BTO Research Report No. 245

A Review of Possible Causes of Recent Changes in Populations of Woodland Birds in Britain

Authors

D. Vanhinsbergh, R.J. Fuller and D. Noble

Report of work carried out by The British Trust for Ornithology
as part of the JNCC / BTO Partnership

November 2003

British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU
Registered Charity No. 216652

British Trust for Ornithology

A Review of Possible Causes of Recent Changes in Populations of Woodland Birds in Britain

BTO Research Report No. 245

D. Vanhinsbergh, R.J. Fuller and D. Noble

Published in November 2003 by the British Trust for Ornithology
The Nunnery, Thetford, Norfolk, IP24 2PU, UK

ISBN 1-902576-98-5

CONTENTS

Page No.

Page No.

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Summary

(1) Large declines in the breeding populations of several woodland birds have occurred in Britain in recent decades. This report provides a summary of these population and range changes. It considers the extent to which such declines may be occurring on mainland Europe and reviews the possible causes. Possible causes of population declines are reviewed under four broad headings: (a) Large-scale environmental change, (b) Large-scale trends in land management and land-use, (c) Fine-scale trends in habitat quality, and (d) Pressures from other organisms. The strongest hypotheses are identified and associated research needs are discussed.

(2) The BTO's Common Birds Census data were analysed using Generalised Additive Models to generate smoothed indices which identify underlying trends. The CBC trends suggest that 12 out of 32 woodland species have declined by more than 25% and 9 species increased by more than 25%, between 1966 and 1999. The 12 declining species with estimated percent population changes are: Spotted Flycatcher *Muscicapa striata* (-85%), Lesser Spotted Woodpecker *Dendrocopos minor* (-81%), Lesser Whitethroat *Sylvia curruca* (–79%), Lesser Redpoll *Carduelis cabaret* (–78%), Tree Pipit *Anthus trivialis* (-75%), Willow Tit *Parus montanus* (-74%), Marsh Tit *Parus palustris* (-68%), Woodcock *Scolopax rusticola* (-61%), Dunnock *Prunella modularis* (-58%), Willow Warbler *Phylloscopus trochilus* (-53%), Song Thrush *Turdus philomelos* (-48%), Bullfinch *Pyrrhula pyrrhula* (-38%). Caution is needed in interpreting the changes of Lesser Redpoll, Tree Pipit and Woodcock mainly due to concern that the data may not be sufficiently representative of the population. The CBC contains relatively few coniferous plots and the majority of plots are in the southern half of Britain; consequently the data may not be fully representative of British woodlands. These declines in abundance have generally been accompanied by contractions in range as shown by estimates of range change derived from the two breeding birds atlases (ca. 1970 and 1990).

(3) Several woodland species for which a population trend could not be calculated from CBC data showed a reduction in occupancy of 10-km squares between the two atlases: Long-eared Owl *Asio otus*, Nightingale *Luscinia megarhynchos*, Hawfinch *Coccothraustes coccothraustes* and Capercaillie *Tetrao urogallus.* For the latter three species there are also independent data indicating a reduction in numbers. Declines may also be occurring in Pied Flycatcher *Ficedula hypoleuca* and Wood Warbler *Phylloscopus sibilatrix.*

(4) The population trends of the declining species show a variety of temporal patterns. Some have declined more or less steadily, but in other species the decline started in the late 1970s or early 80s, while others show an initial increase followed by a decrease. The geographical patterns of range change also vary between species. The declining species also show much variation in life history and ecological attributes. They include migrants and sedentary species, habitat specialists and habitat generalists, species with open nests and hole-nesters, ground-nesters and birds that nest in the shrub or field layer, and species that vary in foraging sites and diet.

(5) A review was undertaken of the available information on population trends of woodland birds in mainland Europe. Based on essentially qualitative data, most of the species that are declining in Britain appear to be stable, or show no clear trend in many parts of Europe. However, these apparent population trends must be interpreted cautiously because high quality long-term data are unavailable for many countries. Quantitative studies indicate that major declines have recently occurred in several woodland birds in France; in contrast data from the Netherlands and Poland do not show this pattern. If the declines have indeed been more pronounced in Britain than in most parts of Europe, this could either mean that conditions have deteriorated in Britain more than elsewhere in Europe, or that wider-scale

processes are affecting population dynamics causing some species to gradually withdraw at the western edge of their European range.

(6) Four potential causes of decline were considered that related to **large-scale environmental change**.

(i) Changing environmental conditions (climate or habitat change or both) on the winter grounds of long-distance migrant birds. This is almost certainly a significant factor in the declines of several migrant species.

(ii) Climate change on the breeding grounds. This could be significant for some long-distance migrants which may find it difficult to adjust the timing of their breeding to match the changing phenology of insect food supplies; they may also be at a competitive disadvantage with resident species that may adapt more readily to climate change, and even benefit from such changes e.g. from milder winters.

(iii) Large-scale changes in the health of trees have occurred in recent years, including reduction in crown density of oak in Britain. It is concluded that this is unlikely to be responsible for the observed declines.

(iv) There is concern that widespread declines in availability of invertebrate food may have occurred for a variety of reasons including climate change, diffuse pollution and surrounding land management. If such food reductions have taken place, this could be an important factor contributing to declines in some woodland birds.

(7) Eight potential causes were considered that related to **large-scale trends in land management and land-use**.

(i) Agricultural intensification may have reduced the quality of non-woodland habitats that are used by some species of woodland birds e.g. hedgerows and field margins used by Bullfinches. The quality of woodland edges as habitats for birds may have deteriorated as a result of grazing pressure, trimming and spray drift.

(ii) Fragmentation and loss of woodland is unlikely to be a major factor in the declines because these have occurred within many individual woods and wooded landscapes that have not become fragmented in recent times. The scale of recent habitat loss has been insufficient to explain the declines.

(iii) Changes in age structure of woodland may be significant, especially for species associated with young conifer plantations (e.g. Lesser Redpoll, Tree Pipit).

(iv) Recent changes in tree species composition of woodland are not thought to be drivers of the woodland bird declines.

(v) Reduction in broadleaved woodland management may have reduced habitat quality by shading out low vegetation with the loss of nest sites and food supplies.

(vi) Increased recreational pressure within woodland cannot explain the national declines.

(vii) Increasing road traffic is unlikely to be a major factor.

(viii) Rearing of Pheasants *Phasianus colchicus* may have locally affected habitat quality.

(8) Three possible causes relating to **fine-scale changes in habitat quality** were reviewed.

(i) Intensified grazing and browsing pressure by increasing numbers of deer is very likely to have caused a reduction in habitat quality and contributed to the declines of some woodland birds.

(ii) Changes in the availability of dead wood are not thought to be significant.

(iii) Changes in lichens (important as a prey habitat, for food storage and as nest material) are not considered important.

(9) Three possible factors relating to **other organisms** were considered.

(i) Increasing predation pressure (especially from Grey Squirrels *Sciurus carolinensis*, Great Spotted Woodpeckers *Dendrocopos major* and corvids) could be significant for some declining woodland birds.

(ii) Enhanced inter-specific competition may be occurring between some increasing species and some declining species. Evidence exists that Willow Tits are being ousted from nest sites by Blue Tits *Parus caeruleus* and Great Tits *Parus major*.

(iii) Parasites and disease could be factors in the declines but there is no evidence that this is the case.

(10) We conclude that there is no single general explanation or hypothesis to account for the declines in woodland birds, as there was with agricultural intensification for farmland birds. Individually, the factors discussed in this review may be insufficient to limit bird populations. Some woodland birds could be affected simultaneously by several factors that may interact or combine in a diffuse way sufficient to reduce reproductive output or survival. Changes in food supply, predation, inter-specific competition and physical deterioration of habitat may be acting simultaneously on some species. We also suggest that conditions for woodland birds are probably rather different in Britain to those found at similar latitudes in mainland Europe.

(11) Seven factors emerge from this review as likely contributors to recent declines in woodland birds. We make suggestions about high priority process-based research in these areas, though we also recognise that autecological studies would be valuable.

(i) Pressures on migrants during migration or in winter.
(ii) Climate change on the breeding grounds.
(iii) Reduction in invertebrates.
(iv) Impacts of agriculture on woodland edges and hedgerows.
(v) Reduced management of woodland.
(vi) Intensified pressure from deer.
(vii) Changing predation pressure (squirrels and corvids).

1. INTRODUCTION AND BACKGROUND

Bird populations in the wider countryside of Britain underwent large changes in the second part of the 20th century. The majority of specialist farmland birds declined in the 1970s and 1980s, largely as a result of agricultural intensification (Siriwardena *et al.* 1998, Chamberlain *et al*. 2000, Fuller 2000). It is less widely appreciated that populations of several woodland birds in Britain have also declined considerably in recent decades. This report summarises the extent of these declines and discusses the possible causes. The aim is to establish hypotheses and to identify priority areas of research that will help to elucidate the factors involved.

During the 20th century substantial changes occurred in British woodland. The total area of woodland approximately doubled and marked changes occurred in tree species composition, age structure and management of woodland. These changes were driven principally by shifts in forestry policy and their impacts varied temporally and spatially across the country. Several patterns of change can be identified in the national forest resource over the last century, though it is important to avoid taking too simplistic a view of these changes. As a background to this review, the most pronounced changes are summarised below; for more detail see Peterken & Allison (1989), Avery & Leslie (1990), Spencer & Kirby (1992), Peterken (1993), Fuller (1995).

(1) The area of conifers increased substantially, especially in upland areas of Scotland, largely as a result of afforestation but also through the conversion of broadleaf woodland to conifer plantations, the latter leading to loss of ancient semi-natural stands. This was especially marked since the Second World War and by mid century the area of coniferous woodland exceeded that of broadleaved for the first time in some 7000 years (Peterken 1993). The increase in conifers was achieved mainly through large-scale planting which initially created predominantly single-species stands of even age. The total area of broadleaved woodland in Britain has shown relative stability, though there appears to have been a pre-war increase, followed by a reduction with another increase in the last decades of the century.

(2) There was a large increase in the area of woodland composed of non-native tree species and of the abundance of non-native trees generally; by the 1990s Sitka spruce *Picea sitchensis* was probably the most abundant tree in Britain.

(3) There was widespread post-Second World War clearance of woodland, particularly small woods in areas of intensive arable agriculture. The losses were mainly of coppice woods, often of ancient origin, converted to arable production. Whilst the rate of clearance has dropped, woodland losses have continued, especially to developments including road building and housing.

(4) Many woods will have become more isolated from other woody vegetation due to extensive losses of small woods and hedgerows that occurred mainly after the Second World War. The number of large trees in the countryside outside woodland has diminished, especially through Dutch Elm disease, and this may have further reduced the connectivity between woods.

(5) Large changes have taken place in management systems. Traditional coppice and wood pasture have declined. Many formerly coppiced woodlands have fallen into disuse and been simply neglected for many decades. However, some former coppiced woods have been cleared and converted to agriculture or converted to conifers. Commercially managed coppice has become largely concentrated in south and south-east England and now forms only 2.1% of the total woodland area in England (Forestry Commission 2001). Most commercially managed woodland now operates as high forest, with conifers managed mainly by clear-felling systems and broadleaved stands mainly by group felling.

(6) Scrub habitats have also changed in status during the 20th century (Mortimer *et al.* 2000). Where traditional grazing practices have been abandoned on downland, commons and fens, there has generally been invasion of scrub which in many cases has gradually turned to woodland.

Since approximately 1980 there has been a shift in several patterns of woodland creation and management. These have been driven by a diversity of reasons including the conservation of biodiversity, creation of game habitat, landscape enhancement, social recreation and production of raw materials.

- In most lowland areas there has been a presumption in favour of broadleaves and many former ancient broadleaved that were planted with conifers are now being restored to broadleaves.
- There has been substantial creation of new woodland on farmland, initially through the Farm Woodland Scheme which was introduced in 1988 and subsequently renamed as the Farm Woodland Premium Scheme in 1992.
- Increased rates of hedgerow planting are evident in many regions and this may also eventually help to reduce the isolation of many woods.
- As many of the large new conifer forests have reached the end of their first rotation, the opportunity has been taken to 'restructure' them into smaller and more structurally varied compartments often with a modest broadleaved component.
- 'Community forests' are being established at the edge of urban areas and a 'National Forest' project has commenced in the Midlands.
- There has been a shift away from the use of clear-felling in broadleaved woods to smaller-scale group-felling. There is also growing interest in alternative high forest systems, especially continuous cover, although these remain localised.
- A small-scale revival of coppicing has occurred, especially in ancient woods managed for nature conservation. There is also considerable interest in short-rotation coppice as a renewable fuel source.
- Many areas of open space within woodland, especially rides and glades, are now managed in ways perceived to be sympathetic to wildlife.

These diverse changes in British woods during the 20th century will have affected the extent and quality of habitat for woodland plants and animals in complex ways. Even though woodland constitutes only 11.6% of the total land area of the United Kingdom (Forestry Commission 2001a), it holds more species of breeding birds than any other major habitat (Fuller 1982, 1995). Indeed, Fuller (1995) estimated that 25% of bird species regularly breeding in Britain are associated with closed-canopy woodland and scrub and a further 15% use open scrub or young plantations. Although most British woodland birds are widespread, and few of them are nationally scarce, there is increasing evidence that several species declined markedly in Britain in recent decades (Marchant *et al*. 1990, Gibbons *et al*. 1993, Gregory *et al.* 2001, Baillie *et al.* 2002).

In this report we: (1) provide estimates of population change for 32 British woodland birds and identify those that declined most heavily in woodland in Britain, during the period 1966-1999; (2) compare the attributes of declining and non-declining woodland birds; (3) consider the extent to which woodland bird populations are in decline elsewhere in Europe; (4) use a review of the published literature to discuss the main factors that may have contributed to the declines in woodland birds. The focus of this report is on the 41 species that contribute to the government's 'headline indicators' of woodland bird populations (Anon 1999, Gregory *et al.* 1999, 2001).

We discuss the factors that may have influenced woodland birds in recent decades under the following four main headings, a separate chapter being devoted to each. It is important to recognise that some of these factors may be inter-related and also that some species, perhaps all, are affected by several factors.

Large-scale environmental change:

- winter / migration conditions faced by long-distance migrants;
- climate change in the breeding areas;

- tree condition, including effects of air pollution;
- widespread reduction in invertebrates.

Large-scale trends in land management and land-use:

- agricultural intensification;
- fragmentation and loss of woodland;
- changes in age structure of woodland;
- changes in tree species composition of woodland;
- reduction in management of broadleaved, especially formerly coppiced, woodland;
- increased recreational pressure;
- road traffic;
- game management.

Fine-scale trends in habitat quality:

- intensified grazing and browsing pressure;
- changes in availability of dead wood;
- reductions in lichens.

Pressures from other organisms:

- increasing predation pressure;
- enhanced inter-specific competition;
- parasites and disease.

2. CHANGES IN POPULATIONS AND DISTRIBUTIONS OF WOODLAND BIRDS

2.1 Methods

Bird population data for the period 1966-2000 were obtained from the BTO's Common Birds Census (CBC) (Marchant *et al.* 1990). As we were interested in the changes that had taken place in woodland, only data from CBC woodland plots were used. The number of plots varied between years and ranged between 75 and 120, with most plots situated in southern and eastern England (Marchant *et al.* 1990). Data were analysed using Generalised Additive Models (Fewster *et al.* 2000) to calculate an annual smoothed population index for each species, for the period 1966-2000. Smoothed indices were used as they identify underlying trends and remove extreme estimates of change caused by short-term fluctuations in population levels. The percentage population change between 1966 and 1999 was then calculated for each species as:

$$((\text{index}_{1966} - \text{index}_{1999}) / (\text{index}_{1966})) \times 100$$

Although all available data are used in the models, the change in population status was calculated to the penultimate year (1999 rather than 2000) following the recommendations of Gregory *et al.* (1999) to minimise unreliable last-year-effects of the smoothing process in the models. We have arbitrarily treated a species as declining if it has shown at least a 25% decrease between 1966 and 1999.

CBC woodland plots are concentrated in south and central England and Wales. Scotland, south-west England and northern England are relatively sparsely covered by the project (Marchant *et al.* 1990). Therefore, it is not known how representative of national trends are the population trends based on these plots. Following Baillie *et al*. (2002) trends were classified as: (1) based on reliable data and sufficient data, or (2) data that may not be representative of the bulk of the population because of the region or habitat sampled (e.g. Lesser Redpoll *Carduelis cabaret),* sampling protocols (e.g. nocturnal species such as Tawny Owl *Strix aluco*) or small sample sizes (e.g. Redstart *Phoenicurus phoenicurus*). Low reporting rates on CBC plots meant that population indices were not calculated for nine woodland indicator species, so information on their population status was gleaned from other sources wherever possible.

The British distribution of each species in 1968-72 was compared with that in 1988-91 using presence-absence data from the two breeding bird atlases (Sharrock 1976, Gibbons *et al*. 1993). Changes in distribution were expressed as the percentage change in the number of occupied 10-km squares between the two periods. These atlas surveys provide the best data on the distribution of breeding birds in Britain currently available.

2.2 Estimates of Change for British Populations

The CBC trends suggest that 12 out of 32 woodland species have declined by more than 25% and 9 species increased by more than 25%, between 1966 and 1999 (Table 1). The declining species were: Spotted Flycatcher *Muscicapa striata* (-85%), Lesser Spotted Woodpecker *Dendrocopos minor* (-81%), Lesser Whitethroat *Sylvia curruca* (–79%), Lesser Redpoll (–78%), Tree Pipit *Anthus trivialis* (-75%), Willow Tit *Parus montanus* (-74%), Marsh Tit *Parus palustris* (-68%), Woodcock *Scolopax rusticola* (-61%), Dunnock *Prunella modularis* (-58%), Willow Warbler *Phylloscopus trochilus* (-53%), Song Thrush *Turdus philomelos* (-48%), Bullfinch *Pyrrhula pyrrhula* (-38%).

For several of the apparently declining species, the trends reported here may not be truly representative of the UK population. Most woodland CBC plots do not contain conifer plantations, which is particularly relevant in the interpretation of trends for species that are common in this habitat, such as Lesser Redpoll, Tree Pipit, Goldcrest *Regulus regulus* and Coal Tit *Parus ater*. There are very large areas of suitable habitat in northern Britain, and long-term population trends of these species in Scottish conifer plantations are unknown. Nevertheless, in the absence of a better long-term data set for these species, it would be unwise to discount the CBC index completely. It should also be noted that Tree Pipit has been reliably monitored since 1994 by the BTO/RSPB/JNCC Breeding Bird Survey (BBS), which employs a stratified random sampling design, across the UK, and further declines in some of these woodland species have been detected (Baillie *et al*. 2002; Noble *et al*. in press). Further work is needed to obtain reliable estimates of the woodland populations of the remaining species.

There was a significant positive correlation (Pearson r = 0.49, P<0.01) between the % change in range between the two breeding bird atlases and the CBC trend, across the 32 species (Figure 1), suggesting that long-term changes in abundance were generally accompanied by changes in distribution. This comparison should be interpreted cautiously, because there were different levels of coverage in each atlas (Gibbons *et al.* 1993). As one would expect, changes in range are generally smaller than changes in abundance.

Of the nine woodland indicator species where a population trend could not be calculated, Long-eared Owl *Asio otus*, Nightingale *Luscinia megarhynchos*, Hawfinch *Coccothraustes coccothraustes* and Capercaillie *Tetrao urogallus* all decreased in breeding range between the two atlas periods (Table 1). Reliable quantitative population data on the Long-eared Owl is unavailable but for the other three species there is evidence of a national decline and these are also treated as declining species in this report. Intensive research has established that the Scottish population of the Capercaillie is in serious decline and the prospects for the species are somewhat bleak (Moss 2001, Moss *et al.* 2000, 2001). In the case of the Nightingale there has been a very marked contraction of range towards south-east England. A national survey in 1999 actually estimated a larger overall population than in the previous survey of 1980, but this may merely reflect improved coverage (Wilson *et al.* 2002) and there is evidence of a marked decline in numbers during the 1990s (Fuller *et al.* 1999). Furthermore, the number of juvenile Nightingales ringed on the BTO's Constant Effort Sites (CES) declined significantly between 1983 and 1995 (Peach *et al.* 1998). There is clear evidence of a particularly marked decline in numbers of Hawfinches over the last 10 years based on analysis of local records (Langston *et al.* 2002).

For two other species that were not well covered by the CBC, Pied Flycatcher *Ficedula hypoleuca* and Wood Warbler *Phylloscopus sibilatrix*, there is an indication that populations may have been declining recently. Several long-term nestbox studies in different regions of Britain have reported declines in numbers of breeding Pied Flycatchers since the mid 1990s (Anon 2001) as has the Breeding Bird Survey (Baillie *et al*. 2002). The CBC indices for Wood Warbler suggest little long-term change in numbers (Marchant *et al.* 1990), but the Breeding Bird Survey shows a significant decrease in numbers between 1994 and 2000 (Baillie *et al*. 2002). In addition it is important to recognise that Redstart underwent a major range contraction between the two atlases, largely disappearing from woods in central and south-east England. The CBC shows that the populations of Redstarts decreased markedly in the 1970s with a subsequent recovery, though it has not recolonised those parts of the range from which it disappeared. Wood Warbler has also become extremely scarce in central and south-east England and, like Redstart, its main strongholds are now in the west and north.

This account has concentrated on the declining species but it should be noted that several woodland birds have undergone substantial increases in population size between 1966 and 1999 (Table 1). Five species are estimated to have increased by more than 50%: Nuthatch *Sitta europaea*, Sparrowhawk *Accipiter nisus*, Green Woodpecker *Picus viridus,* Wren *Troglodytes troglodytes,* and Blackcap *Sylvia atricapilla*. A further four species are estimated to have increased by between 25 and 50%, Great Spotted Woodpecker *Dendrocopos major*, Tawny Owl, Robin *Erithacus rubecula* and Great Tit *Parus major*. Studies of increasing as well as of decreasing species would be valuable because (a) some may be competitors or predators of declining species, (b) comparisons of demography, diet and habitat selection may give insights into causes of decline for certain species particularly for pairs of species that are taxonomically or morphologically similar.

2.3 Temporal and Spatial Patterns of Change

Population trends for the 10 species showing estimated population declines of more than 50% are shown in Figure 2. These trends show a variety of forms. Some show a more or less steady decline (e.g. Spotted Flycatcher and Marsh Tit), for some the decline appears to have commenced in the late 1970s or early 1980s (e.g. Tree Pipit, Willow Warbler) while others may have shown an initial increase followed by a decrease (e.g. Lesser Redpoll, Willow Tit). Interestingly, an analysis of long-term ringing data, reaching back to the 1950s, has also indicated that Marsh Tits and Willow Tits have been declining since at least the early 1970s (Perrins 2003). The ringing data for Marsh Tit, however suggest that a marked decline occurred in the late 60s and early 70s with a levelling out since about 1990. According to the ringing data, Willow Tit has been in steady decline since the early 70s which matches the CBC trend very closely.

The pattern of range changes, as documented by the 'change maps' published in Gibbons *et al.* (1993), also shows much variation between species. For example, Marsh Tit has undergone a marked contraction in the north of its range whereas Willow Tit has disappeared from many areas of its former range. Tree Pipit has disappeared particularly from 10-km squares in south and central England, but appears to remain just as widespread in the north and west of Britain as it was in 1970. On the other hand, Lesser Spotted Woodpecker, Lesser Whitethroat and Nightingale have shown contraction in the western and northern parts of their ranges but show little contraction in the south-east.

2.4 Attributes of Declining Woodland Birds

The ecological attributes of the 12 declining species identified in Table 1, plus the three species known to be declining from other sources are summarised in Appendix 1. No single ecological attribute was common to all the declining species; they varied widely in their nesting and feeding ecology. They include (1) long-distance migrants, middle-distance migrants and resident species; (2) specialists of mature broadleaf woodland, mature Pinewoods, young conifer plantations and scrub, as well as more generalist species; (3) species with open nests that nest on the ground or in the shrub or field layer, as well as hole-nesting species; (4) species that use a variety of foraging sites; (5) species that feed on seeds as well as insectivores and non-insect invertebrate specialists.

Numbers of declining, stable and increasing species are shown in relation to selected attributes in Table 2. The table shows that 50% of migrants, 31% of cavity nesters, 27% of foliage insectivores and 57% of ground insectivores are classified as declining species. Fisher exact tests were performed to determine whether, for each of the attributes, the observed distributions of species across trend categories were effectively random. In these 2 x 2 tests the numbers of species were classified as declining or not declining (i.e. stable or increasing). Probabilities that the observed, or more extreme distributions, could arise when the null hypothesis is true were: migrants ($P=0.23$), cavity nesters ($P=0.24$), foliage insectivores ($P=0.15$), ground insectivores ($P=0.17$). Therefore, the numbers of declining species in each of the selected attribute groups was no different to that expected by chance, though it should be noted that the numbers of species involved are small. This observation, together with the diversity of patterns in trends and range changes described above, suggests that there are unlikely to be single factors causing the population declines.

2.5 Population Changes in Woodland Birds in Europe

Are the trends in British woodland birds broadly in line with those on a wider European scale? This question is important because knowledge of European trends may give insights into whether causal factors are specific to Britain. When interpreting British trends relative to those at a pan-European scale, one needs to bear in mind that Britain is positioned at the extreme western edge of the European, and often the world, range. Particularly severe declines in Britain may be part of larger scale dynamics in which a species could be contracting from the peripheral parts of its range, where climatic conditions are most likely to be suboptimal. Such a scenario is most likely to apply to species with strong dispersal rates, especially perhaps to ones associated with unstable habitats and to migrant species. See Fuller *et al.* (1999) for a relevant discussion concerning Nightingale. We return to this issue in section 7.3.

Approximately 15 European countries have annual bird monitoring schemes and trials have been undertaken using data for farmland birds to assess whether valid indices can be produced across countries (Van Strien *et al*. 2001). This method has not yet been applied to woodland birds but some indication of trends in other European countries can be gauged from Tucker & Heath (1994) who presented qualitative trends based mainly on expert judgements. Unfortunately, for many species they only provide information on population declines but a complete summary of the estimated national population trends is available in BirdLife International / European Bird Census Council (2001). Hagemeijer & Blair (1997) give much useful additional information on general population trends in Europe including both declines and increases. We provide very general summaries of the trend assessments in Appendix 2; these relate mainly to the period 1970-1990. These qualitative trend assessments suggest that the recent declines in woodland birds in Britain are not being experienced generally in Europe. A very large proportion of the declining species in Britain (13 out of 15) appear to be generally stable or show no clear trend in mainland Europe. Only Capercaillie and Spotted Flycatcher are documented as showing marked declines both in Britain and mainland Europe. This information needs to be interpreted cautiously because the assessments are likely to vary in accuracy from country to country and it is possible that some declines have gone undetected due to lack of hard data. Given the crudity of this information, what can be derived from more detailed studies?

Population trends of birds in Białowieża Forest, Poland, during 1975 to 1999 do not correspond with those in Britain over the same period. Most of the species that are declining in Britain are either stable or increasing in Białowieża Forest (Wesołowski & Tomiałojć 1997, Wesołowski *et al*. 2002). For example, Spotted Flycatcher, Pied Flycatcher, Marsh Tit and Hawfinch have increased in recent decades while Tree Pipit declined up to the mid 1980s but has since been stable. It is thought that in the case of Białowieża, recent population trends have been influenced mainly by factors operating on a regional scale i.e. outside the forest. In western Poland, woodland birds in farm woods appear to have slightly increased between the mid 1960s and 1990s (Kujawa 2002). The Dutch breeding bird atlas (Hustings & Vergeer 2002) provides summaries of population trends which makes an interesting comparison with the British situation. Examples of species apparently showing contrasting population trends in the Netherlands and Britain include Lesser Spotted Woodpecker, Marsh Tit, Willow Warbler and Hawfinch. France is the only country for which we have an indication that populations of several woodland birds are currently declining. Jiguet *et al.* (2002) provide a summary of recent population changes in France which shows substantial decreases (>40% over the period 1989 to 2001) in breeding numbers of five species that are in decline in Britain: Tree Pipit, Willow Warbler, Bullfinch, Marsh Tit and Willow Tit. Interestingly, Wood Warbler and Nuthatch also appear to be in strong decline in France.

Notwithstanding the data from France, these observations raise the strong possibility that declines in populations of woodland birds are not being experienced in many parts of continental Europe as much as they are in Britain. If true, this could mean that conditions for woodland birds have deteriorated to a greater extent than in other parts of Europe. Alternatively, as indicated above, it is possible that we are seeing a situation where populations of some species are gradually withdrawing at the western edge of their European range as a consequence of wider-scale processes affecting their population dynamics. Interestingly, three species appear to be performing better in Britain than on the European mainland: Redstart, Green Woodpecker and Great Spotted Woodpecker (Appendix 2).

It should be noted that Marchant (1992) concluded that for trans-Saharan migrants in Britain and other northern European countries there was a *very general* concordance of trends among countries. It would be desirable to see more quantitative analyses using annual data before reaching firm conclusions about the European generality or otherwise of population trends.

3. LARGE-SCALE ENVIRONMENTAL CHANGE

3.1 Migration and Winter Conditions

It is well established that climatic conditions faced by migrants on their wintering grounds can affect observed breeding populations. The breeding populations of several species that winter in the Sahel and adjacent regions of Africa, such as the sedge warbler *Acrocephalus schoenobaenus* and whitethroat *Sylvia communis*, fluctuate in relation to winter conditions (Winstanley *et al*. 1974, Baillie & Peach 1992). Furthermore, several species of long-distance migrants, or different populations of the same species, have fluctuated in parallel which is suggestive of effects operating on the winter gounds (Marchant 1992, Siriwardena *et al.* 1998). A demographic analysis of the decline in the British Willow Warbler population has indicated that decreased adult survival is responsible which may signal a problem in the wintering areas (Peach *et al.* 1995a).

Whilst it is highly probable that some of the declines of long-distance migrants are driven mainly by changing environmental conditions (climate or habitat change or both) within their winter ranges, there is a critical lack of information and hard evidence. It would seem especially likely that the widespread decline of the Spotted Flycatcher throughout much of Britain and Europe is linked with pressures on migration or in winter. However, the apparent fact that a migrant may be declining in Britain but not elsewhere in Europe cannot be taken as evidence that winter effects are unimportant. Populations from different parts of the breeding range may occupy different parts of the winter range and experience different winter conditions. Alternatively, general declines may become evident initially at the edge of the breeding range (see section 7.3). It should also be recognised that migrants may have particular problems in adapting to changing climatic conditions on the breeding grounds (Both & Wisser 2001, see section 3.2).

The winter distributions of migrant woodland bird species show considerable variation (Keith *et al.* 1992, Urban *et al.* 1997). The two middle-distance migrants that winter in southern Europe or north Africa (Blackcap and Chiffchaff *Phylloscopus collybita*) have not declined. One of the declining migrants, Lesser Whitethroat, winters in the eastern Sahel which is the region traditionally considered to be most unstable climatically. Four of the declining migrants winter mainly to the south of the Sahel zone, in sub-Saharan or equatorial Africa: Spotted Flycatcher, Tree Pipit, Willow Warbler and Nightingale. Not all long-distance migrants have shown major recent declines, notably Redstart and Garden Warbler *Sylvia borin*.

Most relevant research has tended to focus on the Sahel region which is far north of the winter range of most of the declining migrant woodland species, though some migrate through it. Studies on the Willow Warbler, for example, suggest that the breeding population levels of this species are not strongly associated with conditions in the Sahel, which forms part of its migration route (Baillie & Peach 1992, Marchant 1992). It may be more limited by conditions to the south of this zone, where it actually settles. Clearly there is a need to understand better the conditions within the core wintering ranges of different species of migrant birds (and not just within the Sahel) as well as along their migration routes. Most previous work has focused on effects of climate change, but effects of human activities on habitat quality, for example forest and scrub degeneration through intensified grazing by livestock, should also receive attention. One of the difficulties in pinning down effects of overwinter conditions is that for most species the spatial relationships between winter and breeding areas are poorly understood (Wernham *et al.* 2002). Overwinter conditions in Africa are probably highly variable spatially and consequently may have differential impacts not just among species but also among different components of populations within species. Even relatively small differences in winter distribution may be associated with large differences in overwinter survival. In addition to more work focused directly on the wintering areas, there would be value in continuing to undertake demographic analyses to determine whether population change is driven by pressures operating within or outside the breeding season (cf. Baillie & Peach 1992)

3.2 Climate Change and Weather Patterns on the Breeding Grounds

The British climate has changed markedly since the 18th century, and some of the most marked changes have occurred in the last 30 years. The surface air temperature in the UK increased by a mean of 0.5°C during the 20th century, with warming evident in all four seasons, but more pronounced in summer and autumn (based on the Central England Temperature, Jones & Hulme 1997, Hulme 1999). Three of the four warmest years since 1772 have occurred since the late 1980s (1989, 1990, 1995), and there has been an increase in the frequency of summers with large numbers of hot days (Jones & Hulme 1997, Hulme 1999). In England and Wales, and in Scotland, winters have generally become wetter and summers drier (Jones & Conway 1997) with a greater frequency of droughts, especially in the last 25 years (Jones *et al*. 1997, Hulme 1999). In conjunction with this, the mid-1980s has been a period of relatively little snow (the two longest winter periods with 'little snow' since 1875 occurred in the early 1970s and between the mid-1980s and mid-1990s (Jones *et al.* 1997)). So are these changes likely to explain the recent declines in some woodland bird populations?

There is good evidence that climate change has altered the breeding phenology of wildlife in northern latitudes, with an advance in the egg-laying times of birds (Crick *et al.* 1997, Crick & Sparks 1999), the spawning times of amphibians (Beebee 1995) and the active growing season of plants (Myneni *et al*. 1997). Effects on the population status of different species of plants and animals are less well established. There is an indication that populations or distributions of some insects and birds have increased as a result of an upward rise in temperature (Sparks & Woiwod 1999, Warren *et al.* 2001, Thomas & Lennon 1999). However, large year to year population fluctuations of both birds and insects, in response to annual variations in weather conditions, are still more typical than long-term trends resulting from climate change.

Based on known effects of weather on productivity and survival, one might expect recent patterns of change in climate to have been positive for many birds, though there are some important exceptions (e.g. Capercaillie, see below). An increase in the number of mild winters may explain the recent increase of the Wren in Britain, a species whose survival is severely reduced during cold winters and winters with long periods of snow cover (Peach *et al.* 1995b). However, the populations of other species that are generally susceptible to harsh winters, including Dunnock and Song Thrush, have continued to decline, suggesting that they are limited by factors other than cold winters. It is possible that an increase in winter rainfall has reduced the survival of some birds but there is no direct evidence for this. The survival of the Treecreeper is negatively correlated with winter rainfall (Peach *et al.* 1995), yet this species has not declined (Table 1). Cold wet spring weather may inhibit breeding or cause nest desertion in some woodland birds (e.g. Newton 1972, Perrins 1979, Wiktander *et al.* 1994). However, spring temperature has generally increased in recent decades, and levels of precipitation have varied less markedly in spring than in winter or summer (Jones & Conway 1997). In addition, for most species of woodland birds, there has been no significant increase in nest failure rate in recent years (Crick *et al.* 1998), suggesting that nest failure due to an increase in poor spring weather is not the cause of population declines. It is possible that brief periods of very wet weather during the time when some birds are breeding, which are not evident in the long-term climate trends, have affected female condition, nestling condition or post-fledging survival, but this has not been investigated.

At the level of communities, the overall effects of increasing summer temperatures are likely to have been positive. Lennon *et al.* (2000) examined relationships between bird diversity and climate patterns. There were positive associations between summer temperature and diversity of four assemblages (summer residents, summer visitors, winter residents, winter visitors). Winter temperature and winter precipitation were negatively associated with diversity of each assemblage. These models suggest that an increase in summer temperature would result in a general increase in bird diversity throughout Britain but with variation in the magnitude of the response from place to place. In broad support of this, Thomas & Lennon (1999) suggested that range expansions of British birds between the two breeding bird atlases (approximately 1970 to 1990) were consistent with the pattern expected under climate change.

Despite the above examples of positive effects of temperature on bird populations, there are several reasons for being extremely cautious in dismissing potentially negative effects of climate change. The first is that many species live within a clearly defined ‘climatic envelope’ and that for some, future climate change may result in conditions that lie outside this envelope. Harrison *et al.* (2003) give several examples of how species distributions may be limited by climate and Wilson *et al.* (2002) examine Nightingale distribution in relation to climate. One particular aspect of climate change has emerged as a principal factor in a long-term study of the declining Scottish population of the Capercaillie (Moss *et al.* 2001). Increasingly protracted spring warming has been a major factor responsible for the decline since 1975. Relatively high temperatures in early April are associated with higher success, probably because this has improved the nutritional state of hens and the eventual survival of their chicks. The warming of April temperature has become increasingly delayed so this is a subtle climate change effect. The birds also reared more chicks in years that had warmer and drier weather in late May and early June, but these weather variables did not show a time trend.

A second area of concern focuses on the ability of birds to adapt to changing climate. The optimal period for breeding for many insectivorous birds that depend on Lepidoptera larvae is determined by the peak availability of food, which may represent quite a narrow window during the entire period that caterpillars are available (Naef-Daenzer & Keller 1999). The timing of breeding is crucial because fitness is maximised when chicks hatch at the time of peak food availability (van Noordwijk *et al.* 1995). A critical issue, therefore, with respect to climate change is whether breeding birds could become decoupled from their food supplies. It has been argued that complex changes in temperature patterns within the breeding season potentially could disrupt breeding phenology because they may have different effects on the timing of egg laying and the timing of peak food availability (Stevenson & Bryant 2000). However, Cresswell & McCleery (2003) have shown that Great Tits in central England have the capacity to synchronise hatching dates with peak food supplies, mainly by altering length of the incubation period. This shows that some resident species have the ability to compensate for seasonal changes in food availability. It should be borne in mind that apart from plasticity in individual behaviour, many species are likely to show sufficient variation in individual phenology to ensure that natural selection will allow them to continue to track their food resources.

The situation may be more serious for long-distance migrants. Both & Visser (2001) have shown that although Pied Flycatchers in the Netherlands have advanced their laying dates over the last 20 years in response to increasing spring temperatures, they are not returning any earlier from Africa. The timing of migration in some species is determined by endogenous rhythms which are not altered by climate change. This has potentially serious implications for long-distance migrants that may be unable to adapt the timing of their migration to match changing periods of habitat optimality on the breeding grounds. If the window of maximum food availability is shifting as a result of climate change, migrant birds may suffer reduced breeding success. Interestingly, the Dutch nestbox populations of Pied Flycatchers are declining in rich deciduous forest but not in coniferous and mixed forests (Both 2002). It is suggested that this is a consequence of a change in the timing of food availability in deciduous forest, where the food peak now occurs earlier in the year than in the past, whereas the food peak in coniferous and mixed forest occurs later. The food peak is also relatively narrow in deciduous forest compared with the other forest types (Both 2002). Hence, due to their constrained timing of arrival, Pied Flycatchers may now be unable to exploit the food peaks in deciduous forest but they are able to exploit those of coniferous and mixed forests. Future climate warming may yet lead to negative effects in these latter habitats.

Such effects raise the possibility that resident species may generally be better able to exploit a changing pattern of food availability than migrants. In time, this could exacerbate any existing competition between migrants and residents (Gustafsson 1987, O’Connor 1990). A recent study by Lemoine & Böhning-Gaese (2003) is interesting in this respect. They found that across Europe, the abundance of long-distance migrants during the breeding season was negatively correlated with winter temperature and spring precipitation, and positively correlated with early spring temperature. This model was applied to weather and bird data for the Lake Constance area of central Europe for the period 1980-1992, over which period there had been an increase in winter temperature. It was found that an observed decrease in the proportion of long-distance migrants and an increase in residents and short-distance migrants could be accounted for by the increasing winter temperatures. It should also be noted that the situation could be doubly difficult for migrants because they may be faced with different rates of climate change within the winter and breeding ranges.

Thirdly, climate change may alter woodland environments in ways that are not being adequately monitored. In particular, an increase in the number of hot days in summer and an increase in the frequency of droughts may have reduced the moisture in woodland soils. However, the available data on soil moisture deficit (these data are probably most relevant to grassland) do not show a clear trend, though wide departures from the average have characterised recent years (Marsh 1999). It is possible that land drainage as part of the extensive post-war 'improvement' of agricultural land (Grigg 1989) may have exacerbated the drying out of woodlands in some areas. Relationships between woodland soil conditions and bird populations are poorly understood. One obvious effect is through the availability of soil-dwelling invertebrates, on which several birds feed, including Blackbird, Song Thrush and Woodcock (Snow & Perrins 1998). Some species prefer damp woodland, notably Woodcock (Kalchreuter 1982, Hirons & Johnson 1987) and Willow Tit (Perrins 1979). It is possible that there may be links between soil moisture and the general abundance and availability of invertebrates for sallying and gleaning birds. If this were important, however, one would have expected more general declines in insectivorous woodland birds.

Finally, climate change may benefit certain species which are either predators or competitors of declining woodland species. It is possible, for example, that recent increases in Great Spotted Woodpeckers, Great Tits and Blue Tits are, at least in part, driven by changing climate and that this could be having a deleterious effect on some other species for example Willow Tit (see sections 6.1 and 6.2).

In conclusion, there is direct evidence that climate change is affecting at least one woodland bird (Capercaillie) and it could be starting to affect species of long-distance migrants such as Pied Flycatcher. Although many woodland species, especially residents, may benefit from climate change, in the future there may be complex and subtle effects of climate change on population dynamics that can only be revealed through detailed long-term research. The key mechanisms may act either through (1) inability to adjust to new patterns of habitat optimality, especially relevant in migrant birds, (2) effects on food supply, which will probably act mainly through female condition, food supply for chicks or post-fledging survival, (3) altering the abundance of potential competitors or predators. Maintaining detailed long-term studies is essential to detect such effects. The work on Capercaillie suggests that quite specific (and perhaps regionally specific) components of climate change may be significant to particular species.

3.3 Tree Condition

Deterioration in the health and condition of trees may affect the availability and quality of food for birds that feed on foliage invertebrates in complex ways that are discussed below. Changes in tree condition can arise for many reasons including the abundance and outbreak of defoliating insects, short-term weather events, climate change, air pollution, disease, tree age, soil characteristics, the history of disturbance, squirrel damage and deer browsing (Kenward 1983, Rowe & Gill 1985, Kenward & Parish 1988, Roberts *et al.* 1989, Gill 1992a,b,c, Ling *et al.* 1993, Peterken 1996, Redfern *et al.* 1998). It could be extremely difficult to distinguish between the effects of these agents and there may be interactions between them. For example, trees that are under stress from drought may be less able to cope with additional pressure from defoliating insects or air pollution.

There is thought to have been a general decline in the health of several tree species across Europe in recent decades, largely as a result of air pollution, with the most severely affected areas in central and eastern Europe (United Nations Economic Commission for Europe & European Commission 2002). The condition of selected tree species has been monitored in Britain since 1987 (Hendry *et al.* 2001). There has been no trend in the condition of Sitka Spruce *Picea sitchensis*, Scots Pine *Pinus sylvestris* or Beech *Fagus sylvatica* but there has been a significant deterioration in crown density of Norway Spruce *Picea abies* and Oak *Quercus*. The condition of Oak appears to have deteriorated in the early 1990s and not recovered subsequently (Hendry *et al.* 2001). Although Beech condition does not seem to have declined nationally, there is some evidence of local reduction in the health of Beech (Ling *et al.* 1993 and references therein). Trends in tree condition based on national data should be viewed with caution since these may mask high variability in tree health between different sites which could be of significance to bird populations at local or regional scales. There is large annual and spatial variation in tree health, which depends on many different factors (see above).

Could the decline in Oak condition be significant for woodland birds? Oaks are widespread trees that are especially rich in invertebrates and consequently are important feeding sites for several of the commoner canopy feeders including Blue Tit (Perrins 1979) and Chaffinch (Whittingham *et al.* 2001). In a detailed study of patch use by foraging Great and Blue Tits in deciduous woodland, Naef-Daenzer (2000) showed that abundance of prey was higher on Oak than on Ash *Fraxinus excelsior*, Beech or Hornbeam *Carpinus betulus* and that the tits were preferentially foraging in the Oak. The species that forage mainly within Oak canopies are not, however, among the declining woodland birds. Whilst at first sight it would appear that these changes in tree condition are unlikely to be drivers of recent declines in woodland bird species it is worth looking more closely at the relationships between tree condition and birds. We focus on the issues raised by air pollution but first we outline some of the complexities that may be involved in the relationships between bird abundance and tree health.

In many cases declines in tree health are likely to be beneficial to birds. For example, one of the main factors affecting the health of Oaks in Britain is defoliating insects (Gradwell 1974) and insect damage is thought to be the main cause of the recent reduction in Oak canopy density (Hendry *et al.* 2001). The majority of woodland birds feed on defoliating lepidopteran larvae when there is a superabundance of these insects. Similarly, a decline in the condition of Beech trees often leads to an increase in seed production through masting (Nilsson 1985, Hendry *et al.* 2001) which is likely to benefit many seed-eating birds in the short-term (e.g. Perrins 1979, Nilsson 1987). Increased stress on trees due to drought or air pollution may also increase the susceptibility of trees to insect attack and this may benefit insectivorous birds (van Noordwijk 1990). A decline in tree condition may also benefit some birds by increasing the amount of dead wood. Possible negative effects of a decline in tree health on birds, include a thinning of the crown, which may increase the exposure of birds and nests to predators (e.g. Hake 1991), and leaf loss which may reduce the food for species feeding on foliage/needles or on invertebrates associated with canopy foliage (e.g. Zang 1990).

The potential effects of air pollution have been highlighted by severe dieback of forests in eastern and central Europe. Not surprisingly, the resulting large impacts on forest structure have a marked effect on bird populations, with a decline in species associated with closed, mature woodland and an increase in species associated with more open stands (Šťastný & Bejček 1985, Flousek 1989, Möckel 1992, Graveland 1998). However, there may be more subtle effects of pollution. Studies in Sweden and the Netherlands suggest that both a reduction in the abundance of calcium-rich invertebrates and an increased exposure to aluminium, resulting from an acceleration in the acidification of forest soils, due to air pollution, can lead to an increase in egg shell defects and a lower productivity in some forest passerines (Drent & Woldendorp 1989, Graveland & Wal 1996, Graveland *et al.* 1994, Graveland & Drent 1997). In Scandinavian conifer forests, loss of foliage is linked with reductions in abundance of spiders (Gunnarsson 1990) and with greater levels of vigilence and lower feeding time for Willow Tits (Hake 1991). However, effects at the population level are unclear. Möckel (1992) found that Coal Tits and Crested Tits *Parus cristatus* declined between the mid-1970s and mid-1980s in the acidified forests of the Ore Mountains, but this was attributed to a reduction in the recruitment of juveniles rather than a reduction in nest productivity.

Over recent decades Britain has received lower levels of air pollutants compared with many other parts of Europe and there has been no large-scale dieback of forests comparable to those of central Europe. Is it possible, however, that more subtle effects of air pollution have affected the quality of trees as foraging habitats for birds in similar ways to those described above for Scandinavia and The Netherlands? First, it should be pointed out that the most abundant species that forage for insects within the canopy of mature closed woodland (Coal Tit, Goldcrest, Blue Tit, Great Tit, Chaffinch) have remained stable or increased (Table 1). There is also little evidence that an increase in soil acidification has affected woodland birds in Britain. Ramsay & Houston (1999) found no effect of providing supplementary food on the incidence of egg shell defects in the Blue Tit in an area of west-central Scotland affected by acid precipitation, despite low levels of calcium-rich invertebrates in their study area. They suggested that Blue Tits were able to compensate for a reduction in snail abundance by using alternative calcium sources. Using data from museum specimens, Green (1998) showed that there have been widespread declines in the egg shell thickness of four *Turdus* spp. from Britain since the 19th century, but acidification was only one possible mechanism for this. Furthermore, the impact that egg shell thinning has had on the populations of these species is unknown. Low juvenile survival may account for the decline in the song thrush on farmland in recent years (Thomson *et al.* 1997) and it is possible that this has been reduced by the effects of egg-shell thinning on offspring development, but there is no direct evidence for this. An analysis of BTO nest record cards in relation to levels of acidification across the UK found little evidence of negative effects of increased acidification on the productivity of four invertebrate feeding bird species, including two woodland indicator species, namely the Great Tit and Song Thrush (Chamberlain *et al*. 2000).

There is little evidence of a long-term change in the pH of woodland soils (Howard & Howard 1984a,b), but this has been rarely studied. The pH of woodland soils is dependent on many different factors, including the tree species, stand management, previous land usage and site characteristics (Mitchell & Kirby 1989). A reduction in soil pH, as a consequence of air pollution or other factors, is likely to reduce the availability of some soil-dwelling invertebrates. In a study of the Woodcock (Hirons & Johnson 1987) found that earthworm biomass was positively associated with soil pH and that this appeared to influence selection of feeding sites by the bird. Other species that specialise on soil invertebrates, including Song Thrush and Blackbird, could be affected in similar ways. Interestingly, all three species have shown a decline in woodland in recent years, although it should be noted that the decline in the Blackbird has been less severe than the other two species, and the CBC population indices for the Woodcock may be unreliable (see section 2.2). There is an indication that the nutrient status of woodland soils is changing; between 1990 and 1998 there was a significant increase in the fertility of woodland soils in England and Wales (Haines-Young *et al.* 2000). This general finding is consistent with local studies (McCollin *et al*. 2000). The exact implications of increasing soil nitrogen within woodland for birds and their food is unclear.

In conclusion, whilst there may have been some large-scale changes in the health of trees in recent years it is unlikely that these are responsible for the observed declines in woodland birds. Indeed, there are reasons for thinking that, at least in the short-term, deterioration of tree health may be advantageous to several bird species. There is little direct evidence that air pollution has adversely affected woodland bird populations in Britain. Research on the ecological effects of the reduction in Oak crown density would be valuable.

3.4 General Reduction in Invertebrate Populations

The purpose of this short section is to draw attention to the possibility that, for a variety of reasons, there could have been widespread and general reductions in invertebrates within woodland in recent decades. Some of these reasons have been explored in sections 3.2 and 3.3. Both climate change and deterioration of tree health could potentially affect woodland birds by altering the availability of insect food, either by changing its abundance or its seasonal availability. Drought, for instance, can have major medium-term effects on some invertebrate populations (V.K. Brown pers. comm.). There may be various forms of diffuse pollution, including drift of agricultural sprays, that could affect both the abundance of invertebrates within woodland and the quality of invertebrates as food for birds.

Despite the view that the recent deterioration of Oak condition is caused largely by insect damage, recent years have seen relatively few major defoliation events in Oak woodland in central England

(Harding 2002, C.M. Perrins pers. comm., R.J. Fuller unpublished observation). Large episodic outbreaks of defoliating caterpillars are exploited by most woodland birds and may be linked with higher breeding success of some species and possibly may affect spatial patterns of settlement. Attention has been drawn to the apparent demographic effects of insect food availability on birds in North American forests (Holmes 1990). In European forests the situation is less clear. There is evidence from a 20-year study in Białowieża Forest, Poland, that annual variation in caterpillar numbers may affect *short-term* fluctuations in several insectivorous bird species (Wesołowski & Tomiałojć 1997). The total abundance of crown insectivores was especially strongly correlated with abundance of caterpillars on an annual basis but individual species were less consistently correlated with caterpillar abundance. It should be noted that in Białowieża Forest, annual variation in breeding success of insectivorous birds is driven mainly by predation rather than starvation of chicks (Wesołowski & Tomiałojć 1997).

There is some evidence of large decreases in abundance of invertebrates on farmland (Aebsicher 1991, Donald 1998, Sotherton & Self 2000, Benton *et al.* 2002). As far as we are aware, with the exception of butterflies (e.g. Warren *et al.* 2001), there is no long-term monitoring of invertebrate abundance within woodland and it is possible that large changes have gone undetected in the availability of invertebrates for birds. Long-term abundance data, rather than presence-absence data, are needed to detect such effects. The Rothamsted Insect Survey is potentially a valuable source of information on long-term trends in general insect abundance dating back to the 1960s. Analysis of these data for selected insect taxa could give enormously valuable insights into patterns of change in our insect fauna. The potential has been demonstrated by Benton *et al.* (2002) who analysed a 27 year run of data from a single trap in Scotland demonstrating large non-linear changes in several invertebrate taxa.

4. LARGE-SCALE TRENDS IN LAND MANAGEMENT AND LAND-USE

4.1 Agricultural Intensification and Habitat Change Outside Woodland

It is well established that the intensification of agriculture, particularly through the 1970s and 1980s, has had far-reaching, and frequently detrimental, effects on many farmland birds (Aebischer *et al.* 2000, Chamberlain *et al.* 2000). Some woodland species also use resources outside woodland, and it is possible that they too have been affected by recent changes in agricultural practices. Indeed, the population trends of birds using both woodland and farmland are highly correlated, suggesting that birds that have declined in woodland have also declined in their farmland habitats (Figure 3).

In North America, surrounding land-use affects the nature of bird communities in forests, but this issue has not been specifically examined in Britain. Rodewald & Yahner (2001) found that Pennsylvanian forest bird communities were relatively impoverished in forests situated within agricultural landscapes compared to forests within forested landscapes. The influence of landscape context on North American forest bird communities has also been stressed by Donovan *et al.* (1997) and Chalfoun *et al.* (2002).

In recent decades, the number of hedgerows has declined in Britain (O'Connor & Shrub 1986, Peterken & Allison 1989, Barr *et al.* 1993). Up to the late 1980s, there was a general trend towards lack of hedgerow management, but this seems to have been reversed in the 1990s (Barr *et al.* 1993, Haines-Young *et al.* 2000). British landscapes are very rich in non-woodland trees (Peterken & Allison 1989) but since 1980 there appears to have been a substantial decline in numbers of live trees outside woodland (Forestry Commission 2001b). Furthermore, Dutch Elm disease was responsible for the loss of huge numbers of trees in the 1960s and 70s.

Many typical 'woodland birds' utilise hedges or trees on farmland for nesting or foraging (Fuller *et al.* 2001). Nest productivity may also be as good on farmland with hedgerows as it is within woodland (e.g. Hatchwell *et al.* 1996). The presence and abundance of 'woodland birds' in hedgerows is related to a range of structural and botanical factors which probably affect habitat quality (Osborne 1984, Parish *et al.* 1994,1995, Green *et al.* 1994, Macdonald & Johnson 1995, Sparks *et al.* 1996). These factors differ between species but the most frequent ones affecting abundance of breeding birds are hedge size (height, width, volume) and the quantity of trees (Hinsley & Bellamy 2000, Whittingham *et al.* 2001). Changes in management of hedges and reduction of trees in hedges could, therefore, have led to reductions in bird abundance within many hedgerows. This could be relevant in explaining some of the declines observed in birds within woodland in two ways.

First, some birds may use resources from a combination of habitats, including both woodland and hedgerows. This is especially likely to be the case outside the breeding season, including the post-fledging period when many juvenile birds are dispersing. If the quality of any of these habitats and the resources they provide deteriorates, then survival may be reduced. In landscapes where the woods have poorly structured edges and sparse understories, hedges may offer better quality foraging for some insectivorous and frugivorous species than the woods themselves. There has been little work on the year-round ranging behaviour and habitat use of any species in lowland British landscapes so it is difficult to judge how important this type of effect might be. However, several species are candidates for such dependency on a matrix of woody habitats including both residents (e.g. Bullfinch and Song Thrush) and migrants (e.g. Willow Warbler and Lesser Whitethroat). Interestingly, Hinsley *et al.* (1995) found that the presence of Bullfinches in small woodlands in the East Anglian Fens was related to the amount of hedgerow in the area surrounding the wood. Also, in a study of recently created farm woods, Vanhinsbergh *et al.* (2002) found that woods connected to dense hedgerows with trees were utilised by more species of birds than those connected to hedgerows without trees. These findings could, of course, reflect use of hedgerows as movement corridors as much as a requirement for a combination of woodland and hedgerow habitats. Further research at the individual species level would be extremely valuable at the landscape scale to determine year-round patterns of resource use. Bullfinch would be a high priority for such work (Siriwardena *et al.* 2001).

Second, if hedgerows are optimal habitats, or are effectively acting as a population source for woodlands, then deterioration of hedges could result in a reduction in the woodland component of the population. For most woodland birds this is not the case. Hedgerows are far more likely to be sub-optimal habitats (Krebs 1971), though it should be acknowledged that both hedges and woods provide a continuum of habitat quality and that relative optimality of particular habitats will vary in space and time (Fuller *et al.* 2001). One species for which hedges could be optimal habitats is Lesser Whitethroat for it shows a much stronger preference for hedges than it does for woodland (Fuller *et al.* 2001). There is slight evidence from the CBC that declines on farmland have been less pronounced than those in all habitats (Baillie *et al.* 2002). This may reflect a contraction of Lesser Whitethroat into its preferred habitat, which appears to be tall hedgerows and patches of tall scrub.

Farming practices have also affected the land that immediately surrounds woodland and some woodland birds may use these areas for foraging. The whole pattern of land-use surrounding many woods will have changed greatly in recent decades with the simplification of rotations and the transition of much mixed farming to either predominantly arable or pastoral. This may have been especially important for ground-feeding birds such as thrushes. Pesticides are often applied to field margins (Boatman 1992), many of which run alongside woodlands, and this is likely to influence the availability of seeds and invertebrates for birds using field margins for foraging. Several studies have shown a decline in invertebrates on field margins in response to pesticide applications (Rands 1985, Potts 1986, Feber *et al.* 1996). However, a link between pesticide usage and breeding productivity and breeding numbers of birds has only been established for one farmland bird species, the Grey Partridge *Perdix perdix* (Potts 1986). The effect of pesticides on the abundance of birds using field margins along woodland edges is unknown.

Agriculture has probably had more direct impacts on woodland. The possibility that drainage on farmland has contributed to the drying out of woodland soils was mentioned in section 3.2. Farming activities can strongly modify woodland edges where they adjoin farmland. This modification can come about through four processes: drift of agricultural chemicals, trimming of wood edges, heavy grazing by livestock and a tendency to cultivate right up to the woodland edge. Chemical drift could involve fertilisers leading to eutrophication of woodland edges, herbicides which could reduce semi-natural edge vegetation and insecticides having a direct impact on invertebrates at the woodland edge. None of these factors seems to have been studied in great detail, yet each could be significant for the food resources that are available to some woodland birds. We suggest that there is a need for more work on the circumstances under which chemical drift may be significant for plant and animal communities within woodland, and on the extent to which drift penetrates within woodland. Physical modification of woodland edges through mechanical trimming or intensive grazing, especially by sheep, is widespread but to our knowledge no data exist on recent trends. In livestock areas, some woodland edges may have once been maintained in a similar fashion to hedge laying but this now seems rare.

External woodland edges are extremely important features for many woodland birds because they potentially offer a range of resources that can be scarce in the woodland interior (Fuller & Whittington 1987, Fuller 1995, McCollin 1998). This is likely to be especially true in historically fragmented landscapes such as those of Britain. In eastern North America and Scandinavia there has been much concern that edges, often a consequence of forest fragmentation, are associated with elevated predation and nest parasitism (e.g. Paton 1994, Andrén 1995). However, in ancient cultural landscapes birds have had more opportunity to adapt to edges and they are widely perceived to be positive features for the conservation of biodiversity. Far more attention should be devoted to edges in western Europe and to the factors that influence their quality.

In conclusion, changes in habitats outside woodland could have been important in influencing the population trends of those woodland birds that use these habitats. Further research is needed (a) on how woodland birds interact with habitats outside woodland, especially hedgerows, and (b) to understand the effects of agriculture on the quality of woodland edges as bird habitats.

4.2 Fragmentation and Loss of Woodland

Have changes in the total quantity and spatial pattern of woodland been responsible for the observed changes in woodland bird populations? At first sight, this seems unlikely because the available measures of population change for woodland birds only take account of changes *within* existing woodland (see section 2.1). Furthermore, the total area of woodland is actually increasing at the scale of Great Britain, Scotland and England and Wales (Figure 4). Some caution is needed in the interpretation of these trends in woodland area because they conceal the large losses that have occurred in ancient semi-natural woodland. Approximately 7% of the area of ancient woodland present in about 1930 was converted to other land-uses, mainly agriculture, over the following 50 years (Spencer & Kirby 1992, Peterken 1993). There is no evidence, however, that ancient woods *per se* are of particular importance as bird habitats. However, substantial areas of ancient broadleaved woodland were cleared and replanted with conifers – plantations occupied 40% of the surviving ancient woodland area by the late 1980s (Spencer & Kirby 1992). This represents a major form of habitat loss and fragmentation for those birds, such as Nuthatch and Marsh Tit, that depend specifically on broadleaved woodland (see section 4.4).

Large-scale loss of woodland habitat could theoretically affect population persistence and densities within surviving fragments. This could come about in several ways. If metapopulation dynamics (Hoopes & Harrison 1998, Harrison & Bruna 1999) were operating for woodland birds in British landscapes, loss of small patches could affect population persistence. Alternatively, if some woodland patches acted as population sources and others as population sinks (Pulliam 1988), the loss of source patches could have a severe effect on population survival in other patches. One could also envisage other circumstances whereby loss of certain types of patch could theoretically affect local or regional population persistence, for example in situations where landscape supplementation and landscape complementation were operating (Dunning *et al.* 1992).

The importance of metapopulation dynamics and spatial arrangement of habitat patches for birds remains somewhat questionable in reality; there are few convincing empirical studies (Harrison & Bruna 1999). Even if these processes were appropriate, the scale of loss of ancient woodland in most regions, especially when balanced against the creation of new woodland, is unlikely to have resulted in large-scale declines in woodland bird populations. On the other hand, at the local scale, the loss and fragmentation of woodland could well have altered the status of certain species through reduced habitat availability and possibly by increasing isolation. This view is supported by work in eastern England by Hinsley *et al.* (1995, 1996). They found that several species avoided breeding in small woods (<1ha), including Treecreeper, Nightingale, Marsh Tit, Long-tailed Tit, Jay and Chiffchaff. They also discovered that the amount of woodland in the surrounding landscape or the distance to the next wood could affect the probability of recording Treecreeper and Long-tailed Tit. Both these species were more likely to be present in woods that were less isolated from other woods and they were probably reluctant to cross open ground.

Dispersal ability is an important factor determining the significance of woodland isolation for woodland birds. Two British woodland species that are thought to be particularly sedentary are Nuthatch and Marsh Tit (Matthysen & Schmidt 1987, Nilsson 1989). In the case of Nuthatch it appears that its absence from suitable habitat in parts of eastern England is a consequence of woodland isolation (Bellamy *et al.* 1998). There is also evidence that habitat fragmentation negatively affects settlement rate and patch occupancy by Nuthatches (Matthysen & Currie 1996). The fact that Nuthatch, one of the species predicted to be most sensitive to loss of broadleaved woodland and to increasing isolation of woods, is increasing so strongly (Table 1) rather suggests that effects of recent woodland fragmentation are unimportant at a national scale.

4.3 Age Structure of Woodland

The wooded area of Britain has increased markedly in recent decades (Figure 4) and most of Britain's woodland is now managed as plantations. The total amount of planting and restocking increased massively during the 20th Century (Figure 5). This pattern was driven entirely by the planting of conifers; broadleaved planting remained relatively stable up to the second world war but declined thereafter. The most striking feature is a very large increase during the 1950s with the peak of planting occurring in the 1960s. Since then the amount of planting has decreased, though it remains vastly higher at the end of the 20th century than at the beginning.

The pattern of planting has resulted in large changes in the overall age structure of high forest. The exact age structure at any point in time cannot be worked out from planting statistics alone but these do give an indication of changes in the total quantity of early growth plantations. It is clear that the area of young, relatively open plantations (<20 years) was especially high in the 1960s and 1970s but has decreased somewhat in recent years. Data available in the National Inventory of Woodland for England for high forest can be used to illustrate some of the changes between 1980 and 1998 (Table 25, Forestry Commission 2001b). These data are for high quality timber stands i.e. ones capable of producing sawlogs. Because of the way the statistics are presented, the age class categories (years since planting) are slightly different for the two years. In 1998, there were approximately 123,000 ha of category 1 high forest of <18 years old compared with 190,000 ha of <20 years old in 1980. Defined in this way, young plantations represented approximately 15% of English high forest in 1998 and 25% in 1980. On the other hand, there appears to have been an increase in the area and relative contribution of old stands. In 1998, there were approximately 221,000 ha of stands >68 years old compared with 172,000 ha of >70 years old in 1980. These figures equate to 27% and 23% of the total area of English productive high forest in 1998 and 1980 respectively.

These are the overall patterns. On a local level, changes in the age structure and extent of woodland varied markedly and whilst some regions retained large areas of mature woodland and experienced little replanting, other regions were subjected to large amounts of replanting or woodland clearance (Peterken & Allison 1989, Peterken 1993, Fuller 1995). This local variation in the extent and age structure of woodland make it very difficult to identify the effects of the trends in woodland age on national bird populations. Nonetheless, there will have been strong local effects because the growth stage of woodland is one of the fundamental influences on the composition of bird communities, with many species showing strong associations with particular stages (Fuller 1995). There are many documented examples, from many different types of woodland, showing how the age of the stand strongly affects the bird community (Lack & Lack 1951, Hope Jones 1972, Moss *et al.* 1979, Bibby *et al.* 1985, Fuller & Moreton 1987, Smith *et al.* 1987, Fuller & Henderson 1992, Donald *et al.* 1998). These changes in bird communities are largely driven by the fact that as woodland ages the physical structure of the vegetation alters, often very rapidly. Relationships between vegetation and birds within developing woodland have been illustrated particularly clearly for coppiced woodland (e.g. Fuller & Henderson 1992, Fuller & Green 1998), though similar principles will apply in plantations and farm woodland.

Recently felled or newly planted woodland tends to contain breeding species associated with open ground, such as Meadow Pipit *Anthus pratensis*, Tree Pipit, Skylark *Alauda arvensis* and Woodlark *Lullula arborea*. There are considerable differences in the breeding bird communities that develop in first and subsequent generation plantations, for example Meadow Pipit is more typical of newly afforested land while Tree Pipit is probably more characteristic of restocked land (Fuller 1995). These species rapidly disappear with increasing tree growth, being replaced by ones associated with the thickening low vegetation. In the absence of heavy grazing, a dense field layer and shrub layer may develop which is favoured especially by several migrant species such as *Sylvia* warblers (Ferry & Frochot 1970, Fuller & Crick 1992). In coppiced woodland, most warblers, Nightingales and Dunnocks select coppice of intermediate age, avoiding very young or old stands, and bird diversity tends to be highest in the intermediate growth stages (Fuller & Henderson 1992, Fuller & Green 1998). Closure of the canopy, both in plantations and coppice, may shade out much of this low growth leading to a reduction in those species needing a dense understorey. However, with continued tree growth, hole-nesting species contribute an increased proportion of the bird community (Smith *et al.* 1987, Donald *et al.* 1998). In old stands, the canopy may become slightly more open through self-thinning and treefalls, resulting in a better developed field layer and the return of its associated species, though rarely at such high densities as in the pre canopy-closure period.

Could the changes in age structure of woodlands that have occurred since the 1970s account for the decline in some woodland birds over much the same period? It is very clear that the amount of young woodland habitat decreased over this period, so increases in age of trees on some CBC census plots may not have been fully compensated by felling on other plots. The net effect could have been a decrease in species associated with young growth. The Lesser Redpoll, which favours young conifer plantations (Avery & Leslie 1990, Fuller 1995), has declined markedly according to the CBC data (Table 1), though it is questionable whether this decline has occurred in Scotland where there continues to be much suitable breeding habitat in the form of young conifers (Thom 1986). Several other declining species are often associated with young woodlands, including Tree Pipit, Willow Warbler and Dunnock (Table 1). Maturation of conifer plantations was suggested to be a factor in the contraction of the range of the Tree Pipit (Gibbons *et al.* 1993) – whilst this is probably relevant in central and southern England, it is unlikely to be relevant in much of Scotland where the species appears to be maintaining its numbers and possibly increasing within restocked conifer plantations (G. Shaw pers. comm.). In the case of Willow Warbler, large declines have occurred within suitable habitat in coppiced woodland in eastern England (R.J. Fuller unpublished), so changing age structure is unlikely to be an important factor for this species. Not all birds that use young woodlands have declined – examples include Garden Warbler, Blackcap, Chiffchaff and Wren, though some of these species are not particularly stringent in their requirement for young stands. The maturation of conifer stands planted in the last 40 years has benefited several species notably the Siskin *Carduelis spinus* and Crossbill *Loxia* spp. which have expanded in breeding range (Gibbons *et al.* 1993, Gibbons & Gates 1994). With the exception of Capercaillie, none of the declining species are strongly associated with mature conifers.

In conclusion, it is quite likely that changes in the amount of young woodland have contributed to observed declines, especially in Lesser Redpoll and Tree Pipit, but there are questions about how general any such effects might have been.

4.4 Tree Species Composition

Over the last century there have been huge changes in the tree species composition of British woodlands, dominated by the massive increase in planting of conifers (Figure 5) and an increase in the use of non-native tree species (Locke 1987, Forestry Commission 2001b). At the national scale, the increase in conifers has been dominated by planting of Sitka Spruce, especially in upland Scotland, where substantial areas of Lodgepole Pine *Pinus contorta* also continue to be planted. There have been recent decreases in planting of Scots Pine and Norway Spruce. Recent changes in planting broadleaves have not been so dramatic, though since 1960 the amount of Oak planted has more than halved. Birch *Betula* planting has also decreased substantially. Overall, the amount of Oak woodland declined by an estimated 70,000 ha between 1947 and 1980 (Locke 1987, Peterken & Allison 1989). The numbers of Elms *Ulmus* declined dramatically, following the onset of Dutch Elm disease in the 1960s. Changes in the tree species composition of native woodland also occurred on a local scale in response to natural factors. For example, the death of Beech and Birch trees following the drought of 1976 lead to the replacement of these dominant species by Ash and Lime *Tilia* in Lady Park Wood in Gwent (Peterken 1996).

Relationships between tree species and birds were reviewed by Fuller (1997), with the emphasis on comparing use of native and non-native species. Only a few British birds show a strong association with particular tree species and most woodland birds use a wide range of tree species, both native and non-native. Only one of the declining woodland birds shows a strong dependence on one tree species, the Capercaillie, which is strongly associated with Scots Pine stands. There is no clear evidence that the introduction of non-native species has had a detrimental effect on bird populations at a national scale. Locally, however, the introduction of non-native tree species has probably altered the composition of bird communities. However, such comparisons are difficult to make because one needs to control for effects of tree age.

A study of the introduction of spruce stands into native Scots Pine woodlands in western Norway illustrates the types of change in bird communities that can be caused by introducing stands of locally non-native trees. Specialists of the native Pine woodlands, such as Tree Pipit, Pied Flycatcher and Crested Tit, were found to be completely absent from introduced spruce stands and they declined in relation to the % of spruce cover (Gjerde & Saetersdal 1997). The diversity of the bird community was lower in spruce than in Pine stands but areas containing a mosaic of Pine and spruce stands held the highest bird diversity.

One of the most valid generalisations one can make about tree species preferences is that some species are specialists of broadleaved woods and others are specialists of coniferous woods. Fuller (1997) lists 17 broadleaved specialists and nine conifer specialists. Several of the broadleaved specialists are among the list of declining birds: Lesser Spotted Woodpecker, Nightingale, Pied Flycatcher, Marsh Tit, Willow Tit and Hawfinch but only one conifer specialist is declining, Capercaillie. This does not imply that the national increase in conifers and reduction in broadleaves is responsible for the decline of several species. There are many examples for all six declining broadleaved specialists, of declines that have occurred within woodland that has not greatly changed in tree species composition. Furthermore, several species strongly associated with mature broadleaved woodland have either remained stable or increased in abundance in recent years, including Treecreeper, Chaffinch, Great Tit, Blue Tit and Nuthatch (Table 1).

Turning to individual species of broadleaved trees, the long-term reduction in Oak has almost certainly had implications for woodland birds in Britain, because it is such a strongly favoured tree by several species. However, over the timescales for which changes in bird numbers are presented in Table 1, it is unlikely that this is a significant factor. Indeed, one of the species with the strongest affinities to Oak, the Nuthatch, has undergone the largest increase of all. A decrease in Birch as a result of woodland succession, has been suggested to be a potentially important factor in the decline of Lesser Redpoll in lowland England (Gibbons *et al.* 1993). The effects of the loss of mature Elm from some woods as a result of Dutch Elm disease in the 1970s is unknown, though see section 5.2 for further discussion about implications of the disease.

In conclusion, most woodland birds use both native and non-native trees. Densities of some of these birds may be lower in non-native stands but there is very little firm evidence that national population levels of woodland birds in Britain can be related to recent changes in tree species composition. Even though many species of birds utilise non-native trees for foraging or nesting, non-native stands could represent sub-optimal habitats for many species compared to native stands. Further research is needed to establish how tree species composition affects the dynamics of woodland bird populations, including the relative value of native and non-native stands.

4.5 Reduction in Woodland Management

Many woods have become neglected during the 20th century. This especially applies to former coppice. Coppice that is abandoned rapidly loses its understorey and assumes a relatively stable, simple, multi-stemmed, open structure (Fuller & Henderson 1992, Fuller 1995). Such woods support extremely low densities of breeding birds and low numbers of species. Eventually they may develop a more complex structure as individual trees die and the canopy gradually opens, but this will be a slow process taking many decades. Declining woodland management is evident in other types of woodland too. Many farm woods have become neglected. Within managed woods, owners have tended to reduce stand thinning which has become uneconomic as timber prices have fallen (Gary Kerr pers. comm.).

These processes could have had several effects on habitat quality. In many cases, the resulting canopy closure will have shaded out Bramble *Rubus* and other field / shrub layer vegetation, with possible consequences for warblers and other species that use low vegetation such as Dunnock and Marsh Tit. Loss of open space has occurred within some woods as rides and glades have become grown over; this may have affected Tree Pipits. Increased shading is likely to lead to decline in plant diversity in the field and shrub layers; this would diminish the quality of a year-round food supply for species such as Marsh Tit. There may be a temporary increase in standing dead stems through self-thinning of coppice and the death and decay of early successional trees such as Birch and Aspen *Populus tremula*. This may temporarily improve habitat quality for some hole-nesters, notably Willow Tit.

There are no specific data available on these changes in woodland structure but they do seem to be widespread in lowland woodlands. Interestingly, subtle changes in the structure of hardwood forests in the eastern USA have been recorded by Holmes & Sherry (2001) in forest that had not been disturbed by human activities since the early 1900s. These habitat changes were brought about as a result of natural succession and natural disturbance. Over a 30-year period, large changes in bird communities occurred that were thought to be driven by these habitat changes. There were reductions in numbers of several species associated with early and mid-successional forests and an increase in species associated with mature forests. Similar processes could be taking place in broadleaved woods in Britain where management has not occurred for many years. Such changes would be impossible to detect in the absence of detailed long-term studies of both vegetation and bird communities at specific locations.

4.6 Recreational Pressure

Recreational use of the countryside has increased enormously over the last 50 years. Most Forestry Commission woodlands are open to public access. The number of Forest Enterprise recreational facilities are reported annually. For example, in 2001 in state forests in Great Britain there were 681 car parks, 647 forest walks, 369 picnic sites and 190 cycle trails (Forestry Commission 2001a).

The potential effects of human disturbance will depend on the type of activity, the habitat and the sensitivity of the species. We are unaware of any relevant research in British woodland but published work from the Netherlands purports to demonstrate negative effects of recreational pressure on woodland bird abundance (van der Zande *et al.* 1984, Jansen & de Nie 1986). These correlational studies are inconclusive because birds could have been responding to a range of other factors that were not measured. Nonetheless, there is growing evidence from work in North American forests that recreation can affect bird communities. The composition of bird communities in Colorado forests has been found to be different near to recreational trails than far away (Miller *et al.* 1998). Work in Wyoming showed that some, but not all, species of birds exhibited reduced song output in response to human intruders (Gutzwiller *et al.* 1994, 1997, 1998). These effects could potentially reduce territory quality in moderately or highly disturbed areas and result in reduced breeding productivity. In this connection, the presence of territories in disturbed areas is not necessarily an indication that disturbance is unimportant because there may be subtle effects on territory quality and on the quality of birds that occupy these territories (Fuller 1995).

Whilst there is no clear evidence that human recreational activities are responsible for recent national declines in British woodland birds it would be unwise to dismiss the issue. It is highly probable that there are local impacts. Recently there has been concern that Woodcock are especially vulnerable to human disturbance, especially where dogs are involved. Declines of breeding Woodcock during the 1990s in western Switzerland were attributed mainly to increasing levels of human disturbance (Estoppey 2001).

4.7 Road Traffic

The volume of traffic using British roads has been increasing inexorably for many years. For example, between 1985 and 2002 there was an approximately 45% increase in road traffic and sample annual increases include 5% in 1973, 4% in 1978, 5% in 1984 and 8% in 1989 (www.dft.gov.uk).

The ecological effects are generally poorly understood but there could be several implications for birds. First, direct mortality could have increased as a result of collisions. Second, deterioration of habitat quality may have arisen in some places through pollution, possibly with effects on invertebrate food. Third, the increase in bird and mammal roadkills (especially Pheasants *Phasianus colchicus*, deer and Rabbits *Oryctolagus cuniculus*) has probably provided carrion feeders, especially Crows *Corvus corone* and Magpies *Pica pica*, with extra food and this factor may have contributed to their population increases which in turn could have contributed to higher rates of predation on nesting songbirds. Fourth, visibility of moving traffic may deter birds from living close to roads. Finally, elevated traffic noise could affect territorial behaviour of birds living close to busy roads, in particular it may interfere with song transmission.

It seems very unlikely that traffic could be a major contributor to the declines in woodland birds because all the relevant species show declines in wooded areas away from major roads. Nonetheless, there could be local effects where traffic levels are extremely high. This was found to be the case in the Netherlands where several species appeared to avoid nesting close to major trunk roads (Reijnen *et al*. 1995). In this study, noise was considered to be the main factor causing reduction in habitat quality close to roads rather than visibility of traffic, direct mortality or pollution. A detailed study of Willow Warblers revealed large differences in the population structure of birds close to roads compared with further away. The proportion of first year birds was about 50% higher close to the road and male birds experienced reduced breeding output there (Reijnen & Foppen 1994). Breeding dispersal of first year Willow Warblers using the areas close to roads was higher (Foppen & Reijnen 1994).

4.8. Game Management

Large numbers of Pheasants are reared in British woods. The density of Pheasants released each year, according to the statistics of the National Game-Bag Census, has risen from *ca*. 50 per 100 ha in the mid 1960s to >200 per 100 ha by 1999 (Tapper 1999). Release densities were relatively stable from 1950 until the mid 1970s when a rapid increase started that levelled off in the early 1990s. Some 20 million Pheasants are estimated to be released each year in the United Kingdom (Tapper 1999). These birds represent an enormous biomass.

Some of the habitat management techniques used to improve Pheasant habitat in woodland may be beneficial for some songbirds (Hill & Robertson 1988, Tapper 1999), but there is also a series of potentially negative effects on non-gamebird species which have not been studied adequately. These potential effects include impacts on the structure of the field layer, the spread of disease and parasites, increases in rats and squirrels (potential predators), competition for food etc. Guidelines for good management practice recently developed by the Game Conservancy Trust (2003) seek to minimise adverse impacts. These stress the importance of maintaining a well-developed shrub layer to provide cover for Pheasants. However, achieving this desired habitat structure is not always easy and attempts to stimulate regrowth of the shrub layer by coppicing can often fail due to pressure from deer and shading from the canopy. This can result in woods that appear almost devoid of understorey.

In conclusion, the massive increase in numbers of released Pheasants in recent decades indicates a need to better understand how different intensities of Pheasant rearing affect woodland ecology. Management techniques are also needed that take account of deer impacts and that can be integrated with the needs of forestry.

5. FINE-SCALE TRENDS IN HABITAT QUALITY

5.1 Grazing and Browsing Pressure

Numbers of Red Deer *Cervus elaphus*, Roe Deer *Capriolus capriolus*, Fallow Deer *Dama dama*, Sika Deer *Cervus nippon* and Muntjac Deer *Muntiacus reevesi* have increased in Britain (Chapman *et al.* 1994, Harris *et al.* 1995, Yalden 1999). Although these increases have become strikingly apparent in recent decades, this is part of a far longer-term pattern (Fuller & Gill 2001). There is considerable concern about the intensified deer pressure now being experienced widely through lowland England, but there are long-standing problems of severe browsing by Red Deer in Highland forests (Baines *et al.* 1994, Staines *et al*. 1995). Since the mid 1970s, there has also been a rise in the number of sheep *Ovis* in many parts of Britain, especially in Wales, and south-west and northern England (Fuller & Gough 1999). These increases in sheep have probably resulted in more intensive grazing of some upland woods which were already grazed by sheep, whereas the increases in deer in the English lowlands have resulted in many previously ungrazed or lightly grazed woods becoming heavily grazed. This account focuses principally on the potential effects of deer on birds in lowland woods and draws heavily on a review by Fuller (2001).

The effects on trees and shrubs and woodland structure are well documented (Gill & Beardall 2001). These can be summarised as (a) a reduction in the density and height of woody stems, (b) the removal of other low palatable vegetation (especially Bramble) leading to an open understorey, (c) an increase in unpalatable species (notably grasses) and (d) a likely reduction in the species richness and diversity of trees. In addition there can be complex effects on the structure and composition of the ground flora (Cooke & Farrell 2001, Kirby 2001, Watkinson *et al*. 2001). Whilst generalised impacts can be identified on vegetation, the effects may vary considerably between woodlands, depending on site characteristics, the nature of the surrounding habitat, and the species, density and activity of herbivores (Adams 1975, Putman 1986, Kay 1993). Deer exhibit marked browsing preferences for certain trees and these preferences may vary between woods (Gill & Beardall 2001). Deer browsing and canopy openness may also interact in determining effects on understorey regeneration (DeGraaf *et al.* 1991, Morecroft *et al.* 2001).

Examples of how increased pressure from deer has affected the vegetation structure in particular woods or woodland types are given by Cooke and Farrell (2001), Fuller (2001) and Morecroft *et al.* (2001). The ecological impacts of increased grazing and browsing by large herbivores are far-reaching and complex, potentially cascading through trophic levels (Mitchell & Kirby 1989, Ostfeld *et al*. 1996, Waller & Alverson 1997, Fuller & Gill 2001). These include invertebrates (Feber *et al.* 2001, Stewart 2001), small mammals (Ostfeld *et al.* 1996, McShea 2000, Flowerdew & Ellwood 2001) and birds (Fuller 2001). Many species of woodland birds depend, either for nesting cover or for food, on vegetation in the field or shrub layer (Fuller 1995). It is reasonable to conclude, therefore, that habitat quality for many species could be impaired by severe grazing and browsing pressure. Several correlative or circumstantial pieces of evidence indicate that grazing pressure can affect bird abundance in British woodland (see Fuller 2001 for a more complete discussion).

First, Donald *et al.* (1998) demonstrated that the bird community of parts of the Forest of Dean grazed mainly by sheep (but also Fallow Deer) had a lower proportion of breeding summer visitors, such as Willow Warbler and Blackcap, than ungrazed areas. The reason for this may have been the greater abundance of small broad-leaved trees, in particular Birch, in the ungrazed stands. In winter, the ungrazed plots also held a significantly lower proportion of seed-eating birds, notably finches, perhaps because of a reduction in seed-bearing plants caused by grazing (Donald *et al.* 1997).

Second, during the 1980s and 1990s in Wytham Woods, Oxfordshire, there was a large reduction in breeding populations of species that nest in low vegetation, whereas overall numbers of hole-nesting birds have remained relatively constant (Figure 6, Perrins & Overall 2001). These declines - in species such as warblers, thrushes, Dunnock and Bullfinch - coincide with a dramatic impact by Fallow Deer on the low vegetation structure of the wood, involving the massive reduction of Bramble.

This situation arose because the deer were fenced inside the wood, causing an exceptional grazing pressure which was almost certainly higher than in other woods in the surrounding region.

Third, an increase in pressure from Roe and Muntjac Deer in Bradfield Woods, Suffolk, has caused a reduction in the height and cover of coppice regrowth, together with an increase in coarse grasses (Fuller 2001). These vegetation changes have coincided with a large decrease in Nightingales. Nightingales require a combination of low dense thickets and patches of bare ground within these thickets for feeding (Fuller *et al.* 1999). The intensified browsing in Bradfield Woods has tended to diminish this type of vegetation structure. Experiments are now being carried out in Bradfield Woods to assess whether exclusion of deer affects both vegetation structure and bird distribution.

Experimental evidence that deer can alter woodland bird communities is currently available from two North American studies. In Pennsylvania, 13 ha and 26 ha enclosures were used to simulate four different White-tailed Deer *Odocoileus virginianus* densities ranging from 4 to 25 deer km^{-2} (deCalesta 1994). Enclosures contained both managed and unmanaged forest and each deer density was replicated. After 10 years of browsing, breeding songbirds were counted. Significant effects of deer density were found on ‘intermediate canopy songbirds’ (defined as species that nest at 0.5 – 7.5 m) but not on songbirds that nested on the ground or in the upper canopy. The overall abundance and numbers of species of intermediate canopy-nesters decreased from lowest to highest deer density. The second study was in Virginian forests holding White-tailed Deer densities of >25 km^{-2} (McShea & Rappole 2000). Four pairs of 4 ha study plots were used, one of each pair being fenced to exclude deer. Summer bird numbers were estimated using mist netting in the year before and the eight years following fencing. The exclusion of deer resulted in major changes in the composition of the trapped birds. Numbers of most species increased, whilst those preferring an open understorey declined. Similar results were obtained to those of deCalesta (1994) with increases in intermediate canopy species in exclosures. However, unlike deCalesta, increases were also observed in ground-dwelling birds.

In both of the North American experiments, there was evidence that deer had modified low vegetation structure and it was reasonable to assume that this was the principal cause of the observed differences in bird communities. However, deer can potentially affect woodland birds through other mechanisms (Fuller 2001). Trampling of nests could be a problem where deer density is exceptionally high. Alteration of vegetation structure may result in greater exposure of nests to predators. Complex low vegetation structures may also be important in protecting fledglings against predators once they have left the nest. Deer may directly remove some of the food of birds, for example fruits and large seeds. Indirect effects on food availability may come about as a result of long-term changes in tree and species composition, including reduction in the diversity of young trees and shrubs (Gill & Beardall 2001, Putman *et al*. 1989), and the decrease in small mammals following simplification of the field layer (Flowerdew & Ellwood 2001). None of these potential mechanisms has been adequately studied.

In conclusion, there is good evidence that increasing grazing and browsing pressure, particularly by deer, has had a marked effect on the structure of woodland vegetation in many parts of lowland and upland Britain. Based on knowledge of the requirements of many woodland species this is very likely to have caused a reduction in habitat quality for species that depend on low vegetation. Conversely, species that prefer open structures, notably Redstart and Wood Warbler, may benefit. Experimental studies of the kind undertaken in North America are needed as well as a better understanding of the micro-habitat requirements and year-round food resources exploited by woodland birds. It should not be assumed that responses of woodland species to herbivore pressure are linear; research is needed that examines patterns in biodiversity across gradients of deer density (Fuller & Gill 2001).

The effects of deer on woodland structure are complex and variable. Nonetheless, it is likely that increases in large herbivores have contributed to the declines observed in some woodland bird species – strong candidates include Nightingale, Dunnock, Song Thrush, Willow Warbler, Marsh Tit, Willow Tit and Bullfinch. Following an analysis of demographic change in British Bullfinches, Siriwardena *et al.* (2001) concluded that future work should concentrate on the effects of habitat change, including the alteration of woodland understorey vegetation by deer.

Three final notes of caution are required. First, we can be reasonably certain that local reductions in habitat quality have occurred as a consequence of large increases in deer, but it should not be concluded that deer are the principal causes of decline in any bird species on a large scale. Second, not all changes in woodland structure should be attributed to grazing, since other factors, such as climate change, succession and stand management may have an important influence. Third, the effects of deer on vegetation and birds will vary from one wood to another depending on factors such as canopy shading and it should not be assumed that these effects are consistently negative.

5.2 Availability of Dead Wood and Nest Holes

Dead and decaying wood is widely regarded as an important component of habitat quality for some woodland birds, either by providing nest sites or as a source of food. It is convenient to consider both dead wood and nest holes in the same section even though not all hole-nesting birds place their nests in dead wood. For example in Białowieża Forest, Marsh Tits avoid using holes surrounded by dead wood because these are at greater risk of predation (Wesołowski 2002). Even for such species, however, the processes that allow dead wood to form are broadly important in determining availability of nest holes in live trees. The numbers of holes tend to increase in old stands which have greater quantities of dead wood, and nests located in living trees are often in cavities created through the loss of a dead branch and associated decay of heartwood.

Not all dead wood is of value to birds. The exact state of decay will affect ease of excavation, the potential quality of the nest site and suitability as a microhabitat for wood-boring insects (see below). Nonetheless, certain types of dead and decaying wood appear to be an important resource for at least two species of declining woodland birds in Britain. Uniquely among British tits, Willow Tits excavate their nest cavity in soft deadwood (Cramp & Perrins 1993). Lesser Spotted Woodpeckers commonly excavate nest holes in dead or dying wood and appear to have a greater preference for making their holes in dead wood than Green or Great Spotted Woodpeckers (Osborne 1982, Glue & Boswell 1994). Outside the breeding season they also depend heavily on insect larvae associated with small dead branches (1 to 5 cm diameter) as a food source (Olsson *et al.* 1999), although in the breeding season they rely on insects in the foliage (Wiktander *et al.* 1994). In addition to these specific dependencies, it is possible that dead wood has a more general indirect benefit to insectivorous birds. The quantity of dead wood at different stages of decay may have considerable influence on the overall abundance of insects in various woodland habitats, as many saproxylic invertebrates in their larval stages depend on dead wood, though as adults they require open space with nectar and pollen sources (Warren & Key 1989) at which time they may be preyed upon by a wide range of bird species.

Whilst there is no reliable quantitative information on the historical changes in dead wood in British woodland, several factors are likely to have generated increased amounts of deadwood in recent years. The storms of 1987 and 1990 caused the death of many trees and extensive branch loss in south-eastern England (Kirby & Buckley 1994). The storm of 1987 appeared to double the amount of dead wood in some unmanaged English woodlands in the years immediately following the storm (Kirby *et al.* 1998), although this increase may have been short-lived in some areas due to the clearance of dead timber soon after the storm. The drought of 1976 also caused considerable tree death in some areas, particularly of Beech and Birch (e.g. Peterken & Jones 1987, Peterken 1996). Dutch Elm disease, which reached its peak in Britain during the 1970s, temporarily increased the abundance of dead trees in many parts of the countryside (Osborne 1983). Larvae of the *Scolytus* beetles that spread the fungal pathogen are abundant on recently dead trees and formed a food source for woodpeckers and tits (Osborne 1985). This was a temporary glut, however, for felling of the dead Elms became normal practice. Many woods in lowland England, especially former coppice, have long been neglected and this has probably led to an increase in the total amount of dead wood within them because dead wood is less abundant in managed than unmanaged stands (Peterken & Mountford 1995, Kirby *et al.* 1991, 1998). However, within abandoned coppice, the temporal pattern of change in dead wood may be complex possibly involving an initial increase followed by a decline (see section 4.5).

There is now more awareness and appreciation of the biodiversity value of old trees and dead wood amongst woodland managers than was the case 30 years ago. Nonetheless, locally there may have been recent reductions in amounts of dead wood as a result of woodland management activities, especially following the 1987 and 1990 storms. With the rising popularity of wood-burning stoves, some woods may have seen more intensive extraction of dead wood. In woods that are open to public access there has probably been some removal or management of old trees for safety reasons. Elsewhere there will have been some harvesting of mature broadleaved stands containing living trees with dead branches. Overall, however, we suggest that these factors are unlikely to have been sufficient to create a net decrease in dead wood over the last three or four decades.

Given the above, it seems unlikely that change in the availability of dead wood is the key factor in the declines of woodland birds. However, caution is needed in reaching a firm conclusion on this issue. There may have been local changes in dead wood availability that have affected local status of some species. The effects of different factors on dead wood availability are likely to have varied considerably between different woods (Kirby & Buckley 1994, Peterken 1996, Kirby *et al.* 1998), depending on the scale of tree death, the woodland management practices adopted, tree species composition and stand age. Kirby *et al.* (1998) carried out an inventory of dead wood across 63 woodland sites throughout Britain, including managed and unmanaged sites. The values they obtained ranged from zero, in recently cut coppice, to over 100 $m^3 ha^{-1}$ in undisturbed stands. High spatial variability was strongly associated with the age and management of the stand and episodic events, notably storms and drought. Considerable local variation in the factors affecting dead wood availability makes it extremely difficult to establish how changes in dead wood may have affected national bird populations. This is further complicated by the fact that dead wood may be present in several different forms: as standing dead trees, fallen trees, fallen branches, stumps, or as dead parts of living trees. Different types of dead wood may have different consequences for birds. It is possible that subtle changes in the *types*, rather than the *quantity*, of dead wood may have occurred at many sites; this could be relevant to the two declining dead wood specialists in the following ways. In the case of Willow Tit, where there appear to be potentially suitable sites available, these may in fact not be at a suitable stage of decay for nest excavation. It is possible that storms may actually have reduced the suitability of some woodland areas for Lesser Spotted Woodpeckers by destroying many of the small dead branches which are the preferred foraging sites of the bird outside the breeding season.

Whether or not changes in dead wood resources are important in the declines of some woodland birds, there is a need to improve general understanding of the relevance of dead wood to the ecology of woodland birds. Dead wood is enormously variable in terms of its location within woodland, its size, its state of decay and the quality of habitat that it offers saproxylic invertebrates. Much dead wood within woodland is probably of no value to birds as a foraging and nesting habitat. Some relevant questions are as follows. At what times of year is it used as a source of food by woodpeckers and bark gleaning species? What types of dead wood are important to birds, both for feeding and for nest sites? Are saproxylic insects important dietary components for birds that do not excavate dead wood? Do relationships exist between bird productivity and / or bird abundance and dead wood availability?

A better understanding of microhabitat requirements with respect to dead and decaying wood, would make it more feasible to establish whether changes in dead wood resources have the capacity to affect birds at a population level. Research into the effect of dead wood availability on bird populations is minimal in Britain, though an important exception is the work by Smith (1994, 1997) on Great Spotted Woodpeckers. Much of the work on relationships between populations and dead wood has focused on hole-nesting birds and densities of standing dead trees in North America and Fennoscandia. There is little doubt that availability of nest sites limits populations of some species in some types of woodland (see references in Newton 1994). However, a far more difficult question to answer is whether dead wood availability can limit populations through effects on food availability.

Experiments involving different types of dead wood removal would be required to establish whether this was important.

5.3 Reduction in Lichens

Epiphytic lichens can provide important sites for food location and food storage, as well as offering material for nest construction. In boreal forests, lichens are important habitats for spiders and other invertebrates and they provide major foraging sites for insectivorous birds, including Willow Tit and Crested Tit (Cramp & Perrins 1993). Lichens are also the most regularly used food storage sites in Scandinavian Willow Tits (Cramp & Perrins 1993). The abundance of lichens can be affected negatively by both air pollution and forestry activities, so is it possible that a reduction in lichens has occurred in British woodland with consequences for some insectivorous birds? Studies in Sweden have demonstrated that lichens and associated invertebrates are less abundant on branches on spruce trees in managed than unmanaged forests (Petterson 1996, Petterson *et al.* 1995). This may be because rotations are too short to allow lichens to accumulate. Petterson *et al.* (1995) argued that this could result in reduced food for passerine birds. Lichens tend to be far more abundant and luxuriant in western and northern woods in Britain where air pollution has had the least impact historically. Several of the birds that are declining in British woodland are doing so in regions that have been relatively poor in lichens for many decades i.e. the east and south. There is no evidence that *recent* changes have occurred in the status of lichens in British woods that could have resulted in a significant reduction of habitat quality for birds. Furthermore, the use of lichens by birds in British or other temperate European woodland appears not to have been studied; it is unclear whether lichens are such an important microhabitat feature in temperate as boreal woodland.

6. PRESSURES FROM OTHER ORGANISMS

6.1 Predation Pressure

Predation is the largest cause of nest failure in most birds, and in some cases it may be sufficient to suppress or reduce the breeding population (reviewed by Newton, 1993, 1998). The importance of predation as a factor influencing nest site and microhabitat selection is well established (Martin 1992, 1993, 1998, Martin & Roper 1988, Nilsson 1984, Wesołowski 1996, 2002). Several potential predators of woodland birds in Britain have increased over the last 30 years. The main problem in determining whether this may have contributed to bird declines is that there have been few studies of the role of predation in the population dynamics of woodland birds in western Europe and rather little is known about the relative importance of different types of predator. The main potential predators are discussed below, starting with mammals and then considering avian predators.

The Grey Squirrel (*Sciurus carolinensis*) has increased both in terms of density and range, and it is now almost ubiquitous in England and Wales, and continues to increase in Scotland (Harris *et al.* 1995, Yalden 1999). There is widespread concern that the establishment of this non-native species in much British woodland has resulted in elevated levels of nest predation on songbirds. The potential impacts of the Grey Squirrel could be greater than that of the displaced native Red Squirrel (*Sciurus vulgaris*) because the body size and population density of the former are larger. Squirrels are major nest predators of woodland birds in parts of the USA (e.g. Reitsma *et al.* 1990) but rather little is known about their importance as a predator of European birds. One exception, however, is a study by Nour *et al.* (1993) of nest predation using artificial nests in deciduous forest fragments in Belgium. Based on tooth marks, they found that 45% of nests in which predation was caused by a mammalian predator were apparently attacked by squirrels (presumably Red Squirrels). However, they also found that other mammals such as mice, rats and shrews were important and that 66% of overall nest predation was by birds.

A recent review of the evidence concerning impacts of Grey Squirrels indicates that potentially they are major predators of nesting songbirds but there is a lack of information about their impacts on birds, both in Britain and in North America (Hewson & Fuller 2003). Other main conclusions of this review were as follows. It appears that predation rates by Grey Squirrels may vary considerably between woods, possibly reflecting spatial variation in squirrel density and in the availability of alternative foods. A wide range of songbirds, including ground-nesters and hole-nesters, are potentially vulnerable but canopy nesters, particularly Chaffinch and Hawfinch, seem most at risk. The information currently available is, however, largely anecdotal and there is need for a systematic study involving both autecological work and squirrel removal experiments to establish the relative contribution of Grey Squirrels and other predators to songbird nest losses.

The Red Fox *Vulpes vulpes* is another predator that has probably increased in Britain, although reliable estimates of fox densities are difficult to obtain (Harris *et al.* 1995). Foxes are predators of adult nesting Woodcock (Hoodless & Coulson 1998) and Capercaillie (Moss & Picozzi 1994) but their effect on the populations of these and other ground-nesting birds is unknown. Most other mammalian predators (rodents and mustelids) do not appear to have increased on a wide scale, so they are unlikely candidates for causing declines in woodland birds. It is worth mentioning, however, that Badgers (*Meles meles*) are increasing in parts of southern and eastern England and are potential predators of ground-nesting birds.

Turning to avian predators, the most important are woodpeckers, corvids, owls and raptors. Several of these predators have increased substantially in recent decades (Baillie *et al*. 2002). Great Spotted Woodpecker is a major predator of tit nests (Ludescher 1973, Perrins 1979). The marked increase of this species in Britain over recent decades raises the possibility of a link with the declines in Willow Tit and Marsh Tit. However, an analysis of national population trend data using BTO data has not revealed any relationship between these tits and numbers of woodpeckers or Jays, with the exception of a negative relationship between Willow Tit and Great Spotted Woodpecker on farmland

(Siriwardena 2001, in press). Nonetheless, it remains a possibility that such relationships might exist at local scales. The Great Spotted Woodpecker is also the most serious nest predator of the Lesser Spotted Woodpecker (Cramp 1985).

More generally, there is little evidence of strong relationships between woodland songbird numbers and the abundance of avian predators (McCleery & Perrins 1991, Newton 1993, 1998, Newton *et al.* 1997, Thomson *et al.* 1998). The drawback with many of the existing studies is that they have considered the impact of predators on locally stable or increasing songbird populations, many of which were supplemented with nest boxes. The effect of predators on declining or non-supplemented populations may be much more pronounced; in other words, predation could have an important secondary effect when populations are under pressure from other factors. Furthermore, these studies have tended to focus on relationships with particular predator species, notably the Sparrowhawk *Accipiter nisus* (see review in Newton 1998). It is possible that other, relatively unstudied, avian predators have population effects on some woodland birds under some conditions. There may also be cumulative effects from different predator species that would not be apparent from studying a single predator species. A whole suite of predators may predate the nests of woodland birds (e.g. Marcström *et al.* 1988, Reitsma *et al.* 1990, Andrén 1992, Nour *et al.* 1993). Studies are ideally needed on overall predation pressure, but with the capacity to identify the effects of individual predator species.

Changes in habitat structure or food supplies may increase the likelihood of woodland bird populations being exposed to increased predation (Newton 1998). For example, a reduction in shrub or field layer by grazing herbivores may have reduced the amount of nest cover for some birds and increased their susceptibility to predators (section 5.1). Competition, both intra- and inter-specific, may also force birds to use nest sites, feeding sites or roosts where they are more vulnerable to predators.

Many studies suggest that the level of predation is higher along woodland edges than in the woodland interior (e.g. Andrén 1992, 1995, Paton 1994, McCollin 1998). It has even been suggested that edges can form ‘ecological traps’ for bird species that are attracted to nest at high densities in edge habitats as a result of density-dependent predation (Gates & Gysel 1978). Work in North America indicates that such edge effects are dependent on landscape context (Donovan *et al.* 1997, Chalfoun *et al.* 2002). Predation rates at edges may be relatively high where forest meets agricultural land, compared with edges within forests, e.g. where clearcuts abut mature forest. Predation rates at edges may also be generally higher in landscapes where forest is highly fragmented. In Britain, the small-scale clearance and replanting of woodland has led to an increase in the general patchiness of the woodland landscape (see Introduction), which is likely to have increased the proportion of woodland edge habitat in some areas. It is possible that this has led to increased predation rates in some birds, although there is no direct evidence for this. Even where there has been no recent change in the spatial distribution of woodland, it is possible that predation rates may have increased at the woodland edge as a consequence of increases in predators (notably corvids) associated mainly with surrounding farmland. If this has occurred one would expect population declines of vulnerable species to be especially marked in small woodland patches or in edge, rather than woodland interior, habitats.

The findings of studies undertaken in relatively recently fragmented landscapes of eastern and midwestern North America should not be applied directly to landscapes with a far longer history of fragmentation. In Britain, the current distribution of woodland has been broadly similar for several hundred years; furthermore a high proportion of woodland bird species show selection of woodland edges (Fuller & Warren 1991). It is entirely possible that in these historically fragmented landscapes, edges do not represent such a severe predator trap as they do in recently fragmented landscapes due to the evolution of effective anti-predator traits. Interestingly, Møller (1989) has demonstrated that in Denmark the characteristics of nest sites have a strong effect on risk of predation at the woodland edge: open nests are subject to far higher predation rates than nests that are partially covered by vegetation. Species with open nests (e.g. Skylark) tended to nest further from edges than did species with partially covered nests (e.g. Tree Pipit). There is clearly a need for far more work on relationships between forest edges and the breeding success of birds in European woodland.

Analyses of BTO nest record cards suggests that declines in woodland birds have not been accompanied by declines in nest productivity (Crick *et al.* 1998, Baillie *et al.* 2002). However, this is based on nests from all habitat types, not just woodland. A separate analysis of nest records from woodland habitats is needed to see if there have been any significant trends in the productivity of birds occupying woodlands. Notably, nest record data does not measure post-fledging survival and the predation of young once they have left the nest could be a major factor affecting bird populations, but it is extremely difficult to study in most species. Thus, it is also necessary to study the effect of predators on recruitment. Another important point is that sustained low levels of productivity, caused by fairly constant levels of predation, could be more important in influencing bird populations, than trends in productivity.

6.2 Inter-Specific Competition

Even though there is a degree of separation between the ecology of woodland bird species, several species overlap in terms of their foraging and nesting requirements and, therefore, potentially compete for resources. Inter-specific competition may limit the populations of some species where resources are in short supply (Newton 1998). The resources may be nest sites (usually holes) or feeding sites / food supplies. Isolating the effects of competition from other factors as a cause of numerical change in bird numbers is difficult and requires experimentation to rule out alternative explanations. Nonetheless, several experiments have convincingly demonstrated that competition for nest sites or food supplies can affect local abundance and distribution of forest birds (see review by Newton 1998). It is possible, therefore that changes in population levels, or even behaviour, of competitors may be a causal factor in the decline of some British woodland birds.

One approach to determining whether competition may affect population levels is to assess patterns of change within potentially competing groups of species. This approach has yielded few insights into competitive interactions. Most of the published long-term European studies of forest bird communities suggest that the populations of many species that use similar resources often fluctuate or change in parallel, apparently indicating a general lack of inter-specific compensatory fluctuation (Enemar *et al.* 1984, Hogstad 1993, Wesołowski & Tomiałojć 1997). The problem with these analyses is that subtle effects of competition may be masked by large fluctuations in bird populations between years due to factors such as weather and food supply. Negative correlations between population levels of pairs of species are only circumstantial evidence at best. Conversely, a positive correlation does not necessarily imply an absence of competition. Two ecologically similar species may be declining due, for example to the deterioration of a food resource that they use in common. If one species is dominant it may exclude the other species from that resource, with the result that the subordinate species declines at a faster rate. Despite these criticisms, a comprehensive analysis of population trends of British woodland species using Common Birds Census data (Marchant *et al.* 1990) would be valuable in identifying potential competitive interactions that would be worth exploring further.

Some of the declining woodland species appear to be candidates for the inter-specific competition hypothesis; these include Marsh Tit, Willow Tit and Lesser Spotted Woodpecker. In Sweden, Nilsson (1984) found that Marsh Tits were sub-ordinate in their choice of nest sites to Blue Tits, Nuthatches and Starlings. In the presence of these other species they were forced to use lower nest holes which were more thought to be more susceptible to predators. It is unknown whether Marsh Tits in Britain are subjected to this type of competition, but it could be one explanation for their decline in British woodland, given that Nuthatches and Blue Tits have increased in recent years (Table 1).

The Willow Tit also competes with several other tit species for foraging sites (see reviews by Alatalo 1982, Dhondt 1989) though we are unaware of any specifically British studies of foraging interactions involving Willow Tit. It is possible that increases in other tit species have placed extra pressure on Willow Tit populations through competition for food or nest sites. Preliminary analysis of Marsh Tit and Willow Tit population trends have not found any negative relationships with Blue Tit and Great Tit numbers (Siriwardena 2001, in press). Nonetheless, the most convincing example of how inter-specific competition might have consequences for the population of a declining woodland bird involves these three species. In Lanarkshire, central Scotland, Great Tits and Blue Tits commonly usurp the nest sites of Willow Tits (Maxwell 2002, 2003). Out of 30 Willow Tit ‘pair-years’, Maxwell (2002) reported 18 instances of Blue Tits and 2 of Great Tits taking over nests. It appears that the aggressive takeover frequently occurs just as the nest excavation is being completed. Because Willow Tits invest considerable time and energy in excavating a nest site, its loss could result in a serious delay in breeding. It is unclear how widespread this phenomenon is, though it appears not to be new.

The decline of the Lesser Spotted Woodpecker in Britain has occurred at the same time as an increase in the Great Spotted Woodpecker (Table 1). In Fennoscandia, numbers of Great Spotted Woodpeckers increase in years when there is a heavy seed crop of spruce. In subsequent years with low seed crops, Great Spotted Woodpeckers resort to feeding on invertebrates in dead wood and may then come into competition with Lesser Spotted Woodpeckers. Nilsson *et al.* (1992) suggest that, coupled with an increase in the relative extent of coniferous forest, this could explain the decline of the Lesser Spotted Woodpecker in Sweden, although they provided no direct evidence. Whether similar mechanisms, involving fluctuations in other types of foods exploited by Great Spotted Woodpeckers, might operate in Britain is unknown. These two woodpecker species utilise similar nesting trees (dead Birches are used by both species in many English woods) and, hence, there may also be competition for suitable nesting sites.

Inter-specific competition between woodland birds and other taxa may also have affected some British woodland bird populations. Grey Squirrels commonly use tree cavities and can be an effective competitor with Tawny Owls and other large hole-nesting species (Hewson & Fuller 2003). Grey Squirrels feed on many different types of tree seeds which also form a food for several birds. Similarly, deer may consume large amounts of tree seeds and seed plants that are used as food sources by many seed-eating and insectivorous birds (section 5.1).

It is possible that the widespread feeding of garden birds may have contributed to increasing inter-specific competition by enhancing numbers of Blue Tits and Great Tits. Garden feeding may also be a factor in the increase of Great Spotted Woodpecker and it clearly benefits Grey Squirrels with potential implications for predation rates. As yet there is no evidence to support this idea, but the interaction between garden feeding and the dynamics of bird populations in general should be investigated.

6.3 Parasites and Disease

Could parasites or pathogens be elements in the declines of woodland birds? It is relevant that such factors have not emerged as significant in the declines of farmland birds where one might expect them to be more prevalent due to the fact that, especially in winter, many of these species are highly gregarious. One area that may be especially worth examining is whether the concentration of birds at garden feeders increases the risk of disease transmission. This is unlikely, however, to be a direct factor for any of the declining species of woodland birds as few of them feed heavily at feeders; the most likely candidate would be Marsh Tit.

Newton (1998) thought it likely that parasites and disease were less prevalent as major limiting factors for breeding numbers than predation or food shortage. Nonetheless, he pointed out that many species could experience occasional epidemics with medium-term consequences for population size. Furthermore, he acknowledged that risk of disease was not independent of other factors such as deteriorating food supplies and pollution. Exposure to worsening environmental conditions may reduce the condition of birds to a point where they become more vulnerable to disease.

The second half of the 20th century has seen the emergence of several major diseases in humans and wildlife (Friend *et al.* 2001). Against this background, especially coupled with continuing pressures on habitat quality, ecologists need to be aware that disease could become an increasingly important factor in the dynamics of wild birds.

7. GENERAL DISCUSSION AND CONCLUSIONS

7.1 Multiple Hypotheses: No Simple Stories

There is no overarching hypothesis as there was with agricultural intensification for farmland birds (Fuller *et al.* 1995). In the case of woodland birds there is a diversity of hypotheses which may act in a species-specific manner. Nonetheless certain factors emerge as potentially affecting a wide suite of species and these are among the priorities for research (see section 7.4).

We have discussed the factors that may have affected woodland birds in isolation from one another but this is not the situation in nature. Individually, the factors may be insufficient to limit bird populations. Interactions between different limiting factors may accentuate their effects on birds. For example there may be several interactions between predators and other factors. Birds could become more vulnerable to predation as nesting cover is reduced by deer, or as food supplies diminish and birds are forced to spend more time foraging. Some woodland birds could be affected simultaneously by several factors that, even if not interacting, may combine in a diffuse way sufficient to reduce recruitment or survival. Changes in food supply, predation, inter-specific competition and physical deterioration of habitat may be acting simultaneously on some species. We think it very likely that multiple factors have exerted a combined effect.

The set of factors affecting the population of a species may vary between different geographical locations and between different time periods. This is to be expected as British woodlands vary massively in form and management between different localities and because many woodland birds in Britain are widespread (Gibbons *et al*. 1993). In this connection, it has to be recognised that the CBC woodland plots are not representative of woodland in Britain (see section 2). It cannot be assumed therefore, that the population changes summarised in Table 1 are typical of the whole of the United Kingdom. In particular, there is a need to understand how populations have changed in northern Britain generally and in coniferous forests in all regions. A recent project started by BTO and RSPB (Hewson *et al.* 2003) will help to establish whether changes in breeding populations in broadleaved woodland are ubiquitous or whether they are confined to certain regions.

7.2 Have Changes in Forestry Been Significant?

It may seem surprising that this review has not considered effects of changing management practices (i.e. silvicultural treatments) in forestry as potential drivers of woodland bird declines. We have emphasised the potentially important role of <u>lack</u> of management, including reduction of thinning (section 4.5). Other than this, we are unaware of any general trends in management techniques over recent decades that are potentially damaging to the habitats of woodland birds on a large scale. Pesticide usage within lowland woodland is miniscule compared with farmland, and generally is used locally in tree establishment, with usage levels lower than they were several decades ago (Gary Kerr pers. comm.). Changes in tree species composition are unlikely to have been significant for birds at a national scale (section 4.4) though changes in the age structure of forests may have been (section 4.3). On balance, recent trends in forestry are likely to have been beneficial. Forest policy, as well as the attitudes of many foresters and landowners, have become more sympathetic to the need to consider woodland wildlife both in strategic planning and operational management. The importance of habitat diversity, of open space, of dead wood, and of native tree species are now more widely, though not universally, appreciated and accepted, than they were 30 or 40 years ago. Whilst it is possible that some of the bird declines are a legacy of forestry activities conducted several decades ago we find it hard to identify precisely what these might be. Many of the recent declines have taken place in woods which have undergone little obvious change in management approach and where the overall physical structure and tree species composition has changed little for decades.

7.3 Do Different Processes Affect Woodland Birds in Britain and Europe?

The scale of declines in woodland birds in Britain does not appear to be matched by population changes in Europe (section 2.5). The available information is patchy and uneven in quality but a general pattern emerges that Britain is different to mainland Europe. The findings of the detailed long-term studies in Białowieża Forest are especially compelling (Wesołowski & Tomiałojć 1997, Wesołowski *et al*. 2002). These show that several species in Białowieża Forest have entirely the opposite trends to those documented in Britain.

Conditions for woodland birds are probably very different in Britain to those found at similar latitudes but further east in Europe. Climate is clearly different, but the insularity of Britain and the relatively low cover of woodland in Britain may also be relevant. Woodlands in Britain may be sub-optimal for some species due to factors such as these and this may lead to geographical differences in population dynamics. Several woodland species exhibit different patterns of habitat occupancy in Britain compared with mainland Europe (Fuller 2002). This could be due to a complex of factors including inter-specific competition, within-habitat microclimatic variation, historical landscape change, density-dependent habitat selection, and edge-of-range effects (Fuller 2002).

Species are expected to occupy fewer, and more specific, habitats at the edges of their ranges (Hildén 1965), though we are unaware of any critical tests of this hypothesis. Habitat specificity may increase at the edge of the range because intra-specific competition may be lower (possibly due to lower population density) so that birds concentrate into those habitats where breeding output is maximised. For some species, conditions are likely to be marginal at the edge of the range and consequently their populations may be relatively poorly buffered against change (for example in climate, pollution or habitat) that may be occurring more widely through the breeding range. Under these circumstances population decline, coupled with contraction into optimal habitat, is likely to be most pronounced at the edge of the range. For migrant species, pressures operating within the winter range may cause rapid changes in survival which could potentially manifest themselves initially at the edge of the range (see section 2.5). Factors such as these may be important in accounting for some of the population changes in British woodland birds. The Nightingale in England provides an example of how large-scale population dynamics may combine with local pressures on breeding habitat quality to generate range contraction and habitat shifts at the edge of the range (Fuller *et al.* 1999, Wilson *et al.* 2002). As a caveat to the above reasoning, it should be noted that Blackburn *et al.* (1999) could find rather little evidence that the densities of 32 common bird species in Britain showed systematic variation with respect to the edge of their ranges. Two main problems with such analyses, however, are defining the appropriate geographical scale (which ideally should be considerably larger than Britain) and how best to define local density which will be influenced by the area sampled and the exact habitat type studied.

More geographical comparisons are needed of demography, population dynamics and habitat occupancy on a European scale. Comparisons of the breeding performance of English and Dutch Great Tits indicate that complex differences can exist between populations (Stevenson & Bryant 2000, Cresswell & McCleery 2003). More detailed studies of this kind are needed to understand processes, but there is also a basic lack of knowledge about how habitat occupancy varies in both space and time across geographical gradients in Europe (Fuller 2002).

7.4 Key Hypotheses and Priority Research Areas

The strongest hypotheses accounting for recent declines in a suite of woodland birds are listed below. Process-based research is a high priority in all these areas, though autecological studies would also be valuable, especially where conducted at both the territory and landscape scale (e.g. Miranda & Pasinelli 2001).

(1) pressures on migrants during migration or in winter,
(2) climate change on the breeding grounds,

(3) reduction in invertebrates,
(4) impacts of agriculture on woodland edges and on habitats outside woodland,
(5) reduced management of woodland,
(6) intensified pressure from deer,
(7) changing predation pressure (squirrels, corvids and Great Spotted Woodpecker).

In Table 3 we have tried to summarise the likely importance of the above seven hypotheses in explaining the declines of 15 woodland species of particular conservation concern. The species are those woodland birds listed in Table 1 that have been red-listed or amber-listed as ‘Birds of Conservation Concern’ because they are either declining in numbers or contracting in range (Gregory *et al.* 2002). We have, therefore, excluded woodland species that have been red- or amber-listed essentially because they are rare or localised (Firecrest *Regulus ignicapillus*) or ones that are of particular conservation concern in a European context but not in a UK context (Redstart). We have also excluded Black Grouse and Capercaillie because these two species have received far more research attention than the other species and knowledge now extends well beyond the phase of advancing hypotheses. Important mechanisms in these cases are climate change (Moss *et al.* 2001), grazing pressure (Baines *et al.* 1994, Calladine *et al.* 2002) and collisions with deer fences (Catt *et al.* 1994, Baines & Summers 1997, Summers 1998).

With the exception of (1), each hypothesis is plausible for more than half the species (Table 3). Hypotheses (1), (4), (5) and (6) are strong ones for at least a third of the species and hypotheses (5) and (6) are strong for more than half the species. Hence, the effects on birds of decreasing woodland management and intensifying deer pressure are certainly high priority research areas. Three hypotheses potentially affect all 15 species: reduced invertebrate food supplies, climate change on the breeding grounds and enhanced predation pressure. We need to gain a far better understanding of factors affecting supply of invertebrates within woodland in relation to climate change, woodland management and surrounding land management. Some of these hypotheses could be addressed within integrated programmes of research. For example, work on edge impacts would need to address predation issues. Work on deer impacts would need to take woodland management into account due to the interaction between browsing pressure and canopy closure. Climate change work needs to consider issues of invertebrate abundance as well as phenology. It should, therefore, be possible to design research projects that give multiple insights to the processes that are affecting woodland birds at the present time.

In terms of tractability of research and developing remedies, the most challenging issues of all those identified above are (1) addressing the question of whether migrants are facing increasing difficulties outside Britain, especially in sub-Saharan Africa and (2) climate change. The remaining issues are relatively tractable to research, though they differ in the problems to be overcome in finding satisfactory solutions. The two issues that seem to lend themselves most readily to solutions through targeted environmental initiatives are (4) impacts of agriculture on the woodland edge and habitats outside woodland and (5) reduction in woodland management.

Several other strong hypotheses have also emerged which are specific to certain species of declining birds. Species-specific programmes of work would seem most appropriate in these instances e.g. Bullfinch (hedgerow and woodland edge structure), Woodcock (recreational disturbance) and Willow Tit (inter-specific competition for nest sites). The possible effects of changes in forest age structure on Lesser Redpoll and Tree Pipit is worthy of exploration. There is also a case for modelling studies that seek to understand how changes in the age structure affect wider bird communities in forests.

The other hypotheses considered in this review do not emerge as such strong contenders for explaining the recent declines of woodland species. Nonetheless, there is certainly a need to understand more about several of these issues in the context of British woodland birds. The importance of different tree species in the ecology of woodland birds, the ecological effects of intensive Pheasant rearing and exactly how bird species use dead and decaying wood are all topics that would benefit from scrutiny. The exclusion of habitat fragmentation and habitat loss from the priority list of hypotheses should not be taken as a general indication that these are unimportant conservation issues - this merely reflects our contention that these issues are relatively unimportant in explaining recent declines in woodland birds in Britain.

This review has highlighted factors that may have contributed to the decline of woodland birds in Britain but there are many serious gaps in our knowledge about the ecology of these birds. In this respect we lag behind Fennoscandia and North America that have ongoing traditions of research on forest birds that have established a wealth of information and understanding. This body of work and related reviews of new research directions (e.g. Partners in Flight Research Working Group 2002) can give insights to processes that may be operating here. However, the somewhat unique position of British woodlands, both geographically and climatically, means that findings from studies overseas should be applied with caution. In this respect, it has been suggested that a comparison of habitat use by forest birds across a longitudinal gradient from Ireland, through Britain to Germany and Poland would give valuable insights (Fuller 2002). We emphasise the need to consider processes affecting woodland birds at different spatial scales and in different localities. The complexity of the British woodland landscape and the widespread distribution of most woodland bird species, means that care should be taken in interpreting national population trends with respect to potential limiting factors on a countrywide scale.

We make the following specific recommendations concerning future research aimed at identifying the causes of recent declines and the most appropriate future conservation strategies. As mentioned above, there may be considerable potential for addressing some of these issues simultaneously within integrated programmes of research. (1) Improve basic knowledge of the ecology - including diet, breeding biology and habitat use through the year - of the declining species in a British context. (2) Undertake studies on predation in relation to (a) edge effects (b) the relative importance of Grey Squirrels as nest predators. (3) Examine responses of birds and their food supplies to different levels of deer browsing, both experimentally within selected sites and through observation across spatial gradients of deer density. (4) Take opportunities to study responses of birds and their food supplies to habitat variation created by existing examples of woodland management, including variation in edge structures. This should include testing the soundness of widely accepted conservation management techniques now used in woodland, notably coppice restoration and ride management. (5) Test possible solutions involving habitat manipulation by incorporating them into agri-environment schemes and monitoring the responses of birds over ecologically appropriate periods of time. (6) Develop programmes of research on bird populations living in the vast areas of managed conifer forests, both in the lowlands and uplands. Better information on conifer forests is needed to achieve a more representative understanding of the status of woodland birds in Britain, and to develop approaches for sustaining biodiversity within constraints of commercial production.

Acknowledgements

This review was undertaken mainly under the partnership between the British Trust for Ornithology and the Joint Nature Conservation Committee (on behalf of English Nature, Countryside Council for Wales, Scottish Natural Heritage and the Environment and Heritage Service in Northern Ireland). The summary of population changes at a European scale was completed as part of an EU-funded project on 'Biodiversity Assessment Tools'. The review has benefited from discussions with Richard Bradbury, Dan Chamberlain, Fred Currie, Robin Gill, Andy Gosler, Phil Grice, Chris Hewson, Shelley Hinsley, Jeremy Lindsell, Gary Kerr, Rufus Sage, Gavin Siriwardena, Ken Smith, Chris Perrins and Chris Quine. Ian McLean made helpful comments on a draft of the report. The core ideas in this report were presented and discussed at meetings of the Woodland Bird Group, a forum attended by representatives from UK government agencies, NGOs, institutes and universities (September 2001, January 2002, February 2003). Presentations were also made at a Defra review of research on farm woods (May 2002) and at a workshop of the Forestry Research Coordination Committee (April 2003). These discussions have been helpful in refining the ideas and we are grateful to all those who participated. We thank Su Gough and Nicki Read for their help in preparing the review.

References

Adams, S.N. (1975) Sheep and cattle grazing in forests: a review. *Journal of Applied Ecology*, **12**, 143-152.

Aebischer, N.J. (1991) Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. In: Firbank, L.G., Carter, N., Darbyshire, J.F. & Potts, G.R. (Eds.) *The Ecology of Temperate Fields*. Pp. 305-331. Blackwell Scientific Publications, Oxford.

Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (Eds.) (2000) *Ecology and conservation of lowland farmland birds*. British Ornithologists' Union, Tring.

Alatalo, R.V. (1982) Evidence of interspecific competition among European tits Parus spp.: a review. *Annales Zoologici Fennici*, **19**, 309-317.

Andrén, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, **73**, 794-804.

Andrén, H. (1995) Effects of landscape composition on predation rates at habitat edges. In: Hansson, L., Fahrig, L. & Merriam, H.G. (Eds.) *Mosaic Landscapes and Ecological Processes*. Pp. 225-255. Chapman & Hall, London.

Anon (1999) *A Better Quality of Life – A Strategy for Sustainable Development for the United Kingdom*. Department of the Environment, Transport and the Regions.

Anon (2001) Are Pied Flycatchers declining? *RAS Newsletter* no. 3. BTO, Thetford.

Avery, M.I. & Leslie, R. (1990) *Birds and Forestry*. Poyser, London.

Baillie, S.R., Crick, H.Q.P., Balmer, D.E., Beaven, L.P., Downie, I.S., Freeman, S.N., Leech, D.I., Marchant, J.H., Noble, D.G., Raven, M.J., Simpkin, A.P., Thewlis, R.M. & Wernham, C.V. (2002) *Breeding Birds in the Wider Countryside: their conservation status 2001*. BTO Research Report No. 278. BTO, Thetford. (http://www.bto.org/birdtrends).

Baillie, S.R. & Peach, W.J. (1992) Population limitation in Palaearctic-African migrant passerines. *Ibis*, **134** (suppl.), 120-132.

Baines, D., Sage, R.B. & Baines, M.M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology*, **31**, 776-783.

Baines, D. & Summers, R.W. (1997) Assessment of bird collisions with deer fences in Scottish forests. *Journal of Applied Ecology*, **34**, 941-948.

Barr, C.J., Bunce, R.G.H., Clarke, R.T., Fuller, R.M., Furse, M.T., Gillespie, M.K., Groom, G.B., Hallam, C.J., Hornung, M., Howard, D.C. & Ness, M.J. (1993) *Countryside Survey 1990: Main Report*. Department of the Environment, London.

Beebee, T.J. (1995) Amphibian breeding and climate. *Nature*, **374**, 219-220.

Bellamy, P.E., Brown, N.J., Enoksson, B., Firbank, L.G., Fuller, R.J., Hinsley, S.A. & Schotman, A.G.M. (1998) The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (Sitta europaea L.). *Oecologia*, **115**, 127-136.

Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673-687.

Bibby, C.J., Phillips, B.N. & Seddon, J.E. (1985) Birds of restocked conifer plantations in Wales. *Journal of Applied Ecology*, **22**, 619-633.

BirdLife International / European Bird Census Council (2000) *European Bird Populations: estimates and trends*. BirdLife International (BirdLife Conservation Series No.10), Cambridge.

Blackburn, T.M., Gaston, K.J., Quinn, R.M. & Gregory, R.D. (1999) Do local abundances of British birds change with proximity to range edge? *Journal of Biogeography*, **26**, 493-505.

Boatman, N. (1992) Improvement of field margin habitat by selective control of annual weeds. *Aspects of Applied Biology*, **29**, 431-436.

Both, C. (2002) Decrease of European Pied Flycatchers due to climate change? *Limosa*, **75**, 73-78.

Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296-298.

Calladine, J. Baines, D. & Warren, P. (2002) Effects of reduced grazing on population density and breeding success of black grouse in northern England. *Journal of Applied Ecology*, **39**, 772-780.

Catt, D.C., Dugan, D., Green, R.E., Moncrieff, R., Moss, R., Picozzi, N., Summers, R.W. & Tyler, G.A. (1994) Collisions against fences of woodland grouse in Scotland. *Forestry*, **67**, 105-118.

Chalfoun, A.D., Thompson, F.R. & Ratnaswamy, M.J. (2002) Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology*, **16**, 306-318.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771-788.

Chamberlain, D.E., Warren, R.W., Crick, H.Q.P., Hall, J., Metcalfe, S., Ormerod, S., Whyatt, D. & Vickery, J.A. (2000) *Acidification and terrestrial birds*. BTO Research Report No. 236. British Trust for Ornithology, Thetford.

Chapman, N., Harris, S. & Stanford, A. (1994) Reeves' Muntjac, *Muntiacus reevesi*, in Britain – their history, spread, habitat selection, and the role of human intervention in accelerating their dispersal. *Mammal Review*, **24**, 113-160.

Cooke, A.S. & Farrell, L. (2001) Impact of muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. *Forestry*, **74**, 241-250.

Cramp, S. (Ed.) (1985) *Birds of the Western Palearctic* Vol. IV. Oxford University Press, Oxford.

Cramp, S. & Perrins, C.M. (Eds.) (1993) *Birds of the Western Palearctic* Vol. VII. Oxford University Press, Oxford.

Cresswell, W. & McCleery, R. (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, **72**, 356-366.

Crick, H.Q.P., Baillie, S.R., Balmer, D.E., Bashford, R.I., Beaven, L.P., Dudley, C., Glue, D.E., Gregory, R.D., Marchant, J.H., Peach, W.J. & Wilson, A.M. (1998) *Breeding Birds in the Wider Countryside: their conservation status (1972-1996).* BTO Research Report No. 198. British Trust for Ornithology, Thetford.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526.

Crick, H.Q.P. & Sparks, T.H. (1999) Climate change related to egg laying trends. *Nature*, **399**, 423-424.

deCalesta, D.S. (1994) Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management*, **58**, 711-718.

DeGraaf, R.M., Healy, W.M. & Brooks, R.T. (1991) Effects of thinning and deer browsing on breeding birds in New England oak woodlands. *For. Ecol. Manage.*, **41**, 179-191.

Dhondt, A.A. (1989) Ecological and evolutionary effects of interspecific competition in tits. *Wilson Bulletin*, **101**, 198-216.

Donald, P.F. (1998) Changes in the abundance of invertebrates and plants on British farmland. *British Wildlife*, **9**, 279-289.

Donald, P.F., Fuller, R.J., Evans, A.D. & Gough, S.J. (1998) Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. *Biological Conservation*, **85**, 183-197.

Donald, P.F., Haycock, D. & Fuller, R.J. (1997) Winter bird communities in forest plantations in western England and their response to vegetation, growth stage and grazing. *Bird Study*, **44**, 206-219.

Donovan, T.M., Jones, P.W., Annand, E.M. & Thompson, F.R. (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology*, **78**, 2064-2075.

Drent, P.J. & Woldendorp, J.W. (1989) Acid rain and eggshells. *Nature*, **339**, 431.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169-175.

Enemar, A., Nilsson, L., & Sjöstrand, B. (1984) The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. *Annales Zoologici Fennici*, **21**, 321-338.

Estoppey, F. (2001) A declining Woodcock *Scolopax rusticola* population in the Jorat Forest (Vaud, western Switzerland). *Nos Oiseaux*, **48**, 83-92. (in French)

Feber, R., Brereton, T.M., Warren, M.S. & Oates, M. (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. *Forestry*, **74**, 271-276.

Feber, R.E., Smith, H., & Macdonald, D.W. (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology*, **33**, 1191-1205.

Ferry, C. & Frochot, B. (1970) L'avifaune nidificatrice d'une forêt de chênes pédonculés en Bourgogne: étude de deux successions écologiques. *La Terre et al Vie*, **2**, 153-250.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology*, **81**, 1970-1984.

Flousek, J. (1989) Impact of industrial emissions on bird populations breeding in mountain spruce forests in central Europe. *Annales Zoologici Fennici*, **26**, 255-263.

Flowerdew, J.R. & Ellwood, S. (2001) Impacts of woodland deer on small mammal ecology. *Forestry,* **74**, 277-287.

Foppen, R. & Reijnen, R. (1994) The effects of car traffic on breeding bird populations in woodland. II. Breeding dispersal of male willow warblers (*Phylloscopus trochilus*) in relation to the proximity of a highway. *Journal of Applied Ecology,* **31**, 95-101.

Forestry Commission (2001a) *Forestry Commission Facts and Figures 2000-2001*. Forestry Commission, Edinburgh.

Forestry Commission (2001b) *National Inventory of Woodland and Trees – England*. Forestry Commission, Edinburgh.

Friend, M., McLean, R.G. & Dein, F.J. (2001) Disease emergence in birds: challenges for the twenty-first century. *Auk,* **118**, 290-303.

Fuller, R.J. (1982) *Bird Habitats in Britain*. Poyser, Calton.

Fuller, R.J. (1995) *Bird Life of Woodland and Forest*. Cambridge University Press, Cambridge.

Fuller, R.J. (1997) Native and non-native trees as factors in habitat selection by woodland birds in Britain. In: Ratcliffe, P.R. (Ed.) *Native and non-native in British Forestry*. Pp 131-139. Institute of Chartered Foresters, Edinburgh.

Fuller, R.J. (2000) Relationships between recent changes in lowland agriculture and farmland bird populations: an overview. In: Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (Eds.). *Ecology and Conservation of Lowland Farmland Birds*. Pp 5-16. British Ornithologists' Union, Tring.

Fuller, R.J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. *Forestry*, **74**, 289-298.

Fuller, R.J. (2002) Spatial differences in habitat selection and occupancy by woodland bird species in Europe: a neglected aspect of bird-habitat relationships. In: *Avian Landscape Ecology – pure and applied issues in the large-scale ecology of birds*. Pp 101-111. Proceedings 11th IALE (UK) Conference. International Association for Landscape Ecology (UK).

Fuller, R.J., Chamberlain, D.E., Burton, N.H.K. & Gough, S.J. (2001) Distributions of birds in lowland agricultural landscapes of England and Wales: How distinctive are bird communities of hedgerows and woodland? *Agriculture, Ecosystems and Environment*, **84**, 79-92.

Fuller, R.J. & Crick, H.Q.P. (1992) Broad-scale patterns in geographical and habitat distribution of migrant and resident passerines in Britain and Ireland. *Ibis*, **134** (suppl.), 14-20.

Fuller, R.J. & Gill, R.M.A. (2001) Ecological impacts of increasing numbers of deer in British woodland. *Forestry,* **74**, 193-199.

Fuller, R.J. & Green, G.H. (1998) Effects of woodland structure on breeding bird populations in stands of coppiced lime (*Tilia cordata*) in western England over a 10-year period. *Forestry*, **71**, 199-218.

Fuller, R.J. & Gough, S.J. (1999) Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation*, **91**, 73-89.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. & Carter, N. (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, **9**, 1425 -1441.

Fuller, R.J. & Henderson, A.C.B. (1992) Distribution of breeding songbirds in Bradfield Woods, Suffolk, in relation to vegetation and coppice management. *Bird Study*, **39**, 73-88.

Fuller, R.J., Henderson, A.C.B. & Wilson, A.M. (1999) The nightingale in England: problems and prospects. *British Wildlife*, **10**, 221-230.

Fuller, R.J. & Moreton, B.D. (1987) Breeding bird populations of Kentish sweet chestnut (*Castanea sativa*) coppice in relation to age and structure of the coppice. *Journal of Applied Ecology*, **24**, 13-27.

Fuller, R.J. & Warren, M.S. (1991) Conservation management in ancient and modern woodlands: responses of fauna to edges and rotations. In: Spellerberg, I.F., Goldsmith, F.B. & Morris, M.G. (Eds.) *The Scientific Management of Temperate Communities for Conservation*. Pp 445-471. Blackwell Scientific Publications, Oxford.

Fuller, R.J. & Whittington, P.A. (1987) Breeding bird distribution within Lincolnshire ash-lime woodlands: the influence of rides and the woodland edge. *Acta Oecologica*, **8**, 259-268.

Gates, J.E. & Gysel, L.W. (1978) Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, **59**, 871-883.

Gibbons, D.W. & Gates, S. (1994) Hypothesis testing with ornithological atlas data: two case studies. In: Hagemeijer, E.J.M. & Verstrael, T.J. (Eds.) *Bird Numbers 1992*. Pp 39-48. Statistics Netherlands, Voorburg /Heerlen & SOVON, The Netherlands.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991*. Poyser, London.

Gill, R.M.A. (1992a) A review of damage by mammals in north temperate forests: 1 Deer. *Forestry*, **65**, 145-169.

Gill, R.M.A. (1992b) A review of damage by mammals in north temperate forests: 2 Small mammals. *Forestry*, **65**, 281-308.

Gill, R.M.A. (1992c) A review of damage by mammals in north temperate forests: 3 Impact on trees and forests. *Forestry*, **65**, 363-388.

Gill, R.M.A. & Beardall, V. (2001) The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry*, **74**, 209-218.

Gjerde, I. & Saetersdal, M. (1997) Effects on avian diversity of introducing spruce *Picea* spp. plantations in the native pine *Pinus sylvestris* forests of western Norway. *Biological Conservation*, **79**, 241-250.

Glue, D.E. & Boswell, T. (1994) Comparative nesting ecology of the three British breeding woodpeckers. *British Birds*, **87**, 253-269.

Gradwell, G.R. (1974) The effect of defoliators on tree growth. In: Morris, M.G. & Perring, F.H. (Eds.) *The British Oak: Its history and natural history*. Pp 182-193. Classey, Faringdon.

Graveland, J. (1998) Effects of acid rain on bird populations. *Environmental Reviews*, **6**, 41-54.

Graveland, J. & Drent, R.H. (1997) Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology*, **66**, 279-288.

Graveland, J. & Wal, R.V.D. (1996) Decline in snail abundance causes eggshell defects in forest passerines. *Oecologia*, **105**, 351-360.

Graveland, J., Wal, R.V.D., Balen, J.H.V. & Noordwijk, V. (1994) Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature*, **368**, 446-448.

Green, R.E. (1998) Long-term decline in the thickness of eggshells of thrushes, *Turdus* spp., in Britain. *Proceedings of the Royal Society of London*. Series B, **265**, 679-684.

Green, R.E., Osborne, P.E. & Sears, E.J. (1994) The distribution of passerine birds in hedgerows during the breeding season in relation to characteristics of the hedgerow and adjacent farmland. *Journal of Applied Ecology*, **31**, 677-692.

Gregory, R.D., Noble, D.G., Cranswick, P.A., Campbell, L.H., Rehfisch, M.M. & Baillie, S.R. (2001) *The State of the UK's Birds 2000*. RSPB, BTO and WWT, Sandy.

Gregory, R.D., Rehfisch, M.M., Underhill, L.G., Field, R.H., Atkinson, P.W., Freeman, S.N., Siriwardena, G.M. & Baillie, S.R. (1999) *National and site-based alert systems for UK birds*. BTO Research Report No. 226. BTO, Thetford.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Proctor, D., Gibbons, D.W. & Galbraith, C.A. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern. *British Birds*, **95**, 410-450.

Grigg, D. (1989) *English agriculture: an historical perspective*. Basil Blackwell, Oxford.

Gunnarsson, B. (1990) Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology*, **59**, 743-752.

Gustafsson, L. (1987) Interspecific competition lowers fitness in Collared Flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, **68**, 291-296.

Gutzwiller, K.J., Kroese, E.A., Anderson, S.H. & Wilkins, C.A. (1997) Does human intrusion alter seasonal timing of avian song during breeding periods? *Auk*, **114**, 55-65.

Gutzwiller, K.J., Marcum, H.A., Harvey, H.B., Roth, J.D. & Anderson, S.H. (1998) Bird tolerance to human intrusion in Wyoming montane forests. *Condor*, **100**, 519-527.

Gutzwiller, K.J., Weidenmann, R.T., Clements, K.L. & Anderson, S.H. (1994) Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *Auk*, **111**, 28-37.

Hagemeijer, W.J.M. & Blair, M., (Eds) (1997) *The EBCC Atlas of European Breeding Birds: their distribution and abundance*. Poyser, London.

Haines-Young, R.H., Barr, C.J., Black, H.I.J., Briggs, D.J., Bunce, R.G.H., Clarke, R.T., Cooper, A., Dawson, F.H., Firbank, L.G., Fuller, R.M., Furse, M.T., Gillespie, M.K., Hill, R., Hornung, M., Howard, D.C., McCann, T., Morecroft, M.D., Petit, S., Sier, A.R.J., Smart, S.M., Smith, G.M., Stott, A.P., Stuart, R.C. & Watkins, J.W. (2000) *Accounting for nature: assessing habitats in the UK countryside*. Centre for Ecology & Hydrology and Department of the Environment, Transport and the Regions. HMSO, London.

Hake, M. (1991) The effects of needle loss in coniferous forests in south-west Sweden on the winter foraging behaviour of willow tits *Parus montanus*. *Biological Conservation*, **58**, 357-366.

Harding, D. (2002) Where have all the caterpillars gone? *Quarterly Journal of Forestry*, **96**, 278-283.

Harris, S., Morris, P., Wray, S., & Yalden, D. (1995) *A review of British mammals: population estimates and conservation status of British mammals other than Cetaceans*. Joint Nature Conservation Committee, Peterborough**.**

Harrison, P.A., Vanhinsbergh, D.P., Fuller, R.J. & Berry, P.M. (2003) Modelling climate change impacts on distribution of breeding birds in Britain and Ireland. *Journal for Nature Conservation*, **11**, 31-42.

Harrison, S. & Bruna, E. (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, **22**, 225-232.

Hatchwell, B.J., Chamberlain, D.E. & Perrins, C.M. (1996) The demography of blackbirds *Turdus merula* in rural habitats: is farmland a sub-optimal habitat? *Journal of Applied Ecology*, **33**, 1114-1124.

Hendry, S.J., Boswell, R.C. & Proudfoot, J.C. (2001) *Forest Condition 1997*. Forestry Commission, Edinburgh.

Hewson, C.M. & Fuller, R.J. (2003) *Impacts of Grey Squirrels on woodland birds: an important predator of eggs and young*? BTO Research Report No. 328. British Trust for Ornithology, Thetford.

Hewson, C., Lindsell, J. & Conway, G. (2003) Investigating woodland bird declines. *BTO News*, **244**, 10-11.

Hildén, O. (1965) Habitat selection in birds – a review. *Annales Zoologici Fennici*, **2**, 53-75.

Hill, D. & Robertson, P. (1988) *The Pheasant: ecology, management and conservation*. BSP Professional Books, Blackwell Scientific Publications, London.

Hinsley, S.A. & Bellamy, P.E. (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management*, **60**, 33-49.

Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. (1995) Habitat and landscape factors influencing the presence of individual bird species in woodland fragments. *Journal of Avian Biology*, **26**, 94-104.

Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. (1996) Influences of population size and woodland area on bird species distributions in small woods. *Oecologia*, **105**, 100-106.

Hirons, G., & Johnson, T.H. (1987) A quantitative analysis of habitat preferences of Woodcock *Scolopax rusticola* in the breeding season. *Ibis*, **129**, 371-381.

Hogstad, O. (1993) Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest. *Annales Zoologici Fennici*, **30**, 43-54.

Holmes, R.T. (1990) The structure of a temperate deciduous forest bird community: variability in time and space. In: Keast, A. (Ed.) *Biogeography and Ecology of Forest Bird Communities.* Pp 121-139. SPB Academic Publications, The Hague.

Holmes, R.T. & Sherry, T.W. (2001) Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk*, **118**, 589-609.

Hoodless, A.N. & Coulson, J.C. (1998) Breeding biology of the woodcock *Scolopax rusticola* in Britain. *Bird Study*, **45**, 195-204.

Hoopes, M.F. & Harrison, S. (1998) Metapopulation, source-sink and disturbance dynamics. In: Sutherland, W.J. (Ed.) *Conservation Science and Action*. Pp 135-151. Blackwell Science, Oxford.

Hope Jones, P. (1972) Succession in breeding bird populations of sample Welsh oakwoods. *British Birds*, **65**, 291-299.

Howard, P.J.A. & Howard, D.M. (1984a) *Effects of trees on soil properties, a resampling of J.D. Ovington's plots at Bedgebury*. Developmental paper No. 100 Institute of Terrestrial Ecology, Merlewood.

Howard, P.J.A. & Howard, D.M. (1984b) *Effects of trees on soil properties, a resampling of J.D. Ovingtons's plots at Abbotswood.* Developmental paper No. 101. Institute of Terrestrial Ecology, Merlewood.

Hulme, M. (1999) Air temperature in central England. In: Cannell, M.G.R., Palutikof, J.P. & Sparks, T.H. (Eds.) *Indicators of climate change in the UK.* Pp 6-7. Department of the Environment, Transport and Regions.

Hustings, F. & Vergeer, J-W. (Eds.) (2002) *Atlas van de Nederlandse Broedvogels 1998-2000*. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, Amsterdam.

Jansen, P.B. & de Nie, H.W. (1986) Thirty years of passerine breeding bird monitoring in a mixed wood. *Limosa*, **59**, 127-134. (in Dutch)

Jiguet, F., Boulinier, G., Julliard, R. & Jolivet, A. (2002) Nos oiseaux “communs” sont en danger! *L’Oiseau*, **67**,12-13

Jones, P., Conway, D. & Briffa, K. (1997) Precipitation variability and drought. In: Hulme, M. & Barrow, E. (Eds.) *Climates of the British Isles: present, past and future.* Pp 197-218. Routledge, London.

Jones, P. & Hulme, M. (1997) The changing temperature of 'Central England'. In: Hulme, M. & Barrow, E. (Eds.) *Climates of the British Isles: present, past and future.* Pp 173-195. Routledge, London.

Jones, P.D. & Conway, D. (1997) Precipitation in the British Isles: an analysis of area-average data updated to 1995. *International Journal of Climatology*, **17**, 427-438.

Kalchreuter, H. (1982) *The Woodcock*. Veerlag Dieter Hoffman, Mainz. (In German)

Kay, S. (1993) Factors affecting severity of deer browsing damage within coppiced woodlands in the south of England. *Biological Conservation*, **63**, 217-222.

Keith, S., Urban, E.K. & Fry, C.H. (Eds.) (1992) *The Birds of Africa* Volume IV. Academic Press, London.

Kenward, R.E. (1983) The causes of damage by red and grey squirrels. *Mammal Review*, **13**,159-166.

Kenward, R.E. & Parish, T. (1988) Bark-stripping by grey squirrels (*Sciurus carolinensis*). *Journal of Zoology*, **210**, 473-481.

Kirby, K.J. (2001) The impact of deer on the ground flora of British broadleaved woodland. *Forestry*, **74**, 219-229.

Kirby, K.J. & Buckley, G.P. (Eds) (1994) *Ecological responses to the 1987 Great Storm in the woods of south-east England*. English Nature Science No.23.

Kirby, K.J., Reid, C.M., Thomas, R.C., & Goldsmith, F.B. (1998) Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology*, **35**, 148-155.

Kirby, K.J., Webster, S.D. & Antczak, A. (1991) Effects of forest management on stand structure and the quantity of fallen dead wood: some British and Polish examples. *Forest Ecology and Management*, **43**, 167-174.

Krebs, J.R. (1971) Territory and breeding density in the Great tit, *Parus major*. *Ecology*, **52**, 1-22.

Kujawa, K. (2002) Population density and species composition changes for breeding bird species in farmland woodlots in western Poland between 1964 and 1994. *Agriculture, Ecosystems and Environment,* **91**, 261-271.

Lack, D. & Lack, E. (1951) Further changes in bird-life caused by afforestation. *Journal of Animal Ecology*, **20**, 173-179.

Langston, R., Gregory, R. & Adams, R. (2002) The status of the Hawfinch *Coccothraustes coccothraustes* in the UK 1975-1999. *British Birds*, **95**,166-173.

Lemoine, N. & Böhning-Gaese, K. (2002) Potential impacts of global climate change on species richness of long-distance migrants. *Conservation Biology*, **17**, 577-586.

Lennon, J.J., Greenwood, J.J.D. & Turner, J.R.G. (2000) Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *Journal of Animal Ecology*, **69**, 581-598.

Ling, K.A., Power, S.A. & Ashmore, M.R. (1993) A survey of the health of *Fagus sylvatica* in southern Britain. *Journal of Applied Ecology*, **30**, 295-306.

Locke, G.M.L. (1987) *Census of Woodlands and Trees 1979-1982*. Forestry Commission Bulletin 63. HSMO, London.

Ludescher, F.-B. (1973) Sumpfmeise (*Parus p. palustris* L.) und Weidenmeise (*P.montanus salicarius* Br.) als sympatrishce Zwillingsarten. *Journal für Ornithologie*, **114**, 3-56.

Macdonald, D.W. & Johnson, P.J. (1995) The relationship between bird distribution and the botanical and structural characteristics of hedges. *Journal of Applied Ecology*, **32**, 492-505.

Marchant, J.H. (1992) Recent trends in breeding populations of some common trans-Saharan migrant birds in northern Europe. *Ibis*, **134** (suppl.), 113-119.

Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P. (1990) *Population Trends in British Breeding Birds*. British Trust for Ornithology, Tring.

Marcström, V., Kenward, R.E. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology*, **57**, 859-872.

Marsh, T.J. (1999) Dry and wet soil conditions in southern England. In: Cannell, M.G.R., Palutikof, J.P. & Sparks, T.H. (Eds.) *Indicators of climate change in the UK*. Pp 14-15. Department of the Environment, Transport and Regions.

Martin, T.E. (1992) Breeding productivity considerations: what are the appropriate habitat features for management? In: Hagan, J.M. & Johnstone, D.W. (Eds.) *Ecology and Conservation of Neotropical Migrant Landbirds*. Pp 455-473. Smithsonian Institution Press, Washington.

Martin, T.E. (1993) Nest predation and nest sites: new perspectives on old patterns. *BioScience*, **43**, 525-532.

Martin, T.E. (1998) Are microhabitat preferences of co-existing species under selection and adaptive? *Ecology*, **79**, 656-670.

Martin, T.E. & Roper, J.J. (1988) Nest predation and nest site selection in a population of the Hermit Thrush. *Condor*, **90**, 51-57.

Matthysen, E. & Currie, D. (1996) Habitat fragmentation reduces disperser success in juvenile nuthatches *Sitta europaea*: evidence from patterns of territory establishment. *Ecography*, **19**, 67-72.

Matthysen, E. & Schmidt, K-H. (1987) Natal dispersal in the nuthatch. *Ornis Scandinavica*, **18**, 313-316.

Maxwell, J. (2002) Nest-site competition with blue tits and great tits as a possible cause of declines in willow tit numbers: observations in the Clyde area. *Glasgow Naturalist*, **24**, 47-50

Maxwell, J. (2003) Scottish Willow Tits hanging on. *BTO News*, **244**, 24.

McCleery, R.H. & Perrins, C.M. (1991) Effects of predation on the numbers of Great Tits *Parus major*. In: Perrins, C.M., Lebreton, J.-D., & Hirons, G.J.M. (Eds.) *Bird Population Studies: relevance to conservation and management.* Pp 129-147. Oxford University Press, Oxford.

McCollin, D. (1998) Forest edges and habitat selection in birds: a functional approach. *Ecography*, **21**, 247-260.

McCollin, D., Moore, L. & Sparks, T. (2000) The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation*, **92**, 249-263.

McShea, W.J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology*, **81**, 228-238.

McShea, W.J. & Rappole, J.H. (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer densities. *Conservation Biology*, **14**, 1161-1170.

Miller, S.G., Knight, R.L. & Miller, C.K. (1998) Influence of recreational trails on breeding bird communities. *Ecological Applications*, **8**, 162-169.

Miranda, B. & Pasinelli, G. (2001) Habitat requirements of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in forests of northeastern Switzerland. *Journal fűr Ornithologie*, **142**, 295-305.

Mitchell, F.J.G. & Kirby, K.J. (1990) The impact of large herbivores on the conservation of semi-natural woods in the British uplands. *Forestry*, **63**, 333-353.

Mitchell, P.L. & Kirby, K.J. (1989) *Ecological Effects of Forestry Practices in Long-established Woodland and their Implications for Nature Conservation*. Oxford Forestry Institute Occasional Paper No. 39. Oxford Forestry Institute, Oxford.

Möckel, R. (1992) Effect of 'Waldsterben' (forest damage due to airborne pollution) on the population dynamics of Coal Tit (*Parus ater*) and Crested Tit (*Parus cristatus*) in the western Erzgebirge. *Ökologie der Vögel*, **14**, 1-100. (in German)

Møller, A.P. (1989) Nest site selection across field-woodland ecotones: the effect of nest predation. *Oikos*, **56**, 240-246.

Morecroft, M.D., Taylor, M.E., Ellwood, S.A. & Quinn, S.A. (2001) Impacts of deer on ground vegetation at Wytham Woods, central England. *Forestry,* **74**, 251-257.

Mortimer, S.R., Turner, A.J., Brown, V.K., Fuller, R.J., Good, J.E.G., Bell, S.A., Stevens, P.A., Norris, D., Bayfield, N. & Ward, L.K. (2000) *The Nature Conservation Value of Scrub in Britain*. JNCC Report No. 308. Joint Nature Conservation Committee, Peterborough.

Moss, D., Taylor, P.N. & Easterbee, N. (1979) The effects on song-bird populations of upland afforestation with spruce. *Forestry*, **52**, 129-147.

Moss, R. (2001) Second extinction of capercaillie (*Tetrao urogallus*) in Scotland? *Biological Conservation*, **101**, 225-257.

Moss, R., Oswald, J. & Baines, D. (2001) Climate change and breeding success: decline of the capercaillie in Scotland. *Journal of Animal Ecology*, **70**, 47-61.

Moss, R. & Picozzi, N. (1994) *Management of forests for Capercaillie in Scotland*. Forestry Commission Bulletin 113. Edinburgh.

Moss, R., Picozzi, N., Summers, R.W. & Baines, D. (2000) Capercaillie *Tetrao urogallus* in Scotland – demography of a declining population. *Ibis*, **142**, 259-267.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698-702.

Naef-Daenzer, B. (2000) Patch time allocation and patch sampling by foraging great and blue tits. *Animal Behaviour,* **59**, 989-999,

Naef-Daenzer, B. & Keller, L.F. (1999) The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, **68**, 708-718.

Newton, I. (1972) *Finches.* Collins, London.

Newton, I. (1993) Predation and limitation of bird numbers. *Current Ornithology*, **11**, 143-198.

Newton, I. (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation*, **70**, 265-276.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, London.

Newton, I., Dale, L., & Rothery, P. (1997) Apparent lack of impact of Sparrowhawks on the breeding densities of some woodland songbirds. *Bird Study*, **44**, 129-135.

Nilsson, J-Å. (1989) Causes and consequences of natal dispersal in the marsh tit, *Parus palustris*. *Journal of Animal Ecology*, **58**, 619-636.

Nilsson, S.G. (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica*, **15**, 167-175.

Nilsson, S.G. (1985) Ecological and evolutionary interactions between reproduction of beech *Fagus sylvatica* and seed eating animals. *Oikos*, **44**, 157-164.

Nilsson, S.G. (1987) Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology*, **56**, 921-937.

Nilsson, S.G., Olsson, O., Svensson, S. & Wiktander, U. (1992) Population trends and fluctuations in Swedish woodpeckers. *Ornis Svecica*, **2**, 13-21.

Noble, D.G., Newson, S.N., Baillie, S.R., Raven, M.J. & Gregory, R.D. (in press). Recent changes in UK bird populations measured by the Breeding Bird Survey. *Bird Study*.

Nour, N., Matthysen, E. & Dhondt, A.A. (1993) Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. *Ecography*, **16**, 111-116.

O'Connor, R.J. (1990) Some ecological aspects of migrants and residents. In: Gwinner, E. (Ed.) *Bird Migration*. Pp. 175-182. Springer-Verlag, Berlin.

O'Connor, R.J. & Shrubb, M. (1986) *Farming and birds*. Cambridge University Press, Cambridge.

Olsson, O., Wiktander, U., Holmgren, N.M.A. & Nilsson, S.G. (1999) Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. *Oikos*, **87**, 264-276.

Osborne, P. (1982) Some effects of Dutch elm disease on nesting farmland birds. *Bird Study,* **29**, 2-16.

Osborne, P. (1983) The influence of Dutch elm disease on bird population trends. *Bird Study,* **30**, 27-38.

Osborne, P. (1984) Bird numbers and habitat characteristics in farmland hedgerows. *Journal of Applied Ecology*, **21**, 63-82.

Osborne, P. (1985) Some effects of Dutch elm disease on the birds of a Dorset dairy farm. *Journal of applied Ecology*, **22**, 681-691.

Ostfeld, R.S., Jones, C.G. & Wolff, J.O. (1996) Of mice and mast: ecological connections in eastern deciduous forests. *BioScience*, **46**, 323-330.

Parish, T., Lakhani, K.H. & Sparks, T.H. (1994) Modelling the relationship between bird population variables and hedgerow, and other field margin attributes 1. Species richness of winter, summer and breeding birds. *Journal of Applied Ecology*, **31**, 764-775.

Parish, T., Lakhani, K.H. & Sparks, T.H. (1995) Modelling the relationship between bird population variables and hedgerow, and other field margin attribute. II. Abundance of individual species and of groups of similar species. *Journal of Applied Ecology*, **32**, 362-371.

Partners in Flight Research Working Group (2002) Priority research needs for the conservation of Neotropical migrant landbirds. *Journal of Field Ornithology*, **73**, 329-339.

Paton, P.W.C. (1994) The effects of edge on avian nest success: how strong is the evidence? *Conservation Biology*, **8**, 17-26.

Peach, W.J., Baillie, S.R. & Balmer, D.E. (1998) Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study*, **45**, 257-275.

Peach, W.J., Crick, H.Q.P. & Marchant, J.H. (1995a) The demography of the decline in the British willow warbler population. *Journal of Applied Statistics*, **22**, 905-922.

Peach, W.J., du Feu, C. & McMeeking, J. (1995b) Site tenacity and survival rates of Wrens *Troglodytes troglodytes* and Treecreepers *Certhia familiaris* in a Nottinghamshire wood. *Ibis*, 1**37**, 497-507.

Perrins, C.M. (1979) *British Tits*. Collins, London.

Perrins, C.M. (2003) The status of Marsh and Willow Tits in the UK. *British Birds*, **96**, 418-426.

Perrins, C.M. & Overall, R. (2001) Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. *Forestry*, **74**, 299-309.

Peterken, G.F. (1993) *Woodland Conservation and Management.* Second edition. Chapman & Hall, London.

Peterken, G.F. (1996) *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge.

Peterken, G.F. & Allison, H. (1989) *Woods, Trees and Hedges: a review of changes in the British countryside*. Focus on Nature Conservation 22. Nature Conservancy Council, Peterborough, UK.

Peterken, G.F. & Jones, E.W. (1987) Forty years of change in Lady Park Wood: the old growth stands. *Journal of Ecology*, **75**, 477-512.

Peterken, G. & Mountford, E. (1995) Lady Park Wood Reserve – the first half century. *British Wildlife*, **6**, 205-213.

Petterson, R.B. (1996) Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. *Ecography*, **19**, 221-228.

Petterson, R.B., Ball, J.P., Renhorn, K.-E., Esseen, P.-A. & Sjöberg, K. (1995) Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biological Conservation*, **74**, 57-63.|

Potts, G.R. (1986) *The Partridge: pesticides, predation and conservation*. Collins, London.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.

Putman, R.J. (1986) *Grazing in temperate ecosystems: large herbivores and the ecology of the New Forest*. Timber Press, Portland, Oregon.

Putman, R.J., Edwards, P.J., Mann, J.C.E., Howe, R.C. & Hill, S.D. (1989) Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation*, **47**, 13-32.

Ramsay, S.L. & Houston, D.C. (1999) Do acid rain and calcium supply limit eggshell formation for blue tits (*Parus caeruleus*) in the U.K.? *Journal of Zoology*, **247**, 121-125.

Rands, M.R.W. (1985) Pesticide use on cereals and the survival of grey partridge chicks: a field experiment. *Journal of Applied Ecology*, **22**, 49-54.

Redfern, D.B., Boswell, R.C. & Proudfoot, J.C. (1998) *Forest Condition 1999*. Forestry Commission, Edinburgh, UK.

Reijnen, R. & Foppen, R. (1994) The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway. *Journal of Applied Ecology*, **31**, 85-94.

Reijnen, R., Foppen, R., Ter Braak, C.J. & Thissen, J. (1995) The effects of car traffic on breeding bird populations in woodland. III. Reductions of density in relation to the proximity of roads. *Journal of Applied Ecology*, **32**, 85-94.

Reitsma, L.R., Holmes, R.T., & Sherry, T.W. (1990) Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos*, **57**, 375-380.

Roberts, T.M., Skeffington, R.A. & Blank, L.W. (1989) Causes of Type 1 spruce decline in Europe. *Forestry*, **46**, 167-189.

Rodewald, A.D. & Yahner, R.H. (2001) Influence of landscape composition on avian community structure and associated mechanisms. *Ecology*, **82**, 3493-3504.

Rowe, J.J. & Gill, R.M.A. (1985) The susceptibility of tree species to bark-stripping damage by grey squirrels (*Sciurus carolinensis*) in England and Wales. *Quarterly Journal of Forestry*, **79**, 183-190.

Sharrock, J.T.R. (1976) *The Atlas of Breeding Birds in Britain and Ireland*. Poyser, Berkhamsted, UK.

Siriwardena, G. (2001) Why are ‘brown tits’ declining? *BTO News*, **235**, 23-24.

Siriwardena, G. (in press) The decline of the Willow Tit in Britain: possible roles of habitat, competition and avian nest predation. *Bird Study*.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H., & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24-43.

Siriwardena, G.M., Freeman, S.N. & Crick, H.Q.P. (2001) The decline of the Bullfinch *Pyrrhula pyrrhula* in Britain: is the mechanism known? *Acta Ornithologica*, **36**,143-152.

Smith, K.W. (1994) The effects of the 1987 and 1990 storms on great spotted woodpecker *Dendrocopos major* numbers and nest site selection in two Hertfordshire woods. In: Kirby, K.J. & Buckley, G.P. (Eds.) *Ecological responses to the 1987 Great Storm in the woods of south-east England*. Pp 124-133. English Nature Science No. 23, Peterborough.

Smith, K.W. (1997) Nest site selection of the great spotted woodpecker *Dendrocopos major* in two oak woods in southern England and its implications for woodland management. *Biological Conservation*, **80**, 283-288.

Smith, K.W., Averis, B. & Martin, J. (1987) The breeding bird community of oak plantations in the Forest of Dean, southern England. *Acta Oecologica*, **8**, 209-217.

Snow, D. & Perrins, C.M. (1998) *The Birds of the Western Palearctic*. Concise edition. Oxford University Press, Oxford.

Sotherton, N.W. & Self, M.J. (2000) Changes in plant and arthropod biodiversity on lowland farmland: an overview. In: Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (Eds.) *Ecology and Conservation of Lowland Farmland Birds*. Pp 26-35. British Ornithologists' Union, Tring.

Sparks, T.H., Parish, T. & Hinsley, S.A. (1996) Breeding birds in field boundaries in an agricultural landscape. *Agriculture Ecosystems and Environment*, **60,** 1-8.

Sparks, T.H. & Woiwod, I.P. (1999) Insect abundance. In: Cannell M.G.R., Palutikof, J.P. & Sparks, T.H. (Eds.) *Indicators of climate change in the UK.* Pp 60-61. Department of the Environment, Transport and Regions.

Spencer, J.W., & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, **62**, 77-93.

Staines, B.W., Balharry, R. & Welch, D. (1995) The impact of red deer and their management on the natural heritage in the uplands. In: Thompson, D.B.A., Hester, A.J. & Usher, M.B. (Eds.) *Heaths and Moorland: Cultural Landscapes.* Pp. 294-308. HMSO, Edinburgh.

Šťastný, K. & Bejček, V. (1985) Bird communities of spruce forests affected by industrial emissions in the Krušné Hory (Ore Mountains). In: Taylor, K., Fuller, R.J. & Lack, P.C. (Eds.) *Bird Census and Atlas Studies.* Pp 243-253. Proceedings VIII International Conference on Bird Census and Atlas Work. British Trust for Ornithology, Tring.

Stevenson, I.R. & Bryant, D.M. (2000) Climate changes and constraints on breeding. *Nature*, **406**, 366-367.

Stewart, A.J.A. (2001) The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. *Forestry*, **74**, 259-270.

Summers, R.W. (1998) The lengths of fences in Highland woods: the measure of a collision hazard to woodland birds. *Forestry*, **71**, 73-76.

Tapper, S.C. (1999) *A Question of Balance: Game Animals and their Role in the British Countryside*. Game Conservancy Trust, Fordingbridge.

The Game Conservancy Trust (2003) *Woodland Conservation and Pheasants*. The Game Conservancy Trust, Fordingbridge.

Thom, V.M. (1986) *Birds in Scotland*. Poyser, Calton.

Thomas, C.D. & Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.

Thomson, D.L., Baillie, S.R. & Peach, W.J. (1997) The demography and age-specific annual survival of British song thrushes *Turdus philomelos* during periods of population stability and decline. *Journal of Animal Ecology*, **66**, 414-424.

Thomson, D.L., Green, R.E., Gregory, R.D. & Baillie, S.R. (1998) The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings of the Royal Society of London* B., **265**, 2057-2062.

Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe; their Conservation Status*. BirdLife Conservation Series No.3. BirdLife International, Cambridge.

United Nations Economic Commission for Europe & European Commission (2002) *The Condition of Forests in Europe: 2002 Executive Report*. UNECE & EC, Geneva and Brussels. (www.icp-forests.org)

Urban, E.K., Fry, C.H & Keith, S. (Eds) (1997) *The Birds of Africa* Volume V. Academic Press, London.

Vanhinsbergh, D., Gough, S., Fuller, R.J. & Brierley, E.D.R. (2002) Summer and winter bird communities in recently established farm woodlands in lowland England. *Agriculture, Ecosystems and Environment*, **92**, 123-136.

Van der Zande, A.N., Berkhuizen, J.C., van Latesteijn, H.C., Keurster, W.J. & Poppelaars, A.J. (1984) Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. *Biological Conservation*, **30**, 1-39.

Van Noordwijk, A.J. (1990) The effects of forest damage on caterpillars and their effect on the breeding biology of the great tit, an overview. In: Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (Eds.) *Population Biology of Passerine Birds.* Pp 215-222. Springer-Verlag. Berlin.

Van Noordwijk, A.J., McCleery, R.H. & Perrins, C.M. (1995) Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology*, **64**, 451-458.

Van Strien, A.J., Pannekoek, J. & Gibbons, D.W. (2001) Indexing European bird population trends using results of national monitoring schemes: a trial of a new method. *Bird Study,* **48**,200-213.

Waller, D.M. & Alverson, W.S. (1997) The white-tailed deer: a keystone herbivore. *Wildl. Soc. Bull.*, **25**, 217-226.

Watkinson, A.R., Riding, A.E. & Cowie, N.R. (2001) A community and population perspective of the possible role of grazing in determining the ground flora of ancient woodlands. *Forestry*, **74**, 231-239.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65-69.

Warren, M.S. & Key, R.S. (1989) Woodlands: past, present and potential for insects. In: Collins, N.M. & Thomas, J.A. (Eds.) *The Conservation of Insects and their Habitats*. Pp 155-211. Academic Press, London.

Wernham, C., Toms, M., Marchant, J., Clark, J., Siriwardena, G., & Baillie, S. (2002) *The Migration Atlas: Movements of the Birds of Britain and Ireland.* Poyser, London.

Wesołowski, T. (1996) Natural nest sites of Marsh Tit (*Parus palustris*) in a primeval forest (Białowieża National Park, Poland). *Die Vogelwarte*, **38**, 235-249.

Wesołowski, T. (2002) Anti-predator adaptations in nesting Marsh Tits (*Parus palustris*): the role of nest-site security. *Ibis*, **144**, 593-601.

Wesołowski, T. & Tomiałojć, L. (1997) Breeding bird dynamics in a primeval temperate forest: long-term trends in Białowieża National Park (Poland). *Ecography*, **20**, 432-453.

Wesołowski, T., Tomiałojć, L., Mitrus, C., Rowiński, P. & Czeszczewik, D. (2002) The breeding bird community of a primeval temperate forest (Białowieża National Park, Poland) at the end of the 20th century. *Acta Ornithologica*, **37**, *2*7-45.

Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Perkins, A.J. & Siriwardena, G.M. (2001) Chaffinch *Fringilla coelebs* foraging patterns, nestling survival and territory distribution on lowland farmland. *Bird Study*, **48**, 257-270.

Wiktander, U., Nilsson, S.G., Olsson, O., & Stagen, A. (1994) Breeding success of a Lesser Spotted Woodpecker *Dendrocopos minor* population. *Ibis*, **136**, 318-322.

Wilson, A.M., Henderson, A.C.B. & Fuller, R.J. (2002) Status of the Nightingale *Luscinia megarhynchos* in England at the end of the 20th Century with particular reference to climate change. *Bird Study*, **49**, 193-204.

Winstanley, D., Spencer, R. & Williamson, K. (1974) Where have all the Whitethroats gone? *Bird Study*, **21**, 1-14.

Yalden, D. (1999) *The History of British Mammals*. Poyser, London.

Zang, H. (1990) Population decrease of coal tit *Parus ater* in the Harz Mountains due to forest damage (‘Waldsterben’). *Vogelwelt*, **111**, 18-28. (In German)

Species		Estimated percentage change in abundance (1966-1999)[1]	Reliability of CBC trend [2]	No. 10-km squares occupied in 1968-1972 atlas	No. 10-km squares occupied in 1988-1991 atlas	Change in no. 10-km squares occupied (%)
English name	**Scientific name**					
Spotted flycatcher	*Muscicapa striata*	-85	1	2435	2378	-2.3
Lesser spotted woodpecker	*Dendrocopos minor*	-81	1	889	790	-11.1
Lesser whitethroat	*Sylvia curruca*	-79	1	1094	1271	16.2
Lesser redpoll	*Carduelis cabaret*	-78	2	1979	1754	-11.3
Tree pipit	*Anthus trivialis*	-75	2	1793	1524	-15
Willow tit	*Parus montanus*	-74	1	1220	1100	-9.8
Marsh tit	*Parus palustris*	-68	1	1366	1133	-17.1
Woodcock	*Scolopax rusticola*	-61	2	1693	1204	-28.9
Dunnock	*Prunella modularis*	-58	1	2601	2511	-3.2
Willow warbler	*Phylloscopus trochilus*	-53	1	2590	2602	0.6
Song thrush	*Turdus philomelos*	-48	1	2680	2620	-2.1
Bullfinch	*Pyrrhula pyrrhula*	-38	1	2326	2173	-6.5
Jay	*Garrulus glandarius*	-21	1	1744	1713	-1.8
Chiffchaff	*Phylloscopus collybita*	-20	1	2003	2100	5
Redstart	*Phoenicurus phoenicurus*	-18	2	1661	1327	-20.1
Garden warbler	*Sylvia borin*	-17	1	1833	1867	1.9
Blackbird	*Turdus merula*	-8	1	2722	2664	-1.9
Chaffinch	*Fringilla coelebs*	-4	1	2588	2602	0.7
Long tailed tit	*Aegithalos caudatus*	1	1	2194	2106	-4
Treecreeper	*Certhia familiaris*	13	1	2289	2120	-7.3
Goldcrest	*Regulus regulus*	15	1	2343	2327	-0.6
Blue tit	*Parus caeruleus*	16	1	2518	2480	-1.4
Coal tit	*Parus ater*	24	1	2392	2315	-3.2
Great tit	*Parus major*	30	1	2457	2443	-0.5
Tawny owl	*Strix aluco*	40	1	2305	2054	-10.9
Robin	*Erithacus rubecula*	41	1	2609	2629	1
Great spotted woodpecker	*Dendrocopos major*	47	1	2050	1959	-4.4
Wren	*Troglodytes troglodytes*	51	1	2757	2747	-0.3
Blackcap	*Sylvia atricapilla*	55	1	1923	2048	6.5
Sparrowhawk	*Accipiter nisus*	83	1	1823	2178	19.6
Green woodpecker	*Picus viridis*	97	1	1623	1555	-4.1
Nuthatch	*Sitta europaea*	122	1	1174	1270	8.2
Crested tit	*Parus cristatus*	NA	NA	46	51	10.9
Wood warbler	*Phylloscopus sibilatrix*	NA	NA	1230	1270	3.3
Pied flycatcher	*Ficedula hypoleuca*	NA	NA	546	732	34.1
Firecrest	*Regulus ignicapillus*	NA	NA	20	99	395
Siskin	*Carduelis spinus*	NA	NA	625	1158	85.3
Long-eared owl	*Asio otus*	NA	NA	590	445	-24.6
Nightingale	*Luscinia megarhynchos*	NA	NA	639	457	-28.5
Hawfinch	*Coccothraustes coccothraustes*	NA	NA	459	315	-31.4
Capercaillie	*Tetrao urogallus*	NA	NA	182	66	-63.7

[1] based on smoothed population indices to the penultimate year (1999) derived using GAMS (see Methods).

[2] assessed on the basis of sample size and whether the population in the sites surveyed represent the UK population, following Baillie et al. 2002: (1) data are reliable and mean number of plots surveyed each year where the species was ever recorded exceeded 20, (2) trend based on regions, habitats or sampling protocols that may not represent the bulk of the population.

Table 1 Estimated change in population and distribution of woodland birds based on CBC woodland plots (1966-2000) and the two breeding bird atlases (1968-72 and 1988-1991). Species are listed in order of estimated population change.

	Declining species (n=12)	**Stable species (n=11)**	**Increasing species (n=9)**
Migrants[1] (n=8)	4	3	1
Cavity nesters[2] (n=13)	4	5	4
Foliage insectivores[3] (n=15)	4	9	2
Ground insectivores[4] (n=7)	4	1	2

[1] 'Migrants' includes all trans-Saharan and middle-distance migrants: Tree Pipit, Redstart, Lesser Whitethroat, Garden Warbler, Blackcap, Chiffchaff, Willow Warbler, Spotted Flycatcher.

[2] 'Cavity nesters' includes all hole-nesters, crevice-nesters and open cavity nesters: Tawny Owl, Green Woodpecker, Great Spotted Woodpecker, Lesser Spotted Woodpecker, Redstart, Spotted Flycatcher, Marsh Tit, Willow Tit, Coal Tit, Blue Tit, Great Tit, Nuthatch, Treecreeper.

[3] 'Foliage insectivores' includes all species that feed in summer to a large extent on invertebrates gleaned from foliage in the field, shrub or canopy layers: Wren, Redstart, Lesser Whitethroat, Garden Warbler, Blackcap, Chiffchaff, Willow Warbler, Goldcrest, Long-tailed Tit, Marsh Tit, Willow Tit, Coal Tit, Blue Tit, Great Tit, Chaffinch.

[4] 'Ground insectivores' includes all species that feed on the ground on surface or soil-dwelling invertebrates: Woodcock, Green Woodpecker, Tree Pipit, Dunnock, Robin, Blackbird, Song Thrush.

Table 2 Population trend in relation to selected species attributes. The 32 species for which CBC trends are given in Table 1 are divided into declining (>25% decline), stable (-25% to +25% change) and increasing (>25% increase).

	Woodcock	**Tree Pipit**	**Dunnock**	**Nightingale**	**Song Thrush**	**Wood Warbler**	**Willow Warbler**	**Goldcrest**	**Spotted Flycatcher**	**Marsh Tit**	**Willow Tit**	**Lesser Redpoll**	**Bullfinch**	**Hawfinch**	**Lesser Spotted Woodpecker**
(1) Pressures on migration or in winter (migrants only)		●		●		●	●		●						
(2) Climate change on the breeding grounds	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
(3) Reduction in invertebrates	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
(4) Impacts on the woodland edge			●	●	●		●	○		○	○		●		
(5) Reduced woodland management	●	●	●	●	○		●	○	●	●	●	○	●		○
(6) Intensified pressure from deer	●		●	●	●		●	○		●	●		●		
(7) Changing predation pressure	○	○	○	○	○	○	○	○	○	●	●	○	○	●	●

Table 3 Hypotheses potentially explaining declines in woodland birds of conservation concern in Britain. Solid circles indicate a strong hypothesis, open circles indicate a weaker, but plausible, hypothesis. To qualify as a strong hypothesis there has to be a clear link between the factor concerned and the natural history of the species or a specific observation that suggests a connection (eg. the observation that Great Spotted Woodpeckers have increased and that these are the main nest predators of the Lesser Spotted Woodpecker).

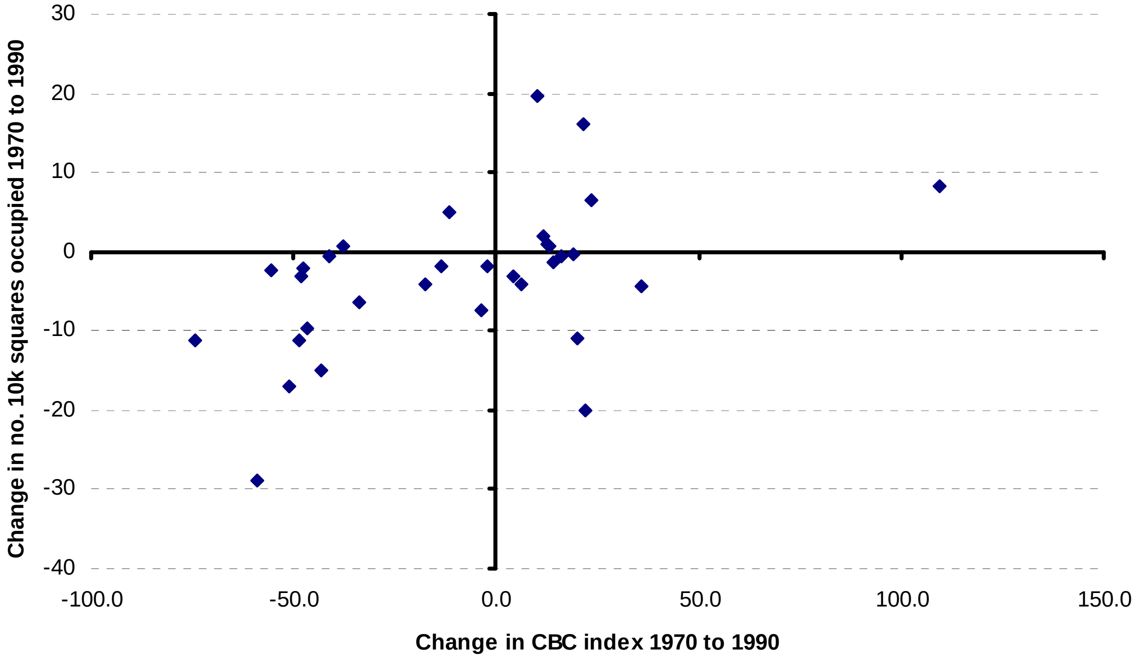
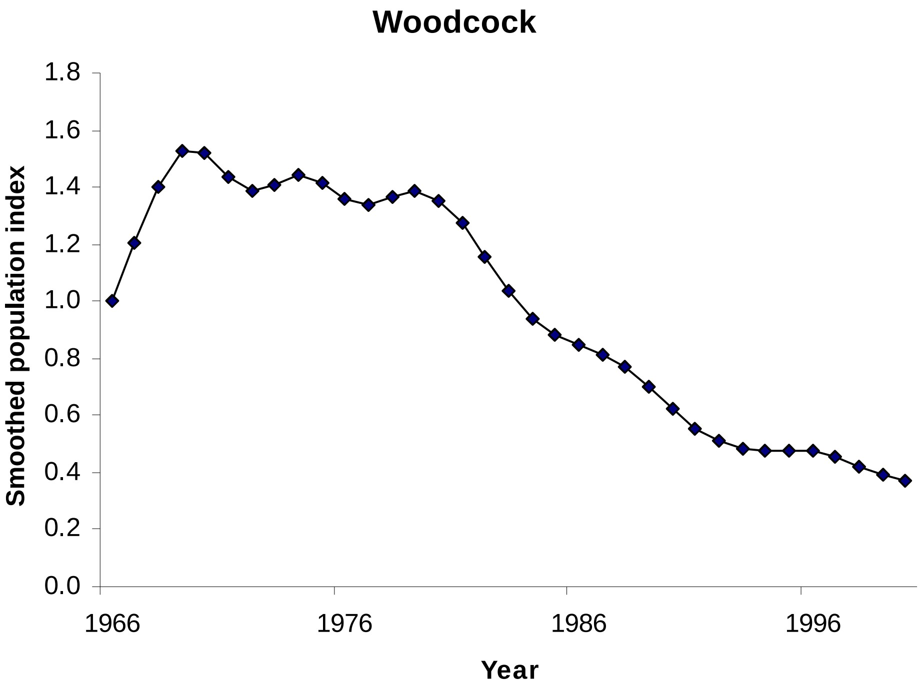


Figure 1 A comparison of changes in breeding ranges of 32 woodland bird species as measured by the occupancy of 10-km squares in the two breeding bird atlases, and changes in abundance as measured by CBC indices for woodland plots between 1970 and 1990.



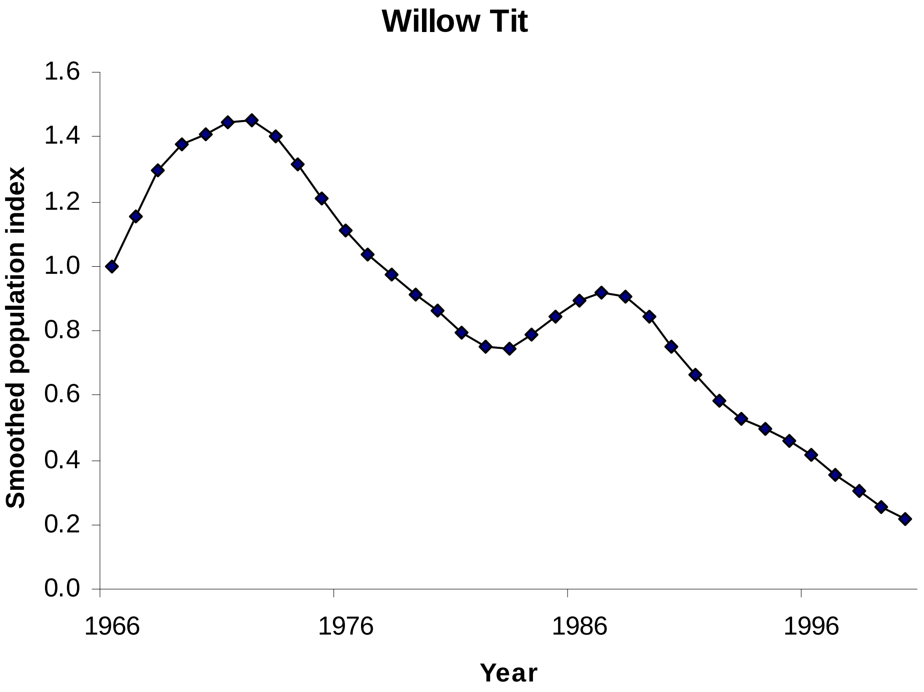
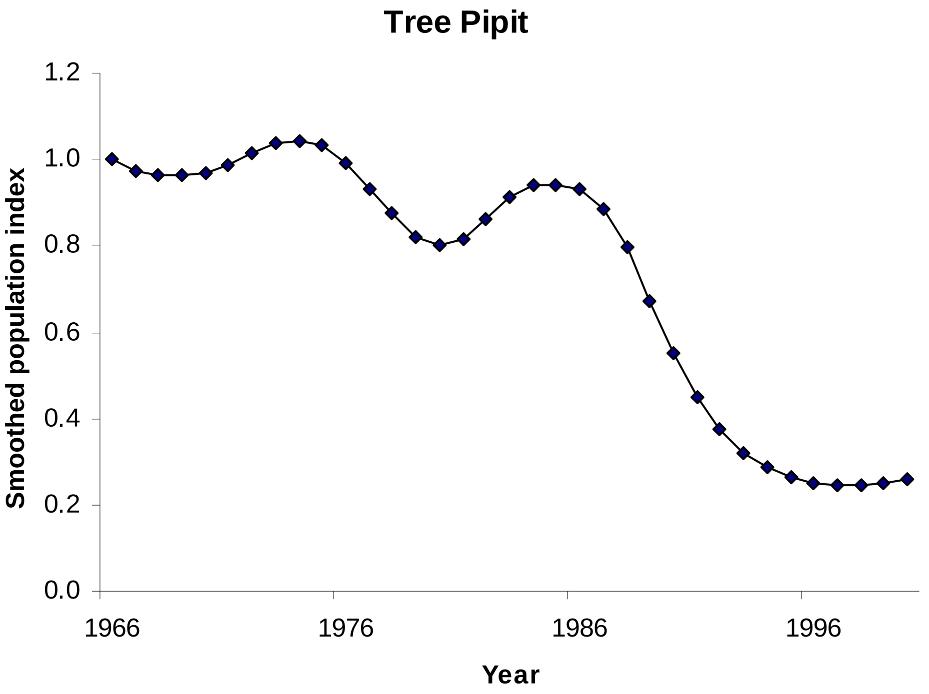


Figure 2 Estimated population trends for British woodland birds that declined by more than 50% between 1966 and 1999. Values are based on smoothed population indices calculated using GAMs (see Methods).



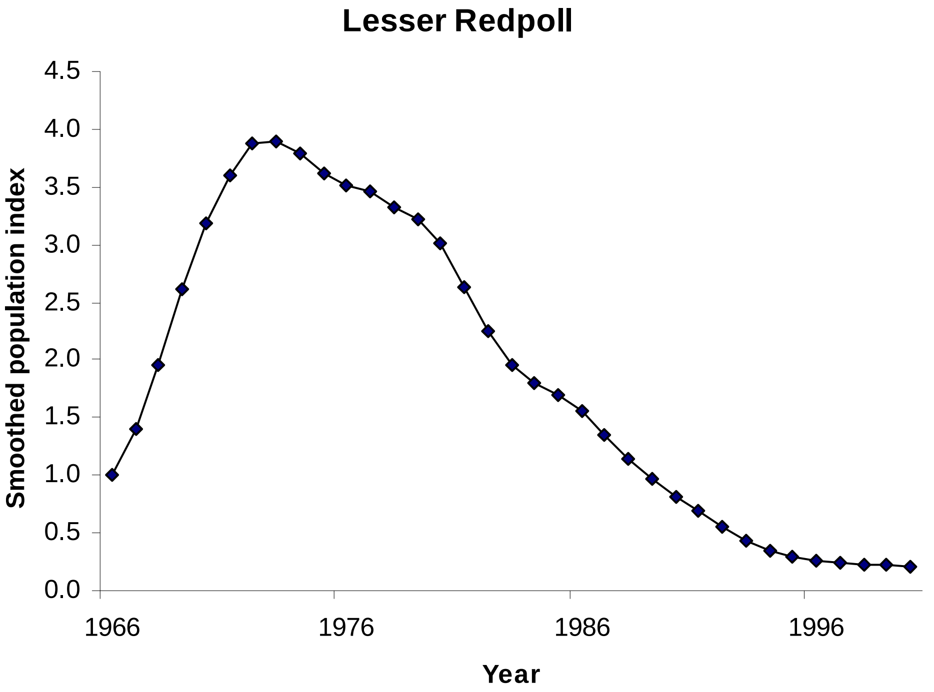
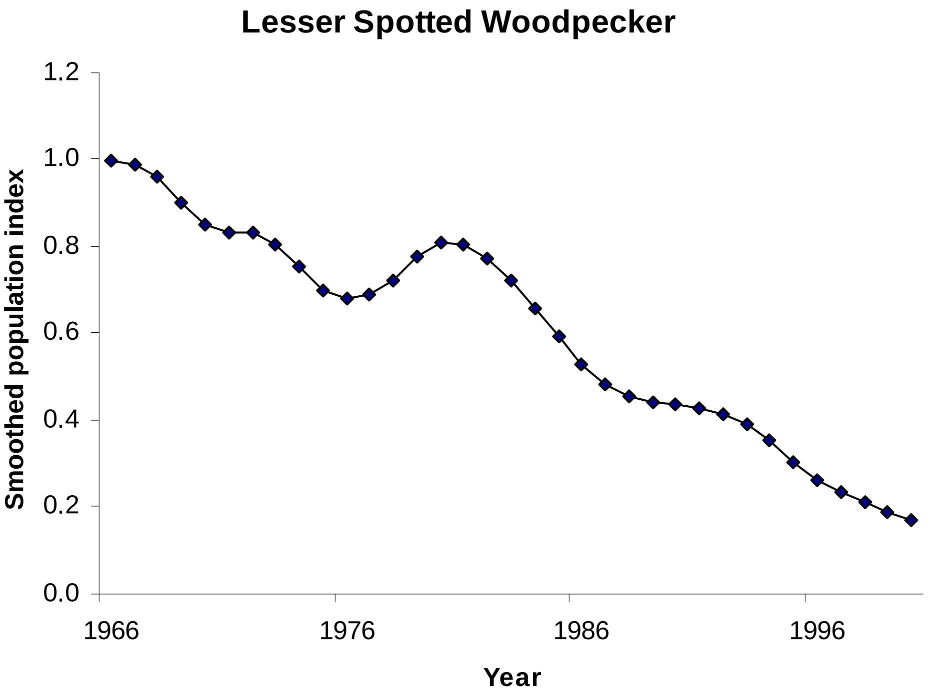


Figure 2 Continued.



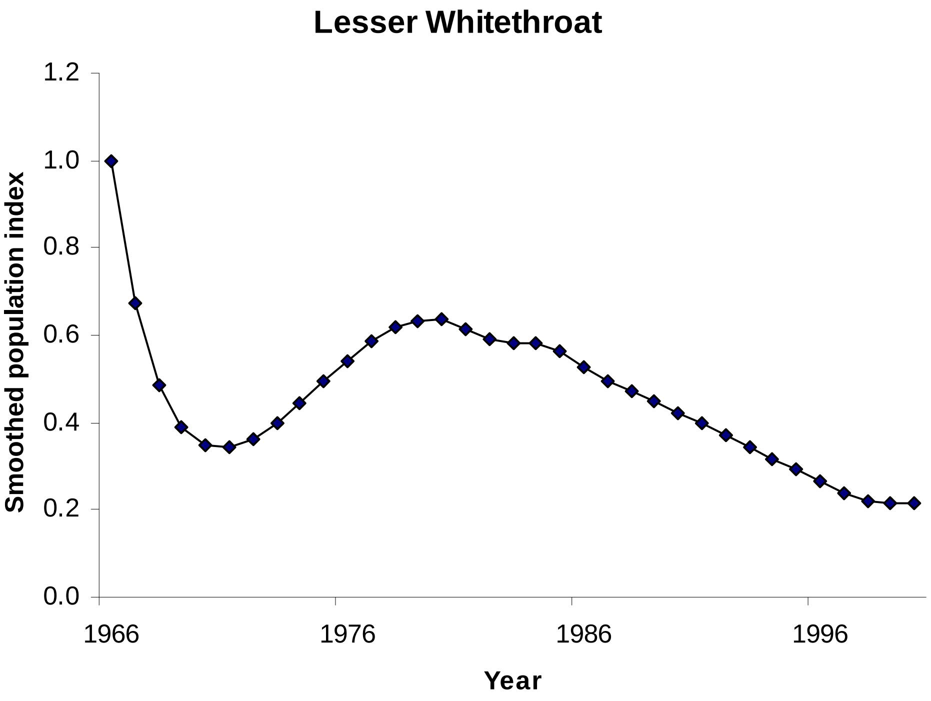
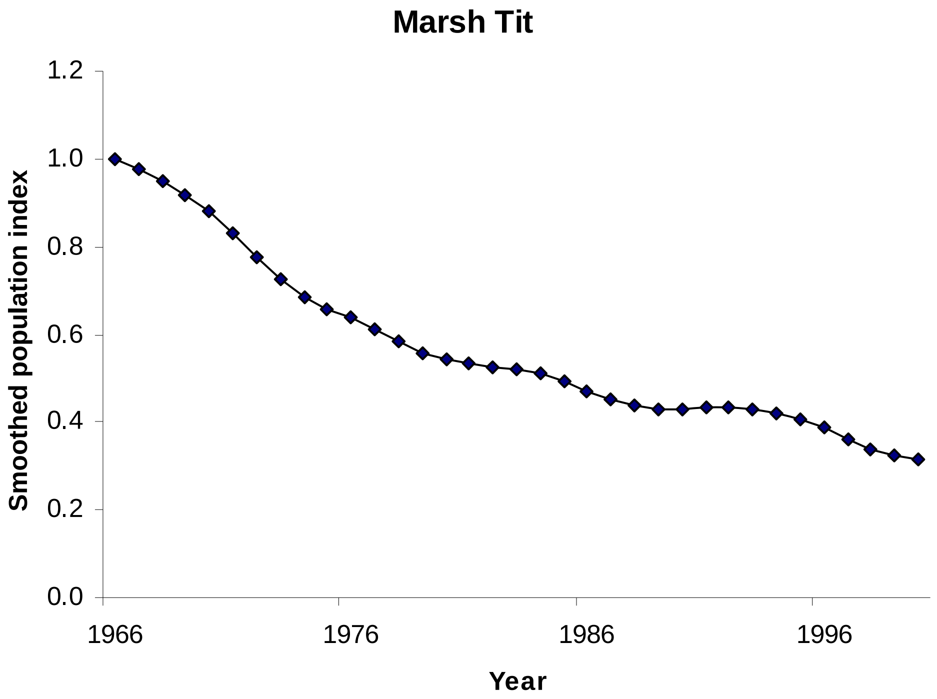


Figure 2 Continued.



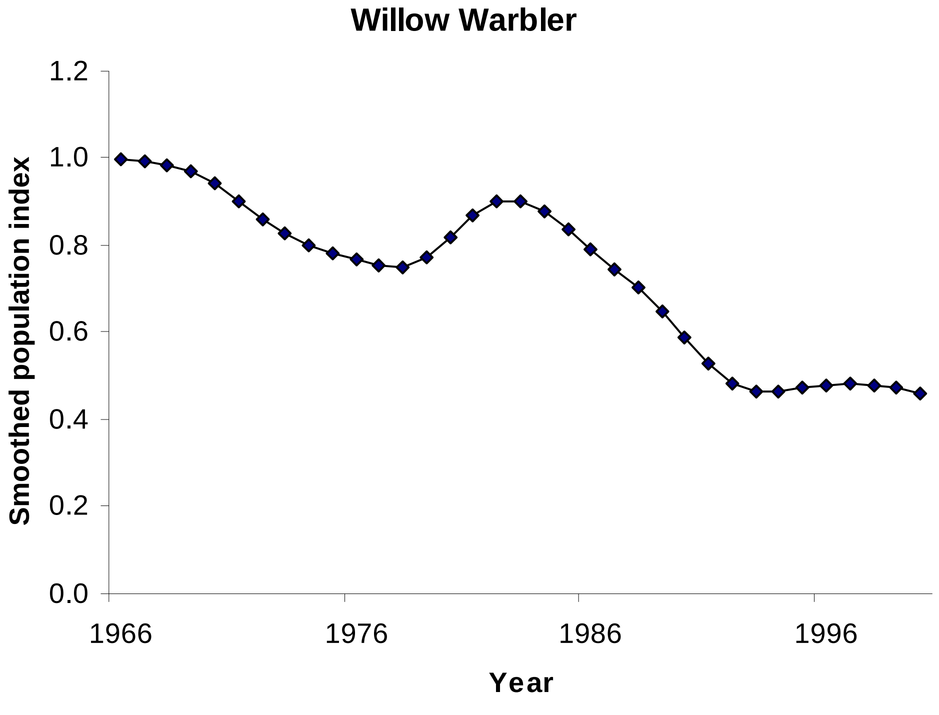
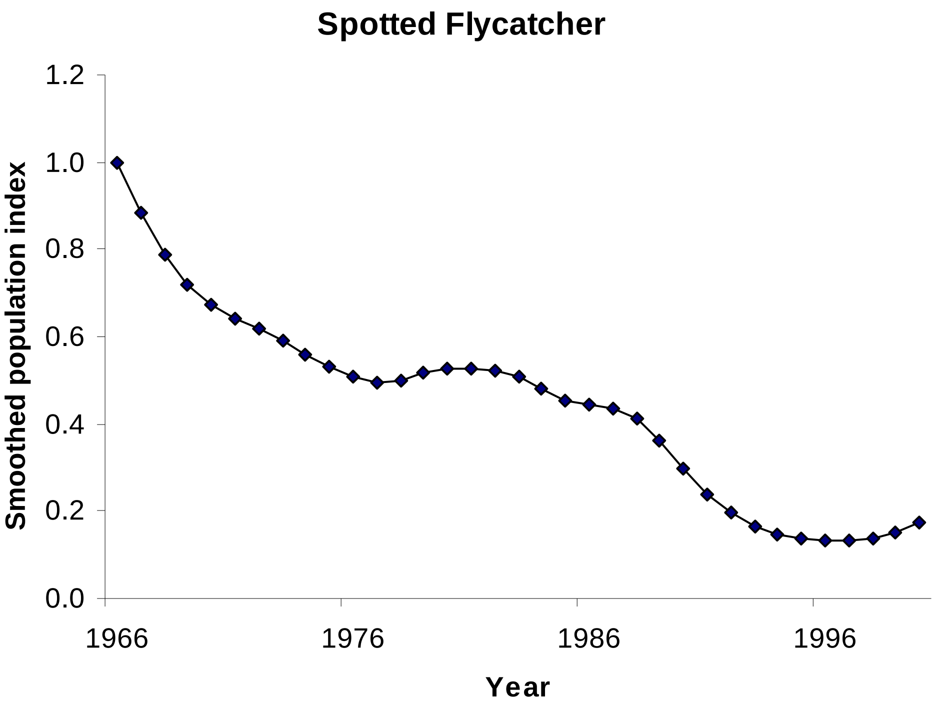


Figure 2 Continued.



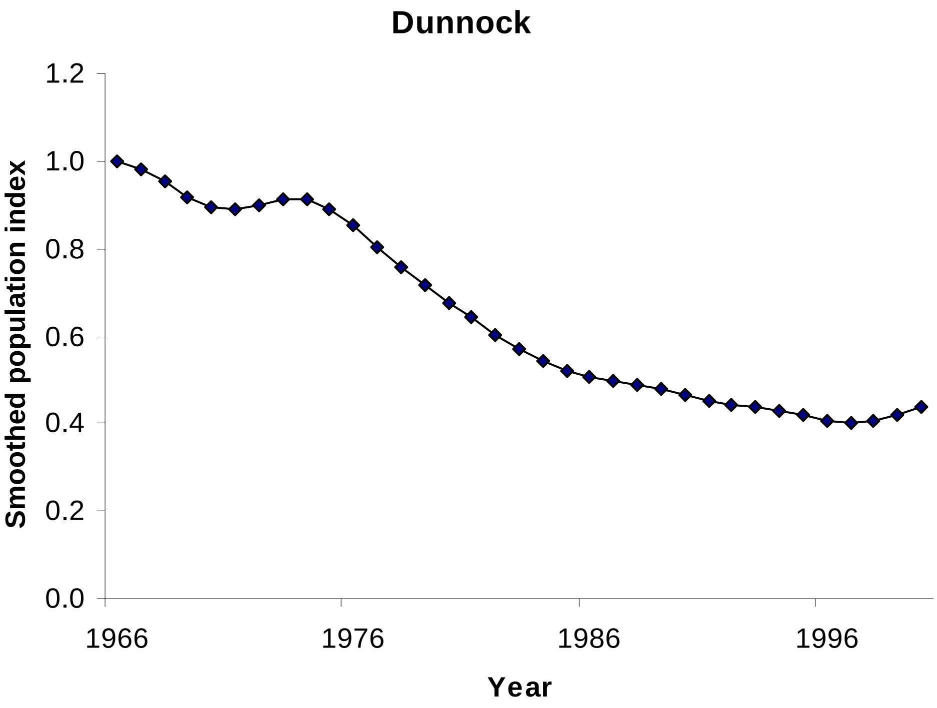


Figure 2 Continued.

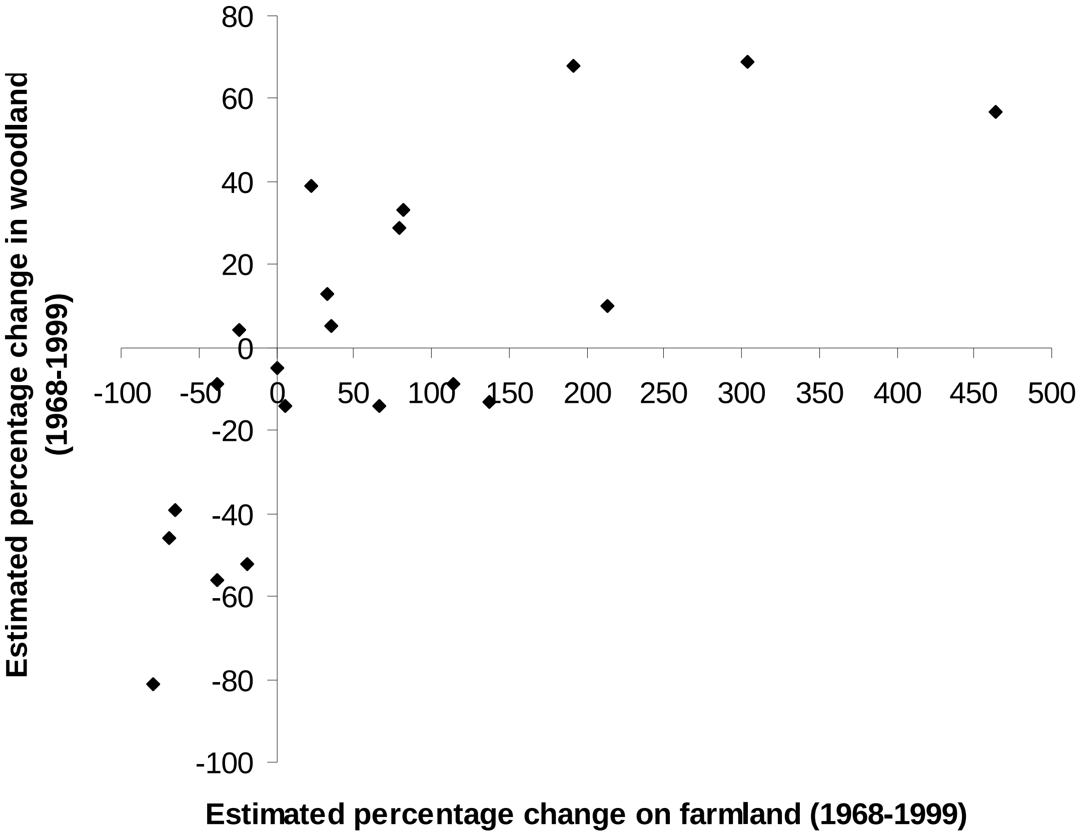


Figure 3 A comparison of estimated population changes on farmland plots and woodland plots for 21 woodland species. The species are those from Table 1 for which sufficiently large sample sizes are available from both woodland and farmland CBC plots. Note that the percentage changes on the two axes are plotted on different scales.

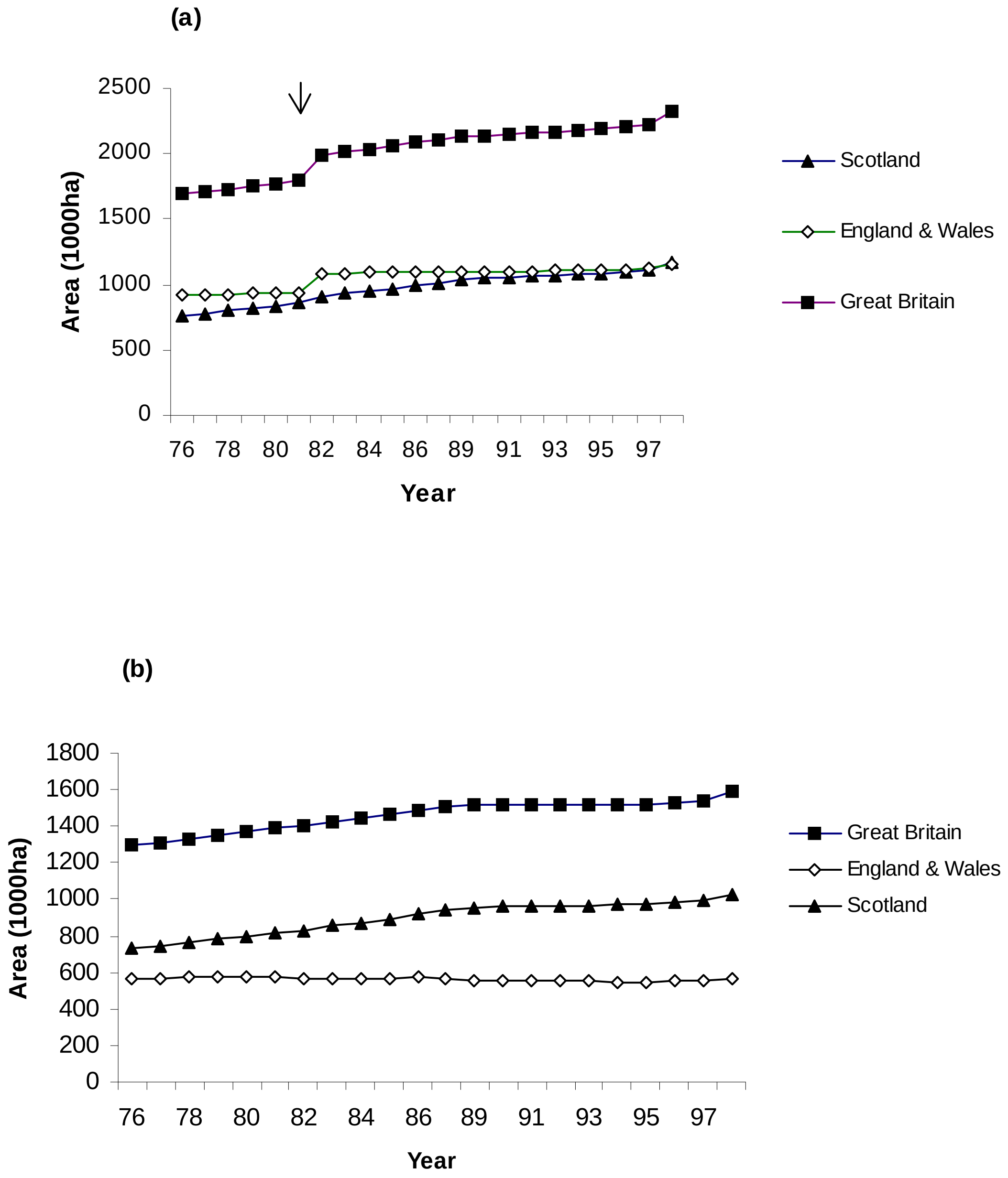
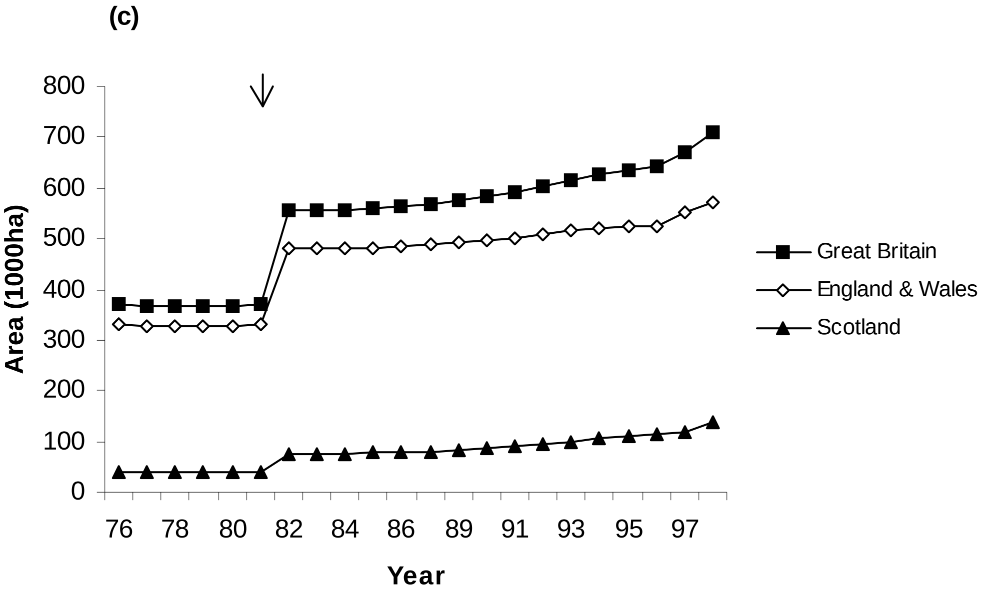


Figure 4 Area of woodland in Great Britain between 1976 and 1999: (a) total productive woodland; (b) productive conifer woodland; (c) productive broadleaved woodland; (d) non-productive woodland. Figures are taken from the Forestry Commission's *Facts & Figures* (1976-1977 to 1998-1999). Productive woodland is defined as woodland where timber production is the main management objective. Non-productive woodland includes areas managed for amenity, conservation and public recreation. The transfer of some woods from non-productive to productive in 1982-1983 caused a large change in the area of woodland in some categories, as indicated by the arrows and does not reflect a true change in woodland area.



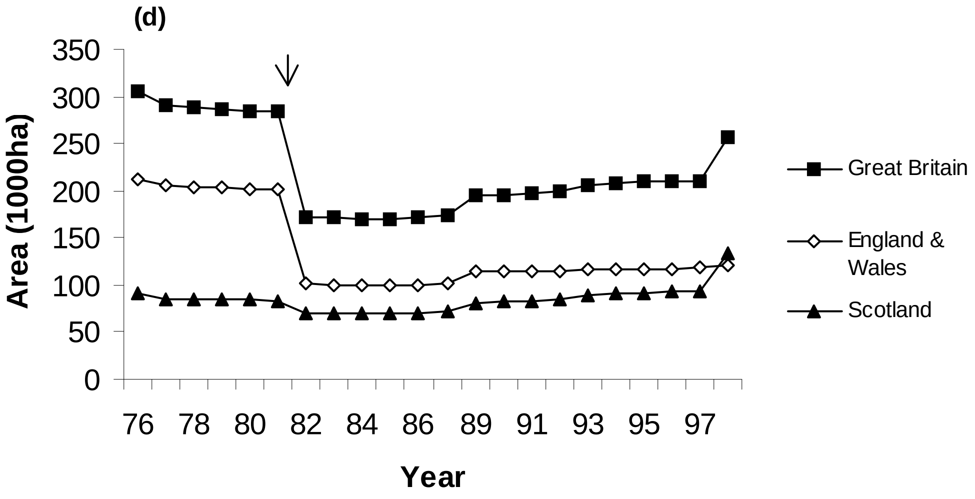


Figure 4 Continued.

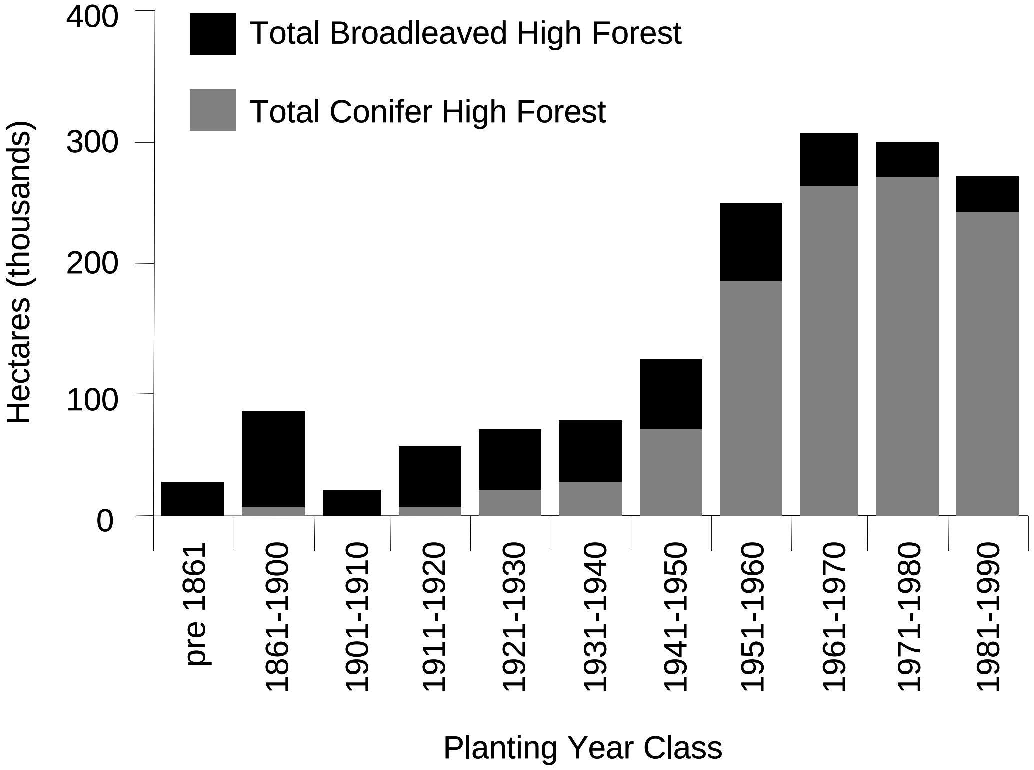


Figure 5 The total area of high forest in Great Britain in the mid 1990s shown by the decade in which it was planted. Most of the current area of conifer forest relates to plantings in the second half of the 20th century, especially since 1960. (Data from Forestry Commission's National Inventory of Woodland and Trees).

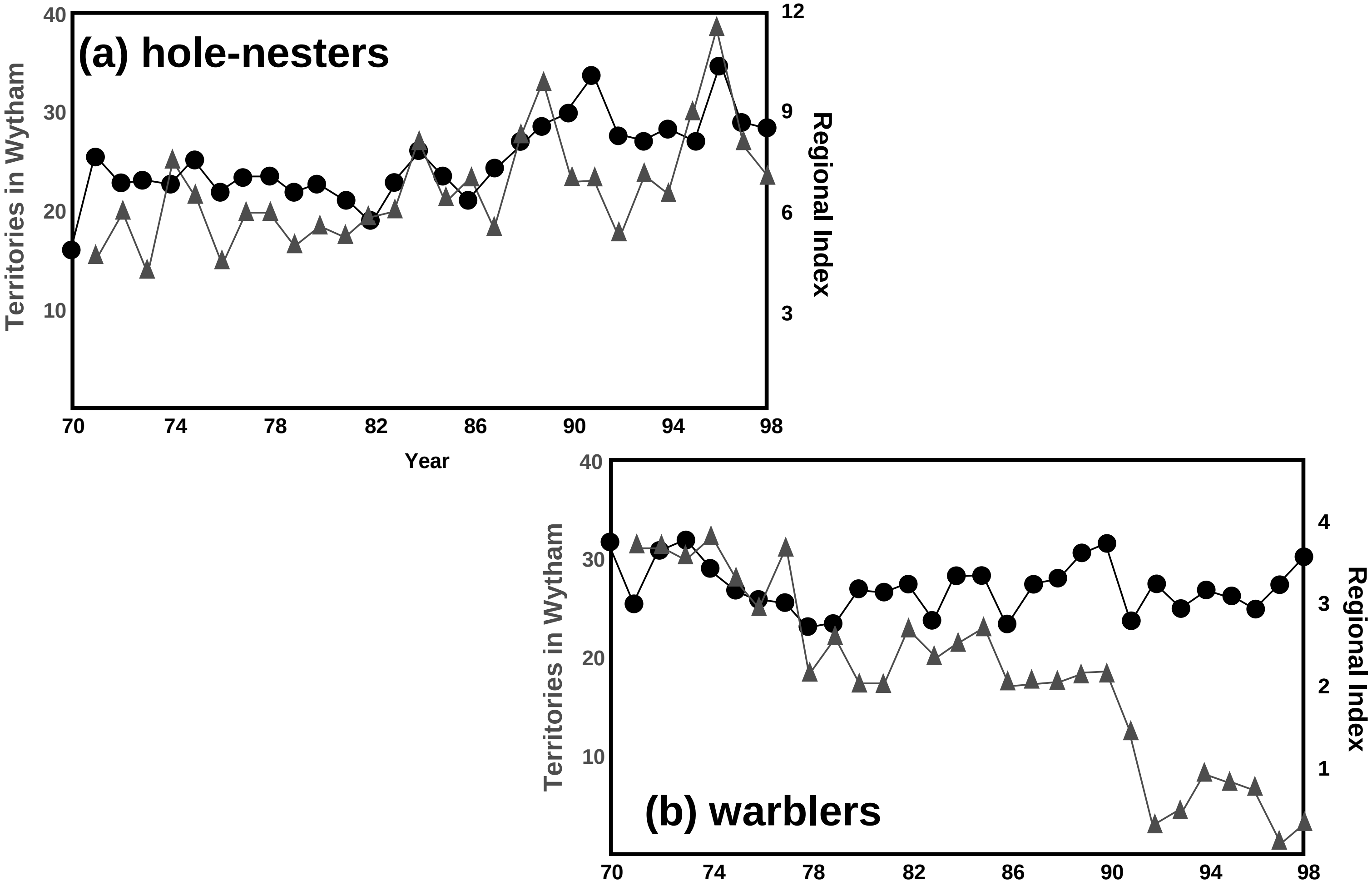


Figure 6 Population trends of (a) hole-nesting birds and (b) warblers in Wytham Woods, Oxfordshire, compared with woods in the same region. The data are drawn from the BTO's Common Birds Census and they show estimated numbers of territories in a 6 ha plot in Wytham Wood (triangles, left axis) and a population index based on CBC woodland plots in Oxfordshire and its adjoining six counties (circles, right axis). Redrawn from Perrins & Overall (2001).

Appendix 1 A summary of attributes of declining woodland birds. Based mainly on information in Fuller (1995) and Snow & Perrins (1998).

Species	**Migratory habit**	**Main habitat in woodland and scrub**	**Typical nest site**	**Diet and foraging sites in breeding season**[1]	**Diet and foraging sites outside the breeding season**[1]	**Comments**
Spotted Flycatcher	Long distance migrant	Mature open broadleaf stands	Open cavity / branch	Insects taken on or close to ground and in the air	--	Prefers open canopy with open spaces
Lesser Spotted Woodpecker	Resident	Mature broadleaf stands	Excavates cavity (usually in deadwood)	Insects, mainly on small diameter branches in canopy	Insects, in particular wood-living larvae	To some extent, a dead wood specialist
Lesser Whitethroat	Long distance migrant	Tall scrub; hedgerows	Bushes, nest usually <2m above ground	Foliage insects from the shrub layer but rarely forages within closed-canopy woodland	--	Avoids most types of woodland but sometimes found at wood edges
Tree Pipit	Long-distance migrant	Open broadleaf stands; young plantations; open scrub	Ground	Insects from the ground and leaf litter	--	In the lowlands usually avoids mature stands, though will use wide rides and glades; in the uplands commonly uses mature birch stands with sparse understorey
Lesser Redpoll	Partial migrant / winter visitor	Young conifer plantations; scrub	Bushes and small trees	Mainly small seeds, some insects; mainly forages in tree canopy, but also field layer or ground depending on food	Mainly birch and alder seeds taken in tree, field layer and on ground	Generally avoids old closed-canopy stands except alder and birch in winter
Willow Tit	Resident	Mainly broadleaf woodland and scrub, occasionally uses coniferous woodland	Excavates cavity in rotting wood (<2m high)	Insects from the field / shrub layer foliage and on dead wood	Insects and small seeds in low foliage and on dead wood	To some extent, a dead wood specialist: appears to prefer damp woodland
Marsh Tit	Resident	Mature broadleaf stands with shrub layer	Uses existing cavity (usually <3m high)	Insects from the shrub layer and low canopy foliage	Seeds and fruits in low canopy, field and shrub layers	Avoids sites with little understorey

Species	**Migratory habit**	**Main habitat in woodland and scrub**	**Typical nest site**	**Diet and foraging sites in breeding season**[1]	**Diet and foraging sites outside the breeding season**[1]	**Comments**
Dunnock	Partial migrant (in north)	Broadleaf, coniferous and scrub with well developed field layer	Field / shrub layer (0.1-2 m high)	Insects, taken mainly on ground but also in field layer	Insects and seeds on ground and in low field layer	Avoids old stands with little understorey; mainly a woodland edge bird
Woodcock	Partial migrant (in north)	Thicket stage broadleaf or coniferous stands	Ground	A ground-feeder, mainly earthworms	As for breeding season	Frequently feeds nocturnally on pasture outside woods
Willow Warbler	Long distance migrant	Open broadleaf woods, young plantations, scrub	Ground	Foliage insects from the tree canopy and shrub layer	--	Avoids closed-canopy woodland but uses mature birch stands with little understorey in upland areas. In lowland mature woods often confined to edges or rides
Song Thrush	Resident	Broadleaf and coniferous stands, especially thicket stage, also scrub	Mainly in shrub layer	Terrestrial vertebrates taken on the ground	As for breeding season	Prefers areas with low cover
Bullfinch	Resident	Broadleaf woods with good shrub layer; dense scrub; thicket stage conifers	Shrub layer (1-3 m high)	Seeds and fruits from the tree, shrub & field layer. Nestlings are fed some invertebrates	As for breeding season	In mature woods often found mainly at edges
Nightingale	Long distance migrant	Mainly dense scrub and broadleaf woods with thick shrub layer	Ground or low field layer	Terrestrial invertebrates, taken on the ground, and fruits.	--	Prefers places with patches of bare or sparsely vegetated ground beneath dense low foliage
Capercaillie	Resident	Semi-natural Scots pinewoods and mature conifer plantations	Ground	Insects (esp. for chicks), heather, bilberry. Feeds on ground and in field layer	Tree canopy on pine needles and buds	Prefers mature Scots pine with dense bilberry *Vaccinium myrtillus*
Hawfinch	Resident	Mainly mature broadleaf woodland	Low or mid canopy	Insects and seeds taken on ground and in trees	Mainly fruits and seeds taken on ground and in trees	

[1] In most cases, species that feed on insects will also consume spiders

Appendix 2 General trends in breeding populations of woodland birds in Europe for the period since approximately 1970, based on information in Tucker & Heath (1994), Hagemeijer & Blair (1997) and BirdLife International/EBCC (2000). Estimated percentage of the European breeding population showing declines of >20% (from Appendix 1 of Tucker & Heath (1994)) are given in parentheses, followed by the European threat status code from BirdLife/EBCC (2000) where: V = vulnerable, D = declining, S = secure and parentheses indicate a provisional status. For Woodcock, the threat status relates to the winter population. Declining species in Britain are defined as ones with a population decline of >25% (Table 1) or for which there is other evidence of recent decline. Stable species have shown population changes of -25% to +25% (Table 1). Increasing species have increased by >25% (Table 1). Asterisks indicate species whose population trends in Britain appear to diverge from those in Europe as a whole.

Species	**European trend and status (Tucker & Heath 1994, BirdLife International / EBCC 2000)**	**European trend (Hagemeijer & Blair 1997)**
Declining species in Britain		
Capercaillie	Status is provisionally secure (13%), (S)	Reduction in numbers throughout range
Woodcock*	Probable decline in E.Europe (3%), V_w	Stable except declines in E.Europe and Britain
Lesser Spotted Woodpecker*	No strong decline (19%), S	Decreases in Fennoscandia
Tree Pipit*	No strong decline (8%), S	Stable
Dunnock*	No strong decline (28%), S	Increase in Fennoscandia; British decline seems unique
Nightingale*	No strong decline (5%), (S)	Mostly stable or increasing
Song Thrush*	No strong decline (13%), S	No clear trend but declines in central Europe, Britain and Ireland.
Lesser Whitethroat*	No strong decline (25%), S	Generally stable
Willow Warbler*	No strong decline (0%), S	No clear trend; only declines in S. Britain and W. Netherlands.
Spotted Flycatcher	Widespread decline (45%), D	Declines of c. 25% in scattered countries
Marsh Tit*	No strong decline (10%), S	Declines in a few countries but no clear trend
Willow Tit*	No strong decline (2%), (S)	No clear trend
Lesser Redpoll*	No strong decline (2%), (S)	Increasing in most areas except Britain
Bullfinch*	No strong decline (8%), S	Apparently stable except in Britain
Hawfinch*	No strong decline (3%), S	Increase over much of its range

Stable species in Britain		
Redstart*	Widespread declines (83%), V	Decreasing in >50% of countries, elsewhere mainly stable
Blackbird	No strong decline (15%), S	No clear trend
Garden Warbler	No strong decline (0%), S	Stable or increasing
Chiffchaff	No strong decline (0%), (S)	No major changes
Goldcrest	No strong decline (0%), (S)	Largely stable
Long-tailed Tit	No strong decline (1%), S	Stable except for major decline in Finland
Coal Tit	No strong decline (4%), S	Largely stable or slightly increasing
Blue Tit	No strong decline (6%), S	No significant trend
Treecreeper	No strong decline (15%), S	Largely stable
Jay	No strong decline (0%), (S)	Largely stable
Chaffinch	No strong decline (8%), S	Increases in several countries incl. Fennoscandia
Increasing species in Britain		
Sparrowhawk	No strong decline (4%), S	General increase in NW Europe
Tawny Owl	No strong decline (8%), S	No clear trend
Green Woodpecker*	Widespread declines (44%), D	Stable or declining
Great Spotted Woodpecker*	No strong decline (1%), S	Generally stable but increases in Britain, Germany, Netherlands
Wren	No strong decline (0%), S	No clear trend
Robin	No strong decline (0%), S	Stable
Blackcap	No strong decline (0%), S	Stable or increasing
Great Tit	No strong decline (0%), S	Stable but increases in Britain, Netherlands and E.Europe
Nuthatch	No strong decline (1%), S	Generally expanding range northwards