earlier, both Blue and Great Tits bred earlier in gardens than in woods". A more detailed investigation of laying dates for Great and Blue Tit was made in urban, suburban and rural habitats at Ghent (Belgium)(51°N) by Dhondt et al. (1984). A clear gradient, from the earliest in urban through suburban to rural, was identified in Great Tit but, again, not with Blue Tit where the earliest laying was suburban and the latest rural. Although Dhondt et al. (1984) discussed the possibility of higher urban temperatures being implicated they concluded that this pattern could not be explained by differences in temperature alone in view of the different laying date gradients between the two species for the same habitats. Instead, they argued that laying date was the result of differences in the timing of food availability and that Great and Blue Tits respond to environmental variations differently.

Differences in food availability have also been cited as the reason why tits breed earlier in Scots pine than in nearby Corsican pine (Lack 1955, Gibb and Betts 1963).

Tit breeding seasons are influenced by general spring temperature (Kluyver 1951, 1952, Perrins 1965, 1979, Van Balen 1973, Blondel 1985). In the Netherlands (52°N), Kluyver (1952) found that the sum of mean daily air temperatures (which he termed 'warmth sum') from mid-March to 20 April (this being the average date of egg formation in the female in his study area) strongly influenced laying date in the Great Tit. Following this principle, Perrins (1965) calculated an index of spring weather derived from an aggregate of mean daily temperatures for the period 1 March-20 April and demonstrated that breeding in Great Tit starts earlier in years with higher index values. Blondel (1985) also found that mean laying dates were influenced by mean air temperatures in the Blue Tit in Ventoux (France)(44°N) but not in Corsica (42°N). This was ascribed to the mildness of the climate and the lack of seasonality on this island. Thus breeding birds did not exhibit the same degree of urgency to start laying that they do in higher latitudes where it is clearly so important to coincide with the single short period of peak food availability.

Whether tits are affected directly by temperature, or indirectly by its

influence on the availability of food, or indirectly by its presaging of other forthcoming environmental changes, has been unclear.

Immediately before first-egg-date, laying Great Tits appear to be influenced by the effect of temperatures on food availability. If there is a sudden drop in air temperatures only those females which have started to lay continue, others delay until the weather becomes warmer (Kluyver 1951). A laying female will have already part-formed eggs and therefore requires less food to complete the clutch than another bird which has not yet started laying (Perrins 1979). Further evidence of the difficulty of obtaining sufficient food in colder weather is shown by lighter eggs being laid following lower temperatures (Jones 1973).

Two recent studies, however, have provided evidence that temperatures can have a direct effect on laying date in tits. Great and Blue Tits roosting in warmer nest-boxes during the pre-breeding period lay earlier than those occupying cooler boxes (O'Connor 1978, Dhondt & Eyckerman 1979). It was demonstrated that mean temperature differences as small as 0.3-0.6°C between boxes could be responsible for earlier laying. Females roosting in warmer boxes lost less weight overnight and could accumulate the necessary energy reserves for egg formation sooner (Dhondt & Eyckerman 1979). Further evidence to indicate how laying date in tits is influenced by slight temperature differences was produced by Perrins (1973). There is a delay of about four days in the mean date of laying for each 1°C reduction in the mean ambient temperature during the period 1 March to 20 April.

Laying date is also known to be influenced by the age of the female. Older birds tend to breed earlier, perhaps due to their increased experience within the breeding habitat (Perrins 1965, Perrins & Moss 1974). One slight variation of this pattern appears to depend upon the age of the female's mate (Harvey *et al.* 1979). A female breeding for the first time paired with an older male will begin egg laying on average one day earlier than a pair both breeding for the first time.

Population density may also affect laying date. When survival from one year to the next is high, both Blue and Great Tits tend to breed earlier than following a winter with higher mortality (Chitty 1967).

Clutch size and the survival of young are negatively correlated with laying date (Perrins 1965, Lack 1966), though this relationship varies between years and between species (Dhondt *et al.* 1983). It follows, therefore, that nestling

survival is clearly enhanced at breeding sites in microhabitats characterised by higher temperatures than elsewhere.

Thus the onset of laying date in tits is influenced by a number of factors including day-length, ambient temperature, availability of food, age of female, weight of female, and habitat.

Of these factors, most workers have tried to account for egg-laying using the proximate environmental controls. These would seem to offer the most reasonable explanation of consistent differences in laying date between different parts of the same wood or between adjacent habitats. Seasonal increases in day-length and seasonal rises in ambient temperatures may be explored further as factors by studying the microclimatic variations within woodlands. Such variations will also influence the availability of insect larvae.

However. it must be stressed here that, except for the nest-box temperatures measured by O'Connor (1978) and Dhondt & Eyckerman (1979), (on only 7 nights and one night, respectively) there is no indication from other studies that any temperatures were recorded over a prolonged period at the study site. Instead, readings were taken from the nearest meteorological station which, sometimes, was many kilometres distant. As will be shown later, such temperature patterns are likely to be quite different from those at the site under examination and should always be used with caution. Thus this study attempts to by measuring address this empirical problem several microclimatological parameters on-site and over a long period of time. It is this approach which has been adopted in Part I as the main avenue to examine what determines breeding success in the Blue Tit in an East Leicestershire woodland. The methods and results are presented in the immediate chapters that follow.

CHAPTER 4

MATERIALS AND METHODS

The effects of microclimatic variations within a specific woodland, Billesdon Coplow, are now examined in detail and are related to the breeding success of the Blue Tit.

The Nest-box Scheme.

Both Blue and Great Tits readily adopt nest-boxes with appropriately sized entrance holes if erected in suitable woodland habitat. Monitoring the progress and development of the eggs and young is greatly facilitated when boxes are visited regularly, generally at weekly intervals. A brief description of this method and an example of the card utilised in this monitoring system, the Nest Record Card, are presented in Appendix 5.

Forty-one small-hole (28mm) nest-boxes were erected throughout Billesdon Coplow in January 1980, followed by nine in February 1981 (in the larch plantation) and a further nine (in the main deciduous wood) in February 1984. The annual total number of boxes situated in each half of the wood from 1980-87 and their positions are presented in Appendix 5. None was positioned along woodland margins adjacent to public highways.

To examine differences between the breeding seasons of Blue Tits on the (predominantly) south- and north-facing slopes, the woodland was divided into two approximately equal areas. This was achieved by drawing an east-west axis, from the western corner of the wood through the crown of the hill to the eastern margin (see Appendix 5).

An intensive programme of marking individual nestling and breeding adult Blue Tits was operated from 1980-87 in order to establish whether differences in egg-laying at Billesdon could be explained by different age-classes of birds in each half of the wood.

Clutch size is defined as the maximum number of eggs laid. Where complete clutches were later found deserted or with fewer eggs than initially counted, (the result of predation), they are included in the analysis but replacement clutches are not. As Blue Tits lay eggs on consecutive days (Perrins 1979, but see Dhondt *et al.* 1983^{1}) the laying date can thus be calculated back accurately despite only once-weekly field visits.

The Weather Stations.

Two weather stations were established in 1983 to record the microclimate of two sites, each believed to be representative of the two parts of the wood. One was sited on a south-facing slope close to the southern margin of the wood, the other was on a north-facing slope near the northern perimeter (Fig. 2.2b). Care was taken to ensure that neither was sited within 30 m of the woodland margin. Consequently, each was positioned further from the woodland margin than the innermost limit of the edge zone (see Ranney *et al.* 1981), whilst continuing to maximise the distance between them. The exact location of each weather station was finally determined by the availability of trees of the same species (pedunculate oak), with similar girth and canopy structure. The tree density and scrub layer height of the immediately surrounding area were also similar.

Ambient dry and wet bulb temperatures were recorded by thermistors (Grant, Type CM-K) placed in small, sleeve-shaped screens. These were painted white on both surfaces and aligned east-west to minimise the effects of direct solar radiation on the probes. Each screen was set at a height of 0.8 m above the ground, and 3.1 m and at a bearing of 220° from the tree supporting the study nest- and control-boxes (Plate 21a).

To determine the extent to which the temperature regime of an occupied nest-box might be affected by an incubating female or by nestlings, а control-box, which would remain unoccupied, was placed just beneath the nest-box (Plate 21b). A thin wire placed across the entrance hole of the control-box prevented its use by birds. At each station the height of the nest-box (3 m), the control-box (2.5 m) and anemometer platform (1.8 m) and their aspect on the tree (200°) were the same (Plate 21b). Dry and wet bulb temperatures in the nestand control-boxes were recorded with paired thermistors. They were threaded through the wall of each box in the same relative positions and were kept clear of nest material. Experience showed that a

¹Interruptions in daily egg-laying may occur in about 6% of Blue and Great Tits.

protective wire gauze was necessary in the nest-box to prevent removal of the lamp-wick sleeve by nesting birds. This was shaped around the probe in such a manner as to exclude possible influence by convective or conductive heat from the gauze.

All temperatures were recorded hourly with thermistors connected to a Grant (Model D) miniature temperature recorder. A calibration test of all thermistors before and after the field experiment showed them to be consistently within $\pm 0.1^{\circ}$ C over the entire temperature range experienced during the field-work. Synchronisation of the hourly recordings made by the Grant D recorder at each station was not achieved but the very small time difference (of a few minutes) between them was considered not to bias the results.

Although the ambient wet-bulb thermistors were not aspirated they will have experienced an airflow exceeding 1 m sec⁻¹, and should therefore provide values about 83% of those achieved when aspirated at a rate in excess of 3 m sec⁻¹ (Unwin 1980). The very still air in the nest- and control-boxes will nevertheless cause inflated wet-bulb readings which should be used with caution (Unwin 1980). However, the readings are used for comparative purposes only in this study. Systematic sampling was adopted to identify any trends.

Total solar radiation was measured (in 1984 only) with a Delta-T tube solarimeter (Model TSL). This was positioned 0.8 m above the ground at a bearing of 220° from the tree and aligned E-W (Plates 21a and 21c). It was connected to a Delta-T millivolt integrator (type MVI) with an 8-digit display. The solarimeter tube was placed one metre north of the screen to avoid being too close to overhanging shrubs. Solarimeter values were read at daily intervals, one directly after the other.

Air-flow was recorded (in 1984 only) by a Cassella omni-directional sensitive cup anemometer fixed on a tree bracket (0.23 m long). Its position, immediately below the two boxes and close to the trunk (Plate 21b), was designed to ensure that recorded air-flow would be very similar to that experienced around the boxes. Closer positioning however might may have affected the behaviour of the breeding birds.

Examples of daily meteorological data collected in 1984 are shown in Appendix 6.

Problems encountered with a miniature temperature recorder in 1983

prevented data being collected from both stations until 16 April. Continuous temperature readings were made thereafter until 23 June, the date on which the nestlings at the southern nest-box fledged. Additional problems encountered with the anemometers has meant that the microclimatic data obtained in 1983 is only included as a supplement to the very comprehensive results obtained the following year.

In 1984, ambient temperature, relative humidity, solar radiation and run of wind were recorded at each weather station, together with the temperature and relative humidity of the nest- and control-boxes, for a continuous period of 112 days, from 1 March to 20 June (the fledging date at the southern nest-box). The results presented in Chapter 5, therefore, are almost entirely taken from these data obtained in 1984.

Diurnal activity in day-active birds is strongly correlated with photoperiodicity (Gwinner 1975). Thus mean temperatures are calculated separately for daytime (sunrise to sunset) and night-time (sunset to sunrise) periods.

In order to summarise differences in temperature patterns between the two weather stations, data were grouped into (arbitrary) 0.2°C units. Such small divisions are adopted as it is clear that a mean temperature of just 1°C higher during the pre-egg laying period can initiate laying by as many as four days earlier (Perrins 1973).

The Sucrose Solution Method.

The two fixed weather stations gave an element of control on the microclimatic investigation and are used to determine the detailed influence of ambient temperature prior to the start of egg-laying. However, it was also clear that a detailed isothermal map of the mean temperature pattern would have to be determined for the entire wood. To produce this, 35 sucrose sensors were exposed for monthly periods from mid-January until mid-June in 1984 and 1985 using a grid at roughly 60 m intervals. Slight variations of this distance were sometimes necessary to avoid sensors being sited within tall, dense vegetation. Each sensor, containing 25 ml of sucrose solution, was suspended centrally in a white plastic plant-pot (acting as a screen) fixed horizontally to a post 0.75 m above the ground (Plate 21c). These screens were north-orientated to minimise possible direct solar radiation effects. Sensors were not placed along the woodland margins adjoining public roads.

However, as pointed out in Chapter 1, the published literature on the practical application of the sucrose solution method was of limited assistance. Thus, data gathered from January to June 1984 was insufficiently validated and are omitted from the following account and results. Only those data obtained between January-June 1985 are presented in this and Chapter 5.

The Theoretical Basis.

The chemical basis of the method is outlined by Lee (1969), Jones (1972), and in many standard text books in physical chemistry, for example Atkins (1982). Briefly, the velocity of a chemical reaction depends on temperature according to the law

$$\ln (k) = c_1 - (c_2/T)$$
(1)

where k is the velocity coefficient and T is the absolute temperature in °K. If the empirical constants c_1 and c_2 can be determined satisfactorily for a suitable reaction, it should be possible to use the extent to which a reaction is completed to find the effective mean temperature over the period in question. Pallmann *et al.* (1940) introduced the rate of inversion of sucrose sugar in acid solution

$$C_{12}H_{22}O_{11} + H_2O + H^+ \rightarrow C_6H_{12}O_6 + C_6H_{12}O_6 + H^+$$
(2)

sucrose water proton glucose fructose

as a suitable reaction. Determining the extent to which the sucrose has been broken down makes use of the fact that, whereas sucrose is dextrorotatory, the inverted mixture is laevorotatory, so that the reaction is easily monitored using a polarimeter.

Using the measured angles of rotation of the initial sucrose (R_0) , the fully inverted mixture (R_∞) , and of any experimental solution (R_t) at time, t, a mean reaction velocity can be found from

$$\bar{k} = [1/(H^+t)] \log[(R_0 - R_\infty)/(R_t - R_\infty)]$$
 (3)

The units of t are immaterial, and H^+ is the hydrogen ion concentration which is, by definition, related to pH as
Chapter 4

$$\log(1/H^{+}) = pH \tag{4}$$

The required rotation angles R_t , R_o and R_∞ are readily obtained using a standard polarimeter. In this study, a Hilger and Watts device was used but more modern automatic instruments are available that have better sensitivity and enable much smaller solution volumes and lower sucrose concentrations to be used.

This simple account conceals a very large number of quite complex experimental decisions.²

In summary these include: (i) the initial solution, (ii) details of the field procedure adopted, (iii) 'tuning' the reaction by selection of a suitable pH value, (iv) determination of R_0 and R_∞ , and (v) the use of the estimated mean reaction velocities, \bar{k} , together with laboratory control sensors exposed to a known temperature regime, to estimate the reaction constants, c_1 and c_2 , by regression. The precise details are as follows:

- (i) In this study, the initial solution used was a standard "Pallmann" mixture made up by dissolving 1500 g of sucrose in 1000 ml of water, buffered at a pH of 1.5 to 1.6.
- (ii) Several methods were explored to determine a satisfactory field technique for using sucrose sensors. Lee (1969) recommends that sensors be frozen before taking them to the field site to prevent hydrolysis, a temperature of -4.7°C being enough to stop hydrolysis. Following this advice, frozen winter of 1983/84. Later polarimetric sensors were deployed in the examination indicated that, owing to low ambient temperatures, many sensors did not thaw for several days (and by unknown periods of time) and some not at all. To eliminate this problem, the following winter all sensors were thawed together by brief immersion in cold tap water immediately prior to taking them to the study site. Lee (1969) also suggests that the sensors can be frozen immediately upon retrieval in order to stop the hydrolysis proceeding any further. Because of practical considerations, in the present study sensors were not frozen for some after leaving the field site. However, all sensors 2.5-3 hours were

²These were explored jointly with Mr D.J. Unwin, Department of Geography, University of Leicester.

subjected to identical temperature regimes during this period, so that, in theory at least, no systematic errors should have been introduced. Moreover, this short retrieval period would account for a maximum error of less than 0.004% in the measure of t employed in equation (3).

Prior to polarimetric examination, it was noted that if the sucrose solution was permitted to thaw slowly, the measured angle of rotation was not stable until the solution reached room temperature, a protracted process. Consequently, several frozen sensors were thawed quickly in cold tap water. This also assists in increasing the translucency of the solution thus facilitating accurate reading of the angles of rotation. An alternative method, outlined by Lee (1969) is to add an antifreeze (salt) to the solution used, making allowances in calibration for the non-linearity this introduces, but this is not practicable if the sensors need to be stored.

(iii) A practical difficulty lies in 'tuning' the reaction rate by careful choice of pH (equations 3 and 4) which interacts with the exposure time of the sensors and the initially unknown mean temperature. This occurs in such a way as to set a limit on t at which all the solution has inverted and the sensor ceases to give useful information.

After a great deal of experimentation, a practical pH value of between 1.5-1.6 was identified as most suitable for this study with its relatively low ambient temperatures and long exposure times. This value is close to the upper end of the range given by Lee (1969) as suitable for winter observation periods of 15-30 days in middle latitudes.

iv) Examination of equation (3) makes it clear that the estimation of the mean reaction velocity is very dependent on the rotation angles assumed for the initial solution, R_0 , and for a fully inverted solution, R_∞ . To determine R_0 a number of fresh samples were used and a mean value obtained. Obtaining samples known to be fully inverted is a little more difficult. The original workers immersed sample tubes in boiling water for 8 hours but this was later shown to produce unwanted secondary reactions. An alternative method is to expose tubes to a constant temperature, taking readings of R_t at, say, 24 hour intervals and extrapolating the curve of the difference in successive R values against time. Lee (1969) provides a detailed analysis of the effect of repeatability of these estimates on the final integrated temperature. Particular care is needed to ensure that very close laboratory control is given to all these

measures and that in a given study all the sensors should use the same batch of sucrose solution.

(v) Finally, with the exception of Lee (1969), published accounts do not offer much guidance on calibration. In the present study, a number of tubes containing sucrose from the same batch as was used in the field and treated to an identical freeze/thaw regime were exposed to isothermal temperature regimes in water baths at 4°, 8°, 9.5°, and 13.5°C for periods of both 16 and 30 days. In each case the procedure adopted was to use equation (3) to estimate the mean reaction velocity \bar{k} . If all has gone according to the basic theory, then from equation (1) it is clear that a plot of ln (\bar{k}) against 1/t(k) should be a straight line. In practice, this linearity was not quite achieved and a feature of all the calibrations undertaken here is a slight, but regular, non-linearity. Nonetheless, over the range of temperatures expected, the relationship in a form suitable for predicting temperature was found to be

 $(1/T) = 0.00380 - 0.000153 \ln(\bar{k})$

with a product moment correlation coefficient of -0.97. It was this equation that was used to find the 'mean' temperatures reported in the next section.

Response of Breeding Blue Tits to Temperature Patterns.

To examine whether laying dates of Blue Tits at Billesdon Coplow were correlated with spatial variations in temperature across the wood the following method was employed. The annual mean first-egg-date for the entire wood was calculated for each year from 1980-87. In turn, these mean dates were compared with the date of laying in all nest-boxes annually and the difference noted (Appendix 5). The mean of these annual differences was determined for each box to establish whether it may be termed an 'early' or 'late' nest-box within Billesdon Coplow. The distribution of these 'early' and 'late' boxes are compared with isothermal patterns as determined by the sucrose solution method.

CHAPTER 5.

RESULTS OF MICROCLIMATIC AND RELATED STUDIES.

The results presented in this chapter are based on the complete data sets collected in 1984. However, a brief summary of some of the main features recorded in 1983 follows the main account.

The commencement date for data recording is in line with that used in other studies (e.g. Perrins 1973), that is, from 1 March onwards. Data collection continued until 20 June, the date of fledging at the southern station nest-box. In addition to a detailed examination of the results based on the data for this period, further attention is also given to the period 1 March-5 May; the latter date here being the date upon which egg-laying commenced in the southern nest-box.

During 1984 the northern weather station nest-box was not occupied thus preventing a direct comparison of laying dates to be made with the southern nest-box. Nevertheless, some measure of the potential difference between laying dates at the two nest-boxes is inferred by the four-day delay in mean first-egg-date experienced in the northern half of the wood over the southern half in that year.

1) Ambient Patterns.

a) Ambient Temperature Pattern.

i) The Weather Stations.

The southern weather station was consistently warmer than the northern station and the differences between mean monthly ambient temperatures at the two stations became progressively greater from March to May (Table 5.1), when a peak difference, of 1.3°C, was recorded.

There is a strong linear relationship between mean daytime air temperatures at the two weather stations (r = 0.98, P<0.001).

Mean differences in ambient daytime and night-time temperatures between the southern and northern stations for the two periods under examination, 1 March-5 May (1984) and 1 March-20 June (1984) are presented in Table 5.1. Daily mean ambient temperature differences clearly demonstrate that the southern station was consistently warmer than the northern one (Fig. 5.1). In both periods the daytime temperatures averaged 1.1°C higher at the southern station. At night the differences were smaller (Fig. 5.1b), with the southern station averaging 0.3°C warmer up to the first day of egg-laying (which occurred at the southern weather station nest-box) and 0.5°C warmer over the entire study period. These differences are statistically highly significant. By using arbitrary 0.2°C divisions, it is apparent that on most days the differences averaged between 0.8-1.2°C during the daytime (Fig. 5.1c) and 0.4-0.6°C at night (Fig. 5.1d). The northern station experienced higher temperatures only 5 times during the day but more frequently at night, though most of these occasions were in March, well before widespread egg-laying commenced in the wood. The peak difference between maximum daytime temperatures was recorded in late April when the southern station was 2.6°C warmer than the northern one. This was one week before egg-laying commenced at the southern station. In the pre-egg-laying period, daily maxima in the south averaged 1.8°C higher than the north (Mann-Whitney U test; U = 1534.5, P<0.01).

ii) The Sucrose Sensors.

The ambient temperature differences recorded at the weather stations appear to be consistent with the patterns demonstrated by mean monthly isotherms for Billesdon Coplow in 1985 (Fig. 5.2). The effective mean temperature differences within the wood in January/February and February/March were small, with a range of 0.8° C and 1.0° C respectively. However, in March/April the range across the site increased to >3.0°C but fell slightly in the April/May to 2.0°C.

Prolonged exposure of sensors to relatively high temperatures can result in near-total inversion of the sucrose thus invalidating those particular sensors from analysis. Some sensors in March/April showed evidence of this near-total inversion at mean temperatures around 13°C. No attempt has been made to estimate temperatures from these sensors; instead they are included as temperatures $>11^{\circ}C$ (Fig. 5.2c), a value which could be accurately measured. Total inversion of all sensors in May/June, however, precludes them from this study. This further highlights the difficulty of finding a single pH value suitable for the wide seasonal range experienced in a study of this nature.

Clear spatial patterns can be identified in the wood from Figure 5.2. In each period, ambient temperatures were consistently higher in the southern half of the wood. A marked temperature gradient, orientated east-west through the crown of the hill, characterised the spatial pattern in both February/March and April/May. With one small exception, highest temperatures were consistently recorded along the S-, SE- and SW-facing edges of the site. In March/April these higher temperatures of the southern margins also extended along part of the NW-facing edge. One further feature of the April/May period was the high temperature recorded within the small clearing in the south-eastern part of the wood. The lowest temperatures, on the other hand, were usually found along the NE-facing edge and especially in the sheltered angle of the wood, mid-way along this margin. This sheltered area could act as a frost pocket in winter. It was also noted that cooler temperatures sometimes penetrated into the region of the larch plantation.

b) Solar Radiation.

Daily total solar radiation amounts received between 1 March-5 May 1984 (Fig. 5.3b) at the southern weather station were consistently higher than those recorded for the northern station. The south received, on average, 19% more radiation than the north during this period; over the entire study period it was 15%.

The differences between the mean solar radiation values (for 5-day periods) at the two stations increased from about 11% in early March to reach a peak of 29% in late April. This peak value coincides with the start of nest-building in the south.

Only after mid-May, when egg-laying had already commenced, did the northern station start to receive equally large daily totals of solar radiation as the solar paths rose. In April, mean ambient daytime temperatures were closely correlated with daily totals of solar radiation both at the southern station (y = 2.7+0.07x, r = 0.62, P<0.001) and at the northern one (y = 3.8+0.06x, r = 0.69, P<0.001).

c) Airflow.

Airflow, measured from 8 March-25 May 1984, showed little difference in the pattern between the southern and northern weather stations. Furthermore, no relationship was established between daily airflow and mean ambient air temperatures (Table 5.2). Consequently, airflow was considered unlikely to account for ambient or nest-box temperature differences observed between the southern and northern stations.

d) Relative Humidity.

Except during periods of rainfall associated with the passage of frontal systems, ambient relative humidity closely followed the diurnal pattern shown in the example in Figure 5.4a. Here, the strong inverse relationship between relative humidity and ambient air temperature is clearly demonstrated. Similar relationships are evident in the nest- and conrol-boxes but the diurnal fluctuations are less marked (Figs. 5.4b, 5.4c).

Mean relative humidity differences between daily ambient and nest-box values at the two weather stations were extremely small. On the 31 sample days these differences were <1%. However, there was a short period after hatching when relative humidity values at the southern nest-box became consistently elevated over ambient (by about 10%). Moreover, the range of values became more constricted in contrast to the usual wider range recorded before hatching (Table 5.3). This pattern was clear evidence of air in the occupied nest-box becoming increasingly saturated during the later part of nestling growth. This trend can be attributed to respiratory evaporation of the nestlings, particularly after their homeothermic development.

2) Nest-box and Control-box Temperature Patterns.

Typically, nest- and control-box temperatures closely followed diurnal ambient fluctuations but exhibited a slight time lapse (Fig. 5.5). Peak box temperatures were generally recorded one hour after peak ambient temperature. Box temperatures also tended to remain slightly higher during the night until dawn. Almost without exception mean nest- and control-box temperatures were higher than ambient.

Mean differences between the southern and northern nest-box temperatures were even greater than between ambient temperatures (Figs. 5.6a, 5.6b). Daytime temperatures averaged 1.4° C and 1.6° C higher at the southern station between 1 March-5 May (1984) and 1 March-20 June (1984) respectively (Table 5.1). Night-time temperature differences averaged 0.7° C for both periods (Table 5.1). Using 0.2° C divisions, daytime temperature differences were mostly between $1.4-1.6^{\circ}$ C (Fig. 5.6c); at night they were mainly $1.0-1.2^{\circ}$ C (Fig. 5.6d). Much

of this difference is accounted for by one particularly noticeable feature. This was the rapid increase in temperature differences in June, especially at night, culminating in those at the southern nest-box being about 3°C (night) or 4°C (day) higher than in the northern nest-box. Comparison of nest-box with control-box temperatures at each station clearly indicates that this feature was confined to the southern nest-box only. Of the four boxes at the two stations, this one alone was used for nesting in 1984 and the temperature regime therein can be related to the various stages of adult roosting, incubation and nestling development.

In the known absence of birds utilising the boxes at the northern station, examination of the temperature differences here provide a basis with which to compare those recorded at the occupied southern nest-box.

Northern daytime nest-box temperatures averaged just 0.1° C and 0.2° C higher than the adjacent control-box between 1 March-5 May and 1 March-20 June respectively (Fig. 5.7b). At night the temperatures in both boxes could be considered as identical; the differences in both periods being <0.01^{\circ}C (Fig. 5.8d).

Since the same materials and dimensions were used in the construction of all boxes at Billesdon Coplow, it seems reasonable to conclude that the temperature differences recorded between the closely paired nestand control-boxes at the southern station would be of the same order as those recorded at the northern one.

This was indeed the case until 5 May during which time mean daytime temperatures were just 0.1°C higher in the southern nest-box. However, after this date, nest-box temperatures rose rapidly and averaged 1.0°C higher (Fig. 5.7a). This same pattern is also clearly evident at night (Fig. 5.8a). These marked differences were the result of a pronounced rise in nest-box temperatures coinciding with the period of nestling growth. The development of these increasingly higher temperatures in the occupied southern nest-box can be followed in Figure 5.9. They are the result of heat loss firstly from the unfeathered bodies of the (ten) nestlings and later through their respiratory evaporation. Examination of night-time temperature differences in Figure 5.8a distinctive pattern. During the period 1 March-31 May reveals a further (hatching-date), night-time temperatures in the southern nest-box were found to consistently average from 0.2-0.6°C higher than the adjacent control-box (Fig. 5.8a). This extremely limited temperature range, which averaged $0.4+0.01^{\circ}$ C

over the period, was not observed in the other (empty) boxes (Figs. 5.7a, 5.7b, 5.8b). This led to the conclusion that the pattern was caused by the metabolic heat loss of an adult Blue Tit roosting nightly in the nest-box where she later nested. That the female will roost nightly in the nest-box during, at least, the egg-laying period and incubation has been documented previously (Perrins 1979). At the southern station, it appears that the bird was utilising the box nightly long before egg-laying commenced.

Daytime temperatures between 1 March-5 May and 1 March-20 June averaged, respectively, 0.9° C and 1.3° C higher at the southern nest-box than ambient (Fig. 5.10a). This was considerably higher than the mean difference of 0.5° C recorded during both periods at the northern station (Fig. 5.10b). The pattern at night was similar; for the two periods under examination, temperatures at the southern nest-box averaged 0.8° C and 1.1° C higher than ambient (Fig. 5.11a) compared with 0.4° C and 0.5° C at the northern station (Fig. 5.11b).

Temperature differences between the two nest-boxes are considerably modified through their elevation in one box by the roosting female, and later by the nestlings. Thus, it is also necessary to compare differences between the empty control-boxes in order to ascertain the temperature pattern that would exist without the presence of birds.

Daytime temperature differences between the control-boxes, which averaged 1.5° C higher at the southern box for both periods under examination, were greater than ambient differences (of 1.1° C from 1 March-5 May and 1.0° C for 1 March-20 June). At night, the temperature differences between the control-boxes were the same as for ambient (with the southern box averaging 0.3° C warmer up to 5 May and 0.5° C warmer from 1 March-20 June).

As described before, problems encountered with recording equipment at the weather stations in 1983 prevented data being recorded continuously from 1 March. Nevertheless, the ambient and nest-box temperatures (for both stations) and the control-box temperature (for the southern station only) were recorded daily from 16 April to the fledging date at the southern nest-box (23 June, 1983). The patterns of temperature differences very closely follow those recorded in greater detail for the following year and described above (Table 5.1). The results are presented in the same order as for 1984 in Figures 5.12-5.16. There is no evidence, therefore, to believe that the microclimatological patterns observed at Billesdon Coplow in 1984 were atypical for that site.

3) Egg-Laying.

Between 1980-87 the mean first-egg-date for Blue Tits in the southern half of Billesdon Coplow was 2-8 days earlier than in the northern half (Table 5.4). The annual start and completion of the laying period was also consistently earlier in the southern half. The spatial pattern of 'early' and 'late' nest-boxes for the 8-year period is presented in Figure 5.17. A clear division exists, with all 'early' boxes in the southern half and most 'late' boxes in the northern part of the wood. The earliest boxes - 9 days earlier than the overall mean for the site - were close to the southern woodland edge and within that area characterised by higher ambient temperatures (see Fig. 5.2). The latest boxes up to 7 days after the mean laying date - were on the north-facing slopes close to the north eastern margin of the wood. These boxes coincided with some of the coolest parts of Billesdon Coplow including that area described possibly as a frost pocket.

Blue Tit clutch size in the southern half of the wood averaged 9.9 ± 0.2 between 1980-87. This compares with the mean clutch size of 9.5 ± 0.3 in the northern half. The average number of nestlings fledging in the southern area (8.5 ± 0.2) was also higher than in the northern part (7.8 ± 0.3) . Thus, approximately 86% of the southern clutches succesfully reached the fledging stage but only 82% did so in the northern half. This is equivalent to a 16% increase in the number of young augmenting the southern woodland population. Clutch size tends to decline during the breeding season but this trend was significant only in the south (Fig. 5.18).

The results presented in this chapter clearly illustrate the importance of temperatures in determining the start of egg-laying in the Blue Tit. These consistent temperature differences are related to a very considerable difference in short-wave radiation between south- and north-facing slopes over the same period. That earlier egg-laying leads to larger clutches from which more nestlings successfully fledge is clearly demonstrated in the southern half at Billesdon Coplow. Spatial differences in mean temperature as small as 1°C can be responsible for a difference of 4 days difference in first-egg-date. The implications of these findings are discussed in the following chapter.

CHAPTER 6

DISCUSSION.

1) Microclimatic Effects.

a) The Temperature Regime.

The egg-laying period of Blue Tits in the southern half of Billesdon Coplow is consistently earlier than in the northern part. Clutch-sizes and fledging success are also higher in the southern half.

Examination of the spatial pattern of 'early', and 'late' nest-boxes (that is, boxes with egg-laying starting before or after the annual average laying dates for the period 1980-87; see p.4.8 for details of the method used) in Billesdon Coplow reveals the following generalised pattern. The earliest egg-laying commences in the southern interior zone on the south-east-facing slopes and is followed shortly after by laying along the south-eastern woodland perimeter. The pattern then continues with simultaneous laying along the southern and northern woodland margins and is concluded by the latest egg-laying in the interior of the northern half. Most nest-boxes in the southern half are 'early' boxes and most in the northern half are 'late' nest-boxes (Fig. 5.17). Although the annual mean difference in laying date between the two parts of the site vary from 2 to 8 days, the average difference between the 'earliest' and 'latest' individual nest-boxes is as much as 16 days for the period 1980-87.

The direct comparison of monthly isothermal patterns with the general timing of egg-laying in Billesdon Coplow can only be made for 1985 in which year sucrose sensors obtained data for the whole wood.

The areas in which the 'early' boxes are situated are all characterised by higher mean temperatures in the period March-May. 'Late' nest-boxes, on the other hand, are located in the cooler parts of the wood. The range of mean temperatures recorded in March/April (1985) by the sucrose method (see note on p.4.5 for data availability), in the period just prior to laying, in Billesdon Coplow was $>3^{\circ}$ C which, by adopting the values suggested by Perrins (1973), should account for a difference in laying dates of 12 days. In fact, the range

of laying dates in 1985 was 21 days, the difference between the first laying date in each half of the wood was 15 days, and the mean difference between the two woodland halves was 7 days. Comparison of the patterns of general first-egg-date with isotherms especially in March/April and April/May show a marked similarity. Although the sucrose sensors and weather stations were not simultaneously, it is believed that the main microclimatic features operated recorded by each method were not atypical of a normal pattern for the wood. If this assumption is correct, the ambient temperature patterns obtained at the weather stations are thus confirmed by the effective mean temperatures recorded by the sucrose sensors. It follows that as control-box temperature differences measured by thermistors between the southern and northern stations were greater than between ambient temperatures for the same sites, even steeper temperature gradients across Billesdon Coplow would result from interpolating isotherm patterns for all nest-boxes. O'Connor (1978) and Dhondt & Eyckerman (1979) both demonstrated the importance of higher nest-box temperature to roosting birds in initiating earlier egg-laying. However, the data obtained by O'Connor (1978) and Dhondt & Eyckerman (1979) are derived from very brief study periods, just 7 nights and one night respectively. The considerably more detailed data from Billesdon Coplow, on the other hand, are based on long, continuous periods. They clearly show that marked temperature differences exist between boxes and, of the two boxes examined, that at the southern station is consistently warmer than the northern box particularly during the daytime. This is attributed to the materials of the control-boxes absorbing the differing amounts of direct solar radiation available at the two sites.

Altitudinal differences between the weather stations (16 m), and the two groups of nest-boxes (north, on average, 4.8 m higher than south), have very limited effect on overall temperature regimes and cannot account for the differences noted between the weather stations. Shanks (1956) has suggested a mean lapse rate for March-June of 0.57°C per 100 m (range 0.54-0.60°C). When this is applied to Billesdon Coplow it gives a mean temperature difference of only 0.03-0.04°C between the nest-boxes. For the two weather stations it would only account for an average temperature difference of 0.09°C.

b) The Pattern of Solar Radiation.

The maximum differences in ambient temperatures between the two parts of the wood occur at the end of April when differences in total solar radiation are also greatest. A significant relationship between solar radiation and ambient daytime air temperature was established at this time. It is at this time also that

Blue Tits in the southern half of the wood commence their egg-laying.

Collmann (1958) suggested that total solar radiation received on а horizontal surface comes from diffuse sky and direct solar radiation in the ratio of approximately 7:4. More recently, Yoshino (1975) quotes a ratio of approximately 5:1. Though diffuse sky radiation values may vary, this source of radiation will be received uniformly on all slopes (Geiger 1965). In view of this, it is clear that temperature variation in spring on south- and north-facing slopes at Billesdon Coplow is caused mainly by differences in the direct solar radiation component. A south-facing slope intercepts a greater proportion of direct solar radiation than falls on an equal area of flat ground (Geiger 1965, Searle 1973). In a study in Trier (West Germany)(50°N), Kaempfert (1942) estimated that the difference between total solar radiation received on а south-facing slope and a north-facing slope, each with gradients similar to those found at Billesdon Coplow, could be as much as 41% in late April/early May. At Billesdon Coplow the difference between the two sites is 29% at this time.

Total solar radiation received on a woodland floor reaches an annual maximum in April (Anderson 1964, Hutchinson & Matt 1977a, 1977b) but decreases progressively until late May in North Temperate latitudes in response to increasing albedo of the expanding leaf canopy (Rauner 1976, Hutchinson & Matt 1977b, Baldocchi *et al.* 1984). The decrease in solar radiation differences noted between the two slopes at Billesdon Coplow in May and June would be caused by foliage development; the difference falling from 17% to 3% over this period. Ultimately about 80% of the total radiation is absorbed by forest canopies (Yoshino 1975) and as little as 5% may reach the woodland floor (Baumgartner 1956). However, this marked decline in light penetration of the canopy occurs after the completion of egg-laying in the wood and so will have no influence on laying date.

Reference was made previously to a small area in the south-eastern part of the woodland interior which was the warmest part in April/May. This part of the wood was clear-felled in the early 1960's and still has an open canopy. This permits direct solar radiation to penetrate to the scrub layer thus elevating near ground temperatures.

Turner *et al.* (1988) have investigated what determines the gradient of species richness of insectivorous birds across the British Isles, from south to north. These authors have also sought to explain species diversity across the British Isles. For this, they initially explored the 'historical' theory, which is

based on the re-establishment and development of ecosystems since the retreat of ice sheets. This was rejected and the 'habitat' theory was next examined. In this, the decline of habitats from south to north in Britain is responsible for declining species diversity. This theory, too. was rejected. Instead. they concluded that greater solar energy amounts would lead to "increased populations of birds on account of the lower metabolic energy required to maintain body functions when the air is warmer" (p.541). They thus related the macro distribution pattern of bird diversity in the British Isles to the solar energy pattern. If this is so for the country as a whole then it is suggested here based on the Billesdon Coplow study that it may be equally important at the micro-distribution level. This might help to explain the diversity (and density) pattern within individual woods or woodland patches where birds will lay eggs earlier in the warmer parts of a habitat than in the cooler parts.

c) The Edge Zone Microclimate.

The physical environment of a woodland margin is distinct from the adjacent woodland interior zone and also from that of the nearby open fields and is termed the woodland edge zone (Odum 1971). Edge zone microclimate is transitional between those of the adjoining interior and open habitats (Geiger 1965, Ranney et al. 1981). Temperature regimes are modified through air-flow (Moen 1974, Grace 1979) and increased radiation. The latter is greater within the edge zone than on the woodland canopy due to the combined effect of direct and diffuse radiation (Hutchinson & Matt 1976, 1977a). Aspect, and time of year, influence direct solar, but not diffuse sky radiation (Geiger 1965, Wales 1967, 1972, Swift & Knoerr 1973). Direct solar radiation, a feature of cloudless days and of clear spells, is greatest along south-facing margins until and SE-facing edges SWmid-April, and along until the end of May (Kaempfert & Morgen 1952). Southern margins are warmest, but it is those facing due east or west which receive the most radiation (Geiger 1965). Monthly mean isotherm patterns at Billesdon Coplow demonstrate this feature. These higher temperatures in the south result in earlier egg-laying in this part of the wood than in the northern half. Microclimate is further influenced by and minimum day temperatures, and aspect, however. Light intensity, maximum relative humidity are all highest on south-west facing slopes (Hartmann et al. 1959, Giles 1981). This is the case along the south-western margin of Billesdon Coplow, situated on a SW-slope, which consistently receives the highest mean monthly temperatures, or nearly so. However, temperatures rapidly decline with increasing distance into the wood at this point. This contrasts with the SE-facing slope where higher temperatures penetrate considerably further into the wood.

Light interception on this slope is believed to be particularly high as demonstrated by the large proportion of asymmetrically shaped trees here found to a depth of about 140 m into the wood. This vegetational feature is described more fully in Chapter 10.

2) Avian Response.

a) Laying Date.

Without explicit reference to microclimate, Perrins (1979) notes that tits start nesting on woodland edges earlier, particularly on south-facing low-lying sites and that clutches tend to be larger in such a habitat. Furthermore, clutch sizes at Marley Wood clearly show a pattern (Perrins 1979; p.207) which could be explained by temperature variations similar to those noted at Billesdon Coplow.

Perrins (1973) has pointed out that a four-day delay in mean first-egg-date is incurred for each 1°C depression of the average temperature in the period 1 March to 20 April. Adopting this period, the mean daytime temperature at the southern station at Billesdon Coplow is 0.9°C higher than the northern one (or 1.1°C higher between 1 March and the date upon which laying at the southern nest-box began, 5 May). These temperature differences would be sufficient to account for the laying-date being four days earlier in at least part of the southern half of the wood. Each day's delay in hatching may lead to a 5% reduction in subsequent survival (Perrins 1973). It therefore follows that at Billesdon Coplow the higher temperatures on the south-facing slopes and along the south-facing woodland edges will encourage earlier breeding and enhance nestling survival.

Prior to breeding, night-time nest-box temperatures can influence the laying date of Great and Blue Tits roosting in them (O'Connor 1978, Dhondt and Eyckerman 1979). At Billesdon Coplow, night-time temperatures between 1 March-5 May the southern nest-box averaged 0.7°C higher. This compares with an ambient difference of 0.3°C between the stations. Considered alone, these night-time nest-box measurements could account for a minimum three-day delay in laying-date in the north.

Furthermore, night-time temperatures in an occupied nest-box are consistently elevated by around 0.5° C by the metabolic heat of the roosting

female. This will have the effect of slightly reducing overnight energy loss in the bird (O'Connor 1978, Warrilow et al. 1978). As a result, the bird would have the reserves necessary for egg-formation at an earlier date (Dhondt & After hatching, Eyckerman 1979). and some 10-14 days before fledging, temperatures rise sharply in the southern nest-box, but not in the other boxes. This feature, which produces a mean box temperature 3.3°C above ambient is explained by metabolic heat loss of the nestlings. Homeothermy develops among nestlings at this stage with a consequent improvement in the heat loss to heat production ratios due to many morphological changes taking place, one of which is feather growth (O'Connor 1975). Consequently, this more efficient insulation will reduce convective and conductive heat loss. The increase box in temperature, therefore, can only be explained satisfactorily by heat loss through respiratory evaporation. This may also explain the increasing saturation of the air. The nest-box environment, with its higher temperatures and relative humidity, would assist nestlings to reduce metabolic heat loss and would allow an increasingly greater proportion of their food intake to be used for body growth.

The lower critical limit of thermoneutrality for an incubating female Blue Tit is approximately 16°C (Haftorn 1982). Below this figure, oxygen consumption rises sharply as ambient temperature falls. A corollary of this would be that tits exposed to ambient temperatures above this threshold, assuming an energy intake above that required for basal metabolism, would have an excess energy accumulation which could be diverted into ovarian development. It is interesting to note that both nest-building and egg-laying at the southern site commenced shortly after both nest-box and ambient daytime temperatures reached 16°C. In the latter part of the nestling period the mean temperature of the occupied box lay within the range 12.6°C (lowest night) to 24.3°C (highest day). The upper parts of these ranges thus fall into the zone of thermoneutrality for the Blue Tit. It seems likely that considerable energy savings are made in this particular environment by the nestlings, and perhaps also the adults which may now reduce their close brooding of the nestlings.

Dhondt et al. (1984) investigated laying dates of Great and Blue Tits in urban, suburban and rural habitats. Great Tits were shown to exhibit a clear gradient in laying dates from urban through suburban to rural sites but Blue Tits laid earliest in suburban and latest in rural habitats. Cities possess their own microclimate, e.g. the urban heat-island effect (see reviews in Geiger 1965, Yoshino 1975), with the core generally experiencing the highest temperatures. Although temperatures will be lower in the suburbs, they will still be higher

than those of adjacent rural areas. Dhondt *et al.* (1984) concluded that whereas laying dates could be correlated with temperature the differences in laying dates were more a response to differences in the timing of food availability.

Older birds tend to lay earlier than younger ones (Perrins 1979), thus it is necessary to examine whether the northern half of Billesdon supports a larger proportion of young birds. The marking scheme (as outlined in Chapter 4) provides, to date, only 11 individuals with multiple nest-box breeding records. Despite this small sample, there is some indication of possible nesting patterns for the wood. Ten of these individuals show site-faithfulness in their nest-box selection. They returned to the same nest-box, or an adjacent one, each year, regardless of its position within the wood. There is therefore no evidence to indicate that, with increasing experience, birds move from the cooler northern part of the wood to the warmer southern half. Furthermore, some individuals nesting in the northern half were known to be 4 or 5 years old, and this provides further evidence that the northern half of the wood does not support young birds alone. It may be assumed from the current evidence that populations in the northern and southern parts of the wood possess similar proportions of each age-class.

b) Clutch Size.

Clutches are significantly larger and nestling survival is higher in the southern part of Billesdon Coplow. Many factors affect clutch-size including habitat (Perrins 1979, Dhondt *et al.* 1984), date of laying (Perrins 1979, this study), lateness of season (Perrins 1979), population density (Perrins 1979), age of female (Perrins 1979), size of nest-chamber (Löhrl 1973, Ludescher 1973, Karlsson & Nilsson 1977), and rate of incubation during egg-laying (Haftorn 1982).

Blue Tits lay slightly larger clutches in woodland where oak is dominant (Perrins 1979). This may be related to food supply. Oak trees are fairly evenly distributed between north and south at Billesdon Coplow and therefore cannot alone account for the variation in clutch-size in the wood. As conifers possess a poorer insect fauna (Perrins 1979), the larch plantation situated in the northern half of the wood could introduce a bias into the results. Recalculation of first-egg-dates after exclusion of the boxes in this habitat provide no change in mean laying dates. However, much of the south-eastern part of the wood is dominated by sycamore (Fig. 2.2b; Plate 11), which is well documented as

being particularly impoverished in insect fauna (see, e.g., Southwood 1961).¹ In spite of this, it is here that Blue Tits generally breed earliest (Fig. 5.17). Clearly the influence of tree species on the start of laying is of minor importance.

If smaller clutch sizes in the northern half of Billesdon Coplow were attributable to higher population density it follows that the proportion of occupancy of nest-boxes might also be greater in the north. However, so small are the annual differences between the two parts of the wood (<4%, except 1984 when the south had 16% greater occupancy) that it seems unlikely that there is a density effect on clutch size. However, this feature is not easy to test as Blue Tits, unlike the Great Tit, may continue to use natural holes despite a surplus of nest-boxes being available (Gibb 1954).

The influence of nest-chamber size on clutch size cannot account for the differences in clutch size at Billesdon Coplow as all boxes were built with the same interior dimensions.

The warmer, southern half of Billesdon Coplow is characterised by earlier laying in the Blue Tit, which leads to larger clutches being laid. Nestling survival is also higher in this part of the wood. It is concluded, therefore, that the differences in laying dates of Blue Tits between the two halves of Billesdon Coplow are accounted for by differences in microclimate, with small temperature variations being particularly important.

 $^{^{1}}$ To illustrate this point, here are quoted (from Southwood 1961) the number of insect species associated with trees commonly found at Billesdon Coplow: oak (284 species); beech (64); Norwegian spruce (37); larch (17); and sycamore (15).

PLATE 1. (see over)

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Sence (flowing westwards). Scale is approximately 10 cm to the kilometre. railway, the Grand Union Canal (adjacent to several study woodlands) and the River evident crossing the area E-W are (north to south) the Leicester-Market Harborough 1970) showing the relative position of 14 study woodlands (numbered W1-W14). Clearly PLATE 1. Wistow Estates. Vertical aerial photograph of the Wistow Estates (taken in








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scene are woodland patches of ash (W5, 0.2 ha), Lombardy poplar (W10, 0.4 ha), pedunculate oak (W11, 0.2 ha and W12, 1.2 ha) and horse-chestnut (W6, 0.2 ha and 641960 showing 6 of the 14 study woodlands on the Wistow Estates. Present in this PLATE 2. Wistow Estates. View looking eastwards towards Wistow Church from G.R. W4, 0.7 ha). June 1988.





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G.R. 641968. Nearest woodland, W9 (0.8 ha), is one of several linear-shaped patches at Wistow which follow the line of the canal. The slightly higher land in the PLATE 3. Wistow Estates. View to the SE from the Grand Union Canal towpath at June 1988. foreground is Boulder Clay underlain by Lower Lias Clays and Limestones but the lower-lying flood-plain of the River Sence in the mid-distance is covered by alluvium.

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PLATE 4. (see over)

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642968), showing the open canopy resulting from some tree-thinning in the 1970's. A including Garden Warbler, Willow Warbler and Whitethroat. June 1988. well-developed scrub layer now forms an important habitat for many bird species PLATE 4. Wistow Estates. The central section of the linear-shaped oakwood, W9 (G.R.

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PLATE 5. (see over)

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ash) whilst there is an almost continuous scrub layer (hawthorn). The patch has a sometimes, as in this case, with closely-spaced hedgerow trees. June 1988. mature woodland edge and is surrounded by farmland. Isolation is reduced through improved connectivity to neighbouring woods by the presence of radiating hedgerows. in all study woodlands. Mature broadleaves form a closed canopy (here being mainly (0.4 ha)(seen here from G.R. 634960) demonstrating vegetational characteristics present PLATE 5. Wistow Estates. The most westerly of the study woodlands at Wistow, W2



PLATE 6. (see over)

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and SW of, Billesdon Coplow. Scale is approximately 10 cm to the kilometre. Bay Fox Covert. Reference is made in the text to the area of parkland adjacent to, Fig. 2.2b); including beech (centre), larch (NE), sycamore (SE) and pedunculate oak (taken in 1970) of Billesdon Coplow (11.4 ha) and Botany Bay Fox Covert (14.9 ha). (elsewhere). Note the main central ride and the more uniform composition of Botany Clearly visible in Billesdon Coplow are zones dominated by different tree types (cf. PLATE 6. Billesdon Coplow and Botany Bay Fox Covert. Vertical aerial photograph




PLATE 7.

(see over)

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PLATE 7. Billesdon Coplow. Views from the south-east: (a) from G.R. 718034, showing relationship to Liassic Marlstone Esarpment; (b) from G.R. 714040, showing steeper S-facing slopes (left) but more gentle gradient of N-facing slope. May 1988.

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PLATE 8.

(see over)

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canopy layer here is dominated by beech with hawthorn (left) forming a discontinuous scrub layer. May 1988. PLATE 8. Billesdon Coplow. View from the crown of the hill looking north. The

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zone were significantly lower than in the southern half of the wood. May 1988. woodland margin downslope. There is a well-developed scrub layer of hawthorn here. characterised by massive beech trees which give way to pedunculate oak closer to the Despite these vegetational charcteristics bird breeding densities in this northern interior PLATE 9. Billesdon Coplow. The north-western part of the wood (looking N) is



PLATE 10.

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along the southern perimeter (looking S). Ornamental shrubs (left) and hedgerows Bird breeding densities here were the highest recorded in the wood. May 1988. (extreme right) provide a varied sub-canopy habitat. Trees are mainly pedunculate oak. PLATE 10. Billesdon Coplow. Shown here is the small southerly extension to the wood



PLATE 11. (see over)

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breeding densities were significantly higher here than anywhere in the northern half of these species, both well documented as supporting impoverished insect fauna, bird mature sycamore (with a few horse-chestnuts) and rhododendron bushes. In spite of the wood. June 1988. PLATE 11. Billesdon Coplow. The south-eastern part of the wood is dominated by



PLATE 12.

(see over)

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margin on the right. June 1988. lowest in the wood. However, bird densities were slightly higher along the woodland wood. Bird breeding densities and ambient air temperatures here were generally the PLATE 12. Billesdon Coplow. A larch plantation dominates the north-eastern part of the

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PLATE 13. (see over)

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of pedunculate oak, as seen here. Hawthorn (left) and bramble (right foreground) PLATE 13. Botany Bay Fox Covert. This 'wet ash-maple' wood has a thin scattering produce discontinuous scrub and field layers. April 1988.



PLATE 14.

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by a closed canopy. May 1988. results in the scrub and field layers being more developed than in parts characterised areas in the interior zone of open canopy, as seen here. Increased light penetration PLATE 14. Botany Bay Fox Covert. Limited tree-thinning in the 1960's has led to



PLATE 15. (see over) zone trees. May 1988. important to scrub warblers and other edge species. Woodland margin is on the right. mid-1970's. Dense field and scrub layers have developed here and are particularly PLATE 15. Botany Bay Fox Covert. Clearing created in the south-western part in the Note the asymmetrically-shaped tree (left of centre) with branching characteristic of edge

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PLATE 16. (see over)

than the adjacent denser woodland, thus encouraging higher bird breeding densities here. May 1988. PLATE 16. Botany Bay Fox Covert. The wide, central ride has lower shade levels



PLATE 17. (see over)

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woods. Scale is approximately 10 cm to the kilometre. entirely closed and the rides are overtopped. Note the high number of neighbouring PLATE 17. Loddington Reddish. Particularly noticeable in this vertical aerial photograph Though the line of several rides can be faintly traced in this view, the canopy is now (taken in 1970) is the uniform tree species composition of the wood ('wet ash-maple').




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PLATE 18.

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species composition and dense, closed canopy. July 1988. gentle slope of the wood on the valley side of the Eye Brook. Note the uniform tree PLATE 18. Loddington Reddish. View (looking SE from G.R. 774028) showing the

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PLATE 19.

(see over)

this area now becoming impenetrable. of tree-thinning in the 1960's. Subsequent planting with conifers has led to most of become totally overgrown. Clearly evident in the western part of the wood is the result this 1970 view. Some rides in the north and western part of the wood have now Leicestershire. Note the main (E-W) central and several shorter intersecting rides in PLATE 19. Owston Big Wood. This is the largest ancient, semi-natural woodland in





PLATE 20. (see over)

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species numbers and breeding densities were markedly lower here than in the smaller Wistow woodlands. layer. The scrub layer comprises a mixture of hazel, hawthorn and willow. Bird mixture of pedunculate oak, wych elm and ash. Bramble forms an impenetrable field PLATE 20. Owston Big Wood. Plot D of the interior zone. The canopy layer is a



PLATE 21. (see over) ۲.

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PLATE 21. Billesdon Coplow. The northern weather station at Billesdon Coplow (1984) showing: (a) the general arrangement of recording equipment; (b) close-up of nest-box (above), control-box and omni-directional sensitive cup anemometer; and (c) white screen with sucrose solution sensor suspended within (foreground), solarimeter (mid-distance) and screen containing wet and dry bulb thermistors. See text for details.



PART II

BIRD BREEDING PATTERNS AND WOODLAND NATURE RESERVE DESIGN.

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Chapter 7

CHAPTER 7

THE APPLICATION OF THE EQUILIBRIUM THEORY OF ISLAND BIOGEOGRAPHY TO CONSERVATION PRACTICE: A REVIEW OF THE LITERATURE.

Whilst Part I has presented detailed findings on the influence of microclimatic variations on the breeding ecology of a specific bird species in a selected wood, Part II now addresses the general distribution of woodlands in East Leicestershire and their associated bird breeding patterns. The association of these breeding density patterns with microclimate is explored. This section concludes with a discussion of the relevance of the findings to avian conservation strategies.

1) The Equilibrium Model.

There have been several attempts recently to derive conservation strategies from the equilibrium theory of island biogeography (see, for instance, Harris 1984). This theory was published first as 'An equilibrium theory of insular zoogeography' (MacArthur & Wilson 1963), and later, with the inclusion of flora, as the 'The theory of island biogeography' (MacArthur & Wilson 1967). This model is widely accepted as the first attempt to explain species-area relationships in terms of a dynamic equilibrium. Earlier studies had used descriptive techniques to identify species-area relationships (e.g. Arrhenius 1921, Gleason 1922, Hamilton *et al.* 1964, Hamilton & Rubinoff 1967).

The equilibrium theory states that the number of species on an oceanic island is determined by a dynamic balance or equilibrium between the immigration of new species and the loss of existing species through extinction. The rate of immigration is high initially but rapidly falls as fewer niches become available with increasing inter-specific competition. In contrast, the rate of extinction is low initially but accelerates as more species colonize and the size of each species' population decreases. Immigration and extinction curves are shown schematically in Figure 7.1. Immigration rates are mainly determined by distance from the species pool or source region of the colonists. It follows that islands which are nearer to the species pool will have higher immigration rates than more isolated islands (Fig. 7.2a). In addition to the distance from the species of the source region will also exert an influence on

immigration rates. Extinction rates are accounted for primarily by area. Larger islands will be characterised by lower extinction rates (Fig. 7.2b). It follows, therefore, that large islands, close to the species' source, will support more species at equilibrium than smaller, more isolated islands owing to higher immigration rates and lower extinction rates. Large islands will also possess higher environmental or habitat diversity and this has a direct effect on species richness. This further explains why higher immigration rates occur on large islands.

The equilibrium model reaffirms the positive relationship that exists between area and species number. Many attempts have been made to quantify this relationship (e.g. Arrhenius 1921, Gleason 1922, Hopkins 1955, Cain & Castro 1959), which is described as a species-area curve (Fig. 7.3a), and it is usually expressed by the equation:

$$S = cAz \tag{1}$$

where S = species number, A = area, and c and z are positive constants (intercept and angle of slope respectively) which vary according to the taxon being examined. Log-transformation of (1) gives a linear relationship between the variables (Fig. 7.3b), and enables the constants c and z to be more readily obtained:

$$\log n S = \log n c + z \log n A \tag{2}$$

The slope of the z-value for a single taxon is steeper for oceanic islands than for continental habitat islands. MacArthur & Wilson (1967) state that values for true islands should fall between 0.20-0.35 which is close to the theoretical value obtained by Preston (1962a, 1962b).

The MacArthur & Wilson model predicts that when the equilibrial number reaches constancy or saturation the species composition will continue to change as new species replace those which are lost through extinction. This process, termed species turnover, is another feature of island biotas and is measured in species/unit time.

Should an island become smaller through a disturbance (for instance, rising sea levels or destructive volcanic activity) the current equilibrial level will then be higher than the new island area can support. Elevated extinction rates cause a re-equilibration to fewer species. This feature is known as relaxation.

2) Modifications to the Equilibrium Model.

Shortly after the basic equilibrium model was described, a number of proposals were made to modify it. Included in these was the claim that extinction rates are influenced by distance from the species pool (Brown & Kodric-Brown 1977) and immigration rates are affected by island size (Whitehead & Jones 1969).

Attempts to validate the equilibrium theory with empirical evidence soon followed its publication. One such study involved a defaunation experiment of small mangrove islands and the monitoring of their subsequent colonisation by arthropods (Simberloff & Wilson 1969, 1970, Wilson & Simberloff 1969). Both in this study and one other, which examined the avifauna of the Californian Channel Islands (Diamond 1969), rates of immigration and extinction, species turnover rates and species equilibria were all determined. These two studies, in addition to others, e.g. Crowell (1973), Mayr (1976), are offered as further examples where island faunas are largely accounted for by the model. Despite this early support of the model, many weaknesses have subsequently been ascribed to it (see, for example, Williamson 1981). There is criticism that habitat heterogeneity of oceanic islands is not considered as a major factor in determining species number (Stoddart 1981, Reed 1983, Rafe et al. 1985). Furthermore, it fails to take into account species diversity (that is, the relative proportion of individuals within the species present), but instead considers only species number (Williamson 1981). It also ignores the biology of individual species, a feature which Berry (1979) believes must be considered. Even the familiar log-transformed species-area relationship has been challenged as a statistical convenience that has little support from empirical evidence (Vincent 1981).

Concern is also expressed over the precise definition of the terms immigration, extinction (Simberloff 1969, McCoy 1982, Williamson 1981) and turnover (McCoy 1982). MacArthur & Wilson (1967) define immigration as "the process of arrival of a propagule on an island not occupied by the species" (p.188). For the purposes of their study they define a propagule as "the minimal number of individuals of a species capable of successfully colonizing a habitable island" (p.190). Williamson (1981) challenges these definitions as being unclear in instances such as single migrants (birds) which may not remain or individuals breeding in a unsuitable habitat where the species could not possibly persist.

Further controversy surrounds species turnover which, as the model the predicts. will accompany colonization process all stages. Some at empirically-derived turnover rates show variation from the values of 0.1-1.0 spp/day as predicted by the equilibrium model. Those presented by Simberloff & Wilson (1969) fall in the lower part of this range, between 0.05-0.5 spp/day. Turnover rates are more rapid on smaller islands than larger ones (Mayr 1965), or in species of a higher trophic level (Hunt & Hunt 1974). Despite this evidence to support turnover, other studies have concluded that it does not exist or has extremely low values (Brown 1971, Lynch & Johnson 1974, Simberloff 1974, Abbot & Grant 1976, McCoy 1982). Indeed, it is suggested by Simberloff (1976) that much of the species turnover is probably attributable to vagrant species and not to true immigrants.

A fundamental feature of the model, the dynamic equilibrium, has been challenged by Abbot & Grant (1976). Investigating immigration and extinction rates of oceanic island avifaunas in Australasia, they found no evidence to support an equilibrium. Diamond's (1969) study, cited previously as clearly supporting the model with empirical evidence, has itself been the subject of criticism (Lynch & Johnson 1974). In particular, the status of transient species (listed by Diamond as immigrants), incomplete censuses and human interference are all challenged as weaknesses.

One major criticism levelled at the equilibrium theory is that, as a hypothesis, it was accepted too readily long before sufficient empirical evidence was available to validate it (Simberloff 1976, Connor & McCoy 1979, Gilbert 1980, Margules *et al.* 1982).

That such conflicting evidence surrounds the equilibrium theory was partly anticipated by its authors. They state that 'we do not seriously believe that the particular formulations advanced in the chapters to follow will fit for very long the exacting results of future empirical investigation' (MacArthur & Wilson 1967, p.v). Among the weaknesses of the theory that MacArthur & Wilson themselves identify are: that the shapes of the immigration and extinction curves are imprecisely known; and it is more difficult to identify individuals as instances of either immigration or extinction than the model supposes.

3) Habitat Islands.

Although the equilibrium theory was originally concerned with oceanic islands the principles of the model have become widely applied to continental

habitat islands (or 'patches'). These are environments surrounded by altered habitat (matrix) which is alien or hostile to the biota of the habitat island. However, the landscape matrix may, unlike the surrounding ocean, support species which are potential colonists. Further, it may assist immigration by providing resting or feeding habitat for migrant or mobilised species. Thus, the degree of isolation of patches is less than that of oceanic islands (Harris 1984, Forman & Godron 1986).

The broader interpretation of the species-area relationship to include habitat islands has included studies which examine, for example, mammals (Brown 1971) and birds (Vuilleumier 1970, Johnson 1975) on mountain peaks, insects in urban parks (Faeth & Kane 1978), invertebrates in lakes (Browne 1981) and avifauna within woodland patches (e.g. Moore & Hooper 1975, Forman *et al.* 1976, Galli *et al.* 1976, Whitcomb *et al.* 1981, Rafe *et al.* 1985).

Disturbance of an oceanic island leads to a reduction in the number of species at equilibrium, through the lowering of the immigration curve. The same effect, termed relaxation, may be created through the destruction of woodland patches thus increasing fragmentation and isolation (Kent 1987).

4) Conservation Strategies and Nature Reserve Design.

Whilst the applicability of the equilibrium theory to explain island biotas has aroused considerable debate, there is little doubt that further controversy has been generated over the attempts to apply it to conservation strategies and nature reserve design. Since Willis first proposed this possible relationship in 1971 (Willis 1974), numerous attempts have been made to derive criteria for nature reserve design from the equilibrium theory (e.g. Willis 1974, Terborgh 1974, 1975, Wilson & Willis 1975, Diamond 1975, May 1975, Sullivan & Shaffer 1975, Blouin & Connor 1985).

The debate has centred on three key issues. These are:

- a) the optimum size for a nature reserve,
- b) the optimum shape for a nature reserve,
- c) the best spatial pattern for a group of related nature reserves.

a) Reserve size.

Initially, there was considerable agreement that the MacArthur & Wilson model could be interpreted as stating that larger reserves are better for preserving greater species numbers than smaller reserves (Terborgh 1974, 1975, Diamond 1975, 1976, May 1975, Sullivan & Shaffer 1975, Wilson & Willis 1975, Diamond & May 1976). Supporting evidence which favours large reserves comes from studies which indicate a decline in species numbers and densities following reduction and isolation of forests (Lynch & Whitcomb 1978, Whitcomb et al. 1981, Karr 1982). Wilson & Willis (1975) further interpreted the model as predicting that one large reserve will support more species than two reserves each of half the original size. On the other hand, Abele & Connor (1979) later demonstrated that, by using a mean slope z value of 0.3 (derived from about 100 species-area relationships), two reserves of half size will hold more species than a single large one (Fig. 7.4), a conclusion reached by other researchers (e.g. Higgs & Usher 1980, Blake & Karr 1984, Woolhouse 1987). Whilst one debate has centred on the option of one large reserve or two half-sized reserves, other studies have compared the species richness of a single large reserve with that of several smaller preserves of equivalent area. Forman et al. (1976) specify that a minimum of three large forests (each at least 40 ha) are required to preserve maximum avian species richness. However, recent evidence suggests that several smaller woods may possess greater species richness than a single large plot of equivalent area (Higgs & Usher 1980, Gilpin & Diamond 1980, Ford 1987).

Many avian studies have examined species-area relationships in woodlands and most have concluded that area is the best predictor of species number (e.g. MacArthur 1971, Moore & Hooper 1975, Forman *et al.* 1976, see summary Fuller 1982, Woolhouse 1983, Rafe *et al.* 1985, Askins *et al.* 1987, Møller 1987).

b) Reserve shape.

Moreover, the model has been interpreted as stating that the optimum shape for a reserve is circular - to minimise the peninsula effect (Diamond 1975, Diamond & May 1976, Butcher *et al.* 1981). This follows the observation that the tip of a peninsula experiences higher extinction rates and lower immigration rates than the base or equivalent areas of mainland, thus supporting fewer species at equilibrium (Simpson 1964, MacArthur & Wilson 1967, Cook 1969, Wilson & Willis 1975). Naturally, it has been concluded that it would be undesirable to include this shape into refuge design. Simberloff (1986) argues, however, that the peninsula effect, even where observed, is supported by

little evidence of such immigration and extinction rates.

There is increasing evidence to indicate that the proportion of woodland edge zone (which Ranney *et al.* 1981 define as having a depth of between about 15-30 m according to aspect) may determine increased species richness and breeding bird densities (Gates & Gysel 1978, Kroodsma 1982a, 1982b, Tiainen *et al.* 1985, Ford 1987, see review Forman & Godron 1986). This effect is manifested through relatively higher species richness in smaller plots, where there is a larger proportion of edge, than in larger woods where there is a high interior to edge ratio.

Some studies have shown that, whilst species numbers increase with increasing area, breeding bird density may decrease (e.g. Gromadski 1970, MacArthur 1971, Ford 1987, Møller 1987). These workers have made little attempt to determine the factors influencing this inverse trend, though Møller (1987) does point out that invertebrate food availability does not decline with decreasing bird density.

Thus if the most desirable criterion for conservation strategies is to maintain the maximum species richness in a region, several smaller reserves, each supporting higher densities, may be more desirable than a single large one (Ford 1987). Though the smaller reserves will, as single units, support fewer species, collectively a group of reserves should have a higher species richness than a single large reserve (Ford 1987). As edge zones support higher faunal densities (see review, Forman & Godron 1986) it follows that, as the total area of edge zone in fragmented preserves will be much greater than in the single large reserve, the strategy for maximising species numbers is to preserve several smaller patches rather than one large reserve of equivalent area. Such a result may stem from the increased habitat heterogeneity that comes from the combined edge/interior ratios of several patches, when compared to the heterogeneity of one large reserve (Reed 1983, Game & Peterken 1984, Simberloff 1986, Woolhouse 1987).

However, as the species-area relationship shows, larger woodlands will support higher species richness, particularly interior species and this might be a further important consideration. Consequently, a single conservation strategy is unlikely to be suitable for all species (Diamond 1976). Different species will require different minimum areas and some require large home territories (Moore & Hooper 1975). It has been suggested that the minimum area should be estimated for key species and this should be the principal determinant for

reserve size (Soulé & Simberloff 1986).

c) Spatial Distribution of Reserves.

As stated previously, the MacArthur & Wilson model holds that rates of immigration are primarily influenced by distance from the species' source region. Thus it may be assumed that the degree of isolation of a reserve is an important factor in determining conservation stategies for fragmented habitat patches.

Diamond (1975) established criteria for designing nature reserves based on his interpretation of the main tenets of the theory (Fig. 7.5). These included that a single large reserve will hold more species at equilibrium than a single small one or several smaller ones of equivalent area. If the original reserve has to be sub-divided, this should be into as few patches as possible. They should be grouped closely together rather than isolated, to help to reduce the possibility of random extinctions, and arranged non-linearly. This would maximise immigration rates and would lower extinction rates between the patches. The reserve should be circular rather than elongated in shape so as to minimise dispersal distances within the patch. Strips of habitat between fragmented reserves would act as corridors or 'stepping stones' and would increase connectivity (which is defined by Forman & Godron (1986, p.591) as "a measure of how a corridor ... is"). This would assist in creating higher connected ... immigration rates and lower extinction rates (Wilson & Willis 1975) and help to reduce the effects of isolation (Harris 1984). However, the connecting strips may also assist the potential spread of threats to wildlife such as disease or fire (Simberloff & Cox 1987).

Although isolation has not been found to be the single best predictor of avian species richness in individual woodlands it is, nevertheless, another contributary factor which controls species numbers (e.g. Johnson 1975, Opdam *et al.* 1984, 1985). It is believed to primarily affect interior species in larger woodlands (Lynch & Whigham 1984, Forman & Godron 1986, Askins *et al.* 1987).

There has followed much support for these criteria, particularly for clustered reserves, from other studies (e.g. Johnson & Simberloff 1974, Johnson 1975, Wilson & Willis 1975, Sullivan & Shaffer 1975, Lynch & Whigham 1984, Opdam et al. 1984, 1985).

d) Other Factors.

Not all studies which have examined species-area relationships have demonstrated area to be the best predictor of species numbers. Other variables such as habitat diversity (Johnson 1975, Picton 1979, Reed 1983, Rafe *et al.* 1985), altitude (Case 1975, Temple 1981), and exposure to the sun (Goldstein 1975) have all been identified.

Habitat heterogeneity, sometimes expressed as foliage height diversity (FHD) (see Chapter 10), has been cited as being responsible for bird species richness (MacArthur & MacArthur 1961, MacArthur *et al.* 1962, Moss 1978, O'Connor 1981, Erdelen 1984, Freemark & Merriam 1986, Møller 1987). In contrast, both Galli *et al.* (1976) and Howe (1984) found that FHD had little or no influence on species richness; here the key variable was found to be woodland area.

Nevertheless, despite all these factors which may influence the species richness of a nature reserve, the general conclusion remains that area is the best predictor of species numbers. This is supported by a wide range of studies from plants on oceanic islands (Johnson *et al.* 1968), to insects in urban parks (Faeth & Kane 1978), and birds in fragmented woodlands (MacArthur 1971, Moore & Hooper 1975, Forman *et al.* 1976, Galli *et al.* 1976, see summary Fuller 1982, Woolhouse 1983, Howe 1984, Lynch & Whigham 1984, Rafe *et al.* 1985, Askins *et al.* 1987, Moller 1987).

There is increasing doubt being expressed as to whether the equilibrium model does in fact make clear recommendations concerning refuge size and refuge shape (Simberloff & Abele 1976a, 1976b, McCoy 1982, Simberloff 1986, Margules *et al.* 1982, Kent 1987). However, although Simberloff (1986) is clearly opposed to the idea that the theory favours single large reserves he does acknowledge that it offers a "testable proposition" (Simberloff 1986, p.324).

As described in Chapter 1, the main aim of this section of the thesis is to determine the extent to which woodland area accounts for avian species richness and breeding bird densities in selected East Leicestershire woodland patches. Should such a relationship exist, a secondary aim will be to identify those other key factors which might also play a part in explaining species numbers and breeding densities within the patches. This should assist the making of recommendations concerning refuge design. Such recommendations might then also apply to similar woodlands in other lowland areas of Britain. Of the avian studies mentioned above in this review of the literature, the two which are particularly relevant for this study of woodland birds in East Leicestershire are Moore & Hooper (1975) and Ford (1987).

CHAPTER 8.

THE BREEDING AVIFAUNA OF SELECTED EAST LEICESTERSHIRE WOODLANDS.

Field Methods.

The field methods described in this section are concerned with two related areas of fieldwork activity, namely the recording of breeding bird species and densities in the various woodlands and the characterisation of these woodlands as habitats for the birds.

1) The Bird Census.

i) Study Woodlands.

Each of the 16 study woodlands (i.e. the Wistow woods, Billesdon Coplow and Botany Bay Fox Covert) was visited between 3 and 7 times and the total time spent in each one varied from 20 minutes (in the smallest, 0.01 ha) to nearly 17 hours (in Billesdon Coplow, 11.4 ha) (see Appendix 4 for details of field visits, including times, dates and weather). If a woodland received just three visits they were spaced at monthly intervals.

Most censuses were undertaken between 1630-1930 hours (range 1400-2000 hours) to coincide with the evening peak of bird song. In addition, all the Wistow woods received one morning visit, between 0930-1100 hours. With very few exceptions visits were made on days of fine weather with little or no wind. All visits were undertaken between 14 April-28 June 1987.

The spot-mapping method was used to monitor the total bird population in each study woodland. Briefly, this method entails mapping (on 1:1000 scale maps) the position of all contacts or registrations of birds exhibiting territorial behaviour. Examples of such behaviour include singing birds, aggression between males, and adults carrying food or nesting material (see Appendix 3 for a full description of this method). Particular effort was made to plot registrations of males singing simultaneously.

ii) Control Plots.

A total of 8 control plots, each of 4 ha, was chosen. Six of these were selected within the core or interior zone of two larger woodlands to investigate the species number and breeding density of an 'interior' avifauna. Of these 6 plots, four were sited at intervals along the main central ride of Owston Big Wood (110.7 ha) and two, which slightly overlapped,¹ in Loddington Reddish (36.2 ha) (Fig. 2.3). Two further plots, sited along the south-western margin of Loddington Reddish to include some edge zone, enabled direct comparison to be made with the avifauna of the two interior plots of this wood. The morphology and vegetation of these control plots have been described previously, in Chapter 2.

Prior to undertaking the census work, the boundary of each control plot was marked out. To do this, a distance of 100 m was measured from the intersection along each ride. One tree standing close to each boundary point was then marked as a locational reference point. False lines were drawn at 90° to the rides through these points to form the perimeter of each 4 ha control plot. Each control plot was sited at the intersection of two rides. The decision to do this was in response to the impenetrable scrub layer throughout both woods.² Walking slowly along the rides, and by using a simple form of triangulation, enabled the exact position of territorial birds to be plotted on maps.

Each control plot was visited three times at approximately monthly intervals between 17 April and 30 June 1987; each visit took 30 minutes and was timed (between 1630-1930 hours) to coincide with the evening peak of bird song and with fine weather (see Appendix 4 for details).

The spot-mapping method, though appropriate for the study woodlands, was unsuitable for use in the control plots. Here, the point-count method was adopted as being the most suitable for monitoring sample populations from within a larger area (details of this are presented in Appendix 3).

¹ In view of the two plots overlapping, particular care was taken in the analysis not to duplicate territories.

 $^{^{2}}$ It should be pointed out that bird species richness and breeding density in these woodland interior plots with their adjacent rides are likely to be slightly higher than in homogenous unbroken interior woodland owing to the 'edge-effect'. This is discussed more fully in Chapters 10 and 11.

In all study woodlands and control plots a cluster of contacts or registrations derived from several visits was used to mark the position of a bird territory or breeding pair of birds. If all the registrations fall within a single woodland patch the breeding territory is clearly allocated to that wood. However, some territories extended beyond the boundary of one study woodland or control plot into an adjacent habitat. For the study woodlands this was usually a neighbouring woodland patch, an adjacent hedgerow or parkland ecotone, but for the control plots it was a continuation of the interior zone of that woodland. In all situations the proportion of territory (either .25, .5 or .75) apportioned to the study woodland or control plot was determined by the ratio of registrations recorded inside and outside the boundary.

No attempt was made to search for nests, in view of the limitation of survey time. However, any located in passing and all occupied nest-boxes were also plotted on the field maps.

A few species presented special censusing problems. Some had extensive territories covering a number of woodland patches, others were semi-colonial nesters with overlapping territories. Species within either of these categories were not counted, just their presence within a woodland patch noted. Included in this group were raptors (Sparrowhawk, Kestrel), game-birds (Pheasant), pigeons (Stock Dove, Woodpigeon, Collared Dove), corvids (Magpie, Jackdaw, Carrion Crow) and Starling. Two species normally associated with riparian habitats, Sedge Warbler and Reed Bunting, but recorded in some Wistow woods, were not mapped either. Although both species have been documented as breeding in dry habitats, including woodland, it is the author's judgement that their presence at Wistow was primarily attributable to the Grand Union Canal being adjacent to occupied woodlands. the An early decision was made not to map the Yellowhammer, as its usual breeding habitat in Leicestershire is farmland hedgerows. It later proved to be widespread in woodlands at Wistow. Inclusion in the breeding density totals of these three species, not generally associated with closed canopy woodland, would have inflated the survey values. However, their presence in study woodlands was noted and are included in appropriate tables. One species alone, Yellow Wagtail, is omitted from all the results. Although recorded in song at one Wistow woodland, it is best known in East Leicestershire as a ground-nesting species associated with moist arable or mixed farmland.

In spite of the intensive nature of the field work, it is possible that some species were overlooked, particularly the Tawny Owl and Woodcock, which are

nocturnal and crepuscular species respectively. For instance, the Tawny Owl is known to have bred, both before and after 1987, in Billesdon Coplow. Furthermore, as both species are shown breeding in some of the larger study woodlands between 1976-84 in the *Breeding Bird Atlas of Leicestershire and Rutland* (Warrilow, in prep.), it follows that they may have occupied these same sites in 1987.

2) The Woodland Habitat.

Wales (1967, 1972) working in New Jersey (40°N) and Ranney *et al.* (1981) working in Wisconsin (43°N), have concluded that the depth of the zone along woodland margins that might be regarded as 'edge' rather than true interior is about 15 m wide for north-, east- and south-facing boundaries but is some 30 m wide on west-facing fringes. Previous British woodland studies have not addressed this problem of edge zone depth definition and so it was decided initially, in the absence of such information, to accept as a reasonable working hypothesis the suggested 15 m depth for the edge zones of the East Leicestershire woodlands used in this study.

In order to calculate the percentage of edge zone and interior zone for each study woodland a grid of 15 m squares was superimposed on large scale maps. Each grid was aligned either with the long axis of the patch, if it was linear in shape, or with the longest straight perimeter if the woodland was non-linear in shape.

The established grid was also used to make a detailed examination of spatial patterns of breeding bird density in Billesdon Coplow and Botany Bay Fox Covert. The procedure adopted can be illustrated by reference to Billesdon Coplow. Figure 8.1a shows the exact position of all registrations (n=852) recorded during field visits to this wood. Through superimposing a grid the total number of registrations per square was determined (Fig. 8.1b). Use of this census technique allowed a mean breeding density for each 15 m square to be calculated, thus permitting comparison of intra-patch differences.

In addition, the census techniques used in all five study woodlands, including Billesdon Coplow and Botany Bay Fox Covert, allowed a mean breeding density for each recorded species to be calculated (as breeding pairs ha⁻¹), thus permitting comparison of between-wood differences. In looking at these differences, the study woodlands were arbitrarily classified into three categories, namely small (<0.5 ha), medium (0.5-2.5 ha) and large (>2.5 ha).

The nature of the edge zone vegetation was also investigated. It is known to possess a greater basal area and higher species richness than that found in the true interior of the wood (Ranney et al. 1981). Characteristically, mature trees within the edge zone display an asymmetrical shape (see Plate 15). Branching is most heavily developed towards the outside of the wood (or towards the main light source); it is absent or nearly so on the woodland side (Levenson 1981). These characteristics were examined in interior one particular woodland, Billesdon Coplow. Here, the position of all such trees was mapped by surveying in April 1987 (Fig. 8.2). The mean direction of the branching was measured with a prismatic compass to $+5^{\circ}$. Distance (in metres) from each tree to the nearest woodland perimeter was measured with tape measure or optical rangefinder (Ranging Measuring Systems, model 620). Calibration of the rangefinder before and after the fieldwork showed no change. Observations during the course of general fieldwork confirmed that edge zone vegetation characteristics could also be demonstrated for the other woodlands and, to a lesser degree, along rides in core zones. However, as a 30 m depth was not identified along the western margin in Billesdon Coplow, this particular depth was not used for the calculations of the interior-to-edge ratios; the 15 m depth value therefore was used for calculating this ratio for all edge orientations.

Finally, inter-patch distance (in kms) was measured from each study wood to the nearest (a) other wood, (b) wood of similar area, (c) larger wood and (d) wood over 10 ha. To further investigate the extent of isolation of each woodland, the number of patches within a 2 km radius of each study site was determined. From the distances between the study woodlands and these neighbouring patches an index of isolation was calculated using a formula as follows:

$$r_i = \frac{1}{n} \sum_{j=1}^n d_{ij}$$

r,

where

= index of the isolation of the patch,

n = number of neighbouring patches (within 2km),

 d_{ii} = distance between patch and any neighbouring patch i.

(Forman & Godron 1986)

The connectivity of the study woodlands with neighbouring patches was investigated by examining the number and structure of hedgerows physically adjoining them. The frequency of trees along these hedgerows was noted from vertical aerial photographs (dated July 1970) and confirmed by ground survey (July 1988). They were scored as follows: hedgerows without trees, 1; hedgerows containing scattered trees, 2; hedgerows with closely-spaced trees, 3. A further score was aggregated to these values: if the particular hedgerow was linked to the neighbouring patch directly (=2); indirectly, (within a distance of about 1000 m along hedgerows; =1); or not at all (greater than 1000 m; =0).

CHAPTER 9

RESULTS

1) Avian Species Composition and Breeding Densities

i) Study Woodlands.

A total of 47 species were recorded in the 16 study woodlands. The maximum species richness recorded in a single woodland was 32 (Billesdon Coplow). Species were divided into four groups according to the range of woodlands in which they were found (Table 9.1).

- a) Group A; species whose presence was not influenced by woodland area and so are termed ubiquitous. However, this group of 17 species is sub-divided (into A1 and A2) depending on whether or not they were present in the smallest patch (0.01 ha). It will be later shown that these species found in the smallest wood were confined not just to this wood but had territories which extended into adjacent hedgerows.
- b) Group B; twelve species found in small (<0.5 ha) and medium (0.5-2.5 ha) patches only. Their presence within this range of patch sizes favours the idea that they are 'edge' species, i.e. mainly associated with the woodland perimeter.
- c) Group C; includes 9 species which were recorded only in medium and large patches (>2.5 ha). Later (in Chapter 10), it will be shown that most within this group are also 'edge' species.
- d) Group D; consists of a further 9 species, which were found only in large woodlands. This feature, together with additional evidence described later, enables them to be classified as 'interior' species (i.e. found primarily or entirely within the woodland core).

The total number of breeding pairs in the Wistow patches, Billesdon Coplow and Botany Bay Fox Covert are presented in Table 9.2 where they are compared with totals from the control plots. These data clearly show that, in addition to having the highest species richness, the fragmented woods at Wistow supported a considerably greater number of pairs than the larger study woodlands or control plots. Confirmation of the higher breeding densities in the more fragmented woods at Wistow is obtained from Table 9.3. Nearly two-thirds of all species mapped (59% of the total number) achieved higher densities at Wistow than elsewhere. Of the common species recorded both in the range of study woodlands and control plots, all had significantly higher breeding densities in the Wistow woods than in the control plots (Table 9.4). Seldom did the breeding densities of individual species at Owston or Loddington Reddish approach the levels recorded in the fragmented woodland at Wistow (Table 9.3).

ii) Control Plots.

A total of 27 species were recorded in the six interior control plots at Owston Big Wood and Loddington Reddish (Table 9.5). Species richness was strikingly similar in each one whilst the maximum number recorded in a single plot was 19. Only eleven species were widespread, being recorded in every plot, or nearly so (Table 9.5). They were Woodpigeon, Great Spotted Woodpecker, Wren, Robin, Blackbird, Song Thrush, Chiffchaff, Willow Warbler, Blue Tit, Great Tit and Chaffinch.

No species was confined entirely to the control plots of Owston Big Wood and Loddington Reddish; all were recorded in at least some of the other 16 study woodlands (Table 9.2). However, for Pheasant, Cuckoo and Willow Tit, their presence was limited to large woods only. Just six species reached their highest breeding densities in woodland core areas (Table 9.3). These were Great Spotted Woodpecker, Chiffchaff, Goldcrest, Long-tailed Tit, Marsh Tit and Willow Tit. It was noticeable that, within the range of study woodlands, these species were generally observed only in medium and large woods (Table 9.1). Analysis of the spatial pattern of territories in Billesdon Coplow and Botany Bay Fox Covert makes it clear that only three species from this list are dependent on the core zone, namely Chiffchaff, Marsh Tit and Jay. The other species listed above require large woodlands to provide their breeding habitat, but not necessarily the interior zone. The highest breeding densities in the control plots were not reached by 'interior species' but instead by Robin, Blue Tit and Wren, all ubiquitous species.

2) Avian Species-area Relationships and Breeding Densities.

Species richness and the number of territories in the 16 study woodlands were significantly correlated with patch size (Table 9.6)(Appendix 7a). Breeding

density was negatively correlated with area (Table 9.7)(Appendix 7b). For both sets of data log-transformation of the variables gave higher correlation coefficients (Appendix 7).

Furthermore, for most species which were widespread in the study woodlands, the number of breeding territories increased with increasing woodland size. Correlation coefficients were calculated for these relationships and are presented in Table 9.8. The strongest positive relationships were those for Blackbird, Blackcap, Blue Tit, Wren and Chaffinch.

3) Avian Breeding Densities and Woodland Edge Zones in Selected Woodlands.

i) Billesdon Coplow.

Bird breeding densities in Billesdon Coplow exhibited clear spatial variations between edge and interior zones in the southern and northern halves of the wood (Fig. 8.1). The mean breeding density of the edge zone was three times greater than that of the core (Table 9.9a). The southern edge zone (facing SW and SE) revealed the highest mean bird density of the wood, and this was significantly higher than both those of the northern edge zone (facing adjacent southern core area. the NW and NE) and The interior zone experienced the lowest densities in the wood but even here the mean density of the southern half of the core was approximately double that of the north. As shown in Table 9.9a the differences between breeding densities of southern edge zones, northern edge zones and interior zones were all highly significant. When compared with each other, mean breeding densities are seen in the following descending order: southern edge zone (average number of registrations = 4.6); northern edge zone (2.0); southern interior zone (1.7); and northern interior zone (0.7).

ii) Botany Bay Fox Covert.

As fewer data were gathered at Botany Bay Fox Covert the results should be assessed with some caution. Nevertheless, the same patterns were found there as at Billesdon Coplow. Again, these differences were, except in one instance, statistically significant (Table 9.9b).

iii) Loddington Reddish.

The higher species richness and breeding density of woodland edges, so

clearly demonstrated at Wistow, Billesdon Coplow and Botany Bay Fox Covert, is also evident at Loddington Reddish (Table 9.5). Species found in the edge, but not in the interior plots, were Turtle Dove, Mistle Thrush, Garden Warbler, Spotted Flycatcher, Nuthatch, Magpie, Jackdaw, Carrion Crow and Bullfinch. The spatial distribution of their territories in other study woodlands confirms many of them as being typical edge species (Table 9.1).

4) Vegetational Characteristics.

i) Interior to Edge Zone Relationships in the Study Woodlands.

The proportion of an edge zone to the total woodland area is determined primarily by patch size and shape. Later (in Chapters 10 and 11), it will be shown that other factors including the degree and aspect of slope, and the presence of rides and clearings, also exert an influence. This relationship is most conveniently described as an interior-to-edge ratio. First, in a large circular or square-shaped woodland (that is, an isodiametric shape, see Forman & Godron 1986), where the majority is interior zone, there is а high interior-to-edge ratio (Fig. 9.1). The ratio declines as patch size decreases until eventually a small patch functions entirely as an edge zone (Galli et al. 1976, Levenson 1981, Forman & Godron 1986). Secondly, an elongated patch has a lower ratio than a circular patch of equal area. If a patch becomes sufficiently narrow (say, approximately 30 m wide, as in a shelter belt) it becomes entirely edge zone independently of area. These principles are summarised diagrammatically in Figure 9.1 but are discussed in detail in Chapter 11.

The interior-to-edge relationships for the 16 study woodlands are expressed as percentages in Table 9.10. Woods at Wistow smaller than 0.2 ha are entirely edge zone. The edge zone accounts for nearly 86% of the total area of the 14 patches at Wistow but only approximately 24% at both Billesdon Coplow and Botany Bay Fox Covert. The presence of a clearing or broad ride within a woodland alters the configuration and the proportion of the edge zone. A small clearing exists in each of four Wistow patches (W7, W9 see Plate 4, W12, W14) and also in Billesdon Coplow. Consequently, the percentage of edge at both sites rises slightly (by approximately 2%, Table 9.10). However, the effect is more marked at Botany Bay Fox Covert where there are three clearings (Plate 15), in addition to a broad ride (Plate 16). Here, the proportion of edge zone is increased by about 9% to one-third of the total wooded area.

ii) The Vegetational Characteristics of the Edge Zone at Billesdon Coplow.

The spatial distribution of all asymmetrically-shaped trees at Billesdon Coplow, together with the mean angle of branch-orientation, is shown in Figure 8.2. The mean orientation of branching of all 'edge-trees' is compared with the mean perimeter aspect for each of the 6 woodland margins in Figure 9.2 (see also Fig. 2.2b for numbered margins). 'Edge-trees' were the outermost trees along all woodland margins and, except along the southern perimeter, none was recorded further than 7-10 m from the physical edge of the wood. Conversely, not all trees on the margins of the wood were 'edge-trees'; several examined along the NE-facing margin showed no signs of asymmetrical branching. The edge zone depth along the southern perimeter of the wood, however, was markedly greater than on the other margins. Where this perimeter is S-facing the edge zone averaged a depth of 39 m and varied from 20-51 m. Most, if not all, trees within the edge zone here were 'edge-trees'. Along the SW-facing margin a few scattered 'edge-trees' were recorded to a depth of about 40 m. The orientation of the branching of 'edge-trees' closely follows the mean woodland perimeter aspect, except on the NE-facing margin where they are rotated further from the mean than on other edges (presumably towards the light source).

One distinctive feature revealed at Billesdon Coplow, is the extent to which slope can enhance the effects of aspect in determining edge zone depth. Many asymmetrically-shaped trees were situated on the steep S- and SE-facing slopes of the hill and were found to a depth of 130-140 m. The branches of these trees were mainly orientated towards the SE.

CHAPTER 10

DISCUSSION

1) Factors influencing Bird Species Richness and Breeding Density in East Leicestershire Woodlands.

a) Woodland Area.

Many studies have suggested that area is the best predictor of bird species numbers in woodland patches (e.g. MacArthur 1971, Forman et al. 1976, Galli et al. 1976, Woolhouse 1983, Howe 1984, Lynch & Whigham 1984, Opdam et al. 1984, Askins et al. 1987, Ford 1987). This view is strongly supported by the species-area relationship that can be clearly demonstrated within the range of woodlands studied in East Leicestershire. Log-transformation of the data results in the linear relationship becoming statistically highly significant. However, it is the second largest study woodland, Billesdon Coplow (11.4 ha), which supports the highest species number (32). Nevertheless, this figure only slightly exceeds the 30 species recorded in the largest wood (Botany Bay, 14.9 ha). Ford (1987), in examining breeding bird populations of 20 Oxfordshire woodlands, recorded the maximum species number (35) in his largest woodland, 18 ha, thus obtaining results similar to those of this study. Excluding the smallest wood in the Leicestershire study which, at 0.01 ha, was too small to support complete breeding territories, all other woods smaller than 0.5 ha held between 13-18 species. These figures are identical to those recorded in Oxfordshire woods of the same size (Ford 1987). Moreover, there is a marked similarity in species number between medium-sized woods (0.5-2.5 ha) in this study and in all but 2 of the 12 patches examined in Oxfordshire. In East Leicestershire these woods supported 18-25 species whilst in Oxfordshire they held 16-26 species. In the two exceptions in Ford's (1987) study the woods held over 30 species, but he makes no special comment on these apparently high species numbers. In general, graphical plots between increasing woodland area and species number produce the familiar species-area curve (Appendix 7)(and, for example, Cain & Castro 1959). The effect of this asymptotic relationship is clearly demonstrated in East Leicestershire where woodlands smaller than 1 ha can support a total species number three-quarters of that found in the richest wood, some 12 times larger. Therefore, even very small patches should not be dismissed as unimportant for avian conservation.
In addition to area, a number of other factors have been suggested as offering a better or additional explanation for variation in bird species numbers in woodlands. These will now be discussed.

b) Habitat Heterogeneity.

Some workers have found that foliage height diversity (FHD), a measure of the complexity of principal vegetation profiles within a woodland, has an influence on bird species diversity (BSD). Studies in Scotland (Moss 1978), Finland (Tiainen et al. 1985) and the United States (MacArthur 1964, MacArthur & MacArthur 1961, MacArthur et al. 1962, Swift et al. 1984) have shown that BSD can be predicted accurately from the number and height of vegetation profiles. On coastal islands the variation in bird species number is mostly explained by the number (Reed 1983) or composition of habitats (Haila & Järvinen 1983). However, several other studies which examined total woodland species numbers found that FHD data made little or no contribution towards an explanation (Galli et al. 1976, Erdelen 1984, Howe 1984, Askins et al. 1987, Ford 1987, Møller 1987). It seems that habitat heterogeneity may have greater influence on species numbers within a single large woodland, rather than between woodlands (Moss 1978). Having examined for the effect of several vegetation variables on bird species richness, Ford (1987) concluded that only one, vegetation density between 1 and 2 m, partly accounted for the total bird numbers. The density of this vegetational layer, however, is inversely related to woodland area. Thus the higher bird density recorded in the smaller woodlands may result from the denser vegetational structure here.

The modified temperature regime, which characterises the woodland edge zone (Wales 1967, 1972, Swift & Knoerr 1973, Moen 1974, this study), encourages higher stem, shrub and tree densities, higher plant species numbers, and more propogule production (Ranney *et al.* 1981). This gives rise to a higher FHD which would, in turn, increase the availability of niches for feeding and nesting birds, leading to an increase in bird species number (Moss 1978).

Whilst no detailed examination of vegetation profiles was carried out for the East Leicestershire woodlands, careful observations, based on numerous field visits, suggest that the evidence for the influence of vegetational complexity on bird species richness remains inconclusive. For example, in the interior control plots of the larger woodlands, where extensive and apparently dense scrub layers of hawthorn, hazel and willow are found, bird species richness and density are relatively low. On the other hand, where scrub has developed in small clearings in some Wistow patches (e.g. W9, see Plate 4; W11 and W12), resulting from limited felling prior to the study period, there are high densities of warblers such as Whitethroat, Garden Warbler and Willow Warbler. However, these species are known to have feeding and nesting strategies which are closely associated with the scrub layer of woodlands.

c) Presence and Proportion of Edge Zone in Woodlands.

The influence of the edge zone on bird assemblages has been briefly reported on by Forman *et al.* (1976), Galli *et al.* (1976), MacClintock *et al.* (1977), Gates & Gysel (1978), Kroodsma (1982a, 1982b, 1984), Tiainen *et al.* (1985) and Ford (1987). Some of these researchers have provided a detailed examination of bird density patterns and species composition either in a single large wood or several fragmented woodlands but none has gone on to relate bird assemblages to the proportion of edge or interior zones.

This present study has demonstrated that edge zones are characterised by higher bird species richness and breeding densities. In larger woodlands, edges facing south, which receive higher direct solar radiation amounts between March-May, have significantly higher bird densities than adjacent core zones or north-facing edge zones.

A group of small fragmented woodlands, such as at Wistow, comprise nearly 90% edge zone. Thus, the characteristic edge zone densities are here evenly distributed across all the patches. Collectively, they can provide a species richness 20-30% higher, and a breeding density 50-80% higher, than single large woodlands of roughly equal area (as demonstrated when they are compared with Billesdon Coplow and Botany Bay Fox Covert respectively). Modified temperature patterns, found in just the relatively narrow edge zones of larger woodland patches, will be present throughout most or all of a small wood patch. As shown in Botany Bay Fox Covert and Owston Big Wood, edge zone characteristics can extend into the woodland interior zone if disturbances such as rides and clearings occur.

In Wisconsin (USA)($43^{\circ}N$), Ranney *et al.* (1981) found that edge zone depths were 10-15 m on N-, S- and E-facing edges but 30 m deep along W-facing margins. Until now, the values given by Ranney *et al.* (1981) have not been tested for higher latitudes or in Western Europe for their universality. However, the distribution of asymmetrically-branching trees at Billesdon Coplow showed the edge zone depth on NW-, NE-, SE- and SW-facing margins of this

wood to be between 7-10 m. Morever, the average edge zone depth on the south-facing margin is about 40 m but varies from about 20 to 50 m. A few scattered asymmetrically-shaped trees are also identifiable to a depth of 40 m from the SW-facing perimeter. Another noticeable effect on the spatial pattern of these asymmetrical trees results from increased direct solar radiation receipt on the steep S- and SE-facing slopes within the woodland interior. This indicates that slope can enhance the effects of aspect to strongly influence the depth of the woodland edge zone. On these slopes it extends about 130-140 m from the southern woodland margin and the woodland here has most trees with their branches generally orientated towards the south-east. This feature has not been reported previously in the literature. It has clear implications for the interior-to-edge ratios of large woodlands which, to date, have been based on sites in flat landscapes (see, e.g., Levenson 1981, Forman & Godron 1986). Usually, such a site would have narrower edge zones than if the same wood occurred on a steep south-facing slope.

An example of the application of this new information might be in the selection of woodland so as to enhance the breeding and conservation of certain avian species. For example, in our uplands quite often the only remaining fragments of natural and semi-natural wood are those confined to the very steepest slopes, where past grazing and felling activities have been limited (e.g. Wistman's Wood). If a choice has to be made between upland woodland fragments as to which ones should be preserved for avian conservation purposes then those with a southerly aspect should be selected, other things being equal. For instance, the Pied Flycatcher is an uncommon summer visitor whose British breeding range is centred predominantly on sessile oak woodlands in Wales. In Rheidol Valley (central Wales), oakwoods occur on both the steep the south-facing and north-facing slopes where the valley has an E-W orientation. Based on the findings at Billesdon Coplow, it is reasonable to speculate that birds of this (and other) species breeding in the south-facing woods do so considerably earlier and have larger clutches than those nesting in woods on the opposite north-facing valley side. The former woods would be mainly composed of edge zone, whilst the latter possess a relatively much narrower edge zone.

d) Woodland Isolation.

The isolation of a wood from neighbouring patches, and particularly from large tracts (which might act as a source of potential colonists), has been advanced as another factor which influences the total species richness of woodlands. This relationship has been demonstrated both in the Netherlands

(52°N)(Opdam *et al.* 1984) and in Maryland (USA) (39°N)(MacClintock *et al.* 1977). Further studies in Maryland by Lynch & Whigham (1984) also found that isolation accounts for some of the variation in the numbers of migratory, interior woodland bird species only. More recently, Askins *et al.* (1987) claimed that isolation was the best predictor of density and numbers of interior species in large woodlands in Connecticut (USA)(42°N). However, other studies of woodland avifauna in North America (Howe 1984), Australia (Howe 1984) and England (Ford 1987), and of the avifauna of farmstead habitat patches in Denmark (Moller 1987), all conclude that isolation has no, or very little, influence on species richness.

Isolation indices, connectivity values, patch density (within a 2 km radius) and inter-patch distances between the study woodlands and neighbouring patches are presented in Table 10.1. The evidence provided from this study indicates that there is a weak inverse relationship between woodland isolation, patch density and species richness (Table 10.2). The majority of species in East Leicestershire woodlands have territories confined to single patches. However, in the Wistow woods some 30 territories, affecting 15 different species, were mapped as extending from one patch into an adjacent wood. But this represents only about 12% of the total territories recorded at Wistow.

Further, the inter-patch distances involved in these cases did not exceed more than 20-30 m, (e.g. W3 to W4, W7 to W8, W10 to W11, W12 to W14). Only two species, Great Spotted Woodpecker and Mistle Thrush, had territories that extended beyond one patch to another for greater distances than these (up to about 200 m). Clearly, these are exceptions to the general pattern for East Leicestershire where most species utilise only one wood for their requirements. For this majority their presence in a particular wood, and their breeding ecology, cannot be explained in terms of the nearness of neighbouring woods.

Summary.

Therefore, although woodland area clearly influences bird species richness, with a positive relationship between the two, the matter is more complex than this would suggest. A group of small woodland patches can hold a much higher species number and breeding density than when the equivalent area is concentrated into one large single woodland.

An explanation for this must lie in the greater proportion of edge zone

that occurs when the total woodland area is made up of several smaller patches. This edge zone will be characterised by a different microclimate with a temperature regime which improves breeding success and heightens species richness and density. This appears to be caused by greater vegetational diversity here which will improve opportunities for feeding and nesting.

Whether woodland is concentrated into a few large tracts or occurs as fragmented small patches, the isolation factor also has to be considered. However, in East Leicestershire most woodlands are seldom more than 1-2 km from a neighbouring patch and connectivity by means of hedgerows is still good (see Chapter 2). Consequently, for most species the isolation factor is probably negligible.

2) The Incidence of Bird Species within the Study Woodlands.

A comparison of the incidence of selected species in woodlands of East Leicestershire with data from Oxfordshire (Ford 1987) and from the considerably larger sample drawn from all parts of Britain by Moore & Hooper (1975) is presented in Table 10.3. In general, most species in East Leicestershire woodlands exhibit an incidence which follows more closely Ford's (1987) data than the national pattern. However, three species in my study show marked differences in their incidence with Ford's (1987) findings. Chiffchaff and Marsh Tit in Leicestershire were confined to woodlands greater than 10.0 ha, as was the tendency nationally. They both had a widespread distribution in Oxfordshire woods, including some smaller than 1 ha. Ford (1987) made comment about the relative scarcity of Song Thrush from his sites, but it was present in over half of the East Leicestershire woodlands of various sizes.

Further attention will now be directed towards three groups of bird species that exhibit a particular incidence in East Leicestershire woodlands worthy of some emphasis. These are (a) ubiquitous, (b) edge, and (c) interior species.

a) Ubiquitous Species.

There are a total of 17 ubiquitous species within the woodlands surveyed in East Leicestershire (Group A). Ford (1987) observed all but four^l of these

¹The four species not observed were Song Thrush, Garden Warbler, Spotted Flycatcher and Treecreeper.

species across a similar range of wooded islands (0.3-18.0 ha) in Oxfordshire. However, he classified only 9 species as being ubiquitous but each occurs in the Leicestershire group. Those species in Group A, the ubiquitous species, can be subdivided on the basis of whether they are found in the smallest wood studied (0.01 ha) in East Leicestershire (Group A1) or not (Group A2). It can be further shown that all Group A1 species have territories that extend beyond the margin of this smallest wood into neighbouring non-wooded habitats. Thus these species emerge as being not confined exclusively to arboreal habitats.

It is interesting to note that Moore & Hooper (1975) list a total of 15 species found in woods of 0.01 ha or less (*sic*). This list includes all but one species placed in Group A1 in East Leicestershire. Moore & Hooper (1975) do not comment on the territorial ranges of these birds, but, based on the data from East Leicestershire, it can be concluded that their list is essentially one of species not strictly confined to woodland habitats rather than one of true arboreal species; a distinction that they do not make.

b) Edge Zone Species.

The study of fragmented woods in New Jersey (USA) by Galli *et al.* (1976), suggests that woodlands smaller than 0.2 ha are composed entirely of edge zone. They concluded that the total avifauna of these small woodlands could be designated 'edge species' - that is, species that would be located mainly or entirely within the edge zone of larger woods.

The woodlands at Wistow smaller than 0.2 ha would fall into this category. However, the data from East Leicestershire suggests that this approach is too simplistic. A distinction can be drawn between true edge species and those species which merely utilise the edge zone in some situations but are less restricted when adjacent non-edge woodland zones are also available. These two categories can be separated by the use of two complementary methods that identify the true edge species.

In the first method the linear relationship between the log of woodland area and the number of breeding pairs is calculated for each species with a high incidence. Those which possess a high correlation coefficient breed as widely in the interior zone as within the edge zone of large woodlands (Table 9.8). As the number of breeding pairs is closely dependent on woodland area these species can be described as size-dependent and they are not true edge species. Those species which exhibit a weak linear relationship between patch

size and total number of pairs are termed size-independent species and are the true edge species in East Leicestershire.

The second method is based on mapping the spatial pattern of individual species' territories and this is used to verify the identifications resulting from the first method.

When these two methods are employed for the ubiquitous species² they reveal that the true edge species are:

Song Thrush, Garden Warbler, Willow Warbler, Spotted Flycatcher and Treecreeper;

and the non-true edge species are:

Wren, Dunnock, Robin, Blackbird, Blackcap, Blue Tit, Great Tit, Chaffinch, Bullfinch.

It was not possible to obtain correlation coefficients by these methods for all species recorded at Wistow because, in some cases, too few data were available. However, when this arose some progress towards a proper classification could still be made by reference to the territorial spatial patterns of the birds concerned. This approach suggests that the following species found in the edge control plots, but not the interior control plots at Loddington Reddish (Table 9.5), and also through a wide range of woodlands (including those of 10 ha or more), may also be true edge species:

Green Woodpecker, Great Spotted Woodpecker, Mistle Thrush, Long-tailed Tit, Nuthatch and Greenfinch;

as may the following species, recorded almost entirely in woodlands of 0.5-2.5 ha:

Lesser Whitethroat, Whitethroat, Goldfinch, Redpoll, Yellowhammer and Reed Bunting.

From the preceding evidence there are 5 species in East Leicestershire woodlands which are indisputably edge species and, based on less firm evidence, a further 12 species probably fall within this category. None of these 17 species were identified as ubiquitous in the Oxfordshire woods by Ford (1987)

²Excluding Stock Dove, Woodpigeon and Starling for which territories were not counted.

but four were described as 'species influenced by area'. By this he meant species whose numbers in each wood were controlled by area. The four species were Great Spotted Woodpecker, Song Thrush, Nuthatch and Treecreeper. The placing of these 4 species in such a category suggests they are not necessarily edge species as they are in Leicestershire.

Of the remaining 13 species in the Leicestershire survey also recorded in Oxfordshire, Ford (1987) described 8 as 'species not influenced by area' and 3 as 'transients'. Those in the first category are species whose numbers are not determined by increasing woodland area. The birds concerned are Green Woodpecker, Mistle Thrush, Garden Warbler, Willow Warbler. Spotted Flycatcher, Long-tailed Tit, Greenfinch and Yellowhammer. In Leicestershire they have been defined as edge species and the evidence from Oxfordshire appears to confirm this classification.

The 'transient' category used by Ford (1987) reflects that his field visits were of generally limited duration, particularly in the larger woods. For instance, he spent only 4 hours surveying the avifauna of his largest wood (18 ha) compared with a total time of 17 hours I spent in Billesdon Coplow (11.7 ha). Species recorded by him on fewer than half of his 5 visits were regarded as 'transients'. These 'transients' were Whitethroat, Goldfinch and Redpoll. All three species are common or fairly common summer visitors. Their presence during the main breeding period for these birds strongly supports the idea that they were in fact territorial and not transient. Furthermore, examination of the different woodland sizes in which they were found in Oxfordshire, leads to the conclusion that they too are 'species not influenced by area', that is, edge species. Two probable edge species in Leicestershire, Lesser Whitethroat and Reed Bunting, were not recorded in Oxfordshire, and consequently no comparison can be offered.

Thus there are some small discrepancies between the findings from East Leicestershire and those from Oxfordshire. Part of the explanation for this probably lies in the fact that Ford spent far less time in the field and admits to problems of identification with some species.

Woodland fragmentation will favour the establishment of both the true and non-true edge species listed above. Indeed, certain species, such as Lesser Whitethroat, Whitethroat, Goldfinch, Redpoll, Yellowhammer and Reed Bunting depend entirely on fragmented wooded landscapes for their breeding.

c) Interior Zone Species.

There is an inverse relationship between woodland area and breeding bird density. This pattern is explained by the relative proportions of interior and edge zones within woodlands. As woodlands become larger the proportion of interior zone also increases. The low breeding density and low species richness of core areas in larger woods is clearly demonstrated in the interior control plots at Loddington Reddish and Owston Big Wood. The total species number recorded in each 4 ha control plot is between 15-19. These totals are approximately equal to that found in a single woodland patch whose area is only one-eighth that of the control plot. Although the control plots examined by Ford (1987) were smaller than in my study (range 0.5-2.0 ha), he also recorded between 11-19 species in each. This suggests that the species-area curve for interior plots is less steep than for smaller fragmented patches (Ford 1987) and few species are added as interior plot size increases from 2.0 to 4.0 ha. Both studies clearly demonstrate the low species numbers which are characteristic of interior zones. The total number of species in the six Leicestershire control plots is 27, compared to a total of 31 species observed in the Oxfordshire survey.

From this list of 27 species, there are just three birds that, having territories confined to the interior zone of woods greater than 10 ha, can be confidently classified as interior species in East Leicestershire woodlands. These are Chiffchaff, Marsh Tit and Jay. Coal Tit is also found only in these larger woods. However, its presence is more likely to be explained by the higher tree species richness in larger woods, including conifers which it prefers (Perrins 1979), rather than by woodland area alone.

The similarity of the composition of interior zone avifaunas between East Leicestershire and Oxfordshire woods is very marked. All but 3^3 of the 27 species which I recorded in my interior control plots were observed by Ford (1987) in his Oxfordshire control sites. On the other hand, I recorded all but 7^4 species of his interior avifauna, but it is possible to readily account for the

³The 3 species absent from Ford's (1987) interior plots were Green Woodpecker, Willow Tit and Jay.

⁴The 7 species absent from East Leicestershire interior control plots were Sparrowhawk, Mistle Thrush, Nuthatch, Jackdaw, Rook, Carrion Crow and Starling.

absence of these species from East Leicestershire woodlands.

In Leicestershire, both the Rook and Carrion Crow are subject to some measure of control in many woodlands through game-keepering practices; the Jackdaw is entirely dependent on the presence of fairly large natural nest-holes which only tend to occur in mature trees with large bole sizes and such trees were frequently absent from the study woodlands; the Starling is now more closely associated with woodland fringes and areas of human habitation in rural environments in the county; the Sparrowhawk, which is, as yet, very thinly distributed in this area (*Breeding Bird Atlas of Leicestershire and Rutland*, Warrilow, in prep.); Nuthatch and Mistle Thrush are found only in edge zones of Leicestershire woodlands.

Thus in considering the conservation value of large woodlands in lowland Britain where the core area is dominant, it should be noted that, in the total interior woodland area of 24 ha surveyed in Leicestershire, the species richness is just 27. This is about two-thirds the total species richness recorded in just 8.8 ha of fragmented woodland at Wistow. Clearly, the mean breeding density of interior woodland zones is markedly lower (7.0 prs ha⁻¹ in the 6 interior plots) than small fragmented woods such as at Wistow (27 prs ha⁻¹).

3) Minimum area Requirements.

In terms of minimum area requirements three categories of birds can be recognised in the East Leicestershire woodlands. First, approximately half the species recorded breed in patches as small as 0.2 ha.

Secondly, there are those species that require somewhat larger territories which will only occur in larger woods or in wooded areas characterised by small inter-patch distances, as at Wistow. In this category are Green Woodpecker, Great Spotted Woodpecker, Mistle Thrush, Nuthatch, Greenfinch and Redpoll and empirical evidence suggests that the minimum area requirement is at least 0.7 ha. This figure is supported by the results of other studies though the minimum area requirement appears to vary across Britain (Moore & Hooper 1975, Ford 1987).

Some species, whilst not found in the very smallest woods in East Leicestershire, do not occur in woods >2.5 ha. In this group are Lesser Whitethroat, Whitethroat, Goldfinch, Redpoll, Yellowhammer and Reed Bunting. This finding conflicts with that of Fuller (1982). He reported that there are no

British bird species more often present in smaller woods (<10 ha) than in large woods (>80 ha). Though this may be the case for Britain as a whole it is not the case in East Leicestershire, neither is it so for Oxfordshire (Ford 1987).

Thirdly, the interior species usually have the largest minimum area requirement. For example, in North America, Askins et al. (1987) have shown this to be as high as 187 ha for some species. In Britain, Moore & Hooper (1975) claim that the requirement for our interior species does not exceed 20 ha. Typical interior species in East Leicestershire are Chiffchaff, Marsh Tit and Jay and their minimum area requirements are apparently met in Billesdon Coplow (11.4 ha), Botany Bay Fox Covert (14.9 ha), Loddington Reddish (36.2 ha) and Owston Big Wood (110.7 ha). When planning general conservation strategies it would therefore seem necessary to identify those bird species which these high specific area requirements. For East Leicestershire, the data have suggests that some reserves should be at least 10 ha in area if interior species are to be preserved. Of course, woods larger than this size will tend to hold more pairs of these interior species and this will help further to ensure their survival.

From the above, it is possible to arrange the bird species of East Leicestershire woodlands in a broad order based on their susceptibility to woodland fragmentation.

Quite clearly, British birds with their lower area requirements will be more tolerant of woodland fragmentation than is the case in North America. There is also some evidence to suggest that certain bird species common to Britain and mainland Europe have higher minimum woodland size requirements in the latter area (Opdam *et al.* 1985). In these cases, the same species will have less tolerance to any subsequent further woodland fragmentation in mainland Europe than in Britain.

A possible explanation of these differences is that the wholesale destruction of forests in Britain occurred so many centuries ago that woodland bird populations have undergone a sufficiently protracted period of relaxation to reach a lower equilibrium level and have become adjusted to the much smaller fragments of forest that remain in this country. In contrast, forest clearance in North America is much more recent and large tracts still remain. Likewise, though to a lesser extent, many areas of mainland Europe (e.g. France, West Germany) still retain a much higher percentage of forest cover than Britain, often concentrated in large blocks or tracts. Thus North American woodland avifauna may still be undergoing a period of relaxation and many still require considerably larger continuous tracts than do British woodland species. Similar reasoning may also explain why many 'big forest' species (Ford 1987) are present in continental Europe but are absent from Britain.

CHAPTER 11.

GENERAL DISCUSSION.

Certain topics, which the findings of the previous chapters have suggested, will now be discussed.

WOODLAND NATURE RESERVE DESIGN.

1) Evaluation Criteria for Assessing the Conservation Potential of Individual Reserves.

Introduction.

In order to provide a context within which to examine the conservation value of woodlands for breeding birds in East Leicestershire a brief review of the literature on the criteria for assessing the conservation potential of habitats is now presented.

The criteria used in the evaluation of nature reserves for conservation purposes may be classified into three groups (Kent & Smart 1981):

- a) The most widespread method adopts an evaluation technique where values are applied to individual criteria such as species richness, species diversity, habitat size and rarity (see e.g., Gehlbach 1975, Ratcliffe 1977, Van der Ploeg & Vlijm 1978, Goldsmith 1987, Margules et al. 1988; see also reviews by Wright 1977, Margules & Usher 1981). These values can be measured directly, or by estimation, (Margules & Usher 1981) and are termed ecological criteria (Goldsmith 1975, 1983). Some other criteria, being more difficult to measure or quantify, are based more on value judgements and are described as conservation criteria (Van der Ploeg & Vlijm 1978, Goldsmith 1983). These include potential value, naturalness, representativeness and recorded history.
- b) Another method evaluates the conservation potential of the fauna or flora of a site by using 'indicator species'. These are a selection of less common species which are considered to account for a large proportion of the 'conservation value' of the flora or fauna

of a site (Peterken 1974, Helliwell 1978). However, this technique tends to emphasise the importance of species rarity, particularly for the few habitats where this method is used, and seldom has a wider or more general use in landscape appraisal (Kent & Smart 1981).

c) The ecological and habitat characteristics of a range of sites within a region are measured by the inventory technique which permits an objective comparison to be made between the sites (Kent & Smart 1981). The criteria adopted for this method include some of the ecological and conservation criteria listed in (a) above.

However, of the three approaches presented here, that of the evaluation method, (a), appears most appropriate for further, more detailed examination in the light of the Leicestershire study, where total bird populations of a range of similar wooded habitats are under study and where quantitative data on species numbers (richness and diversity) and habitat characteristics are available.

Evaluation Criteria.

In the Nature Conservation Review, Ratcliffe (1977) lists the following 10 site criteria for assessment: size: diversity; naturalness, rarity; fragility; typicalness; recorded history; position in an ecological/geographical unit; potential value; and intrinsic value. Many other studies have examined similar criteria. For instance, Tubbs & Blackwood (1971) developed a method for evaluating land in Hampshire particularly in terms of species rarity and diversity of three habitats namely, agricultural land, plantation woodland and unsown vegetation. Goldsmith (1975) considered 6 habitats in Herefordshire each of which was assessed for area, species rarity and richness. Later, in a study of forest reserves in Canada, Goldsmith (1987) ranked in decreasing order of importance the following criteria: plant species number; number of rarities; and area. Gehlbach (1975), on the other hand, defined criteria such as human impact, community representation (that is, commonness and diversity) species significance and educational utility. The few studies cited above demonstrate the point made by Van der Ploeg & Vlijm (1978) that the variation in evaluation criteria found between one study and another reflects the uncertainty of the suitability of criteria for ecological evaluation and the lack of agreement on those of highest priority.

Because of this lack of universal agreement in ranking the principal assessment criteria for conservation potential, no single hierarchy of criteria

exists. However, some progress towards identifying a small group of the most frequently used criteria is possible by examining the results of two reviews in particular. These were conducted by Wright (1977) and Margules & Usher (1981) who investigated a total of 7 and 9 studies respectively. Of these studies, 5 were common to both reviews. Thus, the range of criteria from a total of 11 studies were examined. Their results reveal that the most highly used are species richness or diversity, habitat size or diversity, rarity and naturalness; educational value, threat of human interference and typicalness being only slightly less important. Some criteria, such as availability, recorded history and scientific value, were employed in very few studies. Further support for species richness and area having priority as assessment criteria comes from several other key studies (e.g. Helliwell 1976, Peterken 1981, Goldsmith 1983, 1987, Game & Peterken 1984).

These 'favoured' criteria will now be examined in more detail. Emphasis will be given to those which have a particular relevance in the context of the East Leicestershire findings. It follows that some criteria, which have little relevance to this study, will receive a briefer treatment, e.g. rarity, naturalness.

i) Rarity.

Undoubtedly, the rarity value of certain species generates more interest and results in the provision of more conservation resources, than is the case with common or widespread species. Many members of the general public perceive that the principal function of conservation is to protect rare species (Margules & Usher 1981). This view may be demonstrated by reference to two activities of the Royal Society for the Protection of Birds (RSPB). First, each year many wardens are employed specifically to protect the nest-sites of rare species, especially the large raptors, e.g. Goshawk, Montagu's Harrier, Osprey, Golden Eagle and Peregrine, which arouse much public interest. Increased disturbance by the public, including the unintentional intrusion by hillwalkers or climbers, increased vulnerability through damage to, or loss of, their habitat and the real threat posed by egg-collectors are among the complex problems encountered these species particularly vulnerable. which make Secondly, the RSPB has acquired large tracts of semi-natural habitat that are under pressure from agricultural practices which would lead ultimately to the loss of less common avian species. An illustration of this is the conservation of lowland heath in Dorset primarily to protect a large proportion of the breeding sites of the Dartford Warbler. The British population of this species is estimated at only about 420 pairs (Robins & Bibby 1985) and is confined to the heathlands of

Hampshire, Surrey and Dorset. The conservation of the Dorset habitat by the RSPB is primarily to protect this warbler but it also has the desirable benefit of protecting other flora and fauna indigenous to this ecosystem. However, when viewed in a European context, the Dartford Warbler has a widespread distribution throughout western France and the Mediterranean Basin. Its total population is unknown but some measure of its abundance is provided by the fact that in part of Languedoc (France) alone, where much suitable scrub habitat exists, the numbers are estimated at 12,000 pairs (Yeatman 1976). Therefore, as Margules & Usher (1981) point out, rarity varies with scale. It may be viewed at a local, regional, national or international scale.

In terms of the breeding avifauna of Leicestershire there is only one species, the Black-necked Grebe, which can be classified as a rarity at the national level. However, this bird breeds at a single reservoir site outside the general study area and as such forms no part of this discussion.

However, there are a number of locally rare woodland species which breed in neighbouring woods in East Leicestershire but are absent from the study woodlands. These include the Redstart, Tree Pipit and Nightingale.

Their absence from the study woodlands could be offered as a challenge to the conservation potential of these sites. The presence of these three species would certainly help to diversify the avifauna further and provide more public interest. However, even if one or more of these particular species were present in the woodland sites under investigation it does not follow that their presence could be guaranteed to continue. Their population numbers can fluctuate each season and may drop to zero in specific woods. Further, these species often have requirements for precise vegetation structures within a woodland which may disappear with successional changes. This can make their survival even more uncertain. Therefore concentration on rarity as a criterion can have its drawbacks and limitations. This is well illustrated in East Leicestershire and would also apply to many other lowland woodland areas of similar form and history.

Furthermore, rarity can conflict with typicalness, another criterion for assessing reserve potential. This attempts to include species or communities which are representative or typical of a region. This may form a more rational strategy when considering a woodland conservation policy in an area such as East Leicestershire which has few truly rare avian species.

ii) Naturalness.

Naturalness is used as a criterion to suggest a habitat in its original or near-original state. It is unlikely that there are any true natural habitats remaining in Britain owing to the protracted process of landscape modification which has taken place. Nevertheless, near-natural and semi-natural habitats are many and are usually taken to mean only slightly modified. Semi-natural woodlands, for instance, are those which should receive the highest priority for conservation as they are controlled by natural factors (Peterken 1983). Moreover, these woodlands have higher species richness, more rare species and act as potential species reservoirs (Peterken 1983). But even these woodlands must owe some of their present characteristics to methods such as coppicing and grazing applied since before the Middle Ages.

Naturalness is afforded a high priority by Ratcliffe (1977) in the Nature Conservation Review, following only area and diversity in importance. It is also highly valued by other workers, e.g. Tubbs & Blackwood (1971), Gehlbach (1975) and Everett (1978).

Further, it can only be evaluated through comparison of a site with its surrounding region. In East Leicestershire, where the environment has been modified and controlled by man's activities for centuries, the concept of naturalness hardly applies. This must be the case for most other woodlands in lowland England that are available for actual or potential conservation of avian species. However, Owston Big Wood is a woodland type whose conservation Peterken (1983) strongly advocates since it is less modified by human activities and more controlled by natural factors than most other lowland examples. Further, they have richer communities than more recent woodlands and possess a higher proportion of rare or vulnerable species (Peterken 1983). Certainly, documentation of Owston Wood's flora and fauna show the site to possess rich wildlife communities (Candlish 1977, Jeeves 1985). So perhaps, even though much of Owston Big Wood is not very natural it is still worth conserving on the basis of its few remaining near-natural areas.

It is clear that rarity and naturalness are criteria used for special situations and are not usually of much value for the majority of English lowland sites. Given the strong limitations of these criteria others are sought which are applicable to any site, e.g. area, species numbers and diversity, habitat diversity. These criteria will now be examined.

iii) Area, Species Number and Habitat Diversity.

The relationship between habitat extent and avian species richness is well established, having been demonstrated in many studies including this Leicestershire survey. A large woodland holds more species than a smaller patch. Furthermore, studies which have sought to use the Island Biogeography Theory as a guide in conservation practice have, at least by implication, stressed that maximising the species number is the single most desirable aim. This, it is stressed, is achieved through preserving the largest possible reserve where immigration rates would be high and extinction rates low (e.g. Wilson & Willis 1975, Diamond 1975, May 1975, Diamond & May 1976).

A counter-proposal which followed, argued that a higher species richness could be achieved through two small reserves of equivalent total area, owing to the proportional share of species in each reserve. Detailed empirical evidence from this Leicestershire study has clearly established that small isolated woods support more avian species than an equal area of larger woodland. This finding is in agreement with Ford (1987) and it confirms the more tentative suggestions along these lines by such workers as Helliwell (1976) and Higgs & Usher (1980). This leads to the recommendation that a large number of woodlands per unit area should be preserved in order to conserve maximum species richness (Forman *et al.* 1976, Howe 1984, Lynch & Whigham 1984, Opdam *et al.* 1984, 1985, Møller 1987).

Area, species number and habitat diversity are considered further in the context of the topic which follows.

2) Which is the Optimum Strategy for Conserving Maximum Avian Species Richness in East Leicestershire Woodlands?

Having reviewed the criteria used in the selection of individual sites as nature reserves, attention is now given to the problem of finding the optimum strategy for conserving maximum avian species richness on a regional basis.

To maximise avian species richness in woodlands there are three main strategies which may be considered. These are:

- i) preserve the largest single woodland available;
- ii) preserve a group of closely clustered small fragmented woodlands;

iii) preserve a wide range of woodlands with several small fragmented patches and at least one larger woodland of 10 ha or more.

i) A Single Large Woodland?

Moore & Hooper (1975) recommend that woodlands should be 100 ha or more in order to maximise bird species richness. Owston Big Wood complies with this size recommendation and is the largest semi-natural wood in the region. Since the species-area relationship has been clearly demonstrated for the East Leicestershire woodlands it follows that Owston Big Wood is a suitable site should the single large woodland strategy be followed.

Based on data available from this study, another avian woodland census in East Leicestershire (Jeeves, pers comm), and from extensive field visits made between 1976-84 by the author in conjunction with survey work for the *Breeding Bird Atlas of Leicestershire and Rutland* (Warrilow, in prep), it is possible to make a realistic estimate of the total avian species number for a wood in East Leicestershire of the size and form of Owston Big Wood; this is 41 species.

Briefly, this figure was obtained in the following way. First, the total species richness of the 4 interior plots (covering a total area of 16 ha) was 24 species. Secondly, as this study has clearly demonstrated, interior zone avifaunas are not representative of the total woodland area; the avifauna of the edge zones will possess a different species composition. Therefore, to identify the species most likely to be breeding elsewhere in Owston Big Wood, it is necessary to examine precise data collected from the other large East Leicestershire woodlands and, in particular, their edge zone avifaunas. Adopting this method, a further 13 species, present in Billesdon Coplow, Botany Bay Fox Covert and the edge plots of Loddington Reddish, but absent from the interior zone of Owston Big Wood, can be identified. In general terms, field visits over a 15-year period to Owston Big Wood have confirmed their presence in this wood. Thirdly, in another large (16.5 ha) East Leicestershire mixed deciduous woodland (Great Merrible Wood), Jeeves (pers comm) recorded 35 and 36 breeding species in 1985 and 1986 respectively. Examination of the species compositions there show a very close similarity to those obtained in my study. However, he did record a further 4 species which remained undetected throughout my woodlands. These were Mallard, Woodcock, Tawny Owl and Rook; the absence of three of which in the study woodlands has been explained previously (see pp.8.3, 10.11).

Thus a realistic assessment of the total species number in the 110 ha wood at Owston or in woods of a similar size in the East Midlands is about 41 species. This figure is little different from that of 39 species achieved in just 8.8 ha of fragmented woods at Wistow. Nevertheless, such an alternative offered by these smaller woods for avian conservation would lack true interior species.

In addition to maximising the overall species richness, a wood such as Owston Big Wood will also possess more pairs of interior species than a smaller wood. Thus populations of Marsh Tit, Chiffchaff and Jay will be greater here than in other woods in East Leicestershire.

In addition to the number of birds present in a reserve several other factors of have to be considered when selecting a strategy for conservation.

First, preservation of the single large woodland has a further advantage in being more easily perceived by the general public as a nature reserve than would a series of small, fragmented patches. Moreover, the increased habitat diversity within a single large wood should provide greater intrinsic interest to visitors.

Secondly, a conservation management policy for the single large site would be more easily implemented and administered by a warden than for a series of small fragmented woods. Further, the purchase or leasing of the wood from an existing land-owner should also present fewer problems than would be the case for several fragmented patches acquired from a number of owners.

Owston Big Wood possesses a very high interior to edge ratio and consequently low breeding densities, which characterise interior zones, will be a feature of the total avifauna. Most species present in this core zone will be interior or area-dependent species, and the total number actually represents less than half the potential species pool of East Leicestershire woodlands. The low breeding density could lead to lower survivorship and greater extinction rates for the interior species. It may also be true that the virtual absence of rides over much of the site would further depress these density figures. Edge species and higher breeding densities would be limited to the perimeter of the wood and possibly along the very few rides, which collectively represent a very small proportion of the total woodland area.

Implicit in the strategy of preserving the maximum species number in a

habitat is that all species are equally desirable. But some species may be 'unwelcome' in that they do damage to the other species present by their predatory or other activities. Examples of 'unwelcome' species include mammals such as mink, coypu and grey squirrel, each of which can be highly destructive of other species in the native ecosystem. Although disturbances in woodland such as thinning or felling should lead to colonisation by new avian species it is less easy to identify any woodland birds which would be classified as 'unwelcome'. Predators such as Sparrowhawk and Carrion Crow will have no greater impact here on other breeding birds than in agricultural habitats elsewhere. It is true, however, that colonisation may not be necessarily by truly arboreal species, but instead scrub or ground-nesting species could come in. Whether such non-woodland avian species should be encouraged within a woodland conservation strategy is open to question. Therefore, total species number may not, by itself, be the best measure for assessing a potential reserve.

ii) Several Small Woodlands?

As described above, realistic estimates suggest that around 41 avian species may be breeding in the 110 ha of Owston Big Wood. On the other hand, the 8.8 ha of fragmented woods at Wistow are known to support a total richness of 39 species. Average breeding densities in these small fragmented woods are approximately 4 times greater than in the interior plots of Owston Big Wood and Loddington Reddish. The species composition of the Wistow patches includes a total of 17 species confirmed as edge species and these are found spread throughout these woods. Clearly, these would be present in only a very limited peripheral part of a large wood.

The spatial pattern of fragmented plots would assist colonisation rates through the improved inter-patch connectivity. Such woodland patches are described as stepping-stones (MacArthur & Wilson 1967) whilst their linear shape acts as a strip corridor (Forman & Godron 1986), assisting in movement of species across the landscape.

Small patches are characterised by a microclimate similar to that found restricted to edge zones within large woodlands. This results in a higher habitat diversity across many small patches when compared with a single extensive woodland.

However, small woodlands have a limited proportion of interior zone, and

in the case of the Wistow Woods this amounts to only some 12% of the total area. It follows that the interior avifauna will not be represented, or will be under-represented. For example, species requiring large minimum areas for breeding, such as woodpeckers, are less likely to be present in such habitat patches. However, short inter-patch distances could assist the establishment of such species in a cluster of small woodlands.

Unlike the single large woodland, practical conservation management strategy would be more difficult to execute efficiently in a group of woods such as Wistow. Many problems could be anticipated with the general public, for example, that of access to all the patches or that of perception of such small patches as a genuine nature reserve. However, these problems could be overcome, or at least reduced, if the woodland patches were preserved as part of the total landscape matrix. It might be more ecologically sound to preserve the entire landscape within the Wistow Estates to maximise habitat diversity. This would ensure that, in addition to the woodland remnants, farmland with its hedgerows, water courses and parkland would be preserved to provide a more representative example of the lowland landscape. It is clear that the 39 avian species recorded in the woodlands would be augmented by many additional species present in the other non-wooded habitats neighbouring the patches. Fieldwork conducted throughout the Wistow Estates by this author for the Breeding Bird Atlas of Leicestershire and Rutland resulted in a further 33 species being confirmed as breeding in the varied non-wooded habitats here.

If the prime function of a conservation strategy is to maximise species richness, this study clearly shows that the preservation of several small woodlands with small inter-patch distances should be considered as a more suitable alternative than a single large woodland of equivalent area. The suitability of such a scheme would be enhanced if these small woodlands could be preserved together with their surrounding landscape matrix.

iii) A Combined Strategy?

The problems which characterise the conservation either of a single large woodland or several small patches may be largely overcome by creating a strategy that attempts to combine both. The case can be illustrated by reference to the Wistow Woods in conjunction with Billesdon Coplow, although these woods are not geographically close in the context of East Leicestershire. Since some interior species breed only in the core area of larger woods this conservation strategy should aim to preserve at least one wood over 10.0 ha to support these interior species. Unlike the actual distribution pattern of the woods under examination, for best results this larger wood should be adjacent to, or placed within, the group of fragmented patches.

The East Leicestershire study shows that a range of just 8 woodlands (W3, W4, W7-W9, W12, W14 and Billesdon Coplow), each over 0.5 ha and totalling 18.5 ha, would support a total of 44 species. Moore & Hooper (1975) believe that "only a very few common species are as likely to occur in a 10 ha wood as in one of 100 ha" (p.249). However, when their data for woods of 100ha or over are compared with the species composition of the 8 Leicestershire woodlands listed above, it reveals that only an additional 5 species were present in the Moore & Hooper (1975) nationwide survey. Furthermore, contrary to their findings, none of these species is confined to the few woodlands over 100 ha in Leicestershire (pers. obs.). Data from East Leicestershire provide no support for their conclusion that only woodlands exceeding 100 ha should be considered as worthy of conservation when viewed in the context of lowland England.

iv) Woodland Shape.

The proposal that woodland area alone controls bird species richness and breeding density is too simple an approach. Woodland shape and its influence on the relative proportions of interior and edge zones must also be investigated.

Compared with a rectangular shaped wood of the same area, a circular wood has a smaller proportion of edge zone. This is clearly demonstrated in Figure 11.1 where the depth of the edge zone adopted to demonstrate this principle has been fixed at 15 m irrespective of aspect. In a 50 ha circular-shaped wood the ratio of interior to edge zone is approximately 12:1. A rectangular wood of the same area, but whose length is twice that of the width, has a slightly greater proportion of edge zone than this circular shape. doubling of the length of a rectangular With each wood there is a corresponding decline in the interior to edge ratio of approximately 20%. Thus a 50 ha woodland with a length to breadth ratio of 128:1 would have a width of approximately 62 m (and could be viewed as a long shelter belt). Such a wood has almost 25 ha of both interior and edge zones. The importance of this extensive edge zone to species numbers and breeding densities is clear.

As the total woodland area declines the interior to edge ratio also declines. For instance, a circular wood of 15 ha has an interior to edge ratio

approximately half of that in a 50 ha wood. Similarly a linear-shaped wood of 15 ha, with a ratio of 128:1, is almost entirely composed of edge zone. Although it has been stated previously (in Chapter 9) that patches at Wistow smaller than 0.2 ha are entirely edge zone, examination of Figure 11.1 shows that rectangular-shaped woods can become entirely edge zone at areas as high as 1.5 ha (if the length to breadth ratio is 16:1), or at 3 ha (for a 32:1 ratio) or at 6 ha (for a 64:1 ratio). A further point about linear woods is that they can act as corridors and assist in dispersal of fauna over the landscape. This would be particularly important in reducing the rate of extinctions in neighbouring woodlands.

Thus woodland shape can be as important as woodland area in conservation strategies. Compact shapes will enhance the survival chances of interior species, whilst linear shapes encourage edge species. To encompass both types, the best strategy would be for a reserve framework that includes at least one wood of a compact shape and over 10 ha in area, together with several smaller adjacent woods of linear or irregular shape.

From the previous accounts no single criterion emerges as decidedly superior for determining the basis for nature reserve site selection. Each case has to be decided on its individual merits. This is not surprising since attempts are being made to meet many requirements, some of which are contradictory to one another. However, it is clear that species richness is generally a useful criterion since it can be easily quantified and provides direct inter-site comparisons. Further, it tends also to be a measure of habitat diversity which, in turn, may reflect natural factors as is the case in an ancient semi-natural woodland.

As a strong relationship exists between species richness and habitat size this too has to be considered as a key criterion. It is believed, however, that avian species numbers and breeding densities can be further increased in a large woodland through a carefully controlled management policy for the nature reserve. Such a policy could also benefit other fauna and flora in the reserve.

An account now follows in which the largest study woodland, Owston Big Wood, is used to describe a proposed model to demonstrate this policy.

A CONSERVATION STRATEGY MODEL.

Introduction.

The early view that conservation meant leaving a site alone so that disturbance was kept to a minimum has been replaced in recent decades by the realisation that successful conservation at many sites often requires active the management of habitat. Conservation strategies often advocate that semi-natural woodlands. which meet the criteria of representativeness and naturalness, should be chosen as reserves (Peterken 1981, Harris 1984). In many parts of lowland Britain the first criterion is more easily met than the second, which can seldom be satisfied due to the long history of woodland interference by man. Therefore, it can be argued that it is more reasonable to suggest a conservation strategy which involves active management to produce desired changes in such lowland woodlands rather than a policy of merely protecting the status quo of a reserve whose naturalness is dubiously perceived. A conservation strategy model for a single large woodland is now proposed which is set against the background of findings from the East Leicestershire woodland study.

The largest woodland in the study area, Owston Big Wood, provides a context for describing the model and for assessing the likely consequences of applying such a model to woodlands of this size and type which are typical of many in lowland Britain today. Owston Big Wood is a suitable example for this purpose for three principal reasons. First, on account of its size it already possesses the highest species richness of any of the East Leicestershire woodlands. This provides a higher base level figure upon which to attempt to enlarge further the species numbers and diversity, a prime aim in most strategies. Secondly, it has the greatest potential for permitting any proposed vegetational changes by management techniques whilst still leaving substantial tracts of the wood essentially untouched. These tracts will therefore fulfil the criteria of naturalness or typicalness, within the limitations that these criteria possess in this region. Thirdly, a model which is couched in terms of the more fragmented woods of East Leicestershire, together with the landscape setting in which they occur, runs into the difficulty that the public, and some conservation organisations, seldom perceive such small woodland patches as potential nature reserves. For this reason, a single, large and readily identifiable woodland is currently the most appropriate example to use in this discussion.

on the findings of Part I, it is suggested that the active Based such a woodland should include attempts to improve the management of microclimate of the habitat, thereby enhancing bird populations through improvement of their breeding and survival prospects. To improve microclimate for birds, structural changes to the wood are suggested. These would include clear-felling, selective tree-felling, traditional coppicing and ride widening.

a) Clear-felling.

The first strategy to be employed involves clear-felling areas of the interior zone. By doing this the interior to edge ratio of the woodland would be altered as the total area of edge zone is increased. Further, a secondary growth of scrub would be allowed to develop in the cleared area over successive seasons, thereby encouraging the colonisation of scrub-inhabiting Willow Warbler, Lesser Whitethroat, Grasshopper species, e.g. Warbler. Whitethroat and Yellowhammer. The woodland edge/scrub ecotone would provide suitable breeding habitat for a higher total population of Garden Warbler, which was observed in similar (but smaller) clearings in some Wistow Woods (e.g. W9, W14). Furthermore, the creation of this ecotone could result in the recolonisation of some East Leicestershire woodlands by the Tree Pipit. This species feeds and nests on the ground, but only when it is characterised by low growing vegetation of the form typically found on heathland. However, it also requires isolated trees such as those along a woodland margin to deliver its song (Cramp 1988).

Although it has been clearly demonstrated through this study that the woodland core supports an impoverished avifauna when compared with edge zones and smaller patches, nevertheless there are 3 interior species which are dependent on it for their survival. Therefore, wholesale clear-felling of large areas in the interior must be avoided. Compartments of at least 10 ha or over should always be left intact throughout the wood to safeguard the survival of interior avifaunas.

One further avian species, no longer breeding in Leicestershire but found in adjacent counties, which could markedly benefit from the formation of large clearings is the Nightjar. Typically a bird of the heathland habitat, this species has adapted to breed in clearings within high density conifer plantations in some parts of southern England. A similarly suitable habitat, characterised by low bushes, could be created after clearance in Owston Big Wood. This might allow the Nightjar to re-establish itself in this county.

The proposed clear-felling scheme could be operated on a temporal rotation basis across much of Owston Big Wood, whilst still continuing to maintain some untouched areas. The scheme could resemble the long-rotation method proposed by Harris (1984). In this, he advocates that a central core of old-growth woodland (that is, woodland of 240-years old or over) is surrounded by several radiating stands of woodland managed on a 320-year rotation. This would ensure that at any one time about 25% of the total area would be old-growth and the rest would consist of recruitment stands of different ages. Clear-felling and replanting might then take place on average every 35 years if there were 9 replacement stands. The process of clear-felling is undertaken on alternate stands, thus creating several ecotones between the different ages of stands. However, these figures are based on mature Douglas fir forests in a mountainous region in Oregon, USA, (44°N) and are unlikely to represent realistic proposals for lowland deciduous woodland at higher latitudes, as in Leicestershire. An alternative method, however, might be the traditional coppicing method used for centuries in Britain. This adopted a rotation period varying from 5-25 years. These rotation periods seem more appropriate for Owston Big Wood. This method is described in more detail below.

b) Thinning the Canopy.

A second alternative is to open the canopy through selective tree removal. This would have the effect of increasing net radiation to the woodland floor, which is much reduced with a closed canopy (Lee 1978). A habitat similar to that of the parkland ecotone would be created, except that the ground and scrub layers would soon become sufficiently dense to support many true edge species and scrub species. The edge zone characteristics, together with its associated avifauna, would be found in these small-gap areas of open canopy even when they are located near to the woodland's centre. This expansion of the edge zone should lead to an increase in species numbers and breeding densities into parts of the woodland usually having considerably lower values. This would have the effect of creating small edge zones within the main body of the wood and including the core area.

c) Coppicing.

The third strategy would be based on the re-introduction of the traditional coppicing technique, which has been abandoned since the end of the Second World War in East Leicestershire woodlands. This would involve the coppicing of limited sections of the wood, probably restricted to areas no larger than

about 10 ha, and allowing the new shoots to develop from the stools. Some key mature trees, known as standards, would be left in position and, wherever possible, these would be native species. Through careful selection, a scattering of these trees would again create a habitat similar to that in a parkland ecotone and should attract some true edge species in the woodland core. Two locally rare species which might benefit from this habitat creation are the Tree Pipit, whose nesting habitat details are described above, and the Redstart. This second species is typical of open woodland and parkland where natural nest-holes are present (Cramp 1988). Like the Tree Pipit, its territories also require low growing vegetation.

Coppice has been shown to attract a great variety of avian species during the development of the vegetation in a 25-year coppice cycle. Scrub-inhabiting species will dominate this habitat in the early years following clearing. Many are woodland edge species which would otherwise be absent from the central part of a large woodland. In addition, during this first stage of development there will also be true arboreal species associated with the standards and the adjacent mature woodland edge e.g. Nuthatch, Treecreeper and woodpeckers. This raises the total species number to a level considerably exceeding that found in closed canopy interior zone woodland. Later, coppice between 3-8 years old would have a vegetational structure suitable for many other scrub species including Whitethroat, Yellowhammer, Garden Warbler and Linnet (Stuttard & Williamson 1971). However, it is the Nightingale, largely absent from East Leicestershire woodlands now and afforded rarity status locally, which has been found to breed in coppice of this age in Kent (Stuttard & Williamson 1971). Clearly, the re-introduction of coppicing in Owston Big Wood might lead to the recolonisation of this species here. Furthermore, as it is cut on a rotation this would ensure that coppice of the appropriate age and structure for Nightingale would always be present somewhere in this wood. With canopy closure, the early scrub colonists will be replaced by typical area-dependent species e.g. Blackbird, Robin, which are common throughout core areas of large woods. However, traditional coppicing will allow scrub colonists to find suitable habitat elsewhere within the wood.

As with the process of clear-felling, coppicing could lead to the loss of interior species populations. However, the retention of standards should go some way to redressing this problem. Neither is the concept of operating a clear-felling policy or adopting traditional coppicing techniques incompatible with the proposals of Harris (1984). Clearing parts of the wood in successive years through coppicing or clear-felling produces the variety of additional edge zones

which is a central feature of Harris's (1984) long-rotation scheme. It would also provide an important source of revenue for a proposed nature reserve, realised through the commercial value of mature timber and coppice shoots removed from the wood.

d) Widening or Creating New Rides.

Rides orientated N-S, and especially those which are narrow, have higher shade levels than wider ones or those orientated E-W (Warren 1985). This influences bird breeding densities, as was noted in Owston Big Wood, where higher values were recorded along E-W rides and especially where rides intersected. Thus the positioning and width of the rides is an important consideration which should be incorporated into any management plan for conservation. Attention to such detail will help to establish more suitable microclimates, as the essential elements of the woodland edge zone are recreated in miniature within the main wood. A policy of ride widening is proposed particularly if the adjacent tree height is responsible for protracted periods of shading during the day such as those orientated N-S. Thinning trees along the rides should also have the effect of extending the edge zone depth further into the core zone as temperature fields are modified.

In summary, modification of temperature fields in a bid to extend the total area and distribution of woodland edge zones can be largely controlled in Owston Big Wood by the techniques of clear-felling, canopy-thinning, the introduction of coppicing and ride widening. Care is needed to maintain areas of semi-natural woodland of 10 ha or over to maintain a high population of interior zone species. To increase further the total area of edge zone, tree-felling could be undertaken to create many diverse shapes of wooded stands, particularly linear peninsula shapes (about 20 m wide; entirely edge zone), ring shapes (that is, a clearing with surrounding woodland) and isodiametric shapes. Indeed, the scheme may ultimately be interpreted as an attempt to create tracts of woodland equivalent to a pattern formed by very closely-spaced woodland patches, thus reducing the effect of isolation. A considerably higher habitat heterogeneity and associated species richness than presently in a closed canopy woodland should result from this conservation strategy. Furthermore, the management plan would provide a woodland of greater interest for the visiting public than the existing site.

It is a conservation strategy which calls for much more sensitivity and attention to detail in how woodlands are established and subsequently managed

for their timber resources. As such, it could equally apply to those woodlands that are not official nature reserves and this would do much to improve the conservation prospects of many species throughout lowland Britain.

Clearly, woodland management strategies involving the widening of rides or the thinning of adjacent trees, such as those described above, could have an impact on other fauna and flora. Two examples are given. When ride widening, selective tree-felling and coppicing were introduced into a Dorset woodland to assist with Pheasant rearing, the total numbers and species richness of butterflies in these areas also became appreciably higher than in those parts of the wood characterised by a closed canopy and narrow rides (Robertson *et al.* 1988). With the exception of Warren (1985), who investigated butterfly species richness in relation to the width and orientation of woodland rides, it seems that the importance of the width, distribution and orientation of rides to other fauna and flora is poorly documented. However, Peterken (1981) has noted that the frequency of wood ant nests increases close to ride intersections where shade values are reduced.

FUTURE PROPOSALS.

The Set-aside Scheme.

Introduction.

Current government agricultural policy is attempting to reduce surpluses of arable crops. Under the Set-aside scheme, a non-agricultural use grant is being offered to encourage farmers to set aside land currently in agricultural use for alternative options. This will operate, in the first instance, for a period of 5 years from 1987/88. The conditions stipulate that a minimum area of 20% of the land presently under arable or permanent pasture on a holding must be set aside.

There are three Set-aside options available to farmers. Land can be set aside for:

- i) fallow, either permanently or on an annual rotation;
- ii) non-agricultural purposes, including the provision of tourist (e.g. caravan or camp sites) or sports facilities (e.g tennis courts, golf courses), new farm-based industry, farm accommodation,

farm shops or educational facilities;

iii) tree planting.

As it is the latter use which is of direct concern to the East Leicestershire avian study, the Set-aside woodland option is now described in greater detail.

Farmers can choose between two woodland options. The first is a direct Set-aside of at least 20% of the farm holding to woodland for a period of 5 years. Compensation payments are so structured to encourage the establishment of smaller (0.25-0.9 ha) rather than larger patches (>10 ha) and to plant broadleaved rather than coniferous trees. The minimum area eligible for a grant is 0.25 ha.

Secondly, farmers may set aside land through the Farm Woodland Scheme. The conditions state that between 3 and 40 ha per holding must be planted, in minimum 1 ha patches. The planting of oak or beech will entitle annual grants to be paid for a period of 40 years. Payments will be made for 30 years for other broadleaved trees or mixed woodland containing more than 50% broadleaved trees; 20 years for other woodland; and 10 years for traditional coppice. Grant structure again encourages small (1.0-2.9 ha) rather than large patches (>10.0 ha) to be planted. Tree planting density must be high (at 1100 trees per hectare or averaging 3 m spacings) in order to qualify for a full grant. Lower planting densities are permitted but grants are then calculated on a decreasing *pro rata* basis.

Limited guidance is offered in the literature supplied to farmers concerning the location, size and shape of woodland planted under the Farm Woodland Scheme. Size and shape "should be in proportion to landscape and neighbouring visual features, e.g. ponds and buildings and other woodlands" (MAFF 1988, unpaginated). However, farmers are advised to consider irregular rather than straight-edged perimeters, thus providing woodland with more "sensitive design". They are also encouraged to incorporate open spaces where practicable. MAFF advice also includes comments on the potential marketing of good quality woodland which may be produced in the long term.

Implications of Increased Woodland Planting for Breeding Birds with Reference to the Leicestershire Study.

If all three Set-aside options are received with an equally enthusiastic

response from farmers it should result in a marked increase in total woodland planting during the next 5 years. If, however, the maximum permitted area allotted to new planting under the Farm Woodland Scheme is realised, the potential for a further 36,000 ha of new woodland nationally will be created by the end of the first trial period of 3 years. Areas of lowland England, in particular, will experience therefore an unparalleled increase in woodland acreage as the trees reach maturity in some years time. Such a development will go some way towards replenishing woodland in lowland Britain, where more than half has been removed in the last 40 years.

Certain predictions concerning the impact of this welcome creation of new woodland on avifaunas in lowland England can be made in the light of the results of the East Leicestershire study. Compensation payments in both woodland schemes appear to favour the creation of more smaller (0.25-2.9 ha) rather than larger patches (>10 ha). It follows that if most woodlands planted are 2.9 ha or less in area this will favour colonisation by true edge avian species, non-true edge species (see p.10.8) and ubiquitous species (see p.10.6). Collectively, these species should produce breeding densities and a total species richness similar to that recorded in the Wistow Woods, particularly if there is a high number of woods per unit area. Woods of 10 ha or more are less likely to be established, and there will be even fewer at 40 ha, the maximum permitted extent per holding under the scheme. Thus the creation of woodland suitable for a large population of interior species appears limited. Nevertheless, if planting takes place on Set-aside land adjacent to existing woodlands this could provide sufficiently large tracts for interior species. Moreover, before the newly-planted trees reach maturity, an ecotone would develop similar in type to that within the long-rotation scheme advocated by Harris (1984) and described before. A mature woodland edge zone would adjoin newly planted woodland. As there are grazing restictions on newly planted land, scrub should also develop within this area. This habitat, together with the adjacent mature woodland edge zone, could be of particular importance to many scrub-nesting species. The effect of the juxtaposition of these two habitats would be the same as that which was observed in the small clearings of certain Wistow Woods, e.g. W9, W12, where higher densities of Whitethroat, Garden Warbler, Willow Warbler and Yellowhammer were recorded than in closed canopy woodland.

A much valued priority of the Farm Woodland Scheme targets the planting of native broadleaves and in particular oak and beech. These species are especially rich in insect fauna and will considerably benefit many woodland avian species through the provision of an abundant food source. Furthermore, large-scale planting of sessile oak in lowland England may result in a future eastwards extention of the current breeding range of some species such as Pied Flycatcher. The absence of this species from central and eastern England can largely be explained by the very low density of sessile oak woodland in these parts of the country.

A high planting density is also being encouraged by the grant structure. In the absence of any subsequent thinning, a dense closed canopy would develop when it reaches high forest. In larger woodlands this may depress interior zone densities further but the commercial sale of mature woodland produce should lead to a thinning of the canopy with a consequent modification to the interior zone temperature fields. In due course, management of these new woodlands for timber extraction will necessitate the establishment of rides for access. Care should be taken to ensure that rides orientated N-S are sufficiently wide to prevent high shade levels. These, plus the gaps produced by extraction, will modify microclimate favourably for many nesting species as edge zone characteristics are established around the openings.

Implications of Increased Fragmentation for Breeding Birds with Reference to the Leicestershire Study.

The large-scale clearance of woodland over several centuries has resulted in the inheritance of a present-day landscape characterised largely by small fragmented woodlands with few large tracts. This landscape evolution is perhaps demonstrated nowhere more clearly than in a region such as East Leicestershire. Small patches have been afforded a low priority by conservation bodies and ecologists owing to the conclusion that they are less important as wildlife refuges than larger woods. Their continuing destruction through road-widening schemes, urban development and changing agricultural practices has rarely led to any prolonged public challenge. Their steady loss from the landscape over recent decades has not been interpreted, until recently, in terms of increasing fragmentation. Neither has their destruction been identified as destroying wildlife corridors. More attention on this matter has been directed towards the wholesale removal of hedgerows in Eastern England.

Small patches in East Leicestershire support higher mean breeding densities than are present in larger woods. Those with an area of 0.5-2.5 ha can also support a total species richness three-quarters of that in woodlands of 10 ha or over. The proportional overlap of the avian species number in each small patch

results in a total richness greatly exceeding that of a single 10-15 ha woodland and equal to that found in a 100 ha woodland.

The conservation value of small woodlands is clearly evident from the, East Leicestershire study and particularly when a closely grouped' cluster of patches is considered. Its importance for breeding birds is greater than has been demonstrated hitherto. Loss of a single woodland within such a spatial pattern would lead to decreases in the total species number and breeding density. Avian species with larger minimum area requirements, which occasionally establish territories between neighbouring patches e.g. Mistle Thrush, would also be lost distance becomes too all inter-patch great. Thus the preservation of as fragmented woods of 0.5 ha or over should be recognised as a priority in our landscape. This would also be an acknowledgement of their importance as wildlife corridors, assisting in avian dispersal, raising immigration rates and lowering extinction rates.

Farmers who participate in either the woodland option of Set-aside or in the Farm Woodland Scheme will obviously see planting in terms of the individual requirements of their own farm and not as part of a regional or national scheme. Inevitably, this will lead to the random creation of woodlands totally devoid of an overall strategy. In view of the findings in East Leicestershire, random planting of many small patches would have rather limited value for the potential conservation of woodland avifaunas. It is strongly advised that there should be in the scheme the provision for a regional overview of planting patterns so as to create a cohesive strategy which would greatly benefit avian breeding populations.

To assist in avian dispersal (and presumably that for other animals, e.g. small mammals) woodlands on adjacent participating farms should either be clustered or placed linearly. Woodlands of 10 ha or over should be isodiametric in shape to maximise the total area of the interior zone and thus be of particular benefit to interior species. Canopy thinning in some core areas could lead to altered temperature regimes and, without loss of interior species or a reduction in their total numbers, would encourage true edge species to colonise such parts of the woodland. These woods, with their higher total bird population of both edge and interior species, could then act as avian reservoirs within the landscape. Furthermore, such circular patches are more likely to act as stepping-stones through their higher equilibrium levels. To reduce the effect of fragmentation, some Set-aside woods should be planted between these larger woodlands thus minimising the effects of isolation and improving connectivity.

They could be smaller, linear-shaped patches so as to assist avian dispersal, particularly for sedentary or non-migratory species. This improved connectivity and the use of the larger patches as stepping stones would have the effect of raising immigration rates and lowering extinction rates in the habitat islands. It is predicted, therefore, that the Farm Woodland Scheme and the woodland option of the Set-aside scheme will meet with limited success for conservation purposes unless a regional strategy is developed to offer guidance to participating farmers. Such a strategy should consider also the advantages of incorporating some of the ideas on woodland management outlined in the previous section on the conservation strategy model.

Many of the small woodlands found in the rich agricultural landscape of East Leicestershire owe their existence to the activities of the various foxhunts whose territories cover this region. Few of the woods are used for timber many have a somewhat neglected appearance, production and where scrub undergrowth is often encouraged as part of the programme to maintain fox populations. Rides, unless used frequently by the hunts, can become quickly overgrown with rank vegetation and scrub development. Indeed, this has led to the loss of some rides in Owston Big Wood. Many of the smaller rides are used only infrequently by the random movements of foxes and hunts. The question arises as to what would happen to such woodlands should the activities of the hunts be prohibited. The Co-operative Wholesale Society, the largest land-owner in East Leicestershire, has already banned the hunts from the numerous farms it owns in this area. Others could follow suit as a result of an increasing anti-bloodsports lobby. Indeed, a total ban was included in a recent Labour Party election manifesto.

Such a development might see an accelerating decline in the openness of many woodland rides. This would lead to a pronounced reduction in light penetration, as just one of the ways in which the microclimate along these edge zones would alter. Modifications like this would soon begin to affect bird species numbers and breeding densities and so any conservation model for these East Leicestershire woodlands would have to take account of any possible future changes in their status, ownership and use.

conservationists turned In recent years have their attention to the opportunities afforded by man-made landscapes (e.g urban sites, motorway verges, extractive mineral workings, waste tips, etc.). Activities, problems, suggested solutions and many case studies in this area have been reviewed by Bradshaw et al. (1986). It is shown, for example, how small patches of scrub woodland

growth that has developed in several undisturbed, neglected cemeteries and disused industrial sites in London have become important 'reserves' for avian populations (Goode & Smart 1986). Many of these patches are similar in size to the smallest woodlands at Wistow. Goode & Smart (1986) argue for great attention to design and detail in the establishment of successful urban conservation sites, set against a background of clearly applied ecological principles. It is now argued here that a similar attention to design and detail should permeate those woodlands established regionally under the Set-aside Scheme and the Farm Woodland Scheme (and should also be a key consideration in the conservation model previously discussed).
Chapter 12

CHAPTER 12.

SUMMARY AND CONCLUSION

Summary.

1) Several factors known to influence the start of egg-laying in the Blue Tit were investigated in a mixed deciduous woodland in East Leicestershire. Of these, the spatial differences in microclimate, particularly air temperatures, were found to account for the consistently earlier laying dates in the southern half of the wood.

2) Ambient air temperature, relative humidity, daily wind speed and total solar radiation, were measured daily from 1 March-20 June 1984 (and 16 April-23 June 1983) at two weather stations, together with the temperature and relative humidity of an adjacent nest- and control-box. Each weather station was sited approximately 30 m from the northern and southern margins of the wood respectively.

3) Mean ambient air temperatures were consistently warmer at the southern station than at the northern station for the two periods under examination (from 1 March to the first date of laying at the southern station, 5 May, and from the 1 March to 20 June, the fledging date at the southern station).

4) Sucrose sensors were placed throughout the wood to investigate the spatial pattern of mean monthly temperatures. Values were obtained for the period mid-January to mid-May 1985. The mean monthly temperature patterns determined showed temperatures to be consistently highest along S-, SE- and SW-facing edges of the wood; the lowest temperatures were usually recorded along the NE-facing edge.

The spatial variation of temperatures within the wood, as determined by the sucrose sensors, confirm the pattern of differences recorded at the two weather stations.

5) Daily total solar radiation values were consistently higher at the southern station between 1 March-5 May, and reached a peak difference, of about 30% in late April, when nest-building in the southern half of the wood generally commences. These differences were manifested in higher ambient temperatures at

the southern weather station.

6) Nest- and control-box temperatures exhibited similar diurnal patterns to ambient temperatures. The southern control-box averaged 1.5°C higher than the northern station. At night, the temperature differences between the control-boxes were the same as for ambient for the 2 periods under investigation.

7) The metabolic heat loss of a female Blue Tit roosting overnight in the southern nest-box resulted in temperatures here being elevated by 0.5° C. There was also a temperature elevation of between 3° C-4°C through heat loss from the nestlings during their homeothermic development.

8) Egg-laying in the Blue Tit is consistently earlier throughout the southern half of the wood and the earliest date was recorded close to the southern edge on the steep SE-facing slope and within that area characterised by higher ambient temperatures. The latest laying, on average 3-8 days later, is in the NE part of the wood in that area characterised by the coolest temperatures.

9) Average clutch size was found to be higher in the southern half of the wood, as was the mean number of nestlings successfully fledging. There are approximately 16% more nestlings surviving to augment the southern than the northern population.

10) Individual nestling and adult Blue Tits were marked for recapture methods to determine the extent of site-faithfulness to nest-boxes. It was concluded that breeding adults are extremely site-faithful and do not move from one part of the wood to another.

11) The principles of the equilibrium theory of island biogeography are described and examined in the light of potential nature reserve design.

12) The total breeding avifauna of 16 woodlands in East Leicestershire was measured. In addition, the avifauna of 6 control plots from the core or interior zone of 2 larger woods and two further plots sited along the southern margin of one of these woods were also measured.

13) A total of 47 bird species were recorded in the 16 study woodlands, whilst only 27 species were recorded in the interior control plots.

The total avifauna of all the East Leicestershire woods studied can be

divided into 3 categories namely, ubiquitous species, interior species and true edge zone species. Interior species are found only in woodlands of 10 ha or more where there is a large proportion of interior zone.

14) A clear species-area relationship exists in the 16 study woodlands but breeding densities are negatively correlated with woodland size.

Woodlands having approximately 1/5th the size of the larger study woodlands support up to 2/3rds of their total species richness, stressing the potential conservation value of such small woodland patches and the need for their preservation in the landscape.

15) The spatial variation in breeding density was investigated in one particular wood. It was shown that mean breeding density was clearly highest in the edge zone of the southern half of the wood, being just over twice that of the northern edge zone and six times that of the northern interior zone.

16) In addition, the distribution of all 'edge-trees', possessing structural features characteristic of the edge zone, were mapped in this particular wood. Edge zones were found to be between 7-10 m wide along all margins except that facing south where it extended to an average depth of about 40 m. However, where slope and aspect favourably combined on some S- and SE-facing woodland perimeters there was an enhancement of the edge zone depth to about 130-140 m.

The proportion of edge zone in the 14 smaller study woodlands (range 0.01-2.2 ha) accounted for nearly 86% of the total woodland area but only about 24% in each of the two larger study woodlands (of 11.4 ha and 14.9 ha). The higher breeding density and species richness of the cluster of small woodlands at Wistow is accounted for by the very high proportion of the edge zone in these woods.

Edge zone characteristics also exist along wide rides and around clearings.

17) Isolation and connectivity of woodland patches was also examined. There is a weak inverse relationship between woodland isolation and species richness. This again confirms the need to preserve small woodlands since their destruction leads to increased isolation.

However, most woodlands in East Leicestershire are less than 1-2 km from

neighbouring patches and the relatively high number of hedgerows situated between them improves their degree of connectivity.

18) Minimum area requirements were identified for several species. Approximately half the total number of species in the study woodlands breed in woods as small as 0.2 ha. A further 6 species appear to require territorial areas of at least 0.7 ha, which may be achieved by sometimes extending their territories to link two closely-spaced patches. Apart from the 3 interior zone species, no other species appears to be totally dependent on woodlands of 10 ha or over.

19) The criteria used for evaluating the conservation potential of reserves are presented and the merits of the three most widely accepted criteria, rarity, naturalness and area (the latter is also a surrogate for species number and habitat diversity) are discussed.

Particular emphasis is given to maximising species richness and three alternative strategies are described to achieve this aim. It is concluded that the conservation of a limited range of woodlands, but including at least one >10 ha, would be most desirable.

However, in view of administrative and perceptual problems associated with such a strategy, the alternative strategy of a single large woodland of 100 ha or more is also considered.

20) In addition to area, woodland shape is also shown to account for variable species richness and breeding density. Compared with a rectangular wood of the same area a circular wood has a smaller proportion of edge zone. A small circular wood becomes entirely edge zone at 0.2 ha. Even woodlands as large as 6 ha can be composed entirely of edge zone, with attendant higher species richness and breeding densities, if they possess a long, thin shape such as in a shelter belt. However, such woodland shapes are unlikely to support interior species. Linear shaped woodlands should also assist in avian dispersal by acting as corridors.

21) It is suggested that higher bird species numbers and breeding density can be established in reserves by modifying the edge zone characteristics, including the microclimatic aspects, by careful attention to details such as ride widening, tree-thinning, and coppicing on a cyclical basis.

These conservation strategies should also have a desirable effect on other fauna by increasing their species numbers.

22) Further potential avian conservation strategies are described in the context of possible widespread new-planting through the Set-aside Scheme and the Farm Woodland Scheme. Attention to detail on such questions as size, shape, isolation and ride orientation of future woodlands in lowland Britain is emphasised.

Conclusion.

This thesis has demonstrated that very small differences in microclimate are important in avian breeding ecology. This is especially so in terms of solar radiation receipt as it manifests itself in spatial variations in temperature of as little as a few degrees or so. For at least one common species, the slightly warmer parts of the wood are characterised by earlier egg-laying, larger clutch sizes and a higher survivorship of fledglings into the local population. These same areas of more favourable microclimate also possess higher species numbers and higher breeding bird densities.

These small but significant differences in microclimate are linked to the varying form of the woodland site in terms of how the vegetation structure changes with its location within the wood, with gradient and aspect, with the occurrence of gaps and rides, and particularly with the proportion of edge zone present as determined by the wood's size and shape. The research has shown that in these respects individual small woodland patches are very important in avian conservation, to a level not previously identified. When considered collectively, as a cluster, the importance of these small patches is further markedly heightened. However, such patches of woodland, some often as small as 0.2 ha, are traditionally perceived by most people as hardly worth conserving. This is so whether these woods are considered individually or as a group, and their loss from the landscape rarely causes prolonged concern.

Quite clearly, any future conservation strategy for woodland avifauna should now consider the full range of woodland sizes in a region, recognising that even the smallest fragment of woodland is likely to support a significant proportion of the total local bird population.

The present pattern of numerous small woodlands in East Leicestershire has largely resulted from deliberate plantings, dating from the 18th and 19th

centuries, on former agricultural land so as to create cover for fox-hunting. This explains the extent and distributon of the patchwork. Even where a few more natural woods have persisted in the landscape from Medieval times or earlier, they still reflect a long history of woodland management techniques such as coppicing and clear-felling. Taken together, all the woodlands of East Leicestershire represent a managed landscape, an artefact of the past. In this sense of course, it is no different from the situation to be found in most of lowland Britain and, in fact, in much of our uplands. In broad terms then, the results from this area should be applicable elsewhere.

However, the situation described in East Leicestershire is not static. Already one can see changing attitudes by some present land-owners in the area. For example, the Wholesale Co-operative Society, the largest land-owner in East Leicestershire through its various farm holdings, has recently banned fox-hunting across its land. Following this it has also carried out substantial tree clearing of core areas in some woods so as to encourage a more widespread and denser scrub layer for Pheasant breeding. At the moment, these moves towards a more socially accepted sport are causing internal changes in the woods as trees are removed, rides become choked and gaps begin to fill in. Should the abolition of fox-hunting become more universal several previously maintained woodland patches will either fall into disuse or come under the threat of total clearance, such is their small size. Developments like this could soon break up the distributional pattern of woodlands in East Leicestershire, reducing connectivity between habitats.

A counter-move to any possibly deleterious changes like those outlined above may arise through the provisions of new developments such as the Set-aside and Farm Woodland Schemes. Under these plans, if small areas of tree planting on farms take note of existing woodland patterns and avoid random development then they will do much to enhance the conservation value of the region. To achieve this, attention to detail on such questions as size and shape of the new woodlands will have to be considered. In some cases, interior zone conditions should be aimed for, whilst elsewhere in the same area more emphasis might be called for in the establishment of an edge zone habitat. the case may be, some new small patches should either be Likewise, as clustered order to minimise isolation and reduce inter-patch distance or in spaced so as to improve the links between existing fragments of carefully woodland and thus assist faunal dispersal. The methods by which the new wood is eventually managed are also important. In these and in other ways the Set-aside and Farm Woodland Schemes represent an excellent opportunity to

improve the conservation value of our rural landscapes not only for bird species but for many other species as well.

A number of key factors influencing avian patterns in woodlands have been identified in this study. However, further research is required to investigate whether other fauna (and flora) are likewise affected by similar small-scale features of form, structure and microclimate. The very limited research conducted to date on other woodland species (e.g. butterflies) strongly infers that the correlation between avian ecology and woodland shape, size, structure and heterogeneity may well apply to other animals. When such research data become available we might be much nearer achieving a successful conservation of entire ecosystems rather than just individual species or single animal groups.

The basic Theory of Island Biogeography largely centred initially on size and area but later, with its application to nature reserve design, it came to include shape. Whilst these are important considerations some emphasis has been placed here on additional aspects which include the proportion of edge zones within woodlands, internal heterogeneity and temporal changes such as woodland succession. Consequently, small intrinsic detail has been shown to be important when attempting to maximise species numbers. Thus the simplistic early models are no longer appropriate, providing only the broad brush-strokes for an explanation of total species richness.

Case studies such as this reveal a need to offer a more enlightened and site-specific outlook in the presentation of strategies or models for woodland conservation. Part of the approach also includes the need to guide the general public (and some conservationists) away from the traditional view that gives undue emphasis to a single large habitat or reserve and that it alone is worthy of preservation. Instead, patches within a farmland matrix offer a markedly better alternative if the preservation of species number is the most desirable criterion of conservation success. The conservation of patches within a farmland matrix is an especially appropriate conservation model for the lowlands of England (and surely elsewhere) where the present landscape is not only largely man-made over many centuries but is again yielding to a new set of pressures so that further changes can now be expected in our limited rural resources. APPENDICES.

Appendix 1.

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Tables and Figures.

(see over)

			WOODLAND (LAYE	or CANOPY) R	SCRUB (s) or		ADJAK	ENT HABITAT	S
NUMBER	AREA (ha)	APPROXIMATE SHAPE	PRIMARY TREE SPP.	SECONDARY TREE SPP.	FIELD (f) LAYER	FARMLAND 1 2 3	4	AQUATTIC 5 6 7	ARBOREAL 8 9 10
ТМ	0.01	triangular	pedunculate	ash	hawthorn (s)	*			
ZM	0.4	triangular	ash	beech	hawthorn (s)	*	*		
ЕМ	0.6	linear	pedunculate	sycamore	snowberry (f)		*		*
₩4	0.7	linear	horse chestrut	pedunculate oak, ash,	snowberry (f)	*			*
M5	0.2	rectangular	ash	anne -	hawthorn (s)	*	*	*	
9M	0.2	rectangular	horse	beech	box (s)		*	*	*
LM	0.9	linear	pedunculate	alder	hawthorn (s)	*		*	*
M8	0.7	rectangular	oak pedunculate	and some	hawthorn (s)	*		*	*
6M	0.8	linear	pedunculate	ash, beech	hawthorn (s)	*		*	
OTM	0.4	rectangular	Lombardy	I	blackthorn (s)	*		*	
TIW	0.2	linear	poplar pedunculate	ash	hawthorn (s)	*		*	*
W12	1.2	linear	oak pedimculate	ash	hawthorn (s)	*		*	*
ETW	0.3	triangular	Lombardy	1	blackthorn (s)	*		*	
W14	2.2	linear	popuar pedunculate oak	hawthorn	hawthorn (s)	*		*	*
Note: Famla $\frac{1}{1} = \frac{1}{h}$	ed ad ed ad	jacent habitat	s are as follu c anal	ows: <u>Arboreal</u> 8 = woodlan	ר בזי				
9 0 	astoral	ן 2 = מ וו	iver	10 = garden	5				
4 = n TABLE	uixed 2.1. ME	ain vecetations	al characteri	stics of the	14 study woodlar	ods on the W	isto	Estates.	

Appendix 1

Appendix 1.1

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March	0.9°C**	U	=	325
April	1.2°C	U	=	288.5
May	1.3°C**	U	=	315.5
June	0.7°C	U	=	167.5

b)	Al DAYTIME	MBIENT NIGHT-TIME	NEST DAYTIME	-BOX NIGHT-TIME
1984 1 March-5 May 1 March-20 June	1.1°C 1.1°C	0.3°C 0.5°C	1.4°C 1.6°C	0.7°C 0.7°C
1983 16 April-6 May 16 April-23 June	<0.1°C 0.2°C	0.1°C 0.3°C	0.3°C 0.4°C	0.6°C 0.7°C

TABLE 5.1. (a) Differences between monthly mean temperatures recorded at the southern and northern weather stations at Billesdon Coplow, 1984. In each month temperatures were higher at the southern station.
(b) Differences between mean temperatures at the southern and northern weather stations for the periods indicated, Billesdon Coplow, 1983 and 1984. In each period temperatures were higher at the southern station.

March	r = 0.23 y = 4.12 + 0.01x	r = 0.37 y = 3.09 + 0.01x
April	r = -0.05 y = 9.56-0.02x	r = -0.37 y = 8.79 - 0.05x
May	r = 0.15 y = 8.37 + 0.03x	r = 0.51 y = 6.25 + 0.05x

TABLE 5.2. Correlation coefficients of relationship between daily airflow and mean ambient air temperatures, Billesdon Coplow, 8 March-25 May 1984.

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		AMBI	ENT	NEST	-BOX	CONTR	OL-BOX
		SOUTH	NORTH	SOUTH	NORTH	SOUTH	NORTH
31	May m r	76 66-88	78 61-93	87 74-94	88 81-95	80 71-87	80 66-94
3	June m r	84 67-99	90 74-100	86 68-99	91 83-96	82 71-92	88 77-99
6	June m r	92 80-99	93 79-100	97 92-99	95 92-96	90 84-95	93 85-99
9	June m r	81 59-96	81 57-99	98 88-100	91 86-95	86 80-92	85 67-95
12	June m r	84 72-97	87 76-98	95 90-100	91 89-93	85 78-92	88 81-95
15	June m r	84 63-95	83 55-95	99 96-100	88 84-90	87 81-94	84 73-90
18	June m r	87 72-97	83 66-97	99 96-100	89 85-92	85 81-89	86 76-94
19	June m r	84 70-96	81 66-96	99 95-100	88 84-91	85 81-88	84 76-92

TABLE 5.3. Mean (m) and range (r) of relative humidity values (expressed as %) for ambient, nest- and control-boxes at the southern and northern stations, Billesdon Coplow, on selected days, 1984. 31 May and 19 June were hatching and fledging dates respectively.

Appendix 1

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	SOUTH	NORTH
1980	30 April 21 April-13 May 21	4 May 25 April-16 May 13
1981	3 May 19 April-15 May 19	11 May 1 May-20 May 17
1982	29 April 22 April-9 May 16	4 May 27 April-15 May 15
1983	6 May 2 May-13 May 15	9 May 3 May-16 May 12
1984	4 May 29 April-10 May 17	8 May 2 May-14 May 10
1985	5 May 25 April-13 May 10	12 May 10 May-16 May 9
1986	15 May 12 May-21 May 7	17 May 12 May-23 May 4
1987	1 May 25 April-11 May 11	29 April 26 April-3 May 7

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TABLE 5.4. Mean laying date (top line) of Blue Tit for the southern and northern halves of Billesdon Coplow, 1980-87. Annual range of dates and sample size are presented on the middle and lower lines.

WCCDLAND	W1	WS	WЮ	W11	W1.3	W10	WISTO W2	W WCCD WB	S W4	W8	W9	W7	W12	W14	BC	BB
WCCDLAND AREA	0.01	0.2	0.2	0.2	0.3	0.4	0.4	0.6	0.7	0.7	0.8	0.9	1.2	2.2	11.4	14.9
Al) Species not influenced by area - Group A. 1) Stock Dove 2) Woodpigeon 3) Durnock 4) Blackbird 5) Blue Tit 6) Starling 7) Chaffinch	+ + + 0.5 + 0.5	+ 1.0 1.0 1.0 + 0.5	0.5 1.5 1.0 + 1.0	+ 1.0 0.75 0.5	+ 0.25 1.0 0.5 + 1.0	1.0 1.0 1.0	+ + 0.75 1.5 1.0 + 1.0	+ 1.5 2.5 2.5 + 2.5	+ 1.5 2.0 2.5 + 1.5	+ + 1.5 2.0 1.75 + 2.5	+ 1.0 2.5 2.5 + 2.5	+ + 1.0 2.5 2.75 + 3.5	0.75 2.5 2.25 + 2.5	+ 1.0 3.5 3.0 + 3.0	+ + 6.5 14.0 32.0 + 16.5	+ 5.5 14.5 12.0 + 11.0
A2) Species not influenced by area - Group B. 8) Wren 9) Robin 10) Song Thrush 11) Garden Warbler 12) Blackcap 13) Willow Warbler 14) Spotted Flycatcher 15) Great Tit 16) Treecreeper 17) Bullfinch P)		+ 1.0 + 1.0 +	1.0 1.0 1.0 + 1.0 0.5 1.0	1.0 0.5 1.0 1.5 1.0 1.0 +	+ 1.0 1.0 1.0	1.0 1.0 + 1.0 1.5 + +	1.0 1.0 + 1.0 1.0 1.0	1.5 3.0 2.0 + 1.0 + 1.0 1.0 +	1.5 3.0 1.5 + 1.0 + 2.0 1.5 1.0	3.0 1.75 2.0 + 2.0 1.0 1.0 1.5 1.0	2.0 2.0 0.5 2.0 1.0 4.0 + 1.0 +	2.0 3.25 1.0 1.0 2.0 + 1.0 1.5 +	1.5 1.0 3.0 5.5 + 1.0 2.0 1.0	4.5 1.0 + 2.0 2.0 4.5 + 2.0 1.0 1.0	15.0 13.0 1.0 10.0 3.5 8.5 11.5 3.0 2.0	11.0 10.0 4.0 7.0 9.5 8.0 8.5 5.0 4.0
5) Species confined to smaller and metium patches. 18) Kestrel 19) Collared Dove 20) Sedge Warbler 21) Lesser Whitethroat. 22) Whitethroat 23) Willow Tit 24) Magpie 25) House Sparrow 26) Goldfinch 27) Redpoll 28) Yellowhamer 29) Reed Burting	+	1.0	0.5	0.5 + +	+	0.5 0.5 + +	+	+ 1.0	+ 0.5 1.0 +	2.5 1.0	+ 2.0 + 0.5 + +	2.0	1.5 1.0 + +	+ + 2.0 + +	1.0	
C) Species confined to medium and larger patches. 30) Green Woodpecker 31) Great Spotted Woodpecker 32) Mistle Thrush 33) Long-tailed Tit 34) Coal Tit 35) Nuthatch 36) Jackdaw 37) Carrion Crow 38) Greenfinch		+	+		+++	+ 1.0	+	0.5 1.0 + 2.5	+ + 1.0	+ 1.0 1.5 1.0	0.5	+	+	+ 1.0	1.5 1.5 3.0 1.0 4.5 1.0 + 3.0	2.5 0.5 2.0 3.0 0.5 + 0.5
D) Species confined to larger patches. 39) Sparrowhawk 40) Pheasant 41) Cuckco 42) Lesser Spotted Woodpecker 43) Wood Warbler 43) Wood Warbler 44) Chiffchaff 45) Goldcrest 46) Marsh Tit 47) Jay											+				+ + 4.0 1.0 + 1.0	1.0 + 1.0 2.0 1.0 2.0 1.0
TOTAL NO OF TERRITORIES	1.0	6.5	11.0	8.75	5.75	11.5	9.25	23.5	23.0	31.5	24.0	27.0	25.5	31.5	162.	0 131.0
TOTAL SPECIES RICHNESS	8	14	15	14	13	18	15	21	23	24	25	20	18	24	32	30

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Note: W1-W14 = Wistow Woods BC = Billesdon Coplow BB = Botany Bay Fox Covert. TABLE 9.1. Total number of territories (breeding pairs) and species richness in each study woodland, 1987.

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WOO	DLAND	W	BC	BB	OW	LR
TOTA		0.0	11.4	14.0	16.0	• •
	L AREA (na)	8.8	11.4	14.9	10.0	8.0
1)	Sparrowhawk		+			
2)	Kestrel	+				
3)	Pheasant		+		+	+
4)	Stock Dove	+	+			+
5)	Woodpigeon	+	+	+	+	+
6)	Collared Dove	+				
7)	Cuckoo			1.0		+
8)	Green Woodpecker	+	1.5			0.5
9)	Great Spotted Woodpecker	1.0	1.5	2.5	3.0	0.5
10)	Lesser Spotted Woodpecker			+		
11)	Wren	20.0	15.0	11.0	10.0	8.5
12)	Dunnock	12.75	6.5	5.5	2.0	1.0
13)	Robin	18.0	13.0	10.0	21.0	4.0
14)	Blackbird	23.5	14.0	14.5	9.5	5.0
15)	Song Thrush	9.5	3.0	4.0	1.5	1.5
16)	Mistle Thrush	2.5	3.0	0.5		
17)	Sedge Warbler	+				
18)	Lesser Whitethroat	1.0				
19)	Whitethroat	6.0				
20)	Garden Warbler	12.0	1.0	4.0	5.0	
21)	Blackcap	11.0	10.0	7.0	3.5	2.5
22)	Wood Warbler			1.0		
23)	Chiffchaff	+	4.0	2.0	6.5	2.5
24)	Willow Warbler	23.0	3.5	9.5	8.5	1.0
25)	Goldcrest		1.0	1.0	2.0	1.0
26)	Spotted Flycatcher	5.0	8.5	8.0	1.0	
27)	Long-tailed Tit	1.0	1.0	2.0	3.5	1.0
28)	Marsh Tit		+	2.0	2.0	1.0
29)	Willow Tit	+			2.0	
30)	Coal Tit	2.0	4.5	3.0	4.5	1.0
31)	Blue Tit	23.0	32.0	12.0	14.0	10.0
32)	Great Tit	11.0	11.5	8.5	3.5	2.0
33)	Nuthatch	2.0	1.0	0.5		
34)	Treecreeper	11.0	3.0	5.0	3.0	1.0
35)	Jav		1.0	1.0	1.0	
36)	Magpie	+				
37)	Jackdaw	+	÷			
38)	Carrion Crow	+		+		
39)	Starling	+	+	+		
40)	House Sparrow	+				
41)	Chaffinch	23.5	16.5	11.0	9.5	5.0
42)	Greenfinch	7.0	3.0	0.5		2.0
43)	Goldfinch	9.0	1.0			
44)	Redpoll	2.0				
45)	Bullfinch	3.0	2.0	4 0	2.0	
46)	Yellowhammer	+	2.0	1.0	2.0	
47)	Reed Bunting	+				
	Kood Dunung					
TOTAL	No. OF TERRITORIES	239.75	162.0	131.0	118.5	49.0
TOTAL	SPECIES RICHNESS	39	32	30	24	22

Note: W = Wistow Woods (14 patches), BC = Billesdon Coplow, BB = Botany Bay Fox Covert, OW = Owston Big Wood, LR = Loddington Reddish.

TABLE 9.2. Total number of bird breeding pairs and total species richness in each of the five study woodlands in East Leicestershire, 1987. Highest values for each species are shown in **bold**.

Appendix 1.6

	WOODLAND	w	BC	BB	OW	LR
	TOTAL AREA CENSUSED	(ha) 8.8	11.4	14.9	16.0	8.0
1)	Cuckoo			0.07		÷
2)	Green Woodpecker		0.13			0.06
3)	Great Spotted Woodpecker	0.11	0.13	0.17	0.19	0.06
4)	Wren	2.27	1.32	0.74	0.63	1.06
5)	Dunnock	1.45	0.57	0.37	0.13	0.13
6)	Robin	2.05	1.14	0.67	1.31	0.50
7)	Blackbird	2.67	1.23	0.97	0.59	0.63
8)	Song Thrush	1.08	0.26	0.27	0.09	0.19
9)	Mistle Thrush	0.28	0.26	0.03		
10)	Lesser Whitethroat	0.11				
11)	Whitethroat	0.68				
12)	Garden Warbler	1.36	0.09	0.27	0.31	
13)	Blackcap	1.25	0.88	0.47	0.22	0.3
14)	Wood Warbler			0.07		
15)	Chiffchaff		0.35	0.13	0.41	0.3
16)	Willow Warbler	2.61	0.31	0.64	0.53	0.13
17)	Goldcrest		0.09	0.07	0.13	0.13
18)	Spotted Flycatcher	0.57	0.75	0.54	0.06	
19)	Long-tailed Tit	0.11	0.09	0.13	0.22	0.13
20)	Marsh Tit			0.13	0.13	0.13
21)	Willow Tit				0.13	
22)	Coal Tit	0.23	0.39	0.20	0.28	0.13
23)	Blue Tit	2.61	2.81	0.81	0.88	1.25
24)	Great Tit	1.25	1.01	0.57	0.22	0.25
25)	Nuthatch	0.23	0.09	0.03		
26)	Treecreeper	1.25	0.26	0.34	0.19	0.13
27)	Jay		0.09	0.07	0.06	
28)	Chaffinch	2.67	1.45	0.74	0.59	0.63
29)́	Greenfinch	0.80	0.26	0.03		
30)	Goldfinch	1.02	0.09			
31)	Redpoll	0.23				
32)	Bullfinch	0.34	0.18	0.13	0.13	
tal nu	mber of species with preeding density.	19	5	3	6	2

TABLE 9.3. Mean breeding densities (prs ha⁻¹) for all species mapped at each of the 5 main study sites. Averages are calculated for total woodland area. Highest breeding density for each species is shown in **bold**.

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	WISTOW	7	OWSTC BIG W)N OOD	OBW +	LR
	ā		ā		đ	
Wren	2.95	11	0.63***	4	0.77***	6
Dunnock	2.15	13	0.25***	2	0.25***	3
Robin	3.17	10	1.32**	4	0.91**	6
Blackbird	3.46	12	0.60***	4	0.61***	6
Song Thrush	2.30	8	0.19**	2	0.19**	4
Garden Warbler	3.07	8	0.32**	4	-	4
Blackcap	1.92	8	0.44***	2	0.38***	4
Willow Warbler	3.79	9	0.54***	4	0.48***	5
Blue Tit	3.08	14	0.88***	4	1.00***	6
Great Tit	2.14	10	0.29**	3	0.28**	5
Treecreeper	2.25	9	0.25**	3	0.25**	4
Chaffinch	2.97	14	0.60***	4	0.61***	6
			1		l	

TABLE 9.4. Comparison of mean breeding densities (\bar{d}) (in prs ha⁻¹) of selected species at Wistow and the interior plots of Owston Big Wood (OBW) and Loddington Reddish(LR). The total number of patches (at Wistow) or plots (at Owston Big Wood or Loddington Reddish) in which each species was recorded is shown in **bold**.

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Appendix 1

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		ow	STON I	BIG WO	DOD	LC	DDINC	GTON R	EDDISH
			inter p	ior lots		int p	erior lots	edg plo	ge ots
1)	Pheasant	+		+			+	+	+
2)	Stock Dove					+			
3)	Woodpigeon	+	+	+	+	+	+	+	+
4)	Turtle Dove							+	
5)	Cuckoo						+	0.5	0.5
6)	Green Woodpecker					0.5	+		
7)	Great Spotted Woodpecker	1.0	1.0	0.5	0.5		0.5	• •	
8)	Wren	3.0	4.5	1.5	1.0	4.5	4.0	3.0	4.0
9)	Dunnock		1.0		1.0		1.0	1.0	• •
10)	Robin	6.5	5.5	4.5	4.5	1.0	3.0	3.0	2.0
11)	Blackbird	1.5	3.0	3.0	2.0	2.5	2.5	3.0	2.5
12)	Song Inrush	1.0		+	0.5	1.0	0.5	+	2.5
13)	Mistie Inrush	1.0	1.5	0.5	2.0			1.0	1.0
14)	Garden warbler		1.5	0.5	2.0	1.0	1.6	2.0	1.0
15)	Blackcap	1.5	2.0	1.0	• •	1.0	1.5	2.0	2.0
10)	Unificialit Willow Weakley		2.0	1.5	2.0	1.5	1.0	1.5	1.0
17)	Willow Wardler	2.5	3.5	1.5	1.0	1.0	1.0	2.0	2.0
10)	Goldcrest		1.0	1.0			1.0	1.0	
19)	Spotted Flycatcher	1 1 0	1.0	1.0			1.0	1.0	
20)	Long-tailed 11t	1.0	1.5	1.0		1.0	1.0	1.0	1.0
21)	Marsh Ilt	1.0	1.0	+	1.0	1.0		1.0	1.0
22)	Cool Tit	1.0	2.0	15	1.0		1.0	1.0	10
23)	Rhua Tit	20	5.0	1.5	20	5.0	1.0	1.0	1.0
24)	Great Tit		5.0	4.0	2.0	3.0	5.0	2.5	4.5
23)	Nuthatah	1.0	1.5		1.0	1.0	1.0	2.0	2.0
20)	Treecreener	1.0	1.0		1.0	1.0		1.0	1.0
28)	Iav	1.0	1.0	0.5	0.5	1.0		1.0	1.5
20)	Jackdaw			0.5	0.5				+
30)	Carrion Crow							+	
31)	Chaffinch	25	2.0	40	1.0	15	35	55	40
32)	Bullfinch	1.0	2.0	1.0	1.0	1.5	5.5	1.0	ч. 0
		1.0		1.0				1.0	
TOTAL	NO. OF TERRITORIES	30.5	41.0	26.0	21.0	22.5	26.5	37.0	32.5
TOTAL	SPECIES RICHNESS	19	19	18	16	15	18	24	19
MEAN (prs ha	BREEDING DENSITY	7.6	10.3	6.5	5.3	5.6	6.6	9.3	8.1

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TABLE 9.5. Total number of breeding territories, species richness and mean breeding densities (in prs ha⁻¹) in each of the 6 interior and 2 edge plots in Owston Big Wood and Loddington Reddish. All plots have an area of 4 ha.

	woodland area	logn woodland area
species number	0.72**	0.91***
number of territories	0.95***	0.81***
logn species number	-	0.92***
logn No. of territories	-	0.97***

TABLE 9.6. Correlation coefficients of relationships between species number, territory numbers and woodland area of the 16 study sites. This is based on data in Table 9.1. Plots of these relationships are presented in Appendix 7.

	woodland area	logn woodland area
a) including smallest study woodland (0.01	ha)	
breeding density (prs ha ⁻¹)	-0.46	-0.84***
logn breeding density (prs ha	⁻¹) -	-0.87***
b) excluding smallest study woodland (0.01	ha)	
breeding density (prs ha ⁻¹)	-0.61*	-0.71**
logn breeding density (prs ha	¹) -	-0.80***

TABLE 9.7. Correlation coefficients of relationships between breeding density (prs ha⁻¹) and woodland size if the 16 study sites.

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	correlation coefficient	No. of patches in which spp. recorded
Wren	0.90***	15
Dunnock	0.81***	16
Robin	0.84***	12
Blackbird	0.97***	16
Song Thrush	0.52	12
Mistle Thrush	0.42	6
Garden Warbler	0.43	14
Blackcap	0.94***	11
Willow Warbler	0.69**	13
Spotted Flycatcher	0.56	10
Blue Tit	0.94***	16
Great Tit	0.85***	14
Treecreeper	0.74**	12
Chaffinch	0.90***	16
Greenfinch	0.05	9
Bullfinch	0.87***	10

TABLE 9.8. Correlation coefficients of species-area relationships for selected widespread species in the 16 study woodlands. All data is log-transformed. The number of woodland patches in which each species was recorded is shown in **bold**.

Appendix 1.11

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PORTION OF WOODLAND	I I I I I I I I I I I I I I I I I I I	OTAL NO. F SQUARES	MEAN DENSITY		PORTION OF WOODLAND	ZONE	OTAL NO. E SQUARES	MEAN DENSTIY	
a) Billesdon Coplos					b) Botany Bay Fox Cor	ært.			
1) Complete wood	edge interior	118 380	3.4±0.3 1.1±0.1	t=7.64 P<0.001	1) Complete wood	edge interior	226 460	0.7±0.1 0.5±0.03	t=3.50 P<0.001
2) Southern half	edge interior	64 176	4.6±0.4 1.7±0.1	t=6.40 P<0.001	2) Southern half	edge interior	110	0.9±0.1 0.6±0.1	t=3.24 P<0.01
3) Northern half	edge interior	54 204	2.0±0.2 0.7±0.1	t=5.36 P<0.001	3) Northern half	edge interior	116 231	0.5±0.1 0.4±0.04	t=1.77 n.s.
4) Edge zone	south north	64 54	4.6±0.4 2.0±0.2	t=5.35 P<0.001	4) Edge zone	south	110	0.9±0.1 0.5±0.1	t=3.32 P<0.01
5) Interior zone	south north	176 204	1.7±0.1 0.7±0.1	t=6.89 P<0.001	5) Interior zone	south north	229 231	0.6±0.1 0.4±0.04 I	t=2.91 ×0.01

TABLE 9.9. Mean breeding densities (registrations per 15m²) of edge and interior zones in the southern and northern halves of (a) Billesdon Coplow and (b) Botany Bay Fox Covert, 1987.

Appendix 1

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	AREA (ha)	TOTAL No. 15 m SO	TOTAL No. EDGE SO	TOTAL No.
Wistow	(nu/	10 02		INTERIOR DQ
WI	0.01	1	1	-
W2	0.4	16	15	1
W3	0.6	24	21	3
W4	0.7	30	28	2
W5	0.2	7	7	-
W6	0.2	6	6	-
W7	0.9	41	34	7
			37	4
W8	0.7	34	26	8
W9	0.8	39	34	5
	<u> </u>		36	3
W10	0.4	22	16	6
W11	0.2	9	9	-
W12	1.2	55	48	7
		10	49	6
W13	0.3	13	12	
W14	2.2	98	82	16
	·····		85	13
total	8.8	395	339	56
			348	47
% of total area	a	100%	85.8%	14.2%
			88.1%	11.9%
Billesdon Coplo	w			
				201
total	11.4	502	118	384
			128	374
% of total are:	а	100%	23 5%	76 5%
			25.5%	74.5%
Botany Bay Fo	x Covert			
•	14.0			
total	14.9	689	165	524
			226	463
% of total area	1	100%	23.9%	76.1%
	~	10070	32.8%	67.2%
			UNIC /V	

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TABLE 9.10. Interior to edge relationships of the 16 study woodlands. The first value given for edge and interior squares excludes clearings and rides; figures in **bold** include them.

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		distance	e (in kn				
	nearest other	nearest similar area	nearest bigger	>10 ha	PD	II	CV
		L	I /	4	L		
Wistow W1	0.23	0.22	0.23	6.93	38	1.16	6
W2	0.23	0.44	0.54	7.13	37	1.14	5
W3	0.02	0.02	0.09	6.71	40	0.98	0
W4	0.02	0.02	0.14	6.52	41	0.97	0
W5	0.10	0.22	0.1	6.73	41	1.00	6
W6	0.02	0.22	0.02	6.50	42	1.02	4
W7	0.02	0.02	0.68	7.14	36	0.98	1
W8	0.02	0.02	0.68	7.14	38	1.04	0
W9	0.09	0.09	0.61	7.12	41	1.10	0
W10	0.02	0.02	0.08	6.60	47	1.15	5
W11	0.02	0.02	0.02	6.53	48	1.16	0
W12	0.02	0.64	0.02	6.22	46	1.08	2
W13	0.02	0.2	0.02	6.28	45	1.14	4
W14	0.02	0.92	0.87	5.92	42	1.03	2
Billesdon Coplow	0.02	4.44	0.02	0.02	16	0.97	5
Botany Bay	0.02	6.14	4.62	0.02	17	0.97	8
Loddington Reddish	0.02	1.13	2.24	0.12	31	0.8	6
Owston Big Wood	0.02	2.13	8.74	0.02	15	0.8	35

TABLE 10.1. Isolation indices (II), connectivity values (CV), patch density (within a 2 km radius)(PD) and inter-patch distances between the study woodlands and neighbouring patches.

Appendix 1

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	(a)	(b)
nearest other wood	-0.49	-0.51
nearest woodland of similar area	0.66	0.02
nearest bigger wood	0.48	0.55*
nearest woodland >10 ha	-0.67**	0.02
No. of patches within 2 km	-0.67**	-0.14
isolation indices	-0.65	-0.53

TABLE 10.2. Correlation coefficients of relationships between inter-patch distance variables and species richness in (a) all 16 study woodlands and (b) in the 14 Wistow patches only.

		woodlands (0.1-1.0 ha	ı)	woodlands (1.0-10.0 ha)		
	EAST LEICS	OXFORD	GB	EAST LEICS	OXFORD	GB
Great Spotted Woodpecker	8	0	0	33	33	7
Great Tit	67	70	12	100	100	16
Blue Tit	100.	100	18	100	100	37
Coal Tit	8	0	2	33	11	7
Marsh Tit	0	30	1	0	67	5
Treecreeper	58	10	2	100	89	4
Wren	75	85	37	100	100	51
Song Thrush	58	0	34	67	22	50
Blackcap	58	50	10	67	100	26
Willow Warbler	58	50	13	100	67	39
Chiffchaff	0	20	5	33	100	12
Goldcrest	0	0	1	33	44	9

TABLE 10.3. Incidence of selected species in the woodlands of East Leicestershire compared with values from studies in Oxfordshire (Ford 1987) and Great Britain (Moore & Hooper 1975). Values are expressed as a % of all woodlands investigated.

Figure 2.1

(see over)

Figure 2.1. Togography of the 18 East Leicestershire woodlands selected for this study. These are shown with a dense shading; other woodlands have a more open stipple. Contours are at 5 m intervals. The same orientation and scale are used for all maps as for the Wistow map (3).

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Figure 2.2

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(see over)

Figure 2.2. Billesdon Coplow wood showing: (a) contour pattern at 3 m intervals (within-wood contours are continuous; those outside perimeter are pecked); (b) dominant (upper case) and sub-dominant (lower case) canopy tree species. The sites of the two weather stations (see Plate 21 and Chapter 4 for details) are marked *. Numbers along the woodland perimeter refer to sections between arrows. See Chapter 9 and Figure 9.2 for references to branch orientation of edge trees along these sections.

Tree species are as follows: A, a: ash; B, b: beech; C, c: sweet chestnut; H, h: horse-chestnut; L, l: larch; N, n: Norwegian spruce; O, o: pedunculate oak; P, p: Scots pine; S, s: sycamore







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Figure 2.3. Position of interior control plots at (a) Loddington Reddish and (b) Owston Big Wood. Pecked lines within the woods show rides.

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Figure 5.2. Mean monthly isotherm patterns as determined by the sucrose solution method for Billesdon Coplow, January-May 1985. The maps show mean temperature patterns for the following periods: (a) 20 January-17 February; (b) 17 February-23 March; (c) 23 March-20 April (d)20 April-19 May.









Figure 5.3.

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(see over)
Figure 5.3. Differences (expressed as %) in daily total solarimeter values between the southern (above axis) and northern (below) weather station, Billesdon Coplow, (a) from 1 April-24 June 1983 and (b) 1 March-20 June 1984. See Figure 5.1 for key to symbols.



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Figure 5.4. Typical (a) ambient, (b) nest-box and (c) control-box patterns of temperatures (top) and relative humidity (bottom) at the southern (•) and northern (O) weather stations, Billesdon Coplow, as recorded on 4 April 1984.

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Figure 5.5. Typical ambient (\blacksquare) , nest-box (\bullet) and control-box (\blacktriangle) diurnal temperature patterns for the southern (top) and northern (bottom) weather stations on 2 selected days, Billesdon Coplow.



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Figure 5.6. Mean (a) daytime and (b) night-time temperature differences between nest-boxes at the southern (above axis) and northern (below) weather stations. Billesdon Coplow, 1 March-20 June 1984. A summary is given of these daily differences by using 0.2°C divisions, for (c) daytime and (d) night-time. See Figure 5.1 for key to symbols.



Figure 5.7. Mean daytime temperature differences between nest-box (above axis) and control-box (below) at the (a) southern and (b) northern weather stations, Billesdon Coplow, 1 March-20 June 1984. A summary of these differences is given, by 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.



Figure 5.8. Mean night-time temperature differences between nest-box (above axis) and control-box (below) at the (a) southern and (b) northern weather stations, Billesdon Coplow, 1 March-20 June 1984. A summary of these differences is given, by 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.



Figure 5.9. Influence of nestling development on nest-box temperatures (\bullet) compared with ambient (\blacksquare) and adjacent control-box temperatures (\blacktriangle) at 3-day intervals, southern weather station, Billesdon Coplow, 1983. Number of days after hatching date (h) is shown alongside date.



Figure 5.10. Mean daytime temperature differences between nest-box (above axis) and ambient (below) at the (a) southern and (b) northern weather stations, Billesdon Coplow, 1 March-20 June 1984. A summary of these differences is given. by using 0.2°C divisions. for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.



Figure 5.11. Mean night-time temperature differences between nest-box (above axis) and ambient (below) at the (a) southern and (b) northern weather stations. Billesdon Coplow, 1 March-20 June 1984. A summary of these differences is given, using 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.

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Figure 5.12. Mean (a) daytime and (b) night-time temperature differences between the southern (above axis) and northern (below) weather stations. Billesdon Coplow, 16 April-23 June 1983. A summary of these differences is given, by using 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.

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Figure 5.13. Mean (a) daytime and (b) night-time temperature differences between nest-boxes at the southern (above axis) and northern (below) weather stations, Billesdon Coplow, 16 April-23 June 1983. A summary of these differences is given, by using 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.



Figure 5.14. Mean daytime temperature differences between nest-box (above axis) and ambient (below) for the (a) southern and (b) northern weather stations, Billesdon Coplow, 16 April-23 June and 31 March-23 June 1983 respectively. A summary of these differences is given, by using 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.

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Figure 5.15. Mean night-time temperature differences between nest-box (above axis) and ambient (below) for the (a) southern and (b) northern weather stations, Billesdon Coplow, 16 April-23 June and 31 March-23 June 1983 respectively. A summary of these differences is given, by using 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.



Figure 5.16. Mean (a) daytime and (b) night-time temperature differences between nest- and control-boxes at the southern weather station. Billesdon Coplow, 18 May-23 June 1983. A summary of these differences is given, by using 0.2°C divisions, for the (c) southern and (d) northern weather stations. See Figure 5.1 for key to symbols.

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Figure 5.17. Mean start of egg-laying in nest-boxes at Billesdon Coplow in relation to the annual mean date. The method used is described in Chapters 4 and 5. '+' and '-' are late and early boxes respectively whilst a '0' indicates a mean first-egg-date in that box the same as for the entire wood.

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Figure 5.18. Relationship between clutch size and starting date of laying in the (a) southern and (b) northern halves of Billesdon Coplow, 1980-84.



Figure 7.1. Species equilibrium (S) on an oceanic island as described by the Equilibrium Theory of Island Biogeography (MacArthur & Wilson 1963, 1967). See Chapter 7 for details.

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Figure 7.2. (a) Owing to different rates of immigration, the Theory states that islands nearer to the colonising source have a higher species richness (S_N) than more distant islands with their lower species numbers (S_F) .

(b) Small islands support fewer species (S_S) , and large islands higher species numbers (S_L) , owing to the different rates of extinction. See Chapter 7 for details.




Figure 7.3. Relationship between species number and increasing island (or habitat) area shown (a) arithmetically and (b) after log-transformation.

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Figure 7.4. Using a mean slope z value of 0.3, Abele & Connor (1979) point out that 2 preserves of half size ('B') will support more species than a single large one ('A').

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NUMBER OF SPECIES

Figure 7.5. The design of nature reserves as suggested by Diamond (1975) is as follows: (a) a large reserve is better than a small one; (b) it should be divided into as few fragments as possible; (c) fragments should be as close as possible; (d) fragments should be grouped rather than linear; (e) fragments should be connected by strips of protected habitat; (f) reserves should be as nearly circular as possible. See Chapter 7 for details.

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Figure 8.1. (a) Exact location of all bird registrations (n=852) recorded between 16 April-20 June 1987 at Billesdon Coplow. (b) The same registrations plotted by 15 m squares and presented as totals in each square. The line dividing the southern and northern halves is shown darker.

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Figure 8.2.

(see over)

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Figure 8.2. Distribution and species of all trees exhibiting edge zone characteristics at Billesdon Coplow, 1986. Mean branch orientation is shown as a line on each symbol.

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Figure 9.1.

(see over)

Figure 9.1. Diagrammatic relationship between interior zone (diagonal hatching) and edge zone (stipple) in woodland patches of different sizes and shapes.



Figure 9.2. Orientation of branching of all trees exhibiting edge zone characteristics along each woodland margin (numbered; see Fig. 2.2b) in relation to the mean orientation of that margin (arrows) at Billesdon Coplow, 1986. Un-numbered margins possess no 'edge-trees'.



WOODLAND MARGIN NUMBER (see Fig. 2.2b)

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Figure 11.1. Interior to edge ratios for a variety of woodlands having different sizes and shapes. All values are calculated from edge zone depths assumed to be 15 m wide.

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Appendix 2.

1) Names of bird species mentioned in the text.

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This list follows the conventions and sequence employed by Voous (1973, 1977a, 1977b).

Black-necked Grebe	Podiceps nigricollis C.L. Brehm
Mallard	Anas platyrhynchos Linnaeus
Montagu's Harrier	Circus pygargus (L.)
Goshawk	Accipiter gentilis (L.)
Sparrowhawk	Accipiter nisus (L.)
Golden Eagle	Aquila chrysaetos (L.)
Osprey	Pandion haliaetus (L.)
Kestrel	Falco tinnunculus L.
Peregrine	Falco peregrinus Tunstall.
Pheasant	Phasianus colchicus L.
Woodcock	Scolopax rusticola L.
Stock Dove	Columba oenas L.
Woodpigeon	Columba palumbus L.
Collared Dove	Streptopelia decaocto (Frivaldszky)
Turtle Dove	Streptopelia turtur (L.)
Cuckoo	Cuculus canorus L.
Little Owl	Athene noctua (Scopoli)
Tawny Owl	Strix aluco L.
Nightjar	Caprimulgus europaeus L.
Green Woodpecker	Picus viridis L.
Great Spotted Woodpecker	Dendrocopus major (L.)
Lesser Spotted Woodpecker	Dendrocopus minor (L.)
Tree Pipit	Anthus trivialis (L.)
Yellow Wagtail	Motacilla flava L.
Wren	Troglodytes troglodytes (L.)
Dunnock	Prunella modularis (L.)
Robin	Erithacus rubecula (L.)
Nightingale	Luscinia megarhynchos C.L. Brehm
Redstart	Phoenicurus phoenicurus (L.)
Blackbird	Turdus merula L.
Song Thrush	Turdus philomelos C.L. Brehm
Mistle Thrush	Turdus viscivorus L.

Grasshopper Warbler Sedge Warbler Dartford Warbler Lesser Whitethroat Whitethroat Garden Warbler Blackcap Wood Warbler Chiffchaff Willow Warbler Goldcrest Spotted Flycatcher Pied Flycatcher Long-tailed Tit Marsh Tit Willow Tit Coal Tit Blue Tit Great Tit Nuthatch Treecreeper Jay Magpie Jackdaw Rook Carrion Crow Starling House Sparrow Tree Sparrow Chaffinch Greenfinch Goldfinch Linnet Redpoll Bullfinch Yellowhammer Reed Bunting

Locustella naevia (Boddaert) Acrocephalus schoenobaenus (L.) Sylvia undata (Boddaert) Sylvia curruca L. Sylvia communis Latham Sylvia borin (Boddaert) Sylvia atricapilla (L.) Phylloscopus sibilatrix (Bechstein) Phylloscopus collybita (Vieillot) Phylloscopus trochilus (L.) Regulus regulus (L.) Muscicapa striata (Pallas) Ficedula hypoleuca (Pallas) Aegithalos caudatus (L.) Parus palustris L. Parus montanus Conrad. Parus ater L. Parus caeruleus L. Parus major L. Sitta europaea L. Certhia familiaris L. Garrulus glandarius (L.) Pica pica (L.) Corvus monedula L. Corvus frugilegus L. Corvus corone L. Sturnus vulgaris L. Passer domesticus (L.) Passer montanus (L.) Fringilla coelebs L. Carduelis chloris (L.) Carduelis carduelis (L.) Carduelis cannabina (L.) Carduelis flammea (L.) Pyrrhula pyrrhula (L.) Emberiza citrinella L. Emberiza schoeniclus (L.)

2) Names of plant species mentioned in the text.

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This list follows the conventions and sequence employed by Clapham, Tutin & Warburg (1981).

Norwegian Spruce	Picea abies (L.)
European Larch	Larix decidua Miller.
Scots Pine	Pinus sylvestris L.
Corsican Pine	<i>Pinus nigra</i> Arnold
Western Red Cedar	Thuja plicata
Small-leaved Lime	Tilia cordata Miller
Field Maple	Acer campestre L.
Sycamore	Acer pseudoplatanus L.
Horse-chestnut	Aesculus hippocastanum L.
Box	Buxus sempervirens L.
Bramble	Rubus fruticosus L.
Field Rose, Trailing Rose	Rosa arvensis Hudson
Dog Rose	Rosa canina L.
Blackthorn	Prunus spinosa L.
Hawthorn	Crataegus monogyna Jacq.
Wych Elm	Ulmus glabra Hudson
English Elm	Ulmus procera Salisb.
Walnut	Juglans regia L.
Silver Birch	Betula pendula Roth.
Alder	Alnus glutinosa (L.) Gaertner
Hazel	Corylus avellana L.
Beech	Fagus sylvatica L.
Sweet Chestnut	Castanea sativa Miller.
Pedunculate Oak	Quercus robur L.
Aspen	Populus tremula L.
Lombardy Poplar	Populus nigra 'Italica' Duroi.
Crack Willow	Salix fragilis L.
Great Willow	Salix caprea L.
Common Sallow	Salix cinerea L.
Rhododendron	Rhododendron ponticum L.
Ash	Fraxinus excelsior L.
Snowberry	Symphoricarpus rivularis Suksdorf
Honeysuckle	Lonicera periclymenum L.

3) Names of mammal species mentioned in the text.

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This list follows the conventions and sequence employed in 'A check list of British Mammals', in Lawrence M.J. & Brown R.W. "Mammals of Britain. Their tracks, tráils and signs". Blandford Press, London.

FoxVulpes vulpes L.American MinkMustela vison (Schreber)Grey SquirrelSciurus carolinensis (Gmelin)CoypuMyocastor coypus (Molina).

Appendix 3.

The Breeding Bird Census

The main aim of a breeding bird census is to estimate the total number of breeding pairs (which is usually expressed as the number of territories present) at a particular site.

Bird census methods fall into three main groups as follows:

i) the spot-mapping method, which is the most widely used technique in the British Isles (and where it forms the field technique for the nationally-conducted breeding bird monitoring scheme, the Common Bird Census);

ii) the line-transect method, which is used particularly in Scandinavian countries;

iii) the point-count method, which has become most widely adopted in France and North America.

In brief, the main features of each technique may be summarised as follows.

i) The spot-mapping method (which is described more fully below) monitors the entire breeding population of a complete habitat and, as such, is accepted as the most accurate method (e.g. Blondel 1983). However, it requires several visits with time evenly distributed throughout the habitat and is therefore a particularly time-consuming technique. Moreover, it is only applicable to the breeding season when certain (passerine) birds are exhibiting territorial behaviour in particular habitats (e.g. woodland).

ii) The line-transect method uses a transect of fixed length and width. Population density is then estimated from the birds recorded. This technique is believed to be a more time-efficient method than (i) in terms of the area covered per unit of effort (Emlen 1971, 1977, Shields 1979), hence its popularity in countries with thin observer cover. Moreover, it is applicable throughout the year, is an easy way to sample large areas and is considered by some to be as accurate as the spot-mapping method (Emlen 1971).

iii) The point-count method requires an observer to remain stationary for about 15-20 minutes and to map all bird contacts during that time (Blondel *et al.* 1970). From these data the number of species may be given either in the form of an index of abundance (Indices Ponctuels d'Abondance) or in frequencies (Echantillonnage Frequentiel Progressif; Blondel *et al.* 1981).

For the purposes of this study in East Leicestershire, it was considered most appropriate to census the total breeding population of each study woodland using the spot-mapping method. This was undertaken at each of the 16 sites at Wistow, Billesdon Coplow and Botany Bay Fox Covert. However, to sample parts of the interior zones of Loddington Reddish and Owston Big Wood, a modified point-count method was utilised (after Whitcomb *et al.* 1981). This modification uses plots of a predetermined dimension, 200 m square (4 ha).

Detectability of birds in any survey is species-specific and is dependent on several factors including the time of day, weather, observer speed, habitat structure and the birds' behaviour. In general terms, censusing is considerably more successful if spread over a period of several weeks, is undertaken in calm weather conditions (Robbins 1981a), is timed to coincide with the morning or evening peak of bird song (Robbins 1981b) and survey time is adequate. These criteria were met during almost all visits to Leicestershire woods (see Appendix 4). In addition care was taken to spend much more time on survey work than in most other studies. For instance, for the point-counts, 3x30 minute visits were made to each point in Loddington Reddish and Owston Big Wood. This compares with 3x20 min visits made by Whitcomb *et al.* (1981), 4x8 min visits by DeSante (1981), 1x20 min visit by Scott & Ramsey (1981) and 1x10 min visit suggested by Fuller & Langslow (1984).

The Common Bird Census.

This spot-mapping method (Enemar 1959) has been operated annually in Great Britain since 1962 (by the British Trust for Ornithology) as the so-called Common Bird Census. Through the provision of annual species' indices, it monitors annual changes in populations of common breeding birds.

The methodology is now standardised by the International Bird Census Committee (1969).

Several visits are made to a site and the position of all contacts with birds exhibiting territorial behaviour are mapped. Different symbols are used to designate different activities. An example of Visit B to Billesdon Coplow is shown in Figure A3.1. The symbols are explained in the caption accompanying that figure. After the completion of all visits, the original data are transferred to individual species' maps and clusters of contacts (usually 2 or 3) are used to assess the position of territories. Examples of territories recorded for Willow Warbler and Treecreeper at the 16 study woodlands in 1987 are presented in

Appendix 3

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Figures A3.2 and A3.3 respectively.

Figure A3.1. Map of all contacts registered with birds exhibiting territorial behaviour at Billesdon Coplow on 7 May 1987. Note: this visit is selected for illustration owing to the relatively small number

Note: this visit is selected for illustration owing to the relatively small number of contacts.

B,Bo,B2 a contact with species B (male or female) B,Bo,B2 a contact with species B (male or female) B position of singing bird B position of calling bird E position of aggressive contact between males extent and direction of observed movement B----B simultaneous or contemporary contacts of singing males Species are as follows: B, Blackbird; BC, Blackcap; BF, Bullfinch; BT, Blue Tit; CC, Chiffchaff; CH, Chaffinch: D, Dunnock; GR, Green Woodpecker: GS, Great Spotted Woodpecker; GT, Great Tit; NH, Nuthatch; R, Robin; SF; Spotted Flycatcher; ST, Song Thrush; TC, Treecreeper; WR, Wren; WW, Willow Warbler.



Figure A3.2

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(see over)

Figure A3.2. Distribution of Willow Warbler territories at Botany Bay Fox Covert and Billesdon Coplow (upper map) and in the Wistow patches (lower) in 1987. Note different scales used.

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Figure A3.3

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(see over)

Figure A3.3. Distribution of Treecreeper territories at Botany Bay Fox Covert and Billesdon Coplow (upper map) and in the Wistow patches (lower) in 1987. Note different scales used.

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Appendix 4.

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Dates, tim	es and weatl	ner of field	d visits.						
VISIT No.	VISIT DATE No. of VISIT		TIME of VISIT	TOTAL SURVEN TIME (mins)	CLOUD COVER	GENERAL WEATHER CONDITIONS			
Billesdon	Coplow . (11.	4 ha)							
1	16 April		1820-2000	100	0/8-1/8	calm			
2	7 May		1730-1940	130	0/8	calm			
3	13 May		1635-1935	180	5/8-6/8	strong breeze			
4	20 May		1635-1935	180	1/8-2/8	light breeze			
5	27 May		1645-1915	150	1/8	calm			
6	3 June		1705-1935	150	6/8	strong breeze			
7	20 June		1500-1600	60	6/8	light breeze			
Botany Ba	y Fox Cover	t . (14.9 h	a)						
1	19 April		1840-1950	70	2/8-4/8	strong breeze			
2	7 May		1640-1720	40	0/8	calm			
3	27 May		1405-1635	150	1/8	calm			
4	27 June		1445-1645	120	1/8-3/8	calm			
Loddington	Reddish. (3	6.2 ha)							
1	17 April	nlot A	1730-1800	30	0/8	calm			
-	iii iipiii	plot R	1800-1830	30	0/8	calm			
		plot D	1830-1900	30	0/8	calm			
		plot D	1900-1930	30	0/8	calm			
2	25 May	plot A	1845-1915	30	7/8-8/8	calm			
-	20 1.14)	plot B	1915-1945	30	7/8-8/8	calm			
		plot C	no visit						
		plot D	1945-2015	30	7/8	calm			
3	30 June	plot A	1635-1705	30	8/8	calm			
		plot B	1805-1835	30	8/8	calm			
		plot C	1735-1805	30	7/8-8/8	calm			
		plot D	1705-1735	30	7/8-8/8	calm			
Owston Bi	ig Wood. (1	10.7 ha)							
1	29 April	plot A	1820-1850	30	1/8	calm			
	-	plot B	1750-1820	30	1/8-2/8	calm			
		plot C	1720-1750	30	2/8	calm			
		plot D	1650-1720	30	1/8-2/8	calm			
2	25 May	plot A	1745-1815	30	2/8	calm			
	-	plot B	1715-1745	30	3/8	calm			
		plot C	1645-1715	30	2/8	calm			
		plot D	1615-1645	30	4/8	calm			
3	10 June	plot A	1910-1940	30	6/8-7/8	calm			
		plot B	1835-1905	30	7/8	calm			
		plot C	1750-1820	30	8/8	calm			
		plot D	1715-1745	30	8/8	calm			

TABLE A4.1. General weather conditions, dates, times and duration of field visits made to study woodlands to census breeding avifauna, 1987.

VISIT DATE TIME CLOUD GENERAL							PATCH NUMBER												
No.	vî	f SIT	of VISIT	COVER	WEATHER CONDITIONS	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	14	Apr	1830-1900 1910-1940	3/8 3/8	caln	30							30		30				
2	15	Apr	$1255 - 1325 \\ 1335 - 1405 \\ 1415 - 1425 \\ 1425 - 1455 \\ 1500 - 1510 \\ 1515 - 1520 \\ 1520 - 1530 \\ \end{array}$	7/8-8/8 7/8-8/8 7/8-8/8 7/8-8/8 7/8-8/8 7/8-8/8 7/8-8/8 7/8-8/8	light breeze	30 30 30 5 10													
3	5 1	Hay	1815-1845 1845-1915	1/8-2/8 2/8-3/8	light breeze												30		3
4	9 1	Нау	1005-1015 1020-1025 1030-1100 1100-1110 1115-1125 1140-1200 1200-1220 1230-1250 1255-1310 and 1545-1600 1515-1545	3/8 3/8 1/8-2/8 1/8-2/8 1/8-2/8 3/8-4/8 2/8-4/8 1/8 1/8 0/8-1/8	light breeze								30		3				
5	12 1	May	1710-1740 1955-2025	6/8-7/8 7/8-8/8	strong wind with showers												30		3
6	14 1	Нау	1615-1625 1630-1640 1655-1725	7/8 8/8 8/8	strong wind with showers		10				10	3	0						
7	16	Hay	$\begin{array}{c} 0.945-0.955\\ 0.955-1010\\ 1010-1020\\ 1020-1035\\ 1105-1120\\ 1130-1150\\ 1200-1210\\ 1210-1220\\ and\\ 1750-1810\\ 1810-1840\\ \end{array}$	4/8 4/8 4/8 3/8 3/8 6/8-4/8 4/8 4/8 7/8 7/8-8/8	caln			15	15	10	10	15	15	20	10		30		3
8	21 1	Hay	1900-1930 1940-2010 2015-2025	3/8-4/8 3/8 5/8-6/8	strong breeze						10	3	0	30					
9	23	May	1445-1500	8/8	strong breeze		15												
10	25 1	Нау	1205-1235 1255-1325 1340-1350 1350-1430	8/8 8/8 7/8 7/8	calm			3	0		10	3	10	30	[
11	31	Hay	1800-1830 1830-1845 1900-1940	3/8 3/8-4/8 3/8	light breeze			3	0	15	[4	0	1					
12	20 .	June	0945-1015 1030-1040 1040-1110 1110-1140	1/8 1/8 1/8 2/8-4/8	light breeze									30	10	I	30		3
13	28 .	June	1745-1815 1815-1825 1830-1840 1845-1855	8/8 8/8 8/8 8/8	light breeze	10	10	3	0	10	1								
	TOTAL SURVEY TIME (mins)					20	55	18	0	55	60	23	80	160		20	00	1	18
			то	TAL No. c	f VISITS	3	5	6	6	5	6	7	7	6	6	7	7	7	6

TABLE A4.2. General weather conditions, dates, times and duration of field visits to the Wistow patches (W1-W14), 1987.

Appendix 5.

The Nest-box Scheme at Billesdon Coplow.

A total of 59 small-hole (28 mm) nest-boxes were erected throughout Billesdon Coplow with roughly equal numbers in each half of the wood (Table A5.1, Figure A5.1a). Breeding progress was monitored in each box from mid-April to early July and was recorded on a Nest Record Card (Figure A5.1b). Later, after the breeding season, these cards were submitted to the British Trust for Ornithology, which is responsible for organising the Nest Record Scheme nationally.

Table A5.2 gives the first day of laying in all nest-boxes occupied by Blue Tits between 1980-87 in relation to the annual mean date for the entire wood. The overall mean date for each box is presented in the final column and these values are shown in Figure 5.17 to show the spatial distribution of 'early' and 'late'boxes.

		1980	1981	1982	1983	1984	1985	1986	1987
southern	half	25	27	27	27	32	32	32	32
northern	half	16	23	23	23	27	27	27	27
total		41	50	50	50	59	59	59	59

TABLE A5.1. Number of small-hole nest-boxes erected in the southern and northern halves of Billesdon Coplow, 1980-87.
Figure A5.1

(see over)

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Figure A5.1. (a) Distribution of small-hole (28 mm) nest-boxes at Billesdon Coplow. Horizontal line is used to divide wood into two approximately equal halves.

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(b) Example of a Nest Record Card as used for nest-box 6 in 1982.

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	NO. of	EGGS	or YO	UNG at	each visit. Record here stage of	COUNTY If this record is entered on	Of
D Day	ATE Month	G.M.T.	EGGS	YNG.	if eggs warm; age of γoung; ring nos. etc.	LEICESTERSHIRE ATLAS CARD	Use D
24	APRIL	16.15			NESTBUILDING COMM	LOCALITY (place-name) Grid Ref	
2	MAY	1615	2			COPLOW 709045	5
8		16.15	6		+ I BROKEN.		4
15		5.40	11			ALTITUDE above sea level	
22		1545			9 SITTING	HABITAT RURAL/SUBURBAN/URBAN F	=
١	JUNE	19.30		~		WOODLAND (3)	
5	u	19.30		~			
12	u	16.15		11	RINGED B596376 - 86	NEST BOX SITED ON OAK.	
19		15.45		2	DEAD B596380/82		
					OTHERS PRESUMED	NEST SITE NEST BOX (AI) HOLE IV	81
					FLOUDN.	FRAM PACE OF WOOD BAD CORA	JS JS
						FENCE DIVIDING, SITE SHADE	5

NEST	WDLD									MEAN
-BOX I	HALF	1980	1981	1982	1983	1984	1985	1986	1987	DATE
No.		. 1	. 1		1.2	10	1 0			+3
1	N	+1	+1	+2	+2	+0	70			+5
2	IN N	+3	+5	+10	+3	+7	+2		-3	+2
4	N	-7	+7	=	+4	• •	. 2		C C	+1
5	N	$+10^{-1}$		-1	-4		+3			+2
6	N	+1	+6	=						+2
8	N								-4	-4
9	Ν					=		+7		+3
10	Ν	-5	+5							0
12	N	-	=	-1						0
13	N	+8	+5	+2		2			+2	+4
14	N	. 7	16	1 1 4	1	-3 -5	т 3			-5 +5
15	IN NI	+ /	+0	Ŧ 14	-1	τJ	τJ			+14
10	N	+ 14			+3					+4
18	N	10	+4	+ 3	+8	+5	+4		+3	+4
19	N	-2	+1	+7	-5				=	0
21	N	-5	-6	+1	-					-3
22	N	+5	-		+8					+6
23	S .	+2				-2				0
24	S	+ 1	-1	-7	-5	+3	•		-3	-2
25	S	-10	-1	-4	+2					-3
26	S	-8	-13	=	+1	-6	-4			-5
28	S		-1		+1			+5		+1
29	S					+ 3			2	+ 3
30	5	+11	4	2		-4 _4			+11	+1
31	s s	+10	-4	-2		-4				-2
33	S	-1	+7	+ 8	-3	-2	+3	-1	+2	+1
34	Š	+2	+1	+4	-6	+5			+10	+2
35	Š	-7								-7
36	S		-14							-14
37	S	-6	+3	-7	+2		+2	=		-1
38	S	+6		_					_	+6
41	S		=	-2	-1	=	-	2	-5	-1
42	S	-8	+7	+6			-5	-2		0
44	S	-11	-18	-9	4	=				-9
46	5	+1	+8		-4 15	-2				+5
47 97	s s			_4	-1				+9	+1
04 ⊿0	S	-11	_	+1	-6	+4	-6	+1	-1	-2
50	S	+3			Ŭ		Ŭ		-	+3
51	Š	-10	-15	-7	-6	-4	-13			-9
52	ŝ		-2	-4	-2	+4	+5		-4	0
53	S	+9	-2							+3
54	S		-14	-2	+4	=	+3	-4	-3	-2
56	Ν			+3	-3			+5		+1
57	Ν		+1	+1	. =	-3	+5	-4		0
58	N			-4						-4
59	Ν		+5				+4			+4
60	N		+7							+/
61	N		+13	, 11	. 7	. 0	1.4			+ 13 + 7
62	N C		+11	+11	Ŧ/	79	±4 _0		_ 	-2
61 61	с С					-6	-7		17	-6
65	s S					-0				Υ.
66	Š					-3	-3	=		-2
67	Ň					+2	+8	-1	=	+2
		-								

TABLE A5.2. Date of laying in each nest-box in relation to the mean annual laying date for Billesdon Coplow, 1980-87.

Note:

+ indicates a laying date after the mean annual laying date. = indicates the same laying date as the mean annual laying date.

- indicates a laying date before the mean annual laying date.

Appendix 6.

Examples of meteorological data recorded at the two weather stations, Billesdon Coplow, 1984.

DATE	RUN	OF WIND	SOLAR	RADIATION
APRIL	SOUTH	NORTH	SOUTH	NORTH
1	23853	12731	7016	5410
2	14613	49425	7785	6520
3	27560	30399	10340	8432
4	70831	93480	10674	7854
5	32791	55158	6381	5841
6	11225	38532	1467	1343
7	11361	67167	6247	5461
8	14174	57527	6032	5144
9	12643	51893	4215	3709
10	14710	47583	7473	6745
11	56252	35960	3419	2996
12	32098	14186	11548	10604
13	40113	37296	6518	6238
14	56407	27515	11967	10283
15	60241	75019	5489	4077
16	41025	10280	8117	6722
17	34481	89477	10229	8353
18	59838	23441	8316	7136
19	56888	25928	8204	7021
20	75288	29984	13342	10165
21	60484	28901	11930	9529
22	19594	13032	4877	4238
23	56529	63084	14291	10870
24	47965	40941	15985	11531
25	39283	39245	13429	10160
26	39340	37396	14526	11600
27	30111	10745	13852	10930
28	60652	71591	16265	13288
29	78236	46339	15496	12611
30	80912	11803	13514	10387

Appendix 6.2. Daily total values of run of wind and solar radiation at the southern and northern weather stations, Billesdon Coplow, April 1984. Higher daily values are shown in **bold**. Note the absence of a pattern with airflow but that daily solarimeter totals at the southern station were consistently higher than the northern station. Note also seasonal increase in radiation totals.

1

			1-20
TATION AMBIENT	50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 50 <t< td=""><td>$\begin{array}{c} 6.0+0.6 \\ 4.2+0.4 \\ 5.3+0.4 \\ \hline \end{array}$</td><td>from 1 March rn weather iin table.</td></t<>	$\begin{array}{c} 6.0+0.6 \\ 4.2+0.4 \\ 5.3+0.4 \\ \hline \end{array}$	from 1 March rn weather iin table.
RN WEATHER ST	4 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8 3.8	$\begin{array}{c} 6.7 \pm 0.7 \\ 4.7 \pm 0.4 \\ 5.9 \pm 0.5 \end{array}$	ected daily f 1 and norther below the ma spectively.
NORTHE NEST-BOX (4.1 3.7 3.7 3.7 3.7 3.7 3.7 3.7 3.7 3.7 3.7	6.9+0.7 4.7+0.4 6.0+0.5	cordings (colle om the souther an values are 1 1830-1930 res
TION AMBIENT	4.2 4.2 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.6 3.7 3.8 3.9 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11 3.11	$\begin{array}{c} 7.5+0.7\\ 4.8+0.5\\ 6.3+0.5\\ \end{array}$	<pre>mperature rec fune 1983) frc pril 1984. Me 0430-0530 and</pre>
I WEATHER STA CONTROL-BOX	4.8 4.8 3.9 3.9 3.9 3.1 3.1 3.1 3.1 4.8 4.1 5.3 4.1 111.0 111.0 111.0 111.0 111.0 111.0 111.0 111.0 111.0 111.0 111.0 111.0 10.0 111.0 10.0 111.0 10.0 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.10	8.8+1.0 5.2+0.5 7.3+0.7	of hourly te 16 April-23 J Coplow, 10 A vere between
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Paired readings are from dry (left) and wet (right) bulb thermistors.

Appendix 7.

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Plots of (a) bird species number, (b) number of territories, (c) breeding density and woodland area.

(see over)

Figure A7.1. Plots of species richness (SPPRICH) and woodland area (WDLDARE), East Leicestershire, 1987. In this, and the following figures. variables are plotted arithmetically (left), with the x variable log-transformed (middle) and with both variables log-transformed (right).

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Figure A7.2. Plots of number of breeding pairs (PAIRS) and woodland area (WDLDARE), East Leicestershire, 1987.

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0.01 WDLDARE 14.90	-4.60517 LNWDARE Z.70136 CORRELATE C1 C3	-4.60517 LNWDARE 2.70136 CORRELATE C4 C3
ORRELATION (N=16) PAIRS VS WDLDARE = 0.954	CORRELATION (N=16) PAIRS VS LNWDARE = 0.806	CORRELATION (N=16) LNTERR VS LNWDARE = 0.971
REGRESS Y IN C1 USING 1 PREDICTOR IN C2	REGRESS Y IN C1 USING 1 PREDICTOR IN C3.	REGRESS Y IN C4 USING 1 PREDICTOR IN C3
AIRS = 11.38917 +9.98357*WDLDARE	PAIRS = 44.07466 +21.78166*LNWDARE	LNTERR = 3.20258 +0.69705*LNWDARE
DLUMN COEFFICIENT STDEV T 11.38917 3.99951 2.848 DLDARE 9.98357 0.84134 11.868	COLUMN COEFFICIENT STDEV T 44.07488 7.30523 6.033 LNWDARE 21.78166 4.28248 5.086	COLUMN COEFFICIENT STDEV T 3.20258 0.07834 40.882 LNWDARE 0.69705 0.04592 15.179
= 14.192 DF=14	S = 27.965 DF=14	S = 0.300 DF = 14
-SQUARED = 90.957x	R-SQUARED = 64.886%	R-SQUARED = 94.272X

Figure A7.3. Plots of breeding bird densities (BD) and woodland area (WA) in all 16 study woodlands, East Leicestershire, 1987.

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T 40.887 2.70136

-6.598

Figure A7.4. Plots of breeding bird densities (BD) and woodland area (WA) in 15 study woodlands, with the smallest patch (W1, 0.01 ha) being omitted through giving inflated values.



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ABSTRACT.

MICROCLIMATIC FACTORS IN AVIAN BREEDING PATTERNS: IMPLICATIONS FOR WOODLAND NATURE RESERVE DESIGN.

by

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Temporal variation in the first day of egg-laying of the Blue Tit within a deciduous woodland is accounted for by the small but significant spatial differences in microclimate, particularly temperatures. The warmer areas, which are confined to the southern half of the wood, are also characterised by larger clutch sizes and greater survival of nestlings into the local population.

Furthermore, examination of the total breeding avifauna of this wood shows densities to be highest in the warmer areas and particularly along the south-facing edge zones.

Investigation of 16 woodlands (range 0.01-14.9 ha) shows that bird species richness increases with increasing woodland area but that there is an inverse relationship between breeding bird density and woodland size. However, the total species number and breeding density of 14 small woods are markedly higher than those of a single large wood of roughly equal size. These differences are accounted for by the high proportion of edge zone within a group a small woodlands (86%) compared with the single larger wood (24%). The clear importance of small woodland patches to the total avifauna of East Leicestershire, and presumably other parts of lowland England, is stressed.

The proportion of edge zone is influenced by woodland size, shape, internal structure (including the presence of rides and clearings), slope and aspect. Combinations of these factors can result in edge zone depth being considerably increased in a woodland.

The importance of the edge zone to maximising species numbers is described in relation to various strategies of woodland nature reserve conservation. One such strategy advocates that species numbers and breeding densities in a very large wood can be enhanced by careful attention to management proposals such as ride-widening, tree-thinning and coppicing. The influence of these findings on future large-scale planting is also discussed.