# Modelling the effects of changing habitat characteristics and spatial pattern on woodland songbird distributions in West and Central Scotland

Helen Patricia Creegan

School of Biological and Environmental Sciences
University of Stirling

September, 2004

Submitted for the degree of Doctor of Philosophy

I hereby confirm that this is an original study conducted independently by the undersigned and the work contained herein has not been submitted for any other degree. All research material has been duly acknowledged and cited.

Signature of candidate:

Date:

# Contents

# List of Figures

## Chapter 1

# Chapter 2

## Chapter 3

## Chapter 4

## Chapter 5

# List of Tables

## Chapter 2

## Chapter 3

## Chapter 4

# Chapter 5

# List of Appendices

# Acknowledgements

I would like to thank the following people for their assistance during the completion of this thesis. Firstly, Patrick Osborne my supervisor, for guidance on all stages of this project. Also, Mick Whelan and Andrew Tyler who were my second supervisors during different stages of completing this thesis. Stuart Bradley, John McArthur and Bill Jamieson all provided valuable technical support in the field work, computing and map production areas respectively. Rose Goodacre also provided constant support and advice.

I would also like to thank André Desrochers at the Université Laval, Quebec for his prompt and helpful responses to my queries about his gap crossing work. Professor Colin Pennycuick provided me with bird morphological data. Hugh Semple and his family provided both support and useful information on forestry practices. I would also like to thank Fiona McColm for her encouragement and for discussing her gap crossing work with me.

Several professional bodies contributed to this study. The National Sound Archive supplied me with the mobbing call recordings for the experimental section of this work. The Forestry Commission, especially Mike Steward provided me with information on management at East Loch Lomond, GIS data and maps, and gave me permission to work in their woodlands. Richard Thompson also allowed me access to his book on Restoring Native Woodlands prior to publication. The Central Scotland Countryside Trust gave permission for me to access The Millennium Guide to Scotland’s Forest Resource GIS data from

Highland Birchwoods and allowed me to use the LIFE II Survey data for the Central Scotland Forest. At the RSPB, Mike Trubridge allowed me to analyse the count data collected for the woodlands around Inversnaid, and gave valuable time for discussion and to show me the Inversnaid Reserve. I would also like to acknowledge the late Bill Brackenridge who along with Mike Trubridge collected some of the bird count data for the Reserve. The Meteorological Office provided me with the weather data for Helensburgh.

The staff at the University of Glasgow Field Station at Rowardennan made me very welcome while I was carrying out field work. I would also like to thank the numerous landowners within the Central Scotland Forest who allowed me to carry out field work in their woodlands and who often showed a lot of interest in the work being carried out.

This work was funded by a University of Stirling studentship.

# Abstract

This study investigated bird distributions in relation to local habitat and landscape pattern and the implications which habitat fragmentation may have for woodland birds. There were two sections to the research: an experimental study investigating bird gap crossing behaviour across distances of five to 120m; and an observational study modelling woodland bird distributions in relation to local habitat and landscape scale variables in two study areas (East Loch Lomond and the Central Scotland Forest).

In the experimental study it was hypothesised that bird willingness to cross gaps will decrease with increasing gap distance even at home-range scales and that the rate of decline will vary interspecifically in relation to bird morphology. Song thrush mobbing calls played at woodland edges in the West of Scotland were used to attract birds across gaps and results were compared with the response along woodland edges. Data were obtained for four species: chaffinch, coal tit, robin and goldcrest. The decline in response with distance across gaps and along woodland edge was modelled for each species using generalized linear modelling. Maximum gap crossing distances ranged from 46m (goldcrest) to 150m (extrapolated value for the chaffinch). Goldcrests responded more readily through woodlands. There was no difference between woodland edge and gap response for the coal tit. Robins and chaffinches however responded more readily across gaps than through woodland.

When different response indices were plotted against bird mass and wing area, results suggested that larger birds with bigger wings responded more readily across gaps than through woodland. It is suggested that this relates to differences in bird manoeuvrability within woodlands and ability to evade a predator in gaps. Fragmentation indices were calculated for an area of the Central Scotland Forest to show how willingness to cross different gap distances influences perception of how fragmented the woodlands are in a region. Results are discussed in the context of the creation of Forest Habitat Networks.

The data for the observational section of the work was from bird point counts for 200 sample points at East Loch Lomond in 1998 and 2000 and 267 sample points in the Central Scotland Forest in 1999. In addition a time series of point count data was available for 30 sample points at East Loch Lomond. Additional data was gathered for ten sample points (1998) and two sample points (2000) at East Loch Lomond to investigate effects of observer, time and weather on count data. Generalized linear and generalized additive modelling was carried out on these additional data. Results indicated that biases due to the variation in time and weather conditions between counts existed in the pure count data but that these were eliminated by reducing data to presence and absence form for analysis. Species accumulation curves indicated that two counts per sample point were insufficient to determine species richness. However a sufficiently large proportion of the species was being detected consistently in two counts of ten minutes duration for it to be valid to model them in relation to habitat and landscape variables.

Point count data for East Loch Lomond in 1998 (ELL98) and the Central Scotland Forest in 1999 (CSF99) for the wren, treecreeper, garden warbler, robin, blue tit, blackbird, willow warbler, coal tit, goldcrest, great tit, and song thrush were analysed using generalized additive modelling. In addition models were built for the blackcap (CSF99) and the siskin, redstart and wood warbler (ELL98). Where all relationships were identified as linear, models were rebuilt as GLMs. Models were evaluated using the Area Under the Curve (AUC) of Receiver Operating Characteristic (ROC) plots. AUC values ranged from 0.84-0.99 for ELL98 and from 0.76-0.93 for CSF99 indicating high predictive accuracy. Habitat variables accounted for the largest proportion of explained variation in all models and could be interpreted in terms of bird nesting and feeding behaviour. However additional variation was explained by landscape scale and fragmentation related (especially edge) variables.

ELL98 models were used to predict bird distributions for Loch Lomond in 2000 (ELL00) and for the CSF99. Likewise the CSF99 models were used to predict distributions for ELL98 and ELL00. Predicted distributions had useful application in many cases within the ELL site between years. Fewer cases of useful application arose for predicting distributions between sites. Results are discussed in the context of the generality of bird environment relationships and reasons for low predictive accuracy when models are applied between sites and years.

Models which had useful application for ELL00 were used to predict bird distributions for 2025 and 2050 at East Loch Lomond. Habitat and landscape changes were projected based on the proposed management for the site. Since woodland regeneration rates are difficult to predict, two scenarios were modelled, one assuming a modest amount of regeneration and one assuming no regeneration. Predictions derived from the ELL98 models showed broad-leaved species increasing in distribution while coniferous species declined. This was in keeping with the expected changes in the relative extent of broad-leaved and coniferous habitat. However, predictions from the CSF99 models were often less readily explicable. The value of the modelling approach is discussed and suggestions are made for further study to improve confidence in the predictions.

# Chapter 1: Introduction

## 1.1 Rationale for studying woodland birds

Breeding birds are one of the UK government's 15 'Quality of Life' Indicators of progress towards sustainable development. Although the common bird indicator has been relatively stable since 1970, woodland birds have declined by 22% since the mid-1970s (Gregory *et al*., 2003). The Government has pledged to reverse this long term trend. This has created a policy climate where old forestry practices are being replaced with more sympathetic management techniques designed to enhance both habitat quality and distribution (Forestry Commission, 2003). To take advantage of these opportunities an understanding of factors determining bird distributions is important.

Species distribution depends on local habitat, landscape pattern and dispersal ability (Léscourret and Genard, 1994). Habitat fragmentation influences all three of these parameters. It has therefore been hypothesised as being at least partially responsible for some of the observed avian population declines and there is now considerable evidence that habitat fragmentation can cause declines in avian populations and biodiversity loss (Andrén, 1994; Robinson *et al*., 1995 Bender *et al*., 1998; Schmiegelow and Monkkonen, 2002).

Habitat fragmentation can be defined as the process of subdividing a continuous habitat into smaller pieces. It results from both natural and anthropogenic activities and leads to habitat loss (and conversely the creation of new habitat), reduced patch size and an increasing distance between habitat patches (Andrén, 1994). New habitat creation is often associated with edges, the junctions between different habitat types (Forman and Godron, 1986). These habitat junctions are coupled with changes in microclimate, species composition due to invasion from the neighbouring habitat, and alterations in the intensity of population processes such as parasitism, predation and competition (Alverson *et al*., 1988). Since the habitat changes occurring at edges are affected by such a variety of abiotic and biotic factors, edge extent is not a constant and is subjective to define (Wiens *et al*., 1985; Yahner, 1988; McCollin, 1998).

Some of the observed population declines will be due to the fragmentation associated habitat loss (Schmiegelow and Monkkonen, 2002). Additional losses may be resulting from the fragmentation related habitat changes, notably edge effects one of the most commonly described being an increased rate of nest predation from mammalian and corvid predators at habitat edges. Numerous studies have investigated the effects of increased nest predation at woodland edges (for example, Wilcove, 1985; Andrén *et al*., 1985; Martin, 1988; Small and Hunter, 1988; Haskell, 1995; Bayne and Hobson, 1997; Huhta *et al*., 1998; Hartley and Hunter, 1998; Chalfoun *et al*., 2002; Huhta *et al*., 2004).

However, populations at the landscape scale are also critically affected by the ability and willingness of individuals to cross gaps generated between suitable habitat patches by fragmentation (Fahrig and Merriam, 1994). As birds were perceived as able dispersers (for example, Margules *et al*., 1982; Ambuel and Temple, 1983), this factor was often ignored in early studies. The dispersal ability of woodland birds is such that they are physically able to cross gaps of many kilometres, where dispersal is defined as the process of moving from one location, or habitat patch, to another, often across inhospitable habitat. However, a psychological reluctance may restrict the gap widths that they are willing to cross (Kirby, 1995; Grubb and Doherty, 1999) possibly due to the birds' perception of predation risk (Lima and Dill, 1990). Gap crossing can occur at a range of scales both within and between territories. In population biology it has important implications for population synchrony, colonization, range expansion, and metapopulation processes (Paradis *et al*., 1998). Nevertheless, it is an under-researched topic even at a local scale (although variations in habitat use at this scale evidently occur (Johnstone, 1998; Fuller, 2001)), probably because data are difficult to collect (Haas, 1995).

This study aimed to model bird distributions in relation to variables from the local to landscape scales for two study areas in West and Central Scotland. This represents an extension to earlier bird studies which generally focused on local habitat parameters for explaining bird distributions (for example Lack, 1933; Lack and Venables, 1939; Moss, 1978; James and Wamer, 1982). It is the approach taken in more recent studies which have tried to separate the effects of habitat characteristics and landscape for woodland birds (for example, Ford, 1987; McCollin, 1993; Léscourret and Genard, 1994; Robinson *et al*., 1995; Bellamy *et al*., 1996a; Berg, 1997; Saab, 1999). Dispersal behaviour at home range scale was also investigated through experiments using the playback of mobbing calls to attract birds across gaps. This was a new method developed from work by Desrochers and Hannon (1997). The results from the observational and experimental studies have direct practical application for improving woodland management to maximise avian biodiversity in these study areas, both of which are currently the subject of exciting management initiatives.

## 1.2 Aims and Objectives of the Study

This study used two general approaches:

1. An experimental approach looking at the responses of birds to gaps in woodland cover. This work is covered in Chapter 2.
2. An observational approach based on bird counts and statistical modelling. This work is covered in Chapters 3 to 5.

### *1.2.1 The Experimental Study*

For the experimental study (Chapter 2) it was hypothesised that:

1. Bird willingness to cross gaps will decrease with increasing gap distance at a relatively local scale of five to 120m range.
2. These declines with distance will vary interspecifically in relation to bird morphology.

### *1.2.2 The Observational Study*

The observational study can be subdivided into different sections.

Chapter 3 provides an evaluation of the bird count methodology. It aimed to set limits within which subsequent statistical modelling could be carried out with confidence that significant biases were being avoided. Specifically the following hypotheses were addressed.

1. Biases may exist in point counts in relation to effects of observer, count length, count radius, and the weather conditions on the day of the count and the day preceding the count. However these are likely to vary interspecifically due to differing detectabilities between birds, such that count data can be modelled with more confidence for some species compared with others.
2. Reducing data to presence and absence rather than abundance level should eliminate some of these biases.
3. The numbers of species detected is likely to increase with the number of counts performed at each sample point. Therefore two counts per point may be inadequate to evaluate species richness. However some species should still be detected with high consistency, such that two counts are adequate to determine their distribution.

Based on the conclusions of Chapter 3, modelling was carried out for species which were detected with high degrees of consistency based on two counts per sample point. The following hypotheses were considered in Chapter 4.

1. Bird-habitat association models can be improved by the inclusion of variables measured at a landscape scale since birds actually respond to parameters at a range of scales.
2. Since habitat and landscape patterns are affected by fragmentation and this factor has been implicated in some of the observed declines in woodland

birds (for example, Bellamy *et al*., 2000), the inclusion of fragmentation related variables into models should improve their accuracy.

3. Where generality exists in the identified relationships, models will have predictive accuracy between sites and years.

Models constructed in Chapter 4 were used in Chapter 5 to predict the changes in bird distributions likely to occur at East Loch Lomond over the next 50 years. Specifically the following questions were addressed:

1. How are bird distributions likely to change over the next 50 years at East Loch Lomond?
2. What degree of confidence can be placed in the accuracy of these predictions?
3. How could the modelling be improved to increase the accuracy of predicted distributional changes of the woodland birds?

This chapter was a speculative exercise designed to illustrate the potential value of the modelling and experimental work as a management aid.

Bird species are referred to by their common names throughout this thesis. However a complete list of scientific names of birds referred to in the text is given in Appendix 1.

## 1.3 Description of the Study Sites

This research was carried out in two study sites:

1. West of Scotland – the woodlands of East Loch Lomond, Achray Forest and Loch Ard Forest.
2. The Central Scotland Forest

### *1.3.1 West of Scotland Study Site*

The West of Scotland study site is best considered in terms of a core study area around East Loch Lomond, and a wider study area incorporating Achray and Loch Ard Forests (Figure 1.1). The core study area was used for both the observational and experimental work described in Chapters 2-5, while the wider study area was used purely for the experimental work (Chapter 2) because of the requirement for additional independent locations for this part of the study.

#### 1.3.1.1 East Loch Lomond

The East Loch Lomond study site (ELL) covers an area of approximately 1800 hectares extending from Balmaha in the south to beyond Inversnaid in the north (Figure 1.1). The largest area (approximately 1400ha), between Balmaha and Cailness has been owned by the Forestry Commission since 1952 and is managed by Forest Enterprise. From Cailness north to Inversnaid, the woodland forms part of the privately owned Comer Estate. Beyond Inversnaid the woodland is managed by the Royal Society for the Protection of Birds (RSPB) as a Reserve.

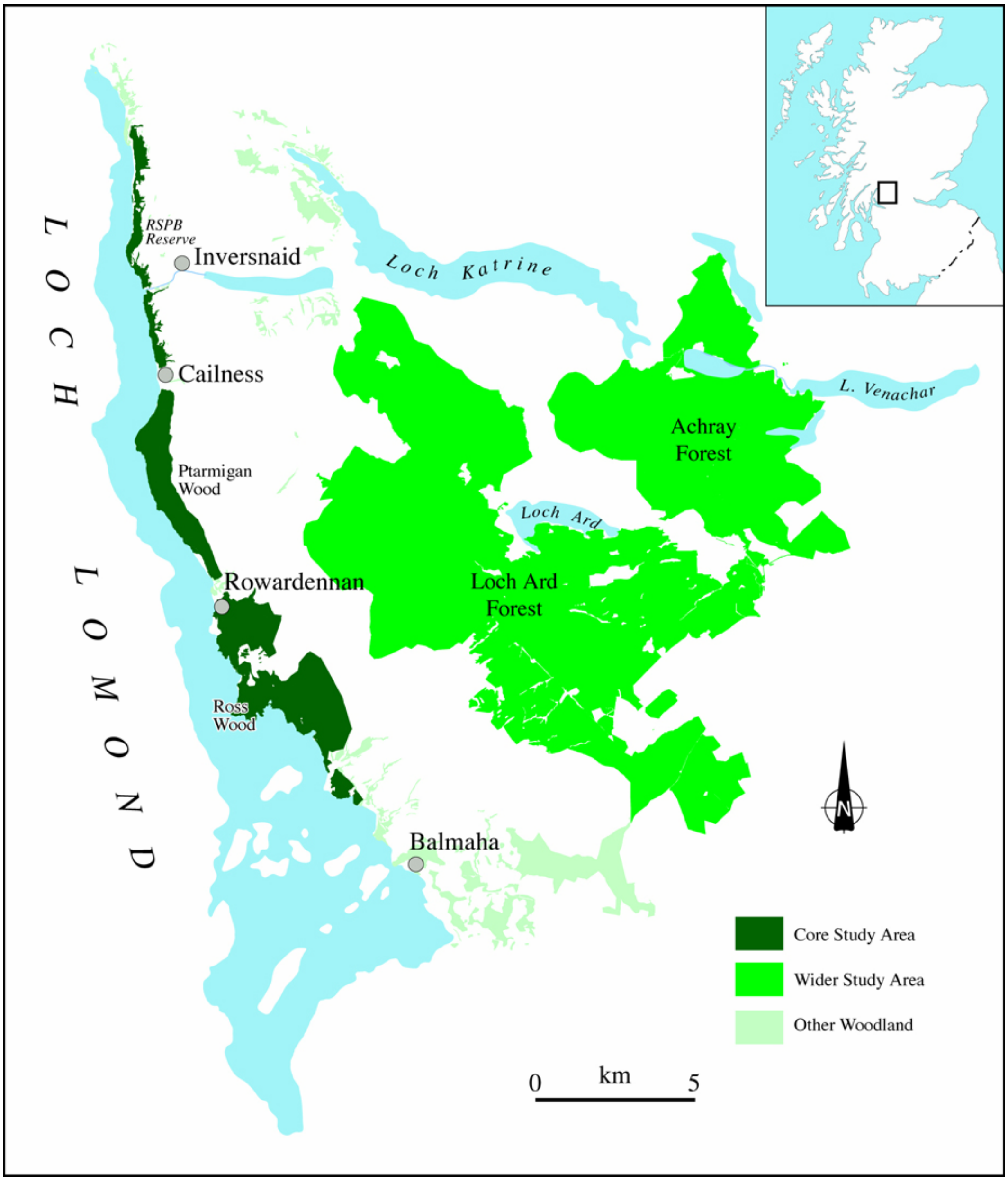

**Figure 1. 1: The West of Scotland study site showing the core East Loch Lomond study area and the wider study area incorporating Loch Ard Forest and Achray Forest. The location of the study area within Scotland is also shown.**

Semi-natural broad-leaved woodlands extend for 16km along the Lochside. Within the Forestry Commission owned area, this woodland lies adjacent to coniferous plantation predominantly planted in the 1950's, though some areas were planted later (Figures 1.2 and 1.3). Semi-natural woodland also occurs along streamsides within the coniferous plantations. The RSPB and Comer Estate woodlands lie adjacent to grazed grassland and heathland (Figure 1.4).

The structure and composition of the semi-natural woodland varies along the length of the Loch due to both natural and past and present anthropogenic influences. For example, the average annual rainfall increases by approximately 100cm from around 152cm to 254cm northwards between Balmaha and Inversnaid, creating differences in soil development. In the south the dominant soil type is a podsol and the woodlands are naturally less diverse than those developed on the brown earth soils in the north (Tittensor and Steele, 1971). Locally, variations in drainage contribute to heterogeneity in plant community development. Species composition also varies with altitude which ranges from around 20m at the lochside to over 350m above mean sea level.

The Loch Lomond area has been populated since around 5000 BP and the woodlands have supported a range of human demands including timber extraction, hunting and livestock grazing (Tittensor, 1970). From the 17th to the 19th centuries the woodlands were managed as a coppice with standards system to provide a continuous supply of a range of woodland products including oak bark and wood (Anderson, 1967). To allow sufficient regeneration within the coppice stools, grazing animals were excluded with varying degrees of success.

Timber extraction has had a selective effect on the species composition. Oak bark and timber were highly valued so other less profitable species such as birch (*Betula* spp.), hazel (*Corylus avellana*), alder (*Alnus glutinosa*), crab apple (*Malus* *sylvestris*) and willow (*Salix* spp.) were removed where possible to allow for greater oak production (Tittensor, 1970). Associated changes in light regime will have altered the composition of the ground flora. At Loch Lomond both the coppice and standards were derived from the native woodland component - oak (*Quercus petraea*). However when stools became exhausted, these were often replaced with the *Quercus robur* oak from England, accounting for the presence of both species and their hybrids in the woodlands today (Cousens, 1963).

Coppice management and exclosure were gradually abandoned in the 19th century due to the decline in value of the oak bark and timber (Anderson, 1967). The last extraction of oak coppice timber occurred between 1914 and 1920 (Shaw, 1976). Emphasis then shifted towards the production of more economically viable, faster growing conifers in plantations, and the semi-natural woodlands became neglected.

The main threats to the semi-natural woodland today are from over-grazing and browsing by the populations of red (*Cervus elaphus*), roe (*Capreolus capreolus*) and fallow (*Dama dama*) deer, feral goats (*Capra* spp.) and domestic sheep (*Ovis* spp.) that occur beside Loch Lomond, and from trampling by walkers. Loch Lomond is a very popular tourist destination (Tittensor and Steele, 1971). While deer occur throughout the area, most of the feral goats are found from Ptarmigan Wood northwards (pers. obs.). Sheep only occur in the extreme north of the RSPB Reserve. Trampling by walkers is especially concentrated around the West Highland Way which runs along the eastern bank of Loch Lomond.

Today, the dominant tree species of the semi-natural woodlands is oak which generally forms a high canopy with occasional breaks due to clearings (Figure 1.5). Towards the northern end of the Loch, ash (*Fraxinus excelsior*) is also a dominant canopy species. The shrub layer comprises birch, rowan (*Sorbus aucuparia*), holly (*Ilex aquifolium*), hazel and hawthorn (*Crataegus monogyna*) and varies from being poorly (Figure 1.6) to reasonably developed (Figure 1.7). Invasive rhododendron (*Rhododendron ponticum*) is widespread over some sections of the woodland. In damper areas, notably along streamsides, significant amounts of alder occur. The dominance of alder along with hazel and hawthorn, also increase relative to oak higher on the slopes of the Comer and Inversnaid woodlands (Figure 1.8). The ground flora consists of typical acid woodland grasses and herbs with more neutral species occurring in the northerly woodlands. Some areas are dominated by bracken (*Pteridium aquilinum*) (Figure 1.5) and less grazed areas have large amounts of bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*) (Figure 1.7).

The coniferous plantations provide a more uniform habitat comprising dense, unthinned, even-aged stands of one or a few tree species and little if any ground cover (Figure 1.9). Spruce (*Picea* spp.) has been most frequently planted, but there are also large areas with larch (*Larix* spp.), pine (*Pinus* spp.) and Douglas fir (*Pseudodtsuga menziesii*). Small areas of western hemlock (*Tsuga heterophylla*) have also been planted. Occasional scattered spindly birch and rowan trees occur among the conifers as well as standing dead trees (snags). Within the Forestry Commission woodlands a few small patches of non-native broad-leaved woodland of beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*) were also present in 1998, though these had been felled by 2000.

Powerline corridors, rides and forest roads create breaks in the woodland cover. These vary in width from less than 10m to over 60m. The vegetation along the edge of the forest roads and in the rides and powerline corridors consists of either grass with scattered willow, birch, broom (*Sarothamnus scoparius*) and gorse (*Ulex europaea*) and occasionally rhododendron, or dense bracken. Areas of clearfell provide wider breaks in the woodland cover. The occurrence of these is increasing in accordance with the Forestry Commission management plan for the site (Mike Steward, pers. comm.). Scattered birch and rowan are left behind when the conifers are felled (Figure 1.3). On the very fertile lower sites that were felled and fenced to exclude deer, in the early 1990s natural regeneration of birch and rowan has been very dense and there is a well-developed field layer of bramble (*Rubus fruticosus* agg.), grasses and herbs (Figure 1.10). Unfenced sites on less fertile soils have however shown no regeneration, and planting with grazing control is being carried out (Figure 1.11).

### 1.3.1.2 Achray Forest and Loch Ard Forest

Both Achray Forest and Loch Ard Forest are owned by the Forestry Commission and contain habitat similar to that seen at East Loch Lomond. Patches of semi-natural oak woodland are embedded in a matrix of dense conifer plantations broken by forest roads, powerline corridors and areas of clearfell. The main difference lies in the greater diversity of ages of blocks of conifers with most development stages between new plantation to mature forest being represented.

**Figure 1. 2: The East Loch Lomond study site in 1998 looking towards Ross Wood. Semi-natural broad-leaved woodland extended along the lochside and lay adjacent to extensive conifer plantation within which patches of clearfell were starting to appear.**

**Figure 1. 3: The East Loch Lomond study site in 2000 looking towards Ross Wood. Felled areas within the conifers were becoming more extensive. The foreground shows how broad-leaved trees within the conifers were left behind once conifers were removed.**

**Figure 1. 4: Semi-natural woodland on Comer Estate at East Loch Lomond. The woodland borders onto grazed grassland and heathland.**

**Figure 1. 5: High canopy semi-natural oak woodland in Ptarmigan wood at East Loch Lomond. The ground layer is heavily dominated by bracken.**

**Figure 1. 6: Semi-natural oak woodland on Comer Estate, East Loch Lomond. Heavy grazing has led to the lack of a shrub layer and a poorly developed grassy ground layer. Although deer fencing has been put up this has been poorly maintained.**

**Figure 1. 7: Semi-natural woodland in Ross Wood, East Loch Lomond. Grazing pressure is low in Ross Wood leading to reasonable shrub development and a good ground cover of heather and bilberry. Ross Wood was under planted with conifers in the 1950s, but these had largely been removed by 2000. This photograph was taken in 1998. A sample point can be seen in the foreground.**

**Figure 1. 8: Alder dominated woodland with a well developed ground layer at Inversnaid, East Loch Lomond.**

**Figure 1. 9: Typical unthinned conifer plantation with no ground vegetation or shrub layer developed at East Loch Lomond.**

**Figure 1. 10: Dense regeneration of birch and rowan in an exclosure on fertile soil at East Loch Lomond. The field layer consists of bramble, grasses and herbs.**

**Figure 1. 11: New planting in an area of clearfell at East Loch Lomond in 2000. Tree tubes have been used outside exclosures to protect the new trees from grazing and browsing.**

### *1.3.2 The Central Scotland Forest*

The Central Scotland Forest (CSF) is the name given to the area covering 160,000ha that lies between Edinburgh and Glasgow (Figure 1.12). It includes the whole of West Lothian, North Lanarkshire and Falkirk and parts of South Lanarkshire and East Dunbartonshire Council areas. Not all of the CSF is actually forest. Only approximately 12.5% of this area is covered with woodland of various types, over half of which (60% - an area of about 10,000ha) is conifer plantation. The rest of the woodland consists of mixed plantations, farm woodlands and shelterbelts, recreation and amenity woodlands, community and urban woodlands and native semi-natural woodland (McPhillimy and Stiven, 1998).

There are a large number of different landowners for the CSF woodlands. The Forestry Commission who planted them in the 1960's, 70's and 80's owns most of the conifer plantations. Public sector bodies are responsible for most of the remainder of the larger CSF woods. These include the local authorities, West of Scotland Water, Scottish Coal, Health Trusts, and conservation bodies such as The Woodland Trust and the Scottish Wildlife Trust. Private estates such as Hopetoun also own quite large areas of woodland. However 65% of the CSF area is under agriculture so many of the smaller woods are owned by farmers. This includes some semi-natural woodlands, most of which are less than five hectares in size (McPhillimy and Stiven, 1998).

Central Scotland is a highly populated area so there are considerable pressures on the woodland from competing land uses. Woodland has been lost to urban and

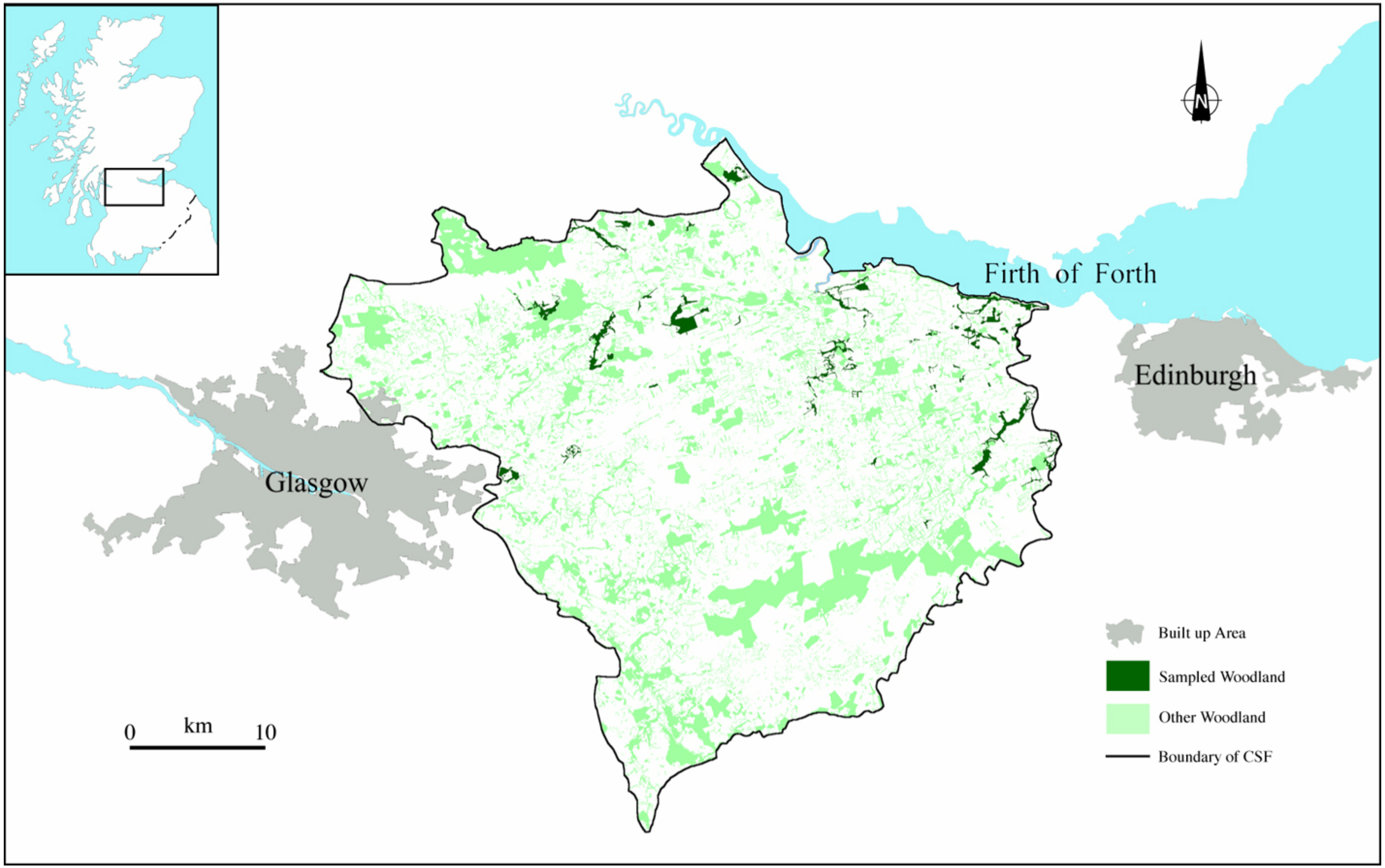

Figure 1. 12: A map showing the extent of the Central Scotland Forest. The location of the forest within Scotland is also shown.

industrial developments and agriculture, especially over the last few centuries, resulting in a highly fragmented native woodland resource (McPhillimy and Stiven, 1998). As at Loch Lomond, native woodlands were felled to meet timber demands for the two World Wars, and subsequently timber production has been concentrated in conifer plantations which have expanded in the area. Urbanisation has also increased significantly. For example, in Central Scotland the built area expanded by 48% between 1940 and 1970 (SNH, 1993). There are also spoil heaps (bings) and other derelict areas resulting from past industry. Some mining activity continues today. Agricultural intensification has resulted in a loss of hedgerows, and many of the remaining semi-natural woodlands are over-mature with limited regeneration.

#### 1.3.2.1 Woodlands sampled within the CSF

A total of 62 separate woodland blocks were sampled within the CSF. These were all located within the West Lothian, Falkirk and North Lanarkshire Council areas (Figure 1.13). Woodland patch size ranged from 0.14ha to 302ha with a median patch size of 9.79ha and a total area of approximately 2300ha. The majority of the woodlands were in private ownership on farms or estates. However a proportion was owned by the various Councils and by the Scottish Wildlife Trust (SWT). The woodlands lay in a matrix of agricultural (Figure 1.14), old industry (Figure 1.15), recreational (Figure 1.16) and urban (Figure 1.17) land uses.

Woodland communities were not sampled in proportion to their occurrence within the CSF. Site selection was constrained to woods for which ownership details were available and access permission could be obtained. The woodlands sampled were predominantly broad-leaved with a semi-natural component. Three general woodland categories can be identified within the sampled woods (after Perkins, 1998): wet willow-birch woodland (Figure 1.17); mesotrophic ash-elm woodland (Figure 1.18); and mesotrophic oak-ash woodland (Figure 1.19). Although some of the woods had a planted coniferous element, notably of spruce, larch and pine species, pure conifer plantations were not sampled. Non-native species (exotics) were common in many of the woodlands. The most frequently encountered non-native tree species were beech (Figure 1.20) and sycamore (Figure 1.21), however other non-native species present included lime (*Tilia x vulgaris*), horse chestnut (*Aesculus hippocastanum*) and sweet chestnut (*Castanea sativa*).

The majority of the sampled woods were mature and a significant number contained over-mature trees. Standing dead trees, generally of elm (*Ulmus* spp.) were a common feature. Where woodlands were enclosed or less accessible (for example, along the steep banks of watercourses) the growth of saplings and young trees was good and there was a well developed ground layer of tall herbs and grass (Figure 1.19). Rhododendron, when present, tended to dominate the shrub layer and bracken was widespread in the ground layer of some woods. However, the majority of the woodlands were unenclosed or only partially enclosed and many of the farm woods were open to domestic grazing. In these cases there was little sapling growth and grassland communities dominated the ground layer (Figure 1.21). A small sample (four sites) of newly regenerating woodland was also included. These woodlands were developing on derelict land often on old spoil heaps (bings) and near urban areas (Figure 1.15 and 1.17)

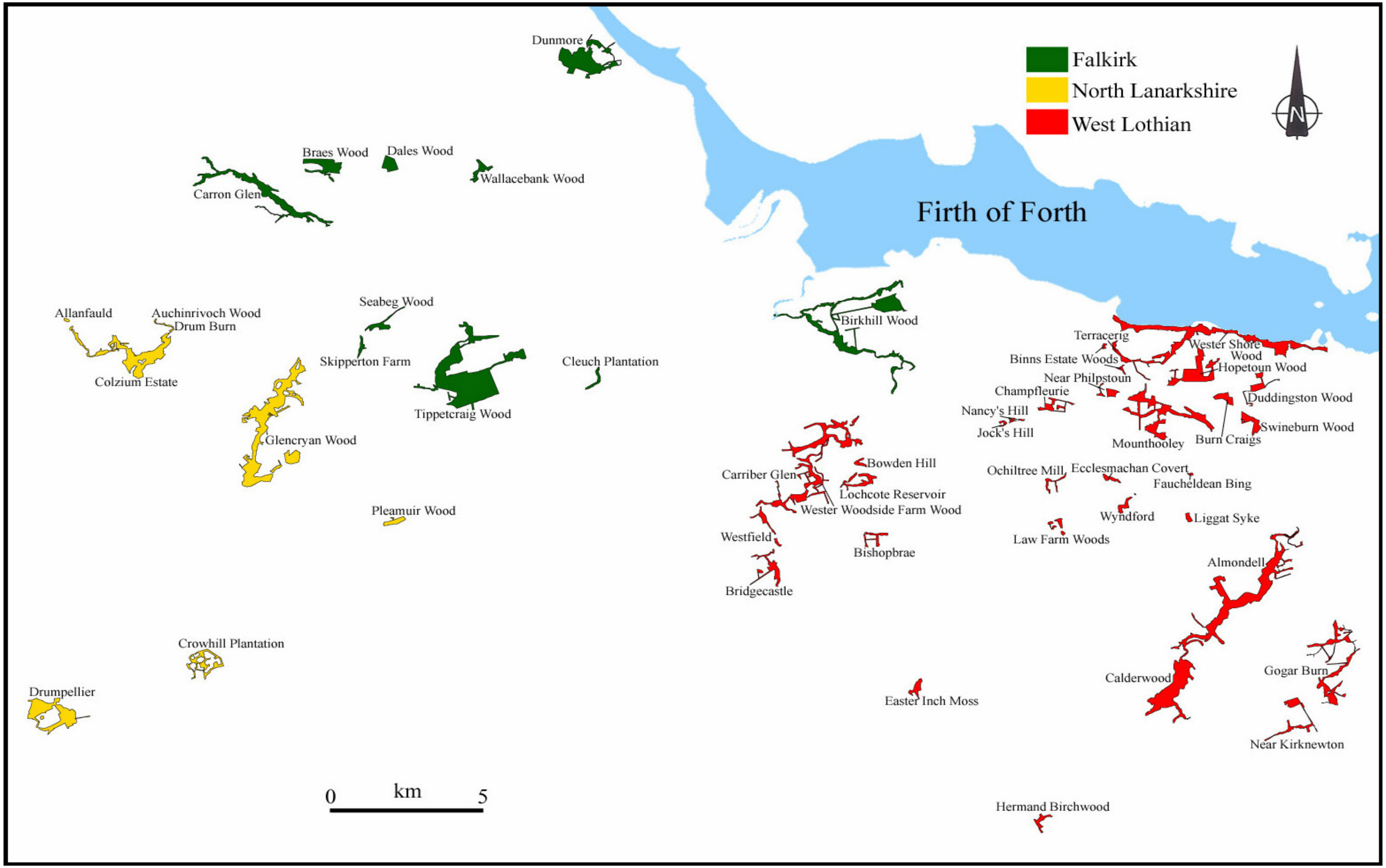

**Figure 1. 13: A map showing the CSF woodlands sampled within Falkirk, North Lanarkshire and West Lothian.**

**Figure 1. 14: Jocks Hill Wood at Parkley Place Farm near Linlithgow, West Lothian. Woodlands often form small discrete blocks in an agricultural matrix within the Central Scotland Forest.**

**Figure 1. 15: Faucheldean bing near Linlithgow, West Lothian. Bings are common remnants of old industry within the CSF and some of them have woodland developing on them.**

**Figure 1. 16: Wallacebank Wood near Larbert, Falkirk. Woodlands often occur on and around golf courses in the CSF.**

**Figure 1. 17: Liggat Syke wet willow-birch woodland near Broxburn, West Lothian. A large portion of the CSF area is urban and there are numerous community and urban woodlands in the area.**

**Figure 1. 18: Cleuch Plantation near Falkirk. This is a typical example of mesotrophic ash-elm woodland within the CSF.**

**Figure 1. 19: Calderwood near Mid-Calder, West Lothian. This is a typical example of mesotrophic oak-ash woodland occurring along a river.**

**Figure 1. 20: A stand of over mature beech within Hermand Birchwood near West Calder, West Lothian. The field layer beneath the beech is poorly developed.**

**Figure 1. 21: Sycamore plantation within Drumpellier Woodland near Coatbridge, North Lanarkshire. The woodland is open to cattle grazing which restricts shrub development and has led to the development of a grass dominated field layer.**

A LIFE II survey of the woods carried out by the Central Scotland Countryside Trust (CSCT) in 1997-1998, found that only seven of the woods sampled in this study were optimally maintained (Perkins, 1998). These included those managed as wildlife reserves. Of the remainder three were classified as partially destroyed and the rest were all sub-optimal. Many of these were declining in condition. The main threats to the woodland come from browsing and grazing, and the spread of exotics and weedy species. Near urban areas there are additional problems of vandalism, and fly tipping.

## 1.4 Woodland Management

Over the past decade there has been an increasing realisation of the social and environmental benefits of native woodlands. This is reflected in a range of policies operating from national down to local level. Relevant policies include the Policy for Sustainable Forestry, (HMSO, 1994a) from which the UK Forest Standard is developed, and the UK Biodiversity Action Plan (HMSO, 1994b) as well as a range of rural development policies. At local level, Forest Strategies are included in local authority Structure Plans, and local Biodiversity Action Plans have been formulated to implement the national policy. Although differing in their specific focus, these policies all promote the expansion and more careful management of our native woodlands. It is this framework which has facilitated the development of the management initiatives at both the East Loch Lomond and Central Scotland study sites.

### *1.4.1 Woodland management at East Loch Lomond*

The Forestry Commission is responsible for implementing government forestry policy in Scotland. As such it has a responsibility to protect and expand the woodland resource and to improve their biodiversity and landscape value. In order to achieve this, Scotland is divided into Forest Districts and a Strategic Plan has been developed by the Forestry Commission for each district. East Loch Lomond comes within the Cowal and the Trossachs Forest District. Within the Strategic Plan for this area the management programme for East Loch Lomond will be an important component in achieving the Commissions' targets for expanding native woodland in Scotland.

The study area also lies within the newly established Loch Lomond and the Trossachs National Park, more than a quarter of which consists of woodland and forest habitat (The National Park Authority, 2003). Of this woodland, a significant amount is owned by the Forestry Commission which consequently has an important role to play in fulfilling the aims of the National Park. The four aims of the National Park are:

- To conserve and enhance the natural and cultural heritage of the area.
- To promote sustainable use of the natural resources of the area.
- To promote understanding and enjoyment (including enjoyment in the form of recreation) of the special qualities of the area by the public.
- To promote sustainable economic and social development of the areas communities.

(The National Park Authority, 2003)

Conservation of the native woodlands and expanding their coverage will contribute towards fulfilling these aims.

Within the Forestry Commission area at East Loch Lomond, the native woodlands are being restored through a programme of conifer clearfelling, and the removal of non-native rhododendron. The management of grazing animals is facilitating natural regeneration of native trees and shrubs. This is involving the use of exclosure fencing and a significantly increased culling programme with due consideration of safety and animal welfare standards. Where regeneration potential is limited, planting of native species is being carried out. The long-term aim for this site is the restoration of the whole of the east bank of the loch to semi-natural native woodland and the complete removal of non-native species. This should be achieved by around 2050. In the short term conifer removal will increase woodland fragmentation at this site. Ultimately, as regeneration progresses and new planting becomes established, this trend should be reversed.

### *1.4.2 The Central Scotland Forest Initiative*

The CSF Initiative was launched in 1989 to aid the regeneration of Scotland's Central Belt. A large number of formal partners are involved in the Initiative, which has been led by The Central Scotland Countryside Trust (CSCT, now renamed the Central Scotland Forest Trust CSFT) since 1995. These include the Scottish Executive, the Forestry Commission, Scottish Natural Heritage (SNH), various Local Enterprise Companies (LECs) and the Local Authorities. Informal partners including voluntary sector organisations such as the RSPB and SWT, and farmers and landowners also play an important role.

The main aims of the Initiative are:

1. To improve the ecological value, by;
    - Enhancing and expanding the semi-natural native woodland resource and,
    - Extending native woodland habitat through the management of other native woodlands and creating new native woodland
2. To develop the social benefits of new and existing native woods through broad public involvement in community woodlands, and by creating native woods for amenity and land reclamation.

(CSCT, 1995)

The Initiative has a target of doubling the total wooded area within the CSF, an increase of 17,000ha, by 2015. Half of this increase is expected to consist of commercial conifer plantations. The remainder of the increase should comprise broad-leaved woodland for general amenity, as farm and community woods and for conservation.

A range of grants is available to encourage the expansion and more sensitive management of woodlands in the CSF. For example, Woodland Improvement Grants, the Farm Woodland Premium Scheme and the Forestry Commission's Central Scotland Forest and Grampian Challenge Fund. The CSF Initiative is providing dividends. For example, during 1999-2000, CSCT was involved in the creation of 220ha of new woodland within the CSF (CSCT, 2001). The net result of the CSF initiative will be a less fragmented woodland resource covering a greater landscape area.

# Chapter 2: An investigation of the gap crossing decisions of woodland birds

## 2.1 Introduction

Habitat fragmentation includes a loss of habitat area and an increasing distance between remaining habitat patches (Opdam *et al.*, 1994; Andrén, 1994). The point at which the effects of fragmentation become greater than that purely due to loss of habitat area will be species specific, depending on dispersal ability (Andrén, 1994; With, 1997). Since birds are highly vagile, it has been suggested that they may be insensitive to habitat fragmentation (Ambuel and Temple, 1983; Margules *et al.*, 1982). Physically they are able to cross gaps of many kilometres in width and energetic cost differentials will be relatively small for gaps of up to one kilometre. However, a psychological reluctance may restrict the gap widths that they are willing to cross (Kirby, 1995; Grubb and Doherty, 1999) possibly due to the birds' perception of predation risk (Lima and Dill, 1990).

There is increasing evidence that habitat connectivity is important for at least some bird species. Patterns of birds in the landscape found in numerous observational studies suggest that wood size and isolation are important determinants of bird species richness (for example, Howe, 1984; Opdam *et al.*, 1984; Opdam *et al.*, 1985; McCollin, 1993; Léscourret and Genard, 1994). Likewise studies based on ringing recoveries and the tracking of marked birds found that fragmentation can inhibit dispersal (Matthysen *et al.*, 1995; Haas, 1995; Grubb and Doherty, 1999). Two categories of gap crossing can be distinguished from these studies. Dispersal gap crossing occurs between natal areas and breeding sites, is relatively rare, and often covers larger distances than the second type of gap crossing - home range gap crossing. Home range gap crossing connects habitat patches within the home range of a bird.

Unfortunately data on willingness to cross gaps is unavailable for most bird species, since it is difficult to collect. This information is essential for a proper understanding of the scale at which individual species perceive the landscape and hence for identifying when they will become sensitive to fragmentation. Such information is especially pertinent since grants are increasingly targeted to areas where they will develop Forest Habitat Networks. New woodland contributes to a Forest Habitat Network where it enlarges and reconnects existing native woodland remnants at either a macro or micro scale (Forestry Commission, 2001). Current guidelines recommend at least 30% woodland cover in the landscape beyond which diminishing returns in ecological benefits occur. Gaps between woodland fragments of up to 30m are acceptable, but an acknowledgement is made that the gap widths which species will cross is crucial (Forestry Commission, 2001). Only limited experimental data apparently underlies these guidelines.

A new technique for studying bird dispersal was suggested by Desrochers and Hannon (1997). They used the playback of avian mobbing calls to elicit directional movements in birds so they could study their response to different habitat configurations in the landscape. Birds carry out mobbing in response to a stationary predator. Several characteristics of mobbing behaviour make it an effective tool for studying bird movement through the landscape. Firstly, mobbing calls cover a wide frequency range making them highly locatable (Shalter and Schleidt, 1977; Klump and Shalter, 1984). Secondly calls will attract both conspecifics and heterospecifics (Curio, 1978; Vieth *et al.*, 1980; Hurd, 1996; Desrochers and Hannon, 1997), possibly due to similarities in mobbing calls of different bird species (Marler, 1955). Thirdly mobbing behaviour occurs, at least in some species, all year round (for example, Hinde, 1952; Curio, 1978).

Most mobbing is carried out within an individuals' home range (Zimmermann and Curio, 1988). Studies have also found that dominant individuals, often the males, tend to mob more than less dominant individuals (Gehlbach and Leverett, 1995). Therefore it is likely that this study investigated home range gap crossing of dominant individuals.

This study used an adaptation of the methodology of Desrochers and Hannon, (1997) to study gap crossing in forest songbirds. It addressed the following questions: (1) What is the effect of narrow gaps (up to 120m) in the woodland cover on the movement of songbirds? (2) How do these effects vary with species, and are these differences related to bird morphology in any way? (3) What is the potential of the playback methodology for obtaining information on avian dispersal behaviour? Data were collected in the West of Scotland study site, however the CSF landscape structure was used to assess how gap crossing ability may influence landscape perception.

## 2.2 Method

### *2.2.1 Study Area*

The habitat was coniferous plantation with a mosaic of spruce, larch, pine and fir species at East Loch Lomond, Loch Ard Forest and Achray Forest in West Central Scotland. Patches of mature semi-natural oak woodland occurred throughout the forests. The coniferous woodland varied in age from newly replanted areas to stands of around 70 years old. The dominant tree age was around 50 years. Thinning had not been carried out so stands were dense and generally had little or no ground vegetation. Gaps in the woodland cover were created by forest roads (Figure 2.1), powerline corridors (Figure 2.2) and clearfelling (Figure 2.3). Most of these gaps were less than 200m wide, although some clearfell areas exceeded this, giving gaps of as much as one kilometre width.

**Figure 2. 1: A typical gap created by a forest road at East Loch Lomond.**

**Figure 2. 2: A typical gap in the forestry plantation at East Loch Lomond due to a powerline corridor.**

**Figure 2. 3: An area of clearfell creating a gap in the tree cover at Loch Ard Forest. This picture also shows one of the patches of semi-natural oak woodland that occurred throughout the study area plantations.**

### *2.2.2 Selection of mobbing call recording*

Recordings of great tits, robins and song thrush mobbing calls were obtained from the National Sound Archive. By looping the recordings it was possible to generate 10 minutes of calls for each of these species and these were used in trials carried out in January 1999. The recording, which elicited the greatest and most consistent response from a range of species, was of the song thrush calls. This was probably due to the superior quality of this recording. Birds are sensitive to the distortion and degradation of recordings (Richards, 1981). The song thrush recording was consequently selected for use in the playback experiments.

### *2.2.3 Playback Experiments*

Experiments were carried out between 9th February and 17th March and 11th July and 27th August 1999 and also between 6th May and 11th August 2000. The song thrush mobbing call recording was used to attract birds across gaps in the woodland cover ranging from five metres to 120m in width. Experiments were carried out under conditions of no rain or strong wind, between half an hour after sunrise and 1600 hours. By performing the experiments in a relatively uniform habitat, avoiding features such as streams (which produce additional background noise) and only collecting data under a limited range of weather conditions sound attenuation should have been relatively constant.

Upon arrival at an experimental site the playback equipment was set up in a woodland edge. This consisted of a CD player in the 1999 experiments and earlier 2000 experiments. Problems with the equipment necessitated a change to a cassette player in the later 2000 experiments. However, output volume and quality was kept the same irrespective of the equipment used. Mobbing calls were audible to the observer up to 190m across a gap and up to 160m through woodland, an audible range exceeding the widest woodland gap studied. Sites of playback experiments were at least 400m apart in the landscape. Based on the audible range of the equipment this should have been sufficient to ensure that experiments were independent. Each location was only used once within any field season.

Once the equipment was set up, a two minute settling period was allowed and was followed by a 10 minute period of observation during which a bird point count following the methodology described in Section 3.2.2 was carried out. In addition during the count any gap crossing or bird movements away from the woodland edge, were recorded. Playback was then commenced and lasted 10 minutes. Two types of experiments were performed – gap experiments and control experiments. Control experiments were important because the probability of response will decline naturally with distance due to the effects of sound attenuation and degradation on the signal. Also birds may not feel the predator poses any threat over greater distances so there would be no need to mob. The control experiments provided a measure of this natural rate of decline. In both gap and control experiments any bird moving to within five metres of the speaker was deemed to be responding. Response was unambiguous since aggressive posturing and calls from the birds almost always accompanied it.

Desrochers and Hannon (1997) identified individual birds within 10m of the woodland edge prior to starting the playback and then followed these to determine whether they responded or not. Replication of this method was attempted in this study, but proved unworkable. Individual birds could not be kept constantly in view within the dense conifer canopy. Thus the methodology had to be adapted. In gap experiments the number and species of any birds, responding at the speaker and crossing the gap was recorded. Experiments where the minimum response at the speaker was less than five birds were rejected to avoid bias. Usually there was an identifiable probable reason for this lack of response. These included a sudden deterioration in the weather conditions, loss of power in the playback equipment when new batteries were needed and the presence of an aerial predator. At least 10 valid gap crossing experiments were carried out for each 10m increment of gap width, except for the width 90-100m. Insufficient sites of this width category were available in the study area. A total of 182 gap crossing experiments were carried out, of which 138 were classed as valid.

Control experiments were designed to measure the response of the birds through woodland. Once playback commenced, the observer walked at a steady pace along the woodland edge until a stationary bird was located within the woodland. This bird was then observed for a minute. If it showed signs of directional movement towards the speakers a marker was placed opposite its original location and it was followed to see if it genuinely was approaching the speaker. Distances between the original location of control birds and the speaker were measured using the markers once the playback had finished. Birds observed once they were already moving towards the speaker were not counted. Control experiments were designed so that approximately equal lengths of observational time during the playback would be carried out at all distances between zero and 120m along the wood edge. Thus there would be an equal probability of detecting a responding bird at all distances within this distance range. A total of 123 control experiments were carried out. Data was obtained from 85 of these.

## 2.3 Data Analysis

Sufficient data for analysis was obtained for four species: chaffinch, goldcrest, coal tit and robin. Since the total number of individuals of each species gap crossing could be sensitive to the population density in the area, data was reduced to presence or absence of gap crossing for each species for both the periods before and after playback commenced. The proportion of experiments in which gap crossing occurred for each species was calculated separately for non-playback and playback time periods for 10m gap increments. It was assumed that there were no significant effects of weather, time of day or time of year. Formal testing of this assumption was not possible. However, since gap and control experiments were randomly distributed with respect to time of day and year, no systematic biases should have been introduced into the data. In addition, experiments were only carried out within a narrow band of weather conditions.

### *2.3.1 Generalized Linear Modelling*

The relationship between probability of response and gap distance was modelled for the playback experiments using generalized linear modelling with a logistic link function assuming a binomial error distribution. The explanatory power of the models was assessed using $D^2$, calculated using Equation 2.1.

$$D^2 = \frac{(null\ deviance - residual\ deviance)}{null\ deviance}$$

*Equation 2.1*

An adjusted measure of $D^2$ was calculated using an adaptation of Weisberg's, (1980) adjusted $R^2$ measure where (*n*) represents the number of observations and (*p*) represents the number of predictors including the constant in the model. This formula is given in Equation 2.2.

$$Adj\ D^2 = 1 - [(n-1)/(n-p)] \times [1 - D^2]$$

*Equation 2.2*

Data for probability of response before the playback was too sparse to allow formal modelling, so this was plotted and best-fit lines were added for illustrative purposes only.

The total number of each species responding along woodland edges was collated for 10m distance increments away from the speaker. Where more than one individual had responded simultaneously along the woodland edge this was counted as a single registration to avoid pseudoreplication since the response of one individual may influence others (Kroodsma, 1986). Poisson regression models were fitted using distance as the predictor. The count data and fitted values were then re-scaled to allow comparison of the response through woodland with that across gaps. This involved extrapolating the regression line for the gap crossing data for each species to a distance of zero metres and rescaling the control data relative to this probability of response value such that the probability of response for both gap and control were the same at zero metres.

### *2.3.2 Calculation of response indices and their relationship with morphological measures*

To facilitate comparison of gap and control responses between the four species, the difference in probability of response for a distance of 50m from the speaker was calculated. In addition, the distance at which the probability of response was effectively zero (taken as the point at which probability reached 0.05) was determined for both gap and control experiments and the difference between these distances was calculated for each species. This required extrapolation of the regression line for the gap response of the chaffinch. These measures were plotted in relation to measures of bird mass, absolute and relative measures of wing span and area, and wing loading. Although these graphs had only four data points on them they were useful to suggest hypotheses worthy of further investigation.

### *2.3.3 Calculation of Landscape Spatial Statistics*

The 10 kilometre squared area of woodland shown in Figure 2.4 was selected from the Central Scotland Forest. All woodland patches classed as open or as having a canopy cover of less than 10% were edited out before landscape metrics were calculated. This decision was based on ground truthing carried out for the woodlands in which bird counts were performed (see Chapter 4). The GIS data was digitised from aerial photographs and contained some inaccuracies. Some areas classed as open woodland were found not to be proper woodland patches at all and this is likely to apply throughout the data set. Eliminating areas classified as having low canopy cover should increase the data accuracy.

Since the whole landscape statistic exercise was only illustrative to demonstrate how gap crossing data can start to be used to interpret how different species may perceive the connectivity of a landscape, the GIS data accuracy was not really important. After editing, the landscape contained a total wooded area of 838.45ha (8.4% cover) of which 567.81ha (5.7%) was broad-leaved woodland and 270.65ha (2.7%) was coniferous or mixed broad-leaved and coniferous woodland.

The total number of patches in the landscape, the median patch size and the mean patch fractal dimensions were calculated for this area assuming non-contiguous fragments to be entirely separate entities. These values were then re-calculated for each bird species, where individual fragments were classed as connected when they were less than the maximum gap crossing distance apart. The maximum gap crossing distance was the maximum distance determined from the generalized linear models for gap crossing under playback conditions for each species. Figure 2.5 illustrates for a single initial fragment how increasing numbers of woodland fragments can be perceived as part of a single patch based on an increasing willingness to cross wider open areas. All calculations were carried out in ArcView 3.2 using Patch Analyst (Elkie *et al*., 1999). Mean patch fractal dimension is a measure of shape complexity taking a value between one and two where a higher value is indicative of greater shape complexity (McGarigal and Marks, 1994).

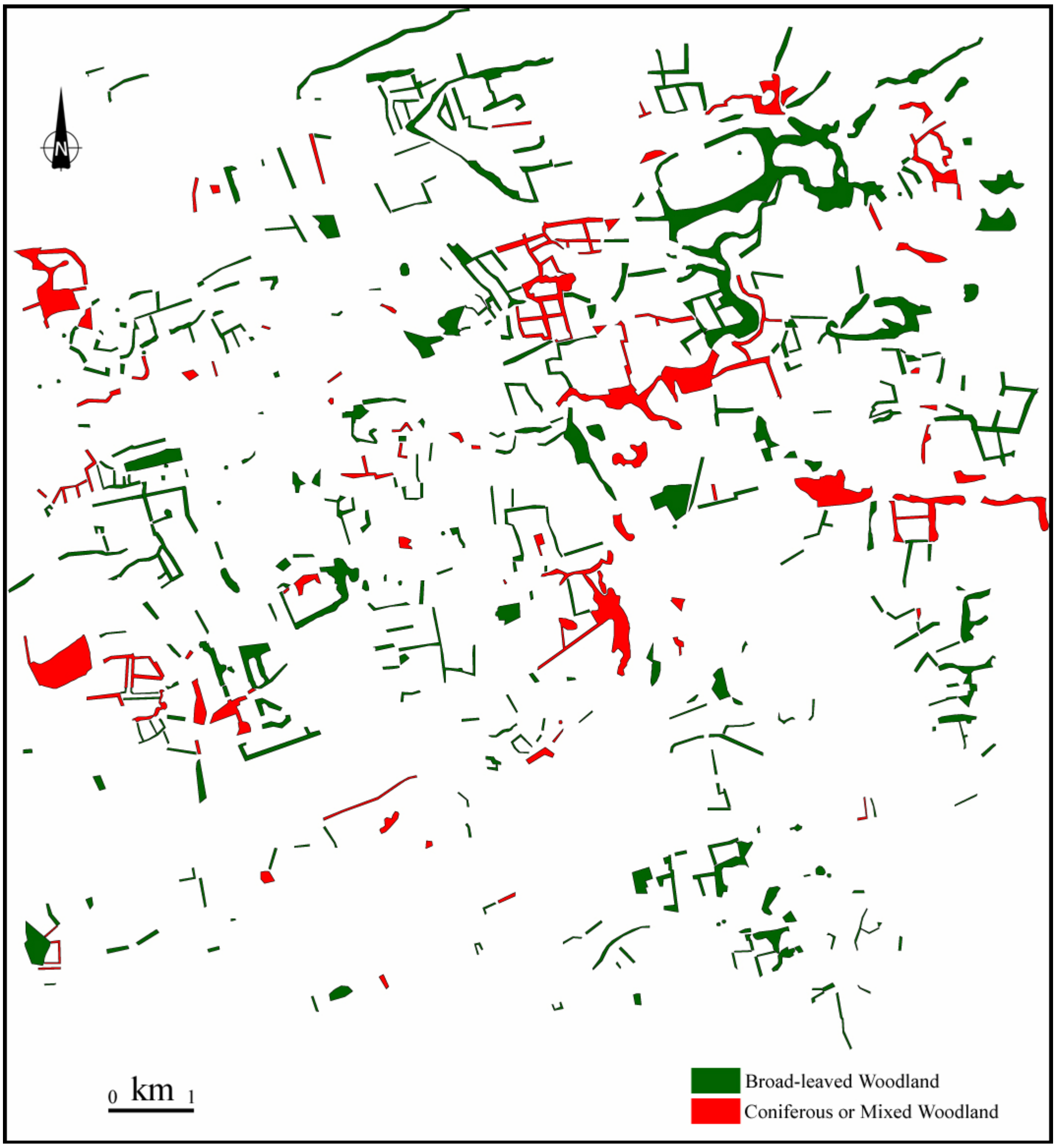

**Figure 2. 4: The 10 kilometre squared area selected from the Central Scotland Forest for calculating landscape metrics for differing gap crossing distances.**

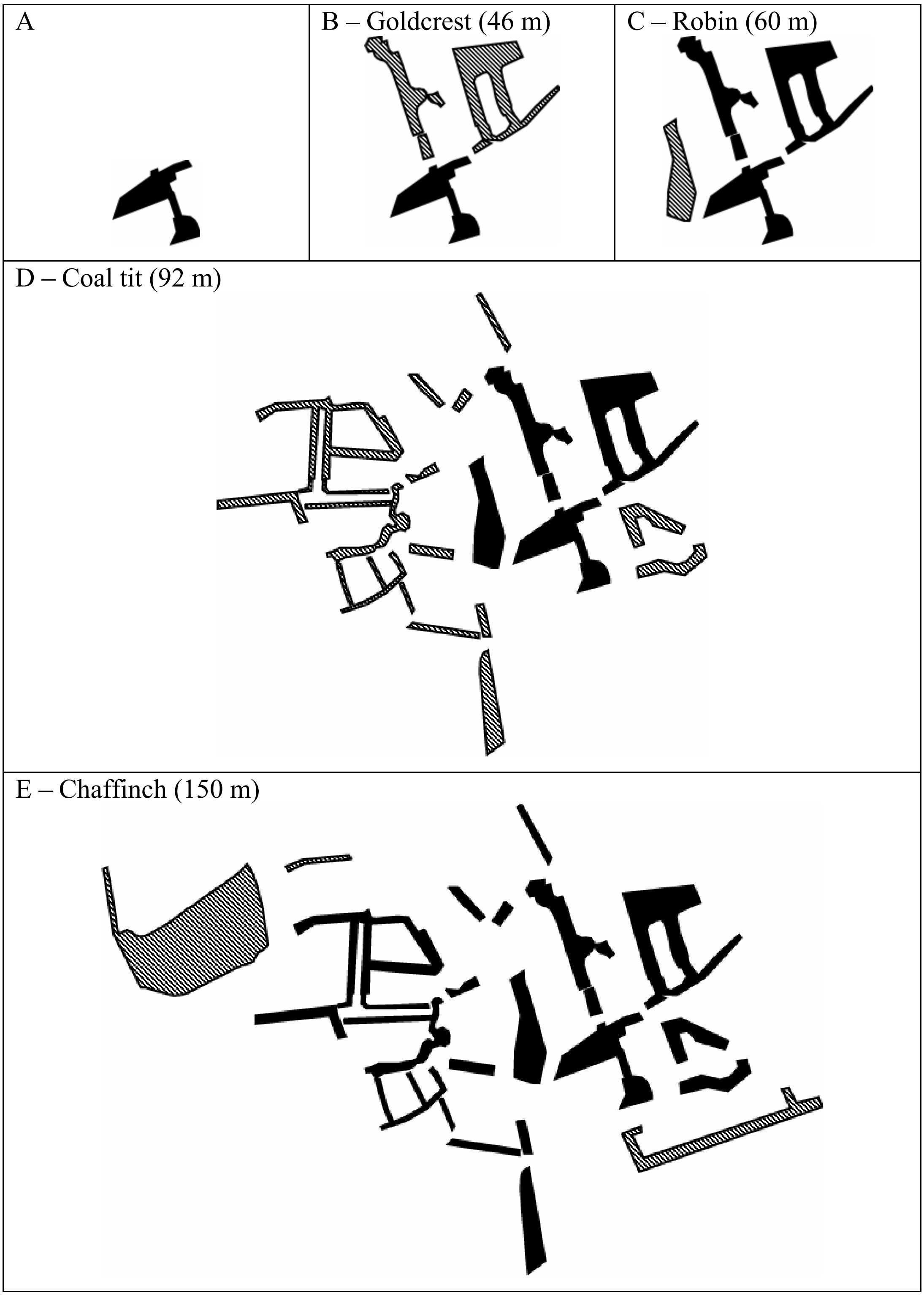

**Figure 2. 5: An illustration from the Central Scotland Forest of how landscape connectivity changes with avian willingness to cross open areas. The patch in Diagram A would be unconnected to any other patch for a bird completely unwilling to cross open areas. Diagrams B to E illustrate which additional woodland patches (distinguished by diagonal shading in each case) become connected to this initial patch as gap crossing distances increase. Gap crossing distances are given in brackets and are the maximum distance that was determined for each species studied in the playback experiments.**

Simplistic assumptions were made in the calculation of the landscape metrics. For example, it was assumed that all woodland fragments contained suitable habitat for each species and that if a fragment fell within the gap crossing range of a particular species it would be equally likely to cross to this fragment irrespective of the fragment dimensions or vegetation composition. There are various reasons why this may not be the case.

The data were collected in the Forestry Commission woodlands of the West of Scotland where birds were being attracted across gaps between large blocks of woodland, not between small fragments. Thus the results were being extrapolated from a less fragmented relatively uniform conifer dominated landscape to a more fragmented and heterogeneous landscape. This was unavoidable. Even if access could have been negotiated for sufficient sites in the Central Scotland Forest the method of data collection may not have been functional for a more fragmented landscape since greater differences in population densities are likely and this could have introduced bias.

Of the four species studied, the robin and chaffinch are ubiquitous occurring in both coniferous and broad-leaved woodland. This can be seen in the Central Scotland Forest bird count data for the robin in Chapter 4. The chaffinch was so widespread in both the Central Scotland Forest and Loch Lomond bird counts that there were insufficient absence points for it to be possible to model it using logistic regression. For these two species it is therefore reasonable to assume that all patches could be used to some degree whether they are broad-leaved, coniferous or mixed. However, the goldcrest and to a lesser degree the coal tit show a strong preference for coniferous woodland and so are less likely to use all patches in the CSF.

No account was taken of the possibility that birds may avoid fragments with particular configurations such as a large edge to interior ratio, but there are interesting possibilities for further study in this area. In addition the extent to which tree containing habitats such as gardens, facilitate dispersal, was not considered.

## 2.4 Results

### *2.4.1 Point Count results*

Because of the time span over which experiments were carried out, detailed analysis of the point count data was not valid. As is discussed in Chapter 3 song output varies with time of day and year and this can affect count results. It was not possible to restrict the period of data collection for the playback experiments as rigorously as for the data used in the empirical models of Chapter 4. Furthermore, interspecific differences in detectability (Emlen, 1971) mean that the total counts for different species are not directly comparable. However, each of the four species analysed for gap crossing behaviour represented over 10% of the total count registrations and were, along with the wren, the most frequently recorded in the bird counts (Table 2.1). This, along with the count data for Loch Lomond discussed in Chapter 4, suggest they were amongst the most abundant species in the area.

**Table 2. 1: The total number and percentage of each species recorded during point counts preceding playback experiments. The four species analysed for gap crossing behaviour are shown in bold italics.**

| Species | Number | % |
|---|---|---|
| ***Goldcrest*** | ***106*** | ***23.19*** |
| ***Robin*** | ***82*** | ***17.94*** |
| ***Coal tit*** | ***70*** | ***15.32*** |
| Wren | 67 | 14.66 |
| ***Chaffinch*** | ***47*** | ***10.28*** |
| Willow warbler | 23 | 5.03 |
| Blue tit | 19 | 4.16 |
| Treecreeper | 11 | 2.41 |
| Blackbird | 6 | 1.31 |
| Great tit | 4 | 0.88 |
| Lesser Redpoll | 4 | 0.88 |
| Siskin | 4 | 0.88 |
| Dunnock | 3 | 0.66 |
| Garden warbler | 3 | 0.66 |
| Long-tailed tit | 3 | 0.66 |
| Bullfinch | 3 | 0.66 |
| Blackcap | 1 | 0.22 |
| Greenfinch | 1 | 0.22 |
| **Total** | **457** | |

### *2.4.2 Birds in gaps under non-playback conditions*

The chaffinch was the most frequently observed of the four species crossing gaps when playback was not being used. They crossed gaps of up to 120m in width. The proportion of experiments with observed crossings for robins and coal tits was less than 0.25 for gaps of up to 10m in width. Maximum observed gap crossing distances were less than 50m for both these species (Figure 2.6). No gap crossing activity was observed for goldcrests.

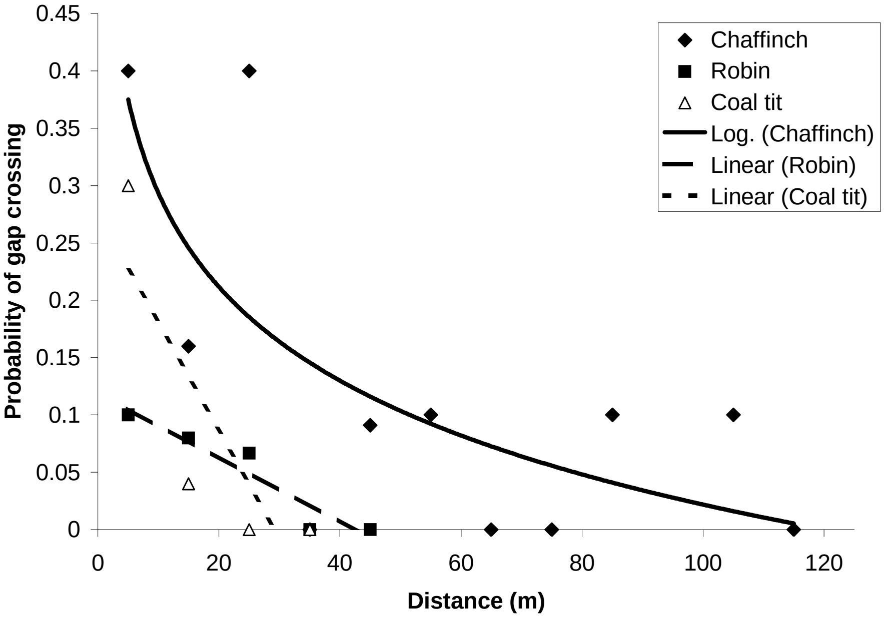

**Figure 2. 6: Probability of gap crossing for chaffinches, robins and coal tits under non-playback conditions. Fitted lines are for illustrative purposes only.**

A comparison of Figure 2.6 with Figures 2.7 to 2.9 shows that the probability of gap crossing over any distance was much lower under non-playback conditions compared with playback conditions for all species based on the data collected in the 10 minutes prior to playback. Likewise the estimated maximum distance of gap crossing was greater for playback experiments than for non-playback time periods.

Occurrences of birds within gaps when no directional movement was occurring were also recorded and these results are given in Table 2.2. As with the gap crossing result under non-playback conditions, the goldcrest was never observed away from the woodland edges. The coal tit was only very rarely observed away from the woodland edge (it was recorded away from woodland edges in less than one percent of counts, which represented only two sightings). Chaffinches and robins used gap habitats with a low frequency.

**Table 2. 2: The total number of individuals of each species making non-directional movements away from woodland edges across all point counts and the percentage of counts on which these were observed.**

| Species | Number | % |
|---|---|---|
| Robin | 28 | 10.73 |
| Chaffinch | 17 | 6.51 |
| Coal tit | 2 | 0.77 |
| Goldcrest | 0 | 0.00 |

### *2.4.3 Playback Experiments*

A total of 1555 birds of 17 different species were recorded at the speaker in the playback and control experiments (Table 2.3). This figure is likely to be an under-estimate since in control experiments the speaker was not constantly in view of the observer. Approximately 90% of recorded respondents comprised the chaffinch, coal tit, goldcrest and robin and these all responded in over 45% of valid experiments. Almost 50% of birds responding were chaffinches, which is unlikely to be directly proportional to their abundance in the environment.

The decline in probability of response with distance was significant for both gap and control experiments for the four species analysed. Distance explained over 50% of variation in response for all models except the goldcrest control model (Table 2.4). Goldcrest control data was relatively sparse, because this was the hardest of the four species to follow as it moved towards the speaker. This could explain the relatively low adjusted $D^2$ in this instance.

**Table 2. 3: The total number (Number) and percentage (%) of each species responding at the speaker for all of the playback and control experiments and the percentage of experiments on which a response occurred (% Expts). Species analysed for gap crossing behaviour are shown in bold italic.**

| Species | Number | % | % Expts |
|---|---|---|---|
| ***Chaffinch*** | ***771*** | ***49.58*** | ***87.50*** |
| ***Goldcrest*** | ***242*** | ***15.56*** | ***49.55*** |
| ***Coal tit*** | ***239*** | ***15.37*** | ***60.71*** |
| ***Robin*** | ***140*** | ***9.00*** | ***46.43*** |
| Blue tit | 43 | 2.77 | 12.05 |
| Great tit | 40 | 2.57 | 10.71 |
| Siskin | 19 | 1.22 | 6.70 |
| Jay | 10 | 0.64 | 1.79 |
| Long-tailed tit | 10 | 0.64 | 4.02 |
| Song thrush | 8 | 0.51 | 2.68 |
| Blackbird | 8 | 0.51 | 2.68 |
| Greenfinch | 7 | 0.45 | 2.23 |
| Wren | 5 | 0.32 | 2.23 |
| Mistle thrush | 3 | 0.19 | 1.34 |
| Treecreeper | 3 | 0.19 | 1.34 |
| Great spotted woodpecker | 2 | 0.13 | 0.89 |
| Willow warbler | 2 | 0.13 | 0.89 |
| **Total** | **1555** | | |

**Table 2. 4: GLM Models for gap crossing (Full Binomial Models) and control (Poisson Models) experiments for the variation in response to mobbing call playback of chaffinches, coal tits, robins and goldcrests with distance. There are 10 null and eight residual degrees of freedom in each model. *** indicates significance at $p \leq 0.001$, ** indicates significance at $p \leq 0.01$ and * indicates significance at $p \leq 0.05$.**

| Species | Gap Crossing Full Binomial Model | | Control Poisson Model | |
|---|---|---|---|---|
| Species | F | Adj. $D^2$ | F | Adj. $D^2$ |
| Chaffinch | 42.38 *** | 0.82 | 30.61 *** | 0.76 |
| Robin | 21.33 ** | 0.66 | 39.59 *** | 0.79 |
| Goldcrest | 12.85 ** | 0.54 | 7.92 * | 0.36 |
| Coal tit | 17.85 ** | 0.62 | 18.40 ** | 0.64 |

The chaffinch and the robin, the two species with the largest maximum gap crossing distances under non-playback conditions (Figure 2.6), were also more likely to respond across gaps than through woodlands for all distances studied

(Figures 2.7 and 2.8). There was no difference in probability of response for gaps and woodland for the coal tit (Figure 2.9). By contrast, the goldcrest responded more readily through woodland than across gaps for all distances (Figure 2.10). The estimated maximum gap crossing distance was greatest for the chaffinch (150m) and least for the goldcrest (46m). The results for the robin and the coal tit fell between these two extremes (Table 2.5).

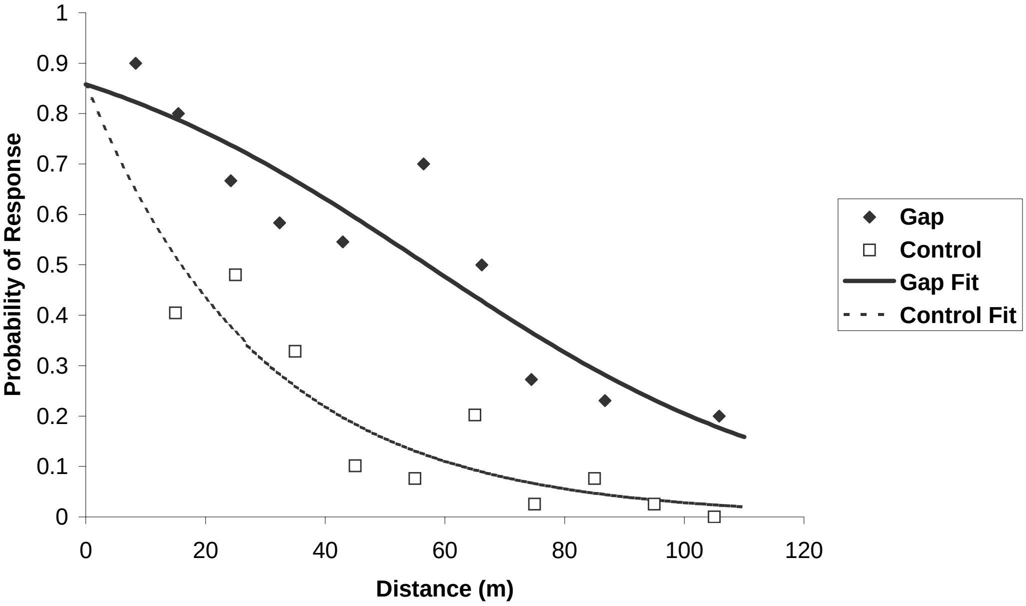

**Figure 2. 7: The effect of distance on probability of response in gap and control experiments for the chaffinch.**

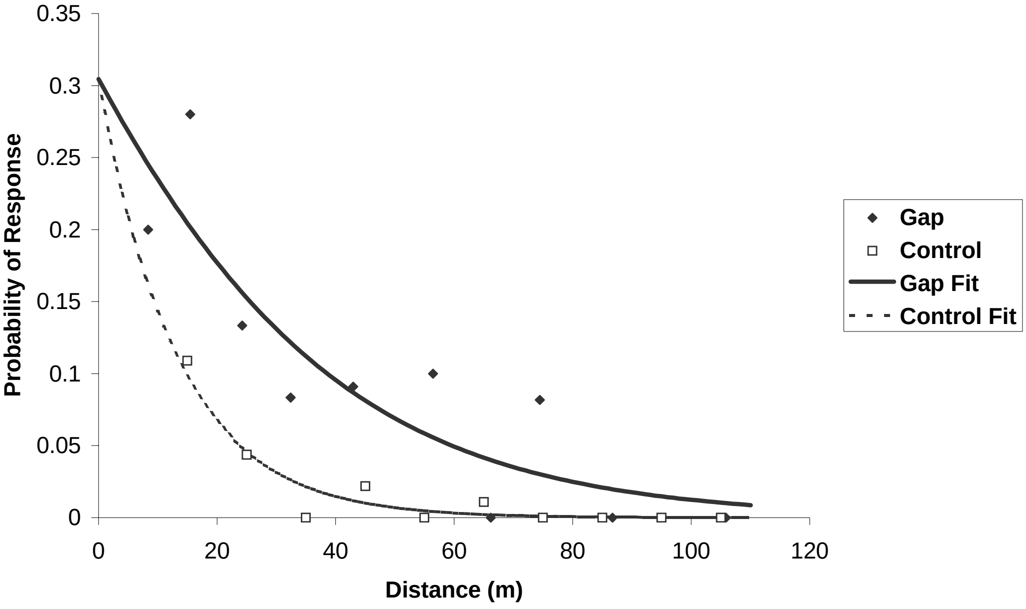

**Figure 2. 8: The effect of distance on probability of response in gap and control experiments for the robin.**

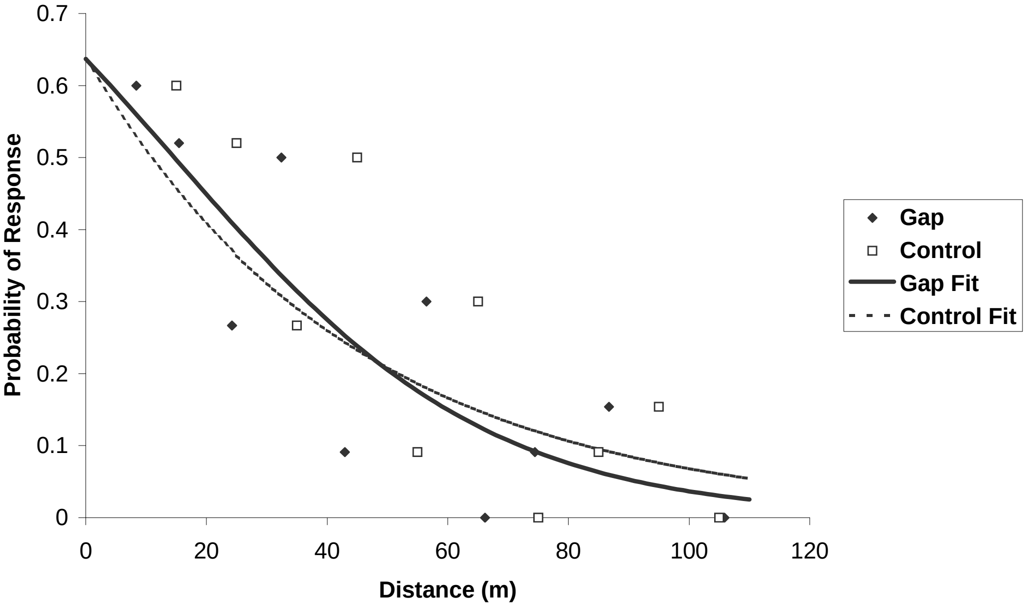

**Figure 2. 9: The effect of distance on probability of response in gap and control experiments for the coal tit.**

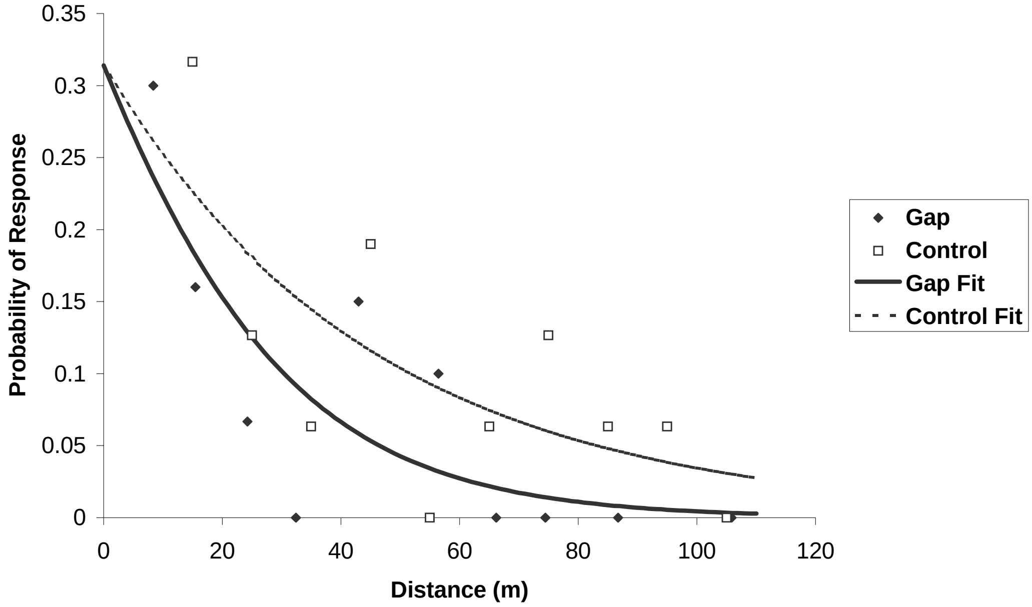

**Figure 2. 10: The effect of distance on probability of response in gap and control experiments for the goldcrest.**

**Table 2. 5: Response indices for the chaffinch, robin, coal tit and goldcrest. Predicted maximum response distances are the points at which the probability of response is 0.05.**

| Index | Species | | | |
|---|---|---|---|---|
| | Chaffinch | Robin | Coal tit | Goldcrest |
| Predicted maximum gap crossing distance (m) under playback | 150 | 60 | 92 | 46 |
| Predicted maximum woodland response distance (m) under playback | 83 | 24 | 113 | 83 |
| Difference between predicted maximum gap and woodland response distance (m) under playback | 67 | 36 | -21 | -37 |
| Predicted maximum gap crossing distance (m) with no playback | 120 | 42 | 29 | 0 |
| Difference between predicted probability of response at 50m for gap and control playback experiments | 0.399 | 0.062 | -0.003 | -0.061 |

## *2.4.4 Gap crossing behaviour in relation to bird morphology*

Although caution must be exercised when data are available for only four species, possible trends were observed in plots of response indices against two of the morphological measures given in Table 2.6. There was a positive linear trend between mass of bird and the difference in the maximum response for gap and control experiments (Figure 2.11). Likewise there was a positive curvilinear relationship between wing area and the difference in probability of response between gap and control experiments at 50m (Figure 2.12).

**Table 2. 6: Morphological measurements for the chaffinch, robin, goldcrest and coal tit. Measurements are from Pennycuick (pers. comm.) (chaffinch), Tatner and Bryant (1986) (robin) and Norberg (1979) (goldcrest and coal tit).**

| | Chaffinch | Robin | Coal tit | Goldcrest |
|---|---|---|---|---|
| Mass (g) | 22.8 | 18.6 | 9.1 | 5.9 |
| Wing span (cm) | 26.2 | 22.2 | 18.0 | 15.6 |
| Wing loading (g/cm$^2$) | 0.204 | 0.263 | 0.169 | 0.167 |
| Wing area (cm$^2$) | 111.8 | 70.8 | 53.8 | 35.4 |
| Aspect Ratio | 6.14 | 7.33 | 6.02 | 5.94 |
| Relative wing area | 0.096 | 0.072 | 0.110 | 0.100 |

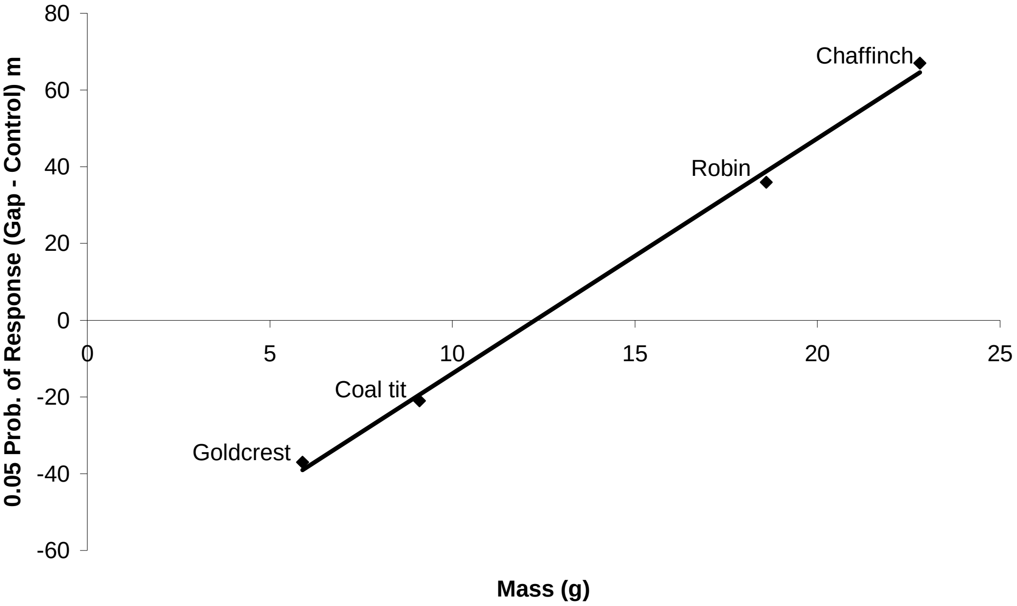

**Figure 2. 11: The relationship between bird mass and the difference in metres between the predicted gap and control distances at which the probability of response was 0.05 under playback conditions.**

**Figure 2. 12: The relationship between wing area and the difference in probability of response at a distance of 50m between gap (G) and control (C) experiments.**

### *2.4.5 Landscape Spatial Statistics*

The total number of patches, mean patch size and mean patch fractal dimension of the landscape of Figure 2.4 for the maximum gap crossing distance for each species under playback conditions, assuming all woodland fragments contribute to landscape connectivity, are given in Table 2.7. Plotting these relationships suggests that the number of patches in the landscape decreases exponentially with increasing gap crossing distance (Figure 2.13) while the median patch size and mean patch fractal dimension increase linearly with gap crossing distance (Figures 2.14 and 2.15 respectively). The scarcity of the data meant that these relationships were not formally modelled.

**Table 2. 7: Landscape spatial statistics for the goldcrest, robin, coal tit and chaffinch where all woodland fragments are assumed to contribute to landscape connectivity. Distance is the maximum gap crossing distance recorded under playback conditions; NumP is the number of patches in the landscape; MedPS is the median patch size and MPFD is the mean patch fractal dimension. Landscape metrics are defined in Section 2.3.3.**

| Species | Distance (m) | NumP | MedPS (ha) | MPFD |
|---|---|---|---|---|
| | 0 | 395 | 0.700 | 1.421 |
| Goldcrest | 46 | 241 | 0.837 | 1.426 |
| Robin | 60 | 219 | 0.877 | 1.428 |
| Coal tit | 92 | 178 | 0.894 | 1.433 |
| Chaffinch | 150 | 111 | 1.016 | 1.436 |

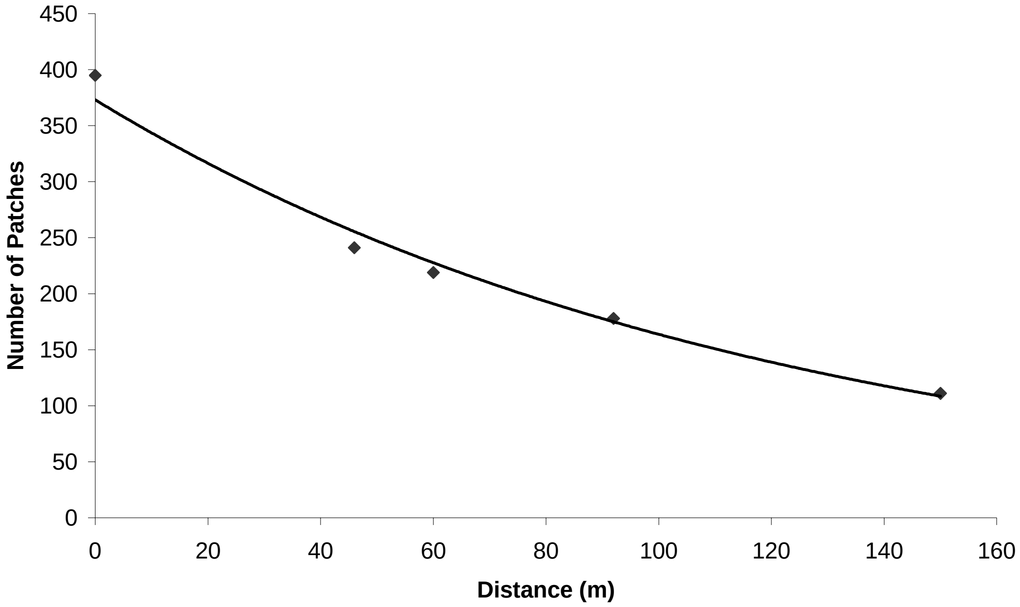

**Figure 2. 13: The change in number of patches in the landscape with maximum gap crossing distance where all woodland fragments are assumed to contribute to landscape connectivity. The fitted line is an exponential curve.**

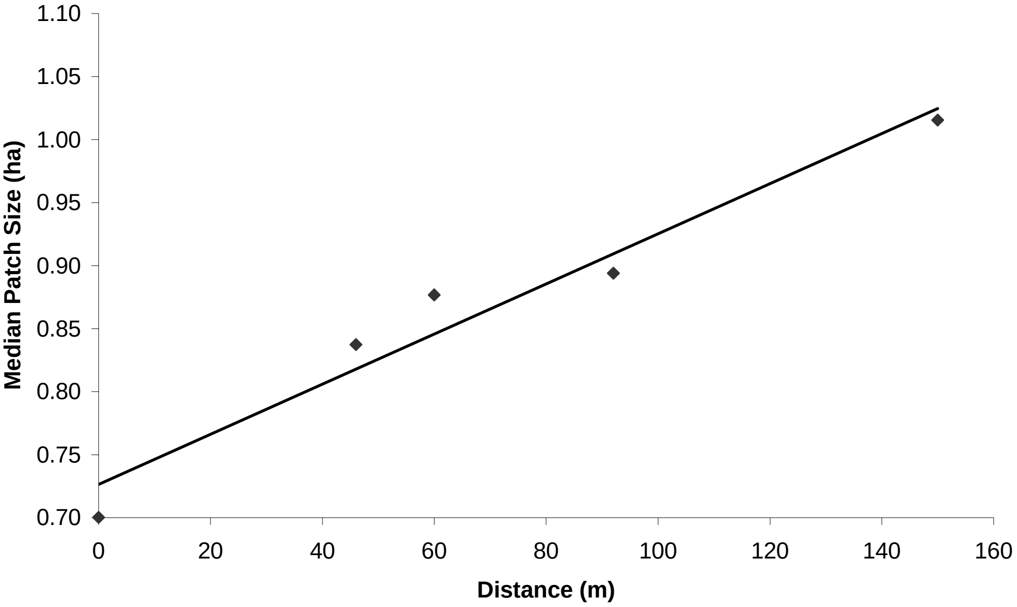

**Figure 2. 14: The relationship between median patch size in the landscape and the maximum gap crossing distance of a species where all woodland fragments are assumed to contribute to landscape connectivity.**

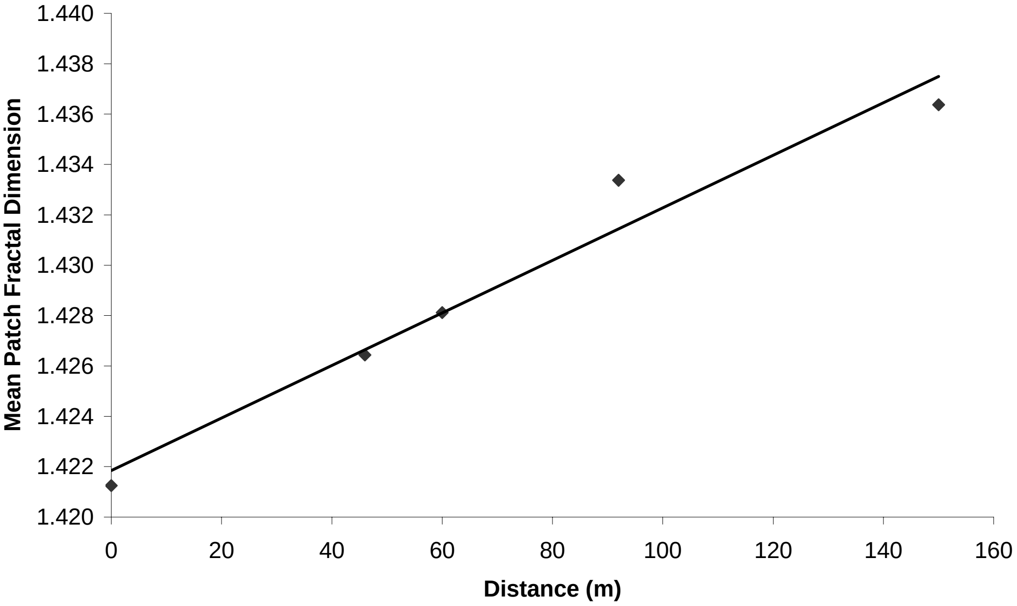

**Figure 2. 15: The relationship between mean patch fractal dimension of the landscape and the maximum gap crossing distance of a species where all woodland fragments are assumed to contribute to landscape connectivity.**

## 2.5 Discussion

### *2.5.1 Evaluation of the methodology*

This study demonstrated that a modified form of Desrochers and Hannons' (1997) mobbing call playback methodology could be used to investigate bird gap crossing behaviour in a different landscape. This was the first attempt to my knowledge, which has been made to replicate their mobbing call methodology to study gap crossing behaviour.

The main limitation to the modified method was that it was highly labour intensive requiring a lot of field work hours to collect a relatively small amount of data. Desrochers and Hannons' (1997) method was also labour intensive, but less so than the modified method. In their gap crossing experiments each playback could potentially contribute more than one observation to the data set, whereas in the modified method at least 10 playback sessions were required to generate a single data point. This required an extensive study area so that sufficient independent sites for playback were available and meant that data had to be collected over a wider time period than was desirable. Motivation to mob may vary at different times of year (Smith and Graves, 1978). This should not have biased the data however, since experiments that did not achieve a minimum level of response were discounted. Some reduction in the field work hours could be made by not measuring gap crossing response for every 10m gap increment. If sufficient gap distances were measured it would still be possible to determine the shape of the relationship between probability of gap crossing and gap distance.

### *2.5.2 Interspecific differences in gap crossing behaviour*

Clear interspecific differences existed in the willingness of woodland birds to cross gaps, supporting the argument for a species-centred approach in looking at landscape pattern (Andrén, 1994; Kirby, 1995; With, 1997; With *et al*., 1997). Of the four species studied the goldcrest was the most inhibited by breaks in the woodland cover. It was never recorded in gaps during the counts preceding playback, responded to playback much more readily through woodland than across gaps and had the shortest maximum gap crossing distance.

By contrast, there was no difference in the probability of response across gaps relative to through woodland for the coal tit, while the chaffinch and robin responded more readily across gaps than through woodland. The control data was designed to measure the decline in response with distance expected due to sound attenuation. Based on this it could be argued that no evidence was found for the coal tit of a behavioural reluctance to cross gaps of increasing width. A similar interpretation could be made for the chaffinch and the robin taking account of the fact that no correction was made for the excess sound attenuation due to the vegetation through woodland. Consequently the audible range of the playback was greater across gaps than through woodland and this could account for the difference in the response curves for these two species.

However, this interpretation of the data is unlikely to represent the whole picture. All response curves differ interspecifically, and with the exception of the coal tit, between woodland and gap intraspecifically. However audibility curves tend to be very similar between bird species, with oscines showing even less variability than non-oscines (Dooling, 1982). Furthermore, none of the curves precisely follow an estimated theoretical sound attenuation curve for the study area even allowing for a shift in the curve for different audible thresholds (Figure 2.16). In all cases the maximum gap distance was within the audible range of the observer, and human audibility thresholds are lower for all sound frequencies than those of oscine birds (Dooling, 1982). Therefore while a sound attenuation effect may account for some of the pattern in the data other factors are also likely to be important.

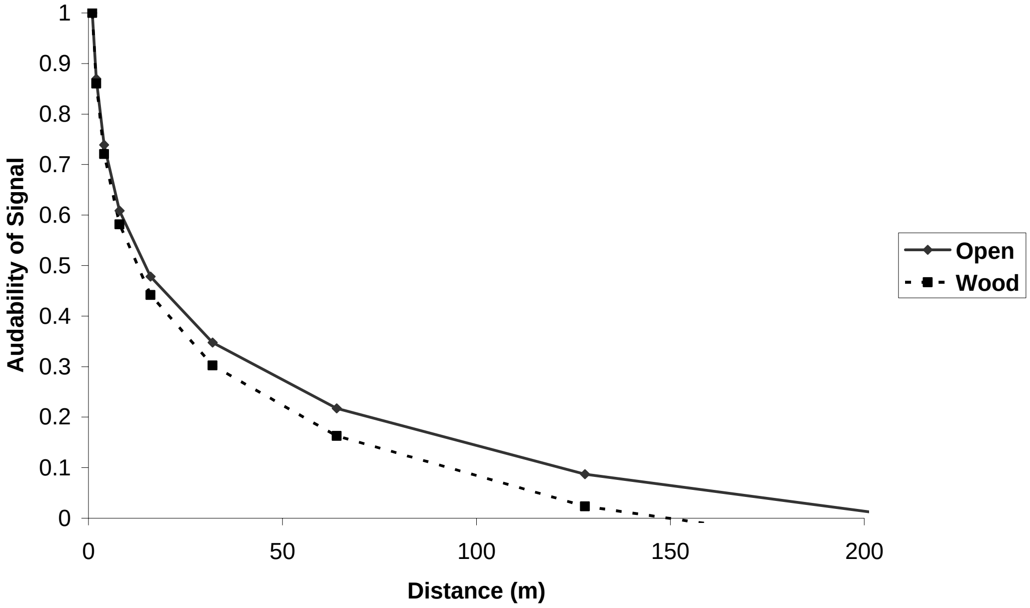

**Figure 2. 16: Theoretical sound attenuation curves for woodland and open habitat for the study area based on the maximum audible range of the signal to the observer.**

One explanation is suggested by the relationships between response indices and morphological parameters. As bird mass increased they responded less readily through woodland and more readily across gaps. Likewise as wing area increased the probability of a response across gaps relative to through woodland increased in a curvilinear way. It is possible that the larger birds with bigger wings were less manoeuvrable within woodland and better adapted to flight in a more open habitat. The coal tit and goldcrest are adapted to low speed, manoeuvrable flight that is advantageous within woodland (Norberg, 1979; Rayner, 1979). The robin and chaffinch may be able to fly faster and be more manoeuvrable in the open and these parameters determine the probability of a bird evading an aerial raptor attack (Rudebeck, 1950; Newton, 1986; Cresswell, 1993). Consequently the perceived risk of crossing wider habitat gaps may be less for robins and chaffinches. Predation risk assessment is likely to be important in gap crossing decisions for the study species since all are prey species for the sparrowhawk (Opdam, 1978; Newton and Marquiss, 1982). Falling victim to a predator eliminates future fitness potential and so should operate as a strong selective force (Lima and Dill, 1990). The effect of predator risk assessment on gap crossing behaviour could be investigated through experiments using a trained sparrowhawk to patrol gaps prior to playback of mobbing calls. The response following presence of an aerial predator in gaps could be compared with response when no predator had been present.

Additional studies would also need to be undertaken to investigate whether the hypothesis that the relative response differences between woodland and gaps relate to morphological adaptations for flight and how this affects the ability to evade a predator. Four species represents too small a sample size to have confidence in the form of the relationships. If comparable gap crossing work was carried out for other woodland species and they followed the predicted patterns, this would increase confidence in the relationships being genuine and not due to chance.

However, the strongest support could be derived from investigating species that may be expected to deviate from the relationship in predictable ways based on other morphological parameters that could affect their manoeuvrability and speed within or outwith woodland.  Examples may be found among the migrant species. All four study species were resident all year round, whereas migrants may be better adapted for long distance flights in open areas (Calmaestra and Moreno, 2001).  Similarly tail morphology can affect flight ability (Balmford *et al*., 1993; Norberg, 1995) and a species with a relatively long tail such as a long-tailed tit may have its flight ability impaired which could affect willingness to cross gaps.

### *2.5.3 Interpretation of the results in terms of Forest Habitat Networks*

It is impossible to say whether the maximum gap crossing distances recorded under playback conditions represent the true maximum gap distances which individuals are prepared to cross within their home range or whether under different motivation greater distances would be crossed.  A study carried out by McColm (1999) where food was used as an attractant indicates that willingness to move away from woodland edges does vary under different stimuli.

Mobbing is a behavioural response to the supposed presence of a predator and entails costs in terms of time and energy expenditure (Curio, 1978), and the risk of being killed or injured (Curio and Regelmann, 1985). Nevertheless the results do suggest that short counts of birds in gaps under-estimate the extent of their home range. In all cases the frequency of occurrence in gaps and the maximum distance crossed increased under playback compared with non-playback conditions. Conservation guidelines based on the gap crossing distances derived from playback experiments will at worst be slightly conservative, leading to Habitat Network designs which err on the side of caution.

The preference of the goldcrest for moving through woodland rather than across gaps suggests that Forest Habitat Networks are important for at least some bird species. The maximum gap crossing distance of this species (the one most reluctant to cross gaps) exceeded the Forestry Commission (2001) guideline of 30m as an acceptable distance between patches in a Forest Habitat Network. Thus for the four study species, a Forest Habitat Network created based on the guidelines would be perceived as connected.

The exercise in calculating landscape metrics demonstrated how gap crossing information could be used to identify how different species perceive landscape connectivity. There was an exponential decline in the number of blocks of unconnected patches in the landscape with increasing gap crossing ability. This could indicate that forest patches in the Central Scotland Forest were relatively randomly distributed, since the relationship mirrors that found by Andrén, (1994). His study demonstrated an exponential increase in the distance between patches as habitat area was reduced in a randomly patchy landscape with less than 20% habitat cover. In the CSF study area the cover was only about 8%.

If the forms of Andrén's (1994) relationships are relatively constant it would be possible to estimate habitat connectivity for any landscape for any of these species based on the percentage cover of habitat in the landscape and how patches were distributed (for example, random, aggregated or over-dispersed). Guidelines for optimal locations for additional habitat creation to bring the landscape total up to the 30% cover recommended by the Forestry Commission (2001) could also be developed.

## 2.6 Conclusion

This study has demonstrated that Desrochers and Hannons' (1997) mobbing call playback methodology could be adapted to investigate gap crossing decisions on a home range scale in a different landscape. The results demonstrate clear interspecific differences in willingness to respond across gaps relative to through woodland. Sound attenuation effects cannot completely account for these results. It is suggested that they may be explained in terms of morphological adaptations to flight and how this affects ability to evade a predator. The gap crossing results can be applied to real landscapes to gain an idea of how the perception of habitat connectivity may vary with different species. This has practical management application, especially for designing Forest Habitat Networks.

# Chapter 3: An investigation of possible sources of bias in the bird point count methodology

## 3.1 Introduction

A key question addressed in this thesis asks what the relative importance of habitat and landscape pattern parameters are as determinants of avian population distributions in fragmented woodlands. A fundamental requirement for answering this question was a suitable method to record avian population distributions in such a way that they could be readily related to habitat and landscape measurements within statistical models. The point count method is a popular technique in this context (for example Askins *et al*., 1987; Blake and Karr, 1987; Bolger *et al*., 1997). This method has the advantage of being less labour intensive than alternative methods such as territory mapping, making it easier to obtain a wider spatial coverage with the data (Gibbons *et al*., 1996). In addition, habitat measurements can be readily associated with each point count, and hence the occurrence of different bird species (Bibby *et al*., 1992). The location of each count can also be identified within a Geographical Information System, facilitating measurements of the landscape in relation to the counts.

The point count method involves a stationary observer counting birds for a fixed time period at locations spread throughout the study habitat. However, the precise details of the method differ between studies. Counts vary in terms of their duration, the length of settling period prior to the count and the time of day at which birds are counted. They also vary in the distance between sample points, the number of counts carried out per point, the use of distance estimates for birds recorded and the range of prevailing weather conditions in which counts are performed (Verner, 1985).

Numerous studies have investigated the impact of varying different count parameters on the results (for example O'Connor and Hicks, 1980; O’Connor, 1980; Best, 1981; Granholme, 1983; Fuller and Langslow, 1984). The conclusions from these studies were used to formulate a sampling method suitable for meeting the objective of this study. The precise methodological details were constrained by the number of fieldwork hours available, given that all work had to be completed by a single observer. In addition, it was desirable for the level of detail collected to be comparable with a pre-existing RSPB data set for Comer Estate (10 points) and the RSPB Reserve (20 points).

The aim of this chapter is to test for any biases in the bird count data collected, and to identify how the impact of these biases could be minimised during data analysis. Specifically the objectives were: (1) to identify the effects of observer, count length and the use of a fixed count radius versus an unlimited count radius; (2) to identify possible biases due to time and weather effects at the time of the counts; (3) to assess the adequacy of two counts only per sample point for determining variations in abundance, distribution and species richness. Answering these questions defines the limitations which must be imposed on subsequent analysis of the East Loch Lomond and Central Scotland Forest bird data.

## 3.2 Field Methodology

The data used to evaluate the bird count methodology came solely from the East Loch Lomond study site. Bird counts were carried out at this site during 1998 and 2000. In addition, a time series of RSPB data was available back to 1987 for 20 sample points and back to 1989 for 10 sample points. It was assumed that conclusions derived from this data would also be applicable to the Central Scotland Forest data.

### *3.2.1 Sample Design*

A total of 170 new sample points were established in the East Loch Lomond woodlands during 1998. Geometric considerations for point location meant that a purely random sample design was not possible. Therefore points were located at each intersect of a randomly orientated grid. Where habitat boundaries necessitated deviation from the pre-defined design, consistent rules were followed for locating the sample point at the nearest acceptable position to the intersect point. This also applied to points that fell along streams. Streams were not avoided because they were often the location of semi-natural broad-leaved woodland of relevance to the management aims of the Forestry Commission for East Loch Lomond. However, where the noise of the water significantly affected the ability to hear birds, the point was moved a small distance away from the streamside.

All sample points were at least 150-200m apart, a distance sufficient to guarantee point independence for a range of woodland birds, but not too great as to make travelling between points overly time consuming (Blondel *et al*., 1981; Morrison *et al*., 1981; Hutto *et al*., 1986; Bibby *et al*., 1992). Likewise, all points were at least 50m from a habitat edge. However, it was not always possible to avoid placing a point less than 50m from an internal linear break in the woodland cover. These gaps never exceeded 20m width and the same habitat type was always present on either side of the gap. The 30 RSPB sample points were incorporated into the sample design giving a total of 200 sample points. However, there was no control over their positioning and a minority were less than 50m from a habitat edge.

Habitats were defined subjectively based on vegetation homogeneity for the purpose of positioning points away from habitat edges. Habitats were not necessarily of a pure broad-leaved or coniferous character where the mosaic of stands was more fine-grained than a 50m resolution. This was justifiable since at this resolution birds would experience a mixed habitat within their territories. However, to ensure that habitat measurements accurately characterised the habitat present, in these cases care was taken to ensure that some of both the broad-leaved and coniferous stands fell within the 20m radius circle used for the habitat measurements described in Section 4.2.5.

Sample points were established in blocks of ten points (19 blocks) or five points (two blocks). One block of points was then sampled on each fieldwork morning. During 1998 one of the blocks containing 10 sample points, designated ‘Block F’ was used to collect control data for evaluating the count methodology. In 2000 the control data were collected using points one and two from a block of 10 points designated ‘Block L’. The RSPB dataset incorporated three study blocks of 10 points each ‘Inversnaid North’, ‘Inversnaid South’ and ‘Comer’.

### *3.2.2 Bird Count Methodology*

Upon arrival at a sample point a two minute settling period was allowed to avoid bias due to any disturbance caused while locating the point. The bird count then involved counting all birds seen and heard over a fixed time period, within specified counting bands around the sample point. In the RSPB data, counts lasted for five minutes only and birds were counted within the bands of 0-20m and an unlimited count radius. By contrast, in 1998 and 2000 counts lasted 10 minutes with registrations for the first and second five minutes of the count period being differentiated. An additional count radius of 20-50m was also included in the data. Although counts employed in different studies have ranged in duration from 2-20 minutes (Scott and Ramsey, 1981), counts of five to ten minutes are now generally considered adequate. Studies suggest that the majority of individuals will have been counted during this time and additional recording time increases the risk of double counting and reduces time available for other independent counts (Dawson, 1981; Morrison *et al*., 1981; Fuller and Langslow, 1984).

In each case bird counts were carried out between late April and the end of June or the beginning of July. This coincided with the breeding season of a wide range of woodland songbirds. Counts were always completed before 11.00 hours BST (British Summer Time), though the first count for the RSPB dataset was often not commenced until a couple of hours after sunrise. All 1998 and 2000 sampling started 20 minutes to half an hour after sunrise. Counts were generally avoided during strong wind (greater than 11km per hour), during light to heavy precipitation, when visibility was obscured due to fog, and under conditions of extreme temperature (less than seven degrees celsius or greater than 24$^{o}$C) (after Verner, 1985). However, if conditions deteriorated after the start of sampling, counts were usually continued and there was not always time to repeat these counts at a later date.

### *3.2.3 The RSPB Dataset*

The RSPB dataset consisted of bird point counts carried out at 30 sample points spread throughout the semi-natural woodland of the Inversnaid RSPB Reserve and the neighbouring Comer Estate. Counts were carried out from the year in which the points were established (1987 for Inversnaid North and Inversnaid South study blocks, and 1989 for Comer study block) through to the year 2000, with no counts in 1997. In most years, each point was counted twice. The year 1994 was an exception when no second count was carried out at any of the points.

Three different observers carried out the point counts, using identical methods (MT, 1987-1994; WRB, 1995-1996; HPC, 1998-2000). There was no overlap between observers and years, and no control counts carried out simultaneously by all three observers were feasible. Habitat measurements made at each point in the year in which it was established and in 1998, suggested that habitat had remained constant throughout the time period with the exception of rhododendron clearance in the early 1990's. This only affected one sample point (Comer 1). Data on rainfall, temperature, cloud cover and visibility on the day of each count and the day preceding each count, were obtained from the Meteorological Office for Helensburgh weather station.

Detailed meteorological data was not available for the study site. The Helensburgh weather station, between 14-30km away from the study site, was the closest station for which a relatively complete set of measurements were available. Meteorological conditions are also affected by altitude. The Helensburgh weather station was at 96m above mean sea level (msl) while the Loch Lomond study site ranged in altitude between 20-400m above msl.

### *3.2.4 Block L Control Data*

The first two points of Sample Block L (points L1 and L2) were used as controls to investigate the effect of weather, time of day and year parameters on counts and to look at the sample effort required to determine bird distributions adequately. Point L1 was in an area of broad-leaved woodland approximately 200m from point L2, located in coniferous woodland. Thus it was possible to move between these two points in a short time. During the 2000 field season sampling was carried out at these points on six mornings, spread evenly throughout the sample period. A total of 10 counts were performed on each of these mornings alternating between the two sample points, giving five counts at each point spread over the typical sample period. This gave datasets for broad-leaved and coniferous woodland where habitat was constant between counts, and time of day, year and weather varied.

### *3.2.5 Block F Control Data*

Study Block F consisted of 10 sample points covering the range of habitat variation present in the study area. Thus it included semi-natural broad-leaved woodland (five points), coniferous woodland (one point), mixed woodland (one point), coniferous clearfell (one point), and young broad-leaved regeneration (two points). Additional variation was incorporated through presence or absence of exclosure fences. The Block F points were counted six times evenly spaced throughout the 1998 field season.

## 3.3 Data Analysis

### *3.3.1 Investigation of the effects of time, weather and observer on bird count data*

The datasets used to investigate effects of time and weather on bird counts were the RSPB dataset from 1987-2000 and the Block L control data gathered in 2000. In addition the RSPB dataset was used to consider the effect which different observers can have on count totals. Analysis of the RSPB dataset considered species individually whereas the Block L analysis looked at species richness.

### 3.3.1.1 Analysis of the RSPB Dataset

Based on field evidence, habitat was assumed to be constant throughout the time span of the data. Hence it was reasonable to suppose that any differences within individual sample points or blocks of points, could be accounted for by time parameters, weather conditions around the time of the count or observer.

The data were analysed using generalised linear or generalised additive modelling (GLM or GAM) (McCullagh and Nelder, 1989; Hastie and Tibshirani, 1990) depending on the shape of the relationships identified between the response and predictor variables. Two sets of models were constructed. Firstly, the response was the total number of individuals of each species counted on each sample day. A Poisson distribution with log link was assumed in these instances. Secondly the proportion of points at which each species had been present in a sample block on each sample day was calculated. This gave responses potentially ranging from zero to one for each species and a full binomial models with logit link were fitted.

Models were constructed using forward stepwise selection, with variables retained where they were significant at the 0.05 level or smaller. Up to four regression splines were fitted for each variable. Adjusted $D^2$ was used as a measure of overall fit of the model, calculated using Equations 2.1 and 2.2. Equation 2.2 can be adapted for GLM or GAMs by making (*p*) the number of parameters in the model rather than the number of variables including the constant (see Guisan and Zimmermann, 2000).

The predictors were Meteorological Office data including temperature, visibility and windiness measures recorded at Helensburgh at 09.00 hours GMT on the day of the count and the day preceding the count. Sample days with incomplete weather data were omitted from the analysis, giving a sample size of 48. Year and day were included as potential predictors where year one was 1987, and day one was 29th April in each sample year. Thus the day variable was defined strictly by the calendar, not taking account of variations in the timing of the bird season in each year, since this information was unavailable. Precise time of day information for each count was largely unavailable, and was in any case confounded by grouping data by study block. Sample block and observer were included as factors. Table 3.1 gives a summary definition of variables included in the final models.

**Table 3. 1: Definition of variables included in the GLM and GAM Models for the RSPB data. Weather variables were measured at 09.00 hours GMT at Helensburgh Weather Station.**

| Variable | Definition |
|---|---|
| BlockID | Factor variable differentiating the three study blocks |
| Observer | Factor variable identifying the individual who performed the counts |
| Year | Year of count where year 1 was 1987 |
| Days | Day of count where day 1 was 29th April |
| WindSpeed1 | Wind speed (knots) on the day of the count |
| Cloud1 | Estimated cloud cover on the day of the count |
| Min1 | Minimum temperature ($^oC$) on the day of the count |
| Min2 | Minimum temperature ($^oC$) on the day preceding the count |

Models were validated using six fold cross-validation (Fielding and Bell, 1997). To evaluate the predictive power of the models Spearman rank correlation was carried out between the predicted and observed values (Pearce and Ferrier, 2001). Rank correlation coefficients were obtained for predictions based on both the full and the cross-validated model in each case.

Response curves were constructed for each parameter in each model. Each curve was constructed by predicting the model response while varying the parameter of interest through the full range of conditions in the data set. All other variables in the model were held constant at their mean values.

### 3.3.1.2 Analysis of the Block L Control data

Analysis of Variance was carried out on the Block L control data to look at whether species richness recorded on a count varied with time of day, year or weather. Data used was 10 minute count data with a 50m restricted count radius. A 50m count radius was used so that the habitat incorporated in the count was purely broad-leaved (Point L1) or purely coniferous (Point L2). This could not be guaranteed for an unlimited count radius because the boundary between the broad-leaved and coniferous woodland fell between the two points, within a distance of 200m. Weather variables included measures of cloud cover, brightness, windiness, temperature and rainfall. These were estimated (percent cloud cover) or measured on simple rating scales in the field at the start of each count (see Table 3.2). Time of day was recorded as minutes after sunrise. Data from the Meteorological Office for Helensburgh were also used as predictors (see Table 3.1 for definitions of variables).

**Table 3. 2: Definition of ratings used for assessing the prevailing conditions at the start of the count.**

| Rating | Prevailing Conditions | | | |
|---|---|---|---|---|
| | **Brightness** | **Windiness** | **Temperature** | **Rainfall** |
| 1 | Dull | No wind | Cold | No rain |
| 2 | Moderately dull | Very slight wind | Cool | Slight rain in the air |
| 3 | Moderately bright | Slight wind | Mild | Light rain |
| 4 | Bright | Moderate wind | Warm | Moderate rain |

## *3.3.2 Investigation of the effects of sample effort on bird count data*

The Block L and Block F datasets were used to investigate the effects of sample effort on count data. Both datasets were used to determine the probability of detecting individual species based on two counts. In addition the Block L data was used to investigate the effects of different numbers of counts on estimates of species richness.

### 3.3.2.1 Analysis of the Block L Control data

To investigate the relationship between sample effort and species richness, species accumulation curves were constructed for each sample point against increasing sample effort, where sample effort was defined as increasing numbers of counts per point. Separate curves were drawn for the five different times of day at which counts were carried out at each point. Mean species richness was calculated for different numbers of counts per point (one to six) using all possible combinations of the individual counts. For two and three counts, combinations were constrained by the fact that the sample period was divided such that a count from each time period needed to be incorporated in the final species richness tally. This constraint did not exist for four or five counts where data collected would inevitably span a large extent of the field season.

Since two counts per point was the maximum achievable based on field work hours available, the effect which this sample effort had on detection probabilities was given additional consideration for each species. Using all possible combinations of two counts, probabilities for detecting individual species were determined based on periods of different duration (five minutes or 10 minutes) and for different areas (50m restricted or unlimited radius). If a species was recorded as present on every possible combination of two counts for a given time of day, it had a detection probability of one at that point and was being recorded with complete consistency. A species absent on all counts at a point would have a detection probability of zero. Probabilities between zero and one represented species not being detected with complete consistency. In some cases a species may be using the habitat, but fail to be detected on all counts. Conversely a species may simply be a transient, not actually using the habitat.

### 3.3.2.2 Analysis of the Block F Control data

The Block F data were less well suited to an investigation of both time and weather effects because time of day and habitat varied simultaneously. Consequently they were only used to give a further look at the probability of detecting individual species based on two counts for a wider range of habitat variation. All possible combinations of two counts were produced, where one count was constrained to come from the first half and one count from the second half of the field season. The overall probability of detecting each species at each sample point was then calculated. The difference between detection probabilities for an unlimited count radius and 50m restricted count radius at each point for 10 minute counts was calculated. Also, the difference between 10 minute and five minute counts for a 50m restricted radius was determined.

To give an overall measure of the probability of detecting species across all of the habitats in the study area the mean probability of detecting each species was calculated for 10 minute counts with a 50m restricted count radius. Data both for Block F and the two Block L points were included in the calculation of the mean. Two means were counted, firstly including all of the probabilities and secondly excluding data where the probability of detection at the individual point was less than 0.5. This second calculation of the mean makes the assumption that where the detection rate is very low, these individuals are transients rather than actually using the habitat. However, it is impossible to test this assumption.

## 3.4 Results

### *3.4.1 Effects of time, weather and observer on bird count data*

#### 3.4.1.1 GLM and GAM models for the RSPB Dataset

The results of the GLM and GAM models assuming a Poisson distribution are given in Table 3.3. These models investigated the effects of time, weather conditions and observer on numbers of individuals counted for each bird species.

Species that occurred with very low frequency could not be modelled without violation of the modelling assumptions. This included the spotted flycatcher, long-tailed tit, lesser redpoll and blackbird. These models have consequently been disregarded. In addition none of the variables were significant for the robin or redstart.

The models for the great tit and the coal tit explained relatively low levels of variation and had adjusted $D^2$ values of less than 0.25. All other models had adjusted $D^2$ values of over 0.35 with the highest explained variation for the treecreeper and willow warbler. With the exception of the great tit the correlation coefficient between the observed and predicted values was over 0.65. In all cases the rank correlation was lower for the cross-validated models. The greatest declines in the coefficients between full and cross-validated models occurred for the great tit, siskin and coal tit.

The factor variable differentiating the three study blocks (BlockID) was the most frequently significant variable in the models. It was only not significant for the great tit, tree pipit, wren and coal tit. Year was significant for six species, though the pattern of change differed greatly between species (Table 3.3 and Figures 3.1 and 3.2). The magnitude of annual fluctuations was greatest for the blue tit, wren and chaffinch with overall rises in numbers for the chaffinch and blue tit and a steady decline for the wren (Figure 3.2). Observer was significant for five species.

**Table 3. 3: GLM and GAM models assuming a Poisson distribution for bird count data in relation to observer, timing of count and weather parameters around the time of the count. Models are additive for all species except the wood warbler, treecreeper and wren. The evaluation includes the Adjusted $D^2$ (Adj. $D^2$) and Spearman correlation coefficients (Correlation) for the association between observed and predicted results for the full model (N=1) and the cross-validated model (N=6). The variable 'Min' represents 'Min1' in the wood warbler and siskin models and 'Min2' in the blue tit model. Full descriptions of the variables in the models are given in Table 3.1. There are 47 degrees of freedom (df) in the null model for each species. The significance of variables in the models is indicated as follows: * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$.**

| Species | Variables | | | | | | | | | | | | | | Evaluation | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BlockID | | Observer | | Year | | Days | | Min | | Cloud1 | | Wind.Speed1 | | Correlation | | |
| | df | F | df | F | df | F | df | F | df | F | df | F | df | F | N = 1 | N = 6 | **Adj. $D^2$** |
| Garden warbler | 2.01 | 6.48 ** | | | | | 3.97 | 6.47 *** | | | | | | | 0.73 | 0.60 | **0.36** |
| Pied flycatcher | 2.00 | 30.80 *** | | | | | 4.00 | 6.48 *** | | | | | | | 0.89 | 0.80 | **0.44** |
| Great tit | | | | | | | 4.00 | 2.92 * | | | | | | | 0.44 | 0.19 | **0.13** |
| Tree Pipit | | | 1.99 | 5.24 ** | | | 4.09 | 6.35 *** | | | | | | | 0.72 | 0.65 | **0.46** |
| Willow warbler | 2.01 | 23.14 *** | 1.99 | 7.24 ** | | | 4.02 | 6.76 *** | | | | | | | 0.86 | 0.76 | **0.62** |
| Wood warbler | 2.00 | 7.33 ** | 2.00 | 9.85 *** | | | | | 1.00 | 7.63 ** | | | 1.00 | 11.98 *** | 0.71 | 0.55 | **0.44** |
| Treecreeper | 2.00 | 4.49 * | 2.00 | 47.56 *** | | | | | | | | | | | 0.89 | 0.86 | **0.68** |
| Wren | | | 2.00 | 33.77 *** | 1.00 | 15.77 *** | | | | | | | | | 0.78 | 0.74 | **0.59** |
| Chaffinch | 1.99 | 6.21 ** | | | 3.99 | 7.67 *** | | | | | | | | | 0.72 | 0.63 | **0.41** |
| Blue tit | 2.03 | 7.47 ** | | | 3.98 | 11.07 *** | | | 4.00 | 4.38 ** | | | | | 0.88 | 0.79 | **0.63** |
| Siskin | 2.05 | 12.66 *** | | | 4.00 | 10.70 *** | | | 4.01 | 5.74 *** | | | | | 0.84 | 0.50 | **0.55** |
| Song thrush | 2.06 | 12.12 *** | | | 4.02 | 4.96 ** | | | | | | | | | 0.70 | 0.54 | **0.40** |
| Coal tit | | | | | 3.98 | 2.70 * | | | | | 3.98 | 3.54 * | | | 0.66 | 0.46 | **0.22** |

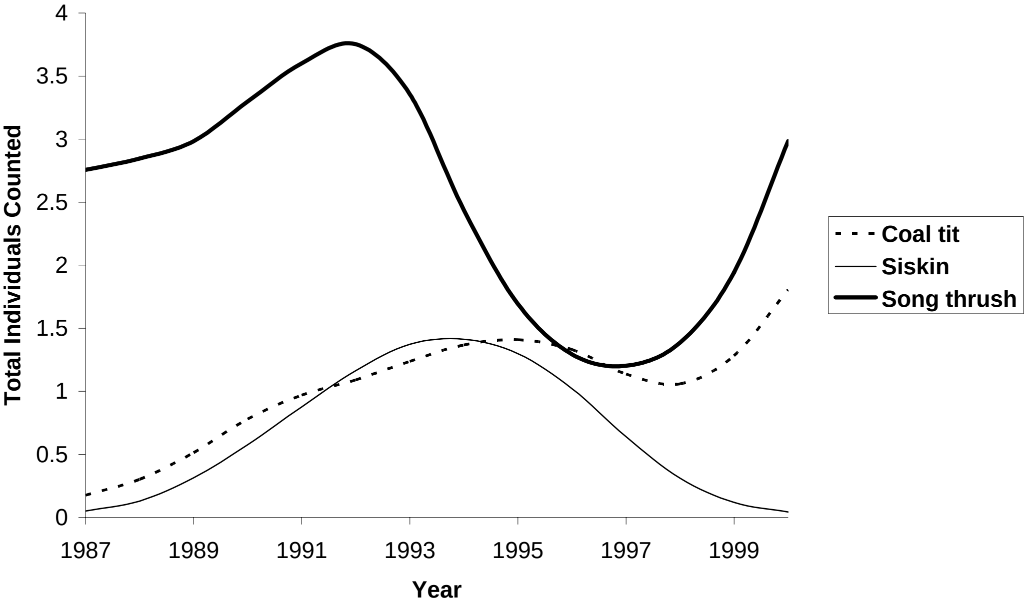

**Figure 3. 1: Response curves for numbers of coal tit, siskin and song thrush in relation to year of count derived from generalized additive models of the RSPB dataset.**

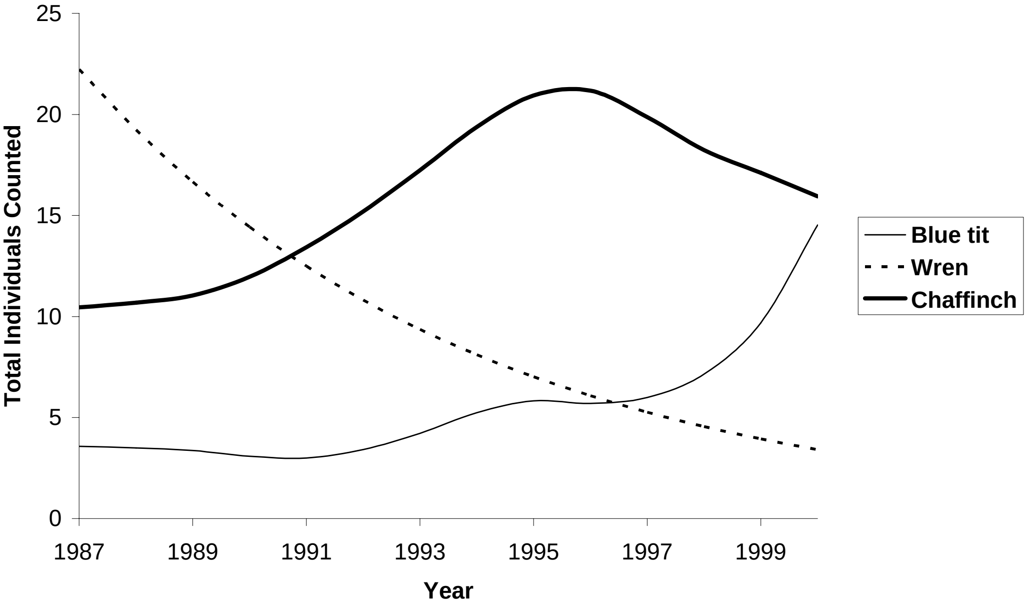

**Figure 3. 2: Response curves for numbers of blue tits, wrens and chaffinches in relation to year of count derived from generalized additive and linear models of the RSPB dataset.**

The day of the count explained significant variation for five species (Table 3.3). There were three main patterns of response to this variable (Figure 3.3). The tree pipit and willow warbler showed a strong steady decrease in numbers counted over the first half of the field seasons. They then had a very small second peak in numbers counted over the second half of the count seasons. By contrast, the great tit and garden warbler initially showed an increase in numbers counted during the first half of the field seasons. This increase peaked earlier in the great tit than in the willow warbler. There was then a decline in the numbers counted until towards the end of the count period where a second peak was reached. The pied flycatcher response curve showed the numbers being counted rising to a plateau around the middle of the count period, and then declining again.

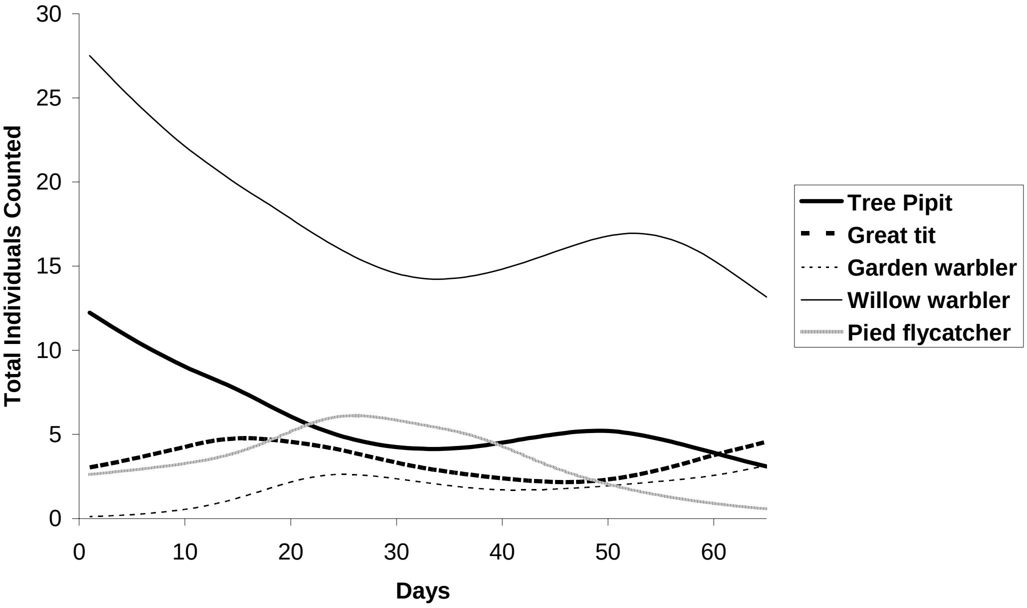

**Figure 3. 3: Response curves for numbers of tree pipits, great tits garden warblers, willow warblers and pied flycatchers counted in relation to day of count derived from generalized additive models of the RSPB dataset.**

Weather variables were significant in models for only five of the species (Table 3.3). The most commonly significant variable was minimum temperature either on the day of the count (siskin and wood warbler, Figure 3.4), or the day preceding the count (blue tit, Figure 3.5). With the exception of the siskin model the relationship between minimum temperature and numbers of birds counted was negative, though not necessarily linear. The siskin showed a different pattern, with a sharp rise in the number of birds counted after a minimum temperature of around 9$^{o}$C. There was a positive linear relationship between the number of wood warblers counted and wind speed on the day of the count (Figure 3.6). The number of coal tits counted initially declined rapidly with increasing cloud cover and then the relationship reached a plateau (Figure 3.7).

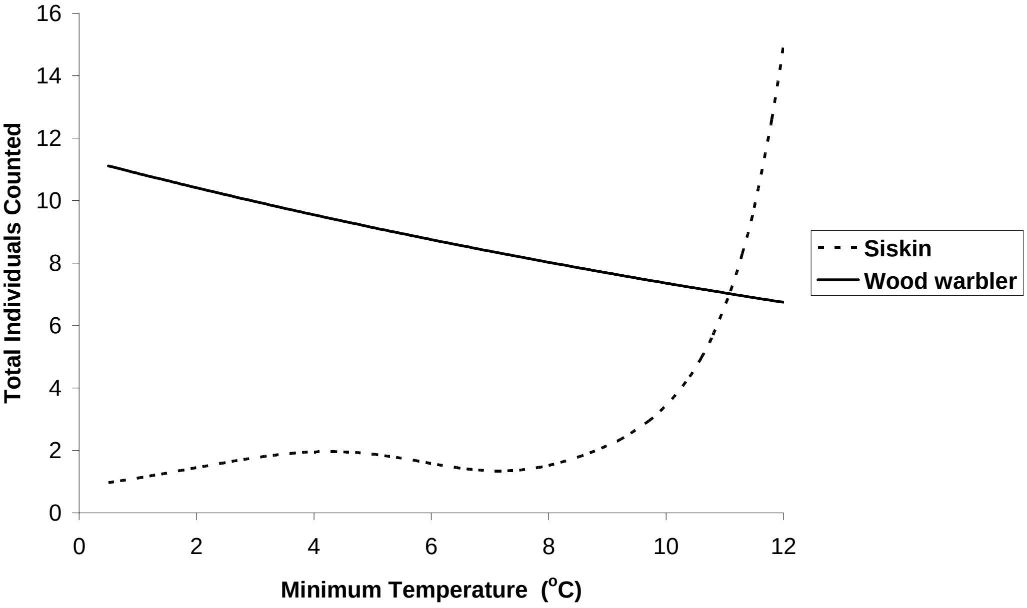

**Figure 3. 4: Response curves for numbers of siskins and wood warblers counted in relation to the minimum temperature on the day of the count (measured at 09.00 hours GMT at Helensburgh Meteorological Station) derived from GAM (siskin) and GLM (wood warbler) models of the RSPB dataset.**

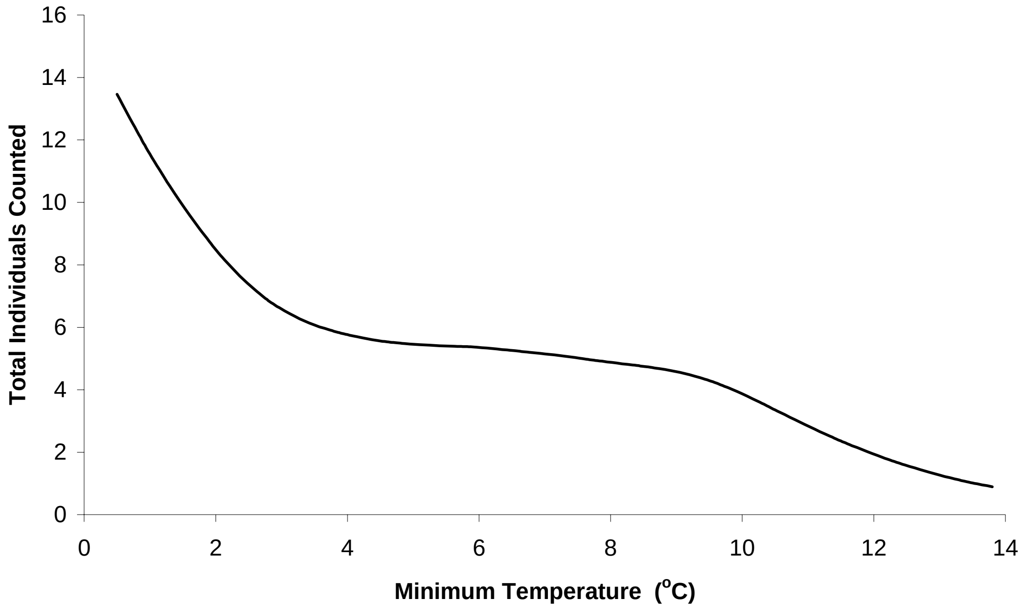

**Figure 3. 5: Response curve for numbers of blue tits counted in relation to the minimum temperature on the day preceding the count (measured at 09.00 hours GMT at Helensburgh Meteorological Station) derived from generalized additive modelling of the RSPB dataset.**

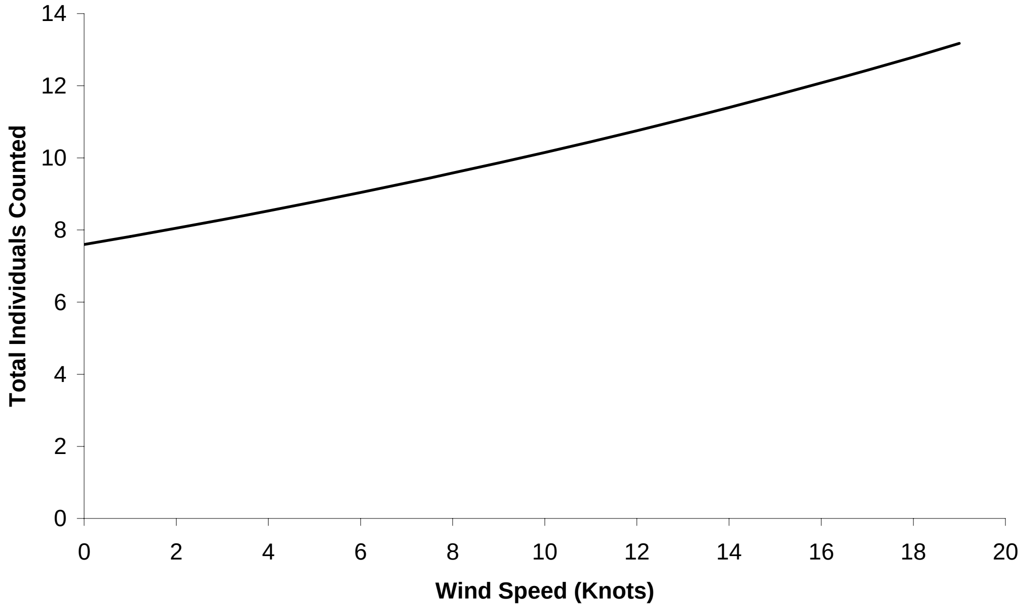

**Figure 3. 6: Response curve for numbers of wood warblers counted in relation to the windspeed at 09.00 GMT at Helensburgh on the day of the count derived from generalized linear modelling of the RSPB dataset**

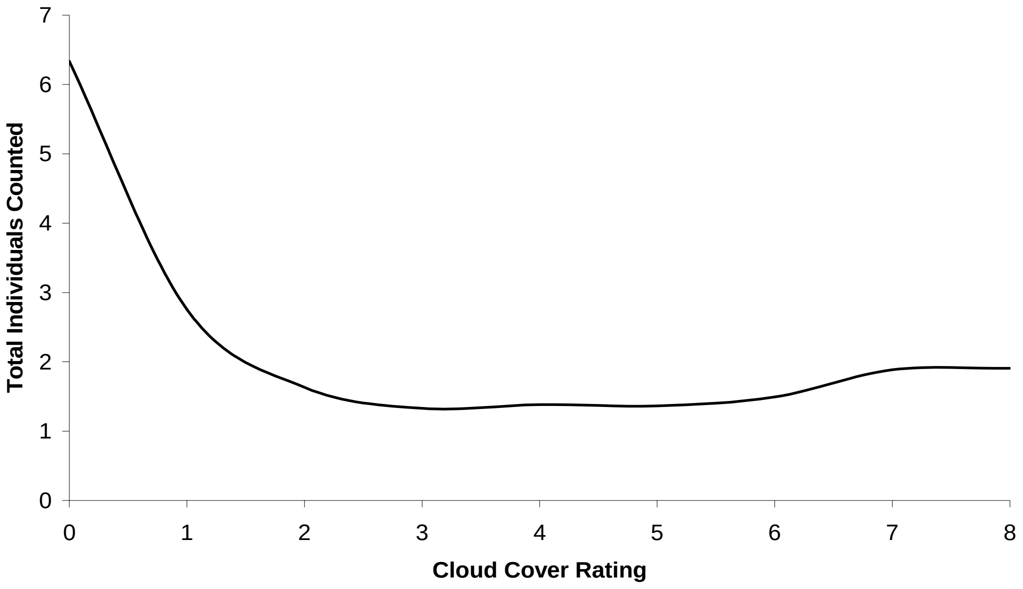

**Figure 3. 7: Response curve for numbers of coal tits counted in relation to the estimated cloud cover at 09.00 hours GMT at Helensburgh Meteorological Station on the day of the count, derived from generalized additive modelling of the RSPB dataset.**

Only the binomial models for three species contained variables significant at the 0.05 level and these results are given in Table 3.4. All of these are GLMs. Observer was significant for the treecreeper and the wren, and sample block was significant for the pied flycatcher. None of the weather or time variables were significant in any models.

**Table 3. 4: Binomial GLM models of the RSPB Dataset for the treecreeper, wren and pied flycatcher where time, weather, observer and block identification parameters were potential predictors. The evaluation includes the Adjusted $D^2$ (Adj. $D^2$) and Spearman correlation coefficients (Correlation) for the association between observed and predicted results for the full model (N=1) and the cross-validated model (N=6). There are 47 degrees of freedom (df) in the null models for each species. The significance of variables in the models is indicated as follows: *** = $p \leq 0.001$.**

| Species | Variables | | | | Evaluation | | |
|---|---|---|---|---|---|---|---|
| | BlockID | | Observer | | Correlation | | |
| | df | F | df | F | N = 1 | N = 6 | **Adj. $D^2$** |
| Treecreeper | | | 2.00 | 50.88 *** | 0.80 | 0.65 | **0.65** |
| Wren | | | 2.00 | 24.29 *** | 0.74 | 0.61 | **0.47** |
| Pied flycatcher | 2.00 | 23.47 *** | | | 0.65 | 0.47 | **0.44** |

### 3.4.1.2 Analysis of Variance for the Block L Control data

The analysis of variance results (Tables 3.5 and 3.6) suggest that species richness was affected by timing of the count and by cloud cover. However, since the interaction between cloud cover and time of day, recorded as minutes after sunrise, was significant or close to significant at the 0.05 level, it is difficult to separate these two influences. Days since the start of the field season was significant at point L1, but not at point L2.

**Table 3. 5: Anova results at point L1 in relation to time and weather parameters. Detailed variable definitions are given in Table 3.1. Colons between variable names indicate the inclusion of interaction terms. Each variable utilized one degree of freedom leaving 23 residual degrees of freedom. Pr(F) is the significance of the F statistic.**

| Variable | F | Pr(F) |
|---|---|---|
| Days | 10.07 | 0.004 |
| Minutes | 3.30 | 0.083 |
| Cloud1 | 6.46 | 0.018 |
| Minutes:Cloud1 | 3.35 | 0.080 |
| Minutes:Days | 0.70 | 0.411 |
| Days:Cloud1 | 3.70 | 0.067 |

**Table 3. 6: Anova results at point L2 in relation to time and weather parameters. Detailed variable definitions are given in Table 3.1. Colons between variable names indicate the inclusion of interaction terms. Each variable utilized one degree of freedom leaving 26 residual degrees of freedom. Pr(F) is the significance of the F statistic.**

| Variable | F | Pr(F) |
|---|---|---|
| Minutes | 9.79 | 0.004 |
| Cloud | 5.70 | 0.025 |
| Minutes:Cloud | 8.42 | 0.007 |

### *3.4.2 Effects of sample effort on bird counts*

#### 3.4.2.1 Species accumulation curves derived from the Block L Control data

The difference in perceived species richness with time of day was reflected in the species accumulation curves (Figures 3.8-3.15) though the curves did all fall within a reasonably narrow band of variation. The species accumulation curves for counts with a 50m restricted radius (Figures 3.8, 3.9, 3.12 and 3.13) were lower than those with an unlimited radius (Figures 3.10, 3.11, 3.14 and 3.15) for all numbers of count combinations, while the differences between curves for five versus 10 minute counts were less obvious. Two counts per sample point does not give a complete measure of species richness at the sample point, since the species accumulation curves for both point L1 and point L2 were still rising at this point. The curves reached a plateau at around four counts per point. However, it is important not to over interpret these patterns because count combinations have been drawn from a small dataset.

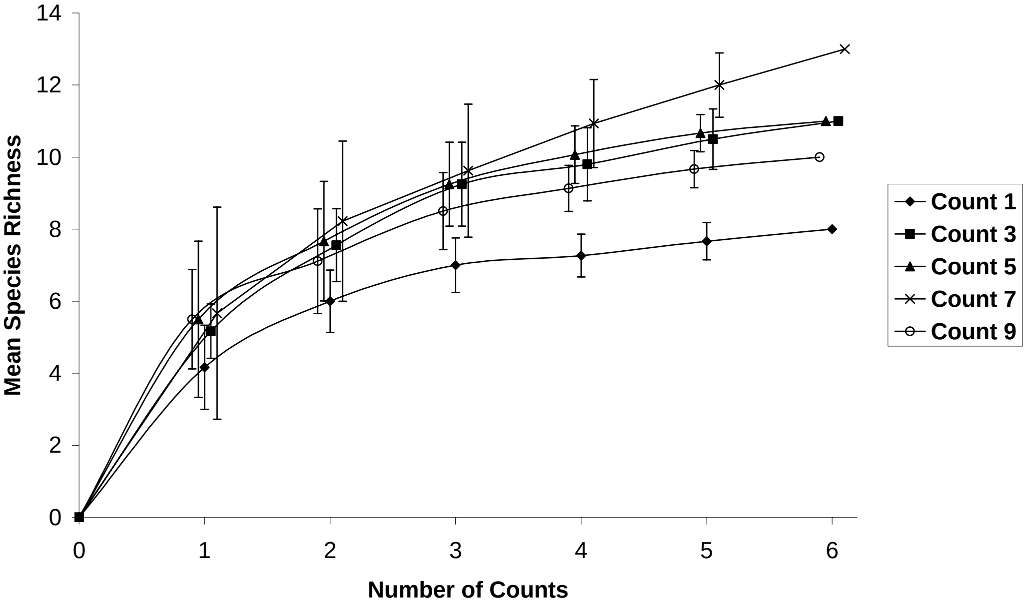

Figure 3. 8: Species accumulation curves for 10 minute count data with 50m restricted count radius for point L1. Error bars are one standard deviation. Points have been jittered so that error bars can be seen for each count.

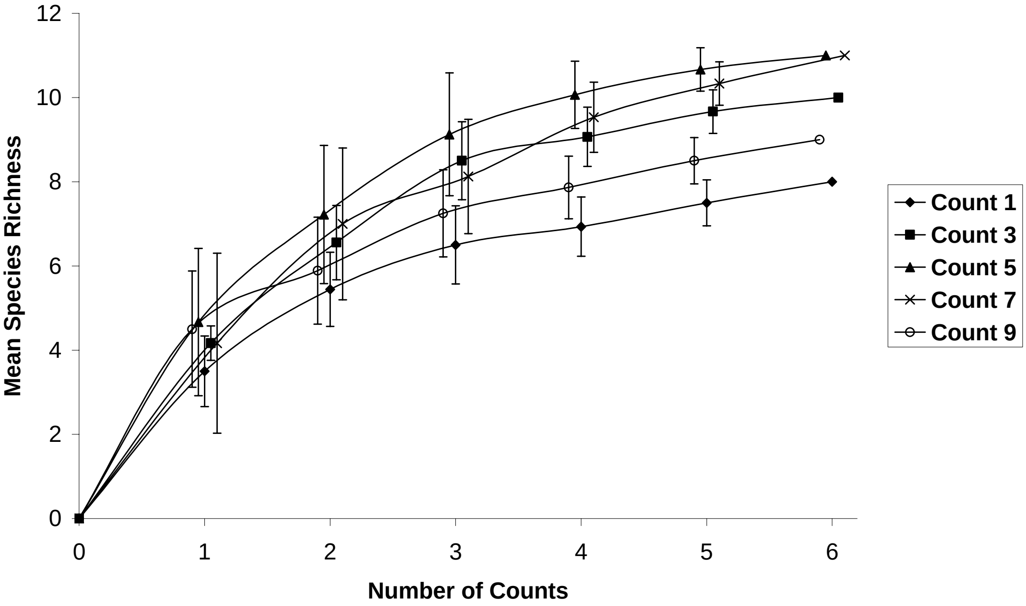

Figure 3. 9: Species accumulation curves for five minute count data with 50m restricted count radius for point L1. Error bars are one standard deviation.

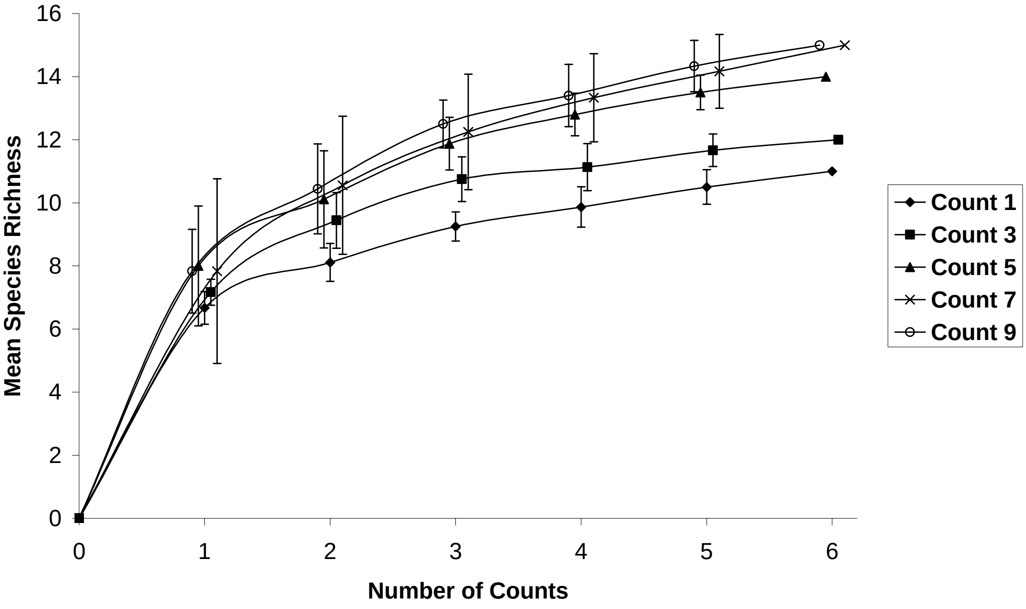

Figure 3. 10: Species accumulation curves for 10 minute count data with an unlimited count radius for point L1. Error bars are one standard deviation.

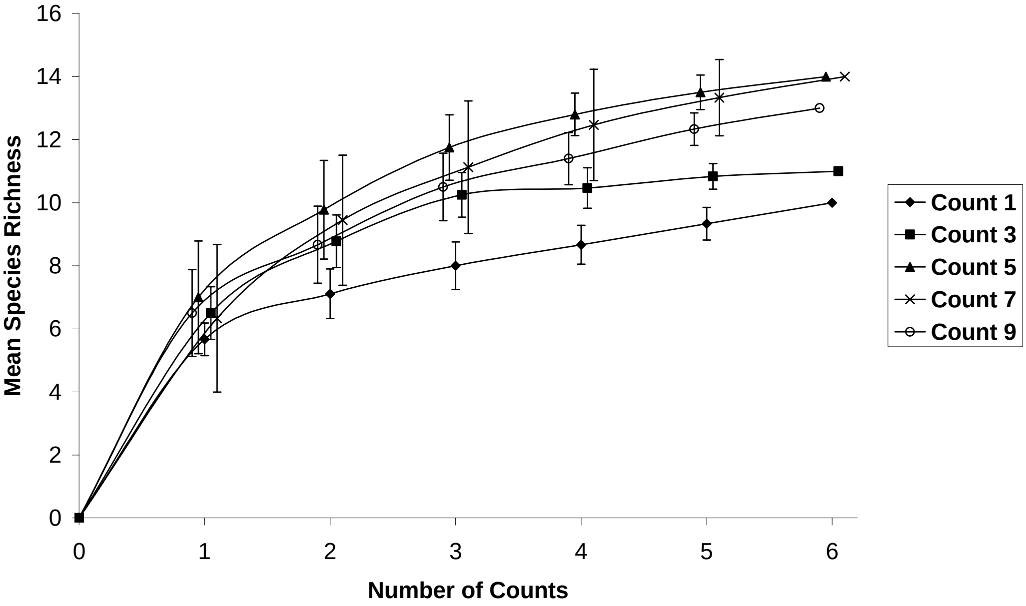

Figure 3. 11: Species accumulation curves for five minute count data with an unlimited count radius for point L1. Error bars are one standard deviation.

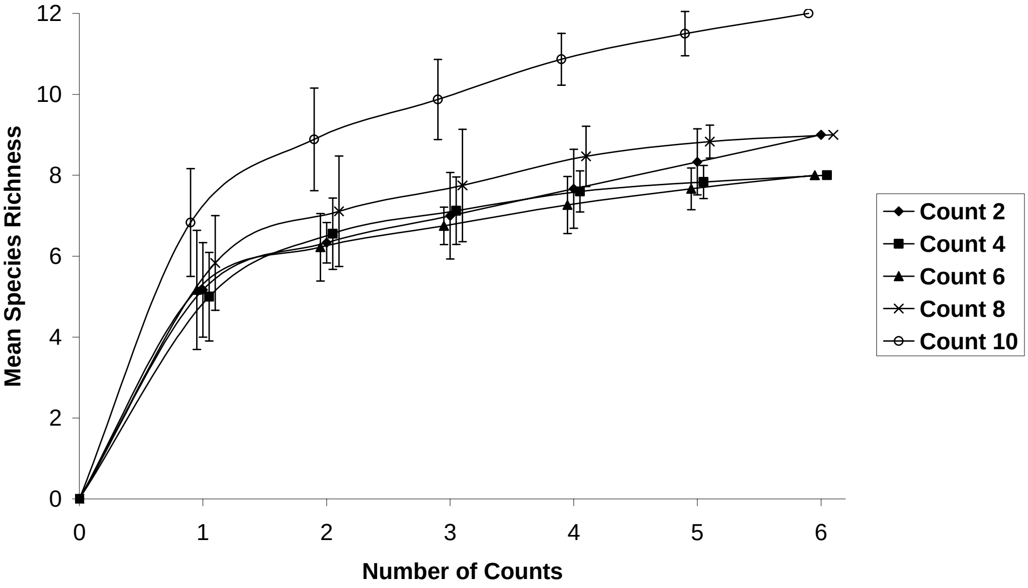

Figure 3. 12: Species accumulation curves for 10 minute count data with 50m restricted count radius for point L2. Error bars are one standard deviation.

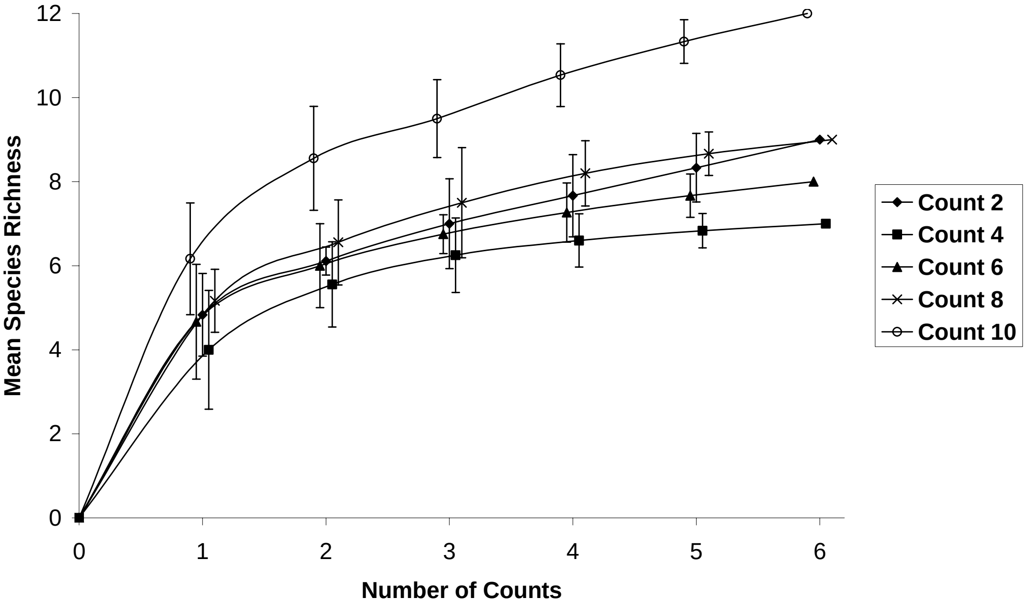

Figure 3. 13: Species accumulation curves for five minute count data with 50m restricted count radius for point L2. Error bars are one standard deviation.

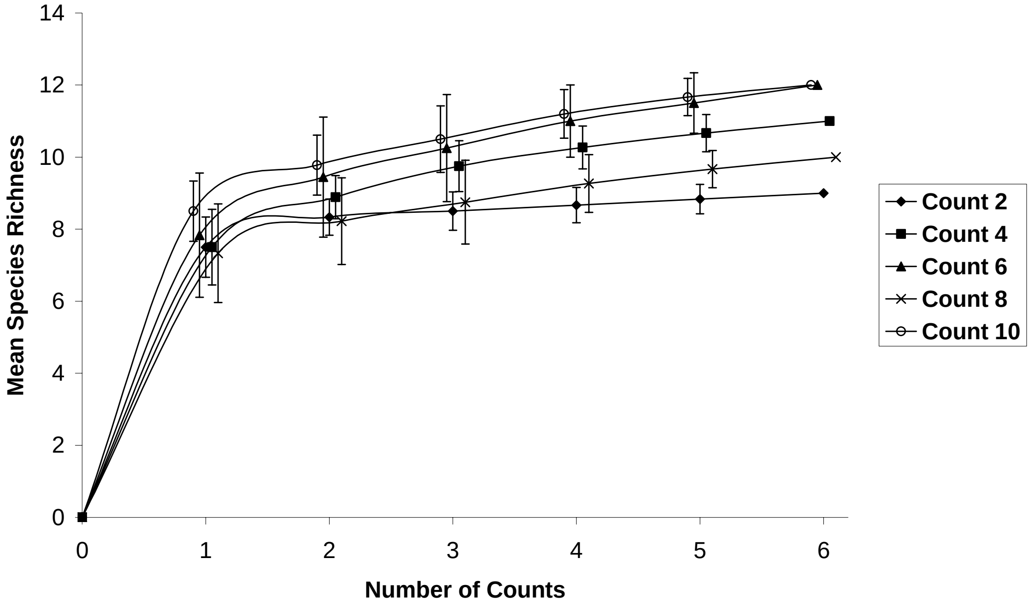

**Figure 3. 14: Species accumulation curves for 10 minute count data with an unlimited count radius for point L2. Error bars are one standard deviation.**

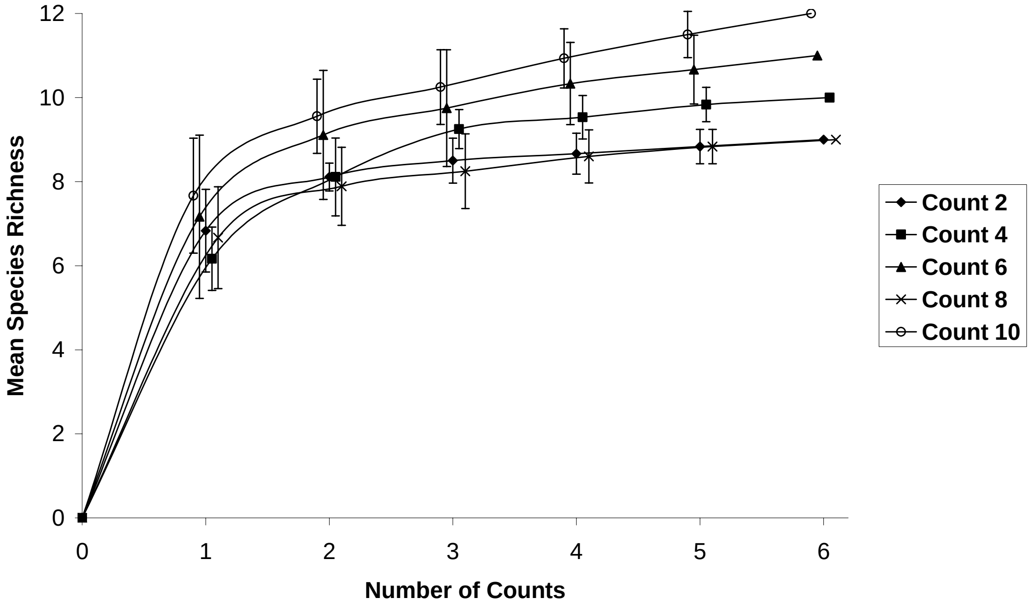

**Figure 3. 15: species accumulation curve for five minute count data with an unlimited count radius for point L2. Error bars are one standard deviation.**

### 3.4.2.2 Probability of bird species detection in two counts using the Block L and Block F Control data

A species that is being detected over two counts with complete consistency should have a probability of detection of either zero or one depending on whether it was present or absent at the point. Any gradation between these extremes introduces an element of uncertainty and the possibility of recording false negatives or false positives. False negatives occur if a species is present but fails to be detected. Conversely false positives may be due to an erroneous identification of a bird, or because a bird is recorded which is a transient, but not actually using the habitat. Tables 3.7 and 3.8 give measures of the consistency with which different species were recorded at points L1 and L2 based on all possible combinations of two counts.

**Table 3. 7: Probability of detecting different bird species based on two counts at point L1 for 10 minute and five minute counts with 50m restricted and unlimited count radii. Figures in bold are detection probabilities of greater than 0.5.**

| Species | 10 Minutes | | 5 Minutes | |
|---|---|---|---|---|
| | 50 m Radius | Unlimited | 50 m Radius | Unlimited |
| Robin | **0.98** | **0.98** | **0.87** | **0.89** |
| Chaffinch | **0.98** | **0.98** | **0.91** | **0.98** |
| Willow warbler | **0.98** | **1.00** | **0.98** | **1.00** |
| Wood warbler | **0.98** | **1.00** | **0.89** | **0.91** |
| Blue tit | **0.78** | **0.87** | **0.58** | **0.71** |
| Redstart | 0.47 | 0.47 | 0.47 | 0.47 |
| Song thrush | 0.38 | **0.80** | 0.31 | **0.76** |
| Treecreeper | 0.38 | 0.44 | 0.33 | 0.44 |
| Wren | 0.29 | **1.00** | 0.24 | **1.00** |
| Blackbird | 0.27 | **0.64** | 0.20 | **0.53** |
| Coal tit | 0.24 | 0.44 | 0.24 | 0.33 |
| Blackcap | 0.13 | 0.20 | 0.13 | 0.20 |
| Garden warbler | 0.07 | 0.20 | 0.00 | 0.13 |
| Dunnock | 0.07 | 0.07 | 0.07 | 0.07 |
| Bullfinch | 0.07 | 0.07 | 0.07 | 0.07 |
| Great tit | 0.00 | 0.13 | 0.00 | 0.07 |

**Table 3. 8: Probability of detecting different bird species based on two counts at point L2 for 10 minute and five minute counts with 50m restricted and unlimited count radii. Figures in bold are detection probabilities of greater than 0.5.**

| Species | 10 Minutes | | 5 Minutes | |
|---|---|---|---|---|
| | 50 m Radius | Unlimited | 50 m Radius | Unlimited |
| Goldcrest | **1.00** | **1.00** | **1.00** | **1.00** |
| Song thrush | **1.00** | **1.00** | **1.00** | **1.00** |
| Chaffinch | **1.00** | **1.00** | **0.96** | **1.00** |
| Coal tit | **0.98** | **1.00** | **0.87** | **0.93** |
| Robin | **0.98** | **0.98** | **0.96** | **0.96** |
| Wren | **0.58** | **1.00** | 0.40 | **1.00** |
| Treecreeper | **0.51** | **0.56** | 0.47 | **0.51** |
| Blackbird | 0.40 | **0.80** | 0.40 | **0.76** |
| Willow warbler | 0.31 | **0.96** | 0.31 | **0.96** |
| Blue tit | 0.13 | 0.24 | 0.07 | 0.18 |
| Chiffchaff | 0.07 | 0.07 | 0.07 | 0.07 |
| Great tit | 0.00 | 0.07 | 0.00 | 0.00 |
| Wood warbler | 0.00 | 0.07 | 0.00 | 0.07 |
| Garden warbler | 0.00 | 0.07 | 0.00 | 0.00 |

The results suggest that there were only small reductions in the probability of detecting species based on five minute counts versus 10 minute counts. Likewise, for most species there was only a slightly reduced probability of detecting species in a 50m restricted count radius compared with an unlimited count radius. At point L1, there were three main exceptions to this. There was a much higher probability of detecting song thrush, wren and blackbird with an unlimited count radius relative to a restricted radius. These are all highly vocal species. At point L2 the probability of detecting the blackbird and willow warbler was much higher for an unlimited count radius than for a restricted radius.

The overall pattern in the results was similar for the Block F data (Tables 3.9 and 3.10). The song thrush frequently showed a large increase in detection probability with an unlimited count radius compared with a 50m restricted count radius. However, this was also observed for tree pipit, goldcrest and redstart at some of the sample points. In some cases the probability of detecting the bird species was high (greater than 0.5) in an unlimited count radius, yet the bird was not recorded at all in the 50m count radius as for example for the song thrush at points F9 and F5.

**Table 3. 9: Detection probabilities based on two counts of 10 minutes with a 50m fixed count radius at Block F points in mature broad-leaved woodland. Figures in bold indicate detection probabilities or differences in probabilities of greater than 0.5. *(i)* is the difference between a fixed 50m count radius and an unlimited radius for 10 minute counts. (ii) is the difference between the 10 minute and five minute counts with a fixed radius of 50m.**

| Species | Mature Broad-leaved Woodland | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F1 | *(i)* | *(ii)* | F2 | *(i)* | *(ii)* | F8 | *(i)* | *(ii)* | F9 | *(i)* | *(ii)* | F10 | *(i)* | *(ii)* |
| Chaffinch | **1.00** | | | **1.00** | | | **1.00** | | | **1.00** | | | **1.00** | | |
| Willow warbler | **1.00** | | | **1.00** | | | **1.00** | | | **1.00** | | -0.22 | **1.00** | | |
| Wren | **1.00** | | | **1.00** | | -0.11 | **1.00** | | | **1.00** | | | **1.00** | | |
| Blue tit | **1.00** | | | **0.78** | | | **0.78** | | -0.44 | **0.78** | | -0.11 | **1.00** | | -0.44 |
| Blackbird | **0.78** | | -0.22 | 0.33 | | -0.33 | 0.00 | | | 0.33 | | | **0.78** | +0.22 | |
| Robin | **0.78** | | | **0.78** | | -0.22 | **0.89** | | | **0.56** | | -0.22 | **0.67** | | |
| Treecreeper | **0.78** | | -0.11 | **0.78** | | | **0.78** | | -0.44 | **0.56** | | -0.22 | **0.89** | | -0.33 |
| Garden warbler | **0.56** | | -0.22 | **0.56** | | | 0.33 | | -0.33 | 0.00 | | | **0.56** | | **-0.56** |
| Great tit | 0.33 | +0.22 | | 0.33 | | | 0.33 | | -0.33 | **0.56** | | -0.22 | 0.00 | | |
| Siskin | 0.33 | | | 0.00 | | | 0.33 | | | 0.00 | | | 0.00 | | |
| Chiffchaff | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | **0.56** | | -0.22 |
| Song thrush | 0.00 | +0.33 | | 0.33 | | | 0.33 | **+0.56** | | 0.00 | **+1.00** | | 0.00 | **+0.89** | |
| Blackcap | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Greenfinch | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Whitethroat | 0.00 | | | 0.00 | | | 0.33 | +0.33 | | 0.33 | | -0.33 | 0.33 | +0.33 | -0.33 |
| Wood warbler | 0.00 | +0.33 | | **1.00** | | | **1.00** | | | **0.67** | | | **1.00** | | |
| Coal tit | 0.00 | | | **0.56** | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Dunnock | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.33 | | |
| Goldcrest | 0.00 | | | 0.00 | | | 0.00 | | | 0.33 | | -0.33 | 0.00 | +0.33 | |
| Long-tailed tit | 0.00 | | | 0.33 | | -0.33 | 0.00 | | | 0.33 | | | 0.33 | | |
| Pied flycatcher | 0.00 | | | 0.33 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Lesser Redpoll | 0.00 | | | 0.00 | | | 0.00 | | | 0.33 | | | 0.00 | | |
| Redstart | 0.00 | +0.33 | | 0.00 | | | 0.00 | | | **0.78** | | | **0.67** | | |
| Spotted flycatcher | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | **0.56** | | |
| Tree Pipit | 0.00 | +0.33 | | 0.00 | **+0.56** | | 0.33 | | -0.33 | 0.00 | **+0.56** | | 0.00 | +0.33 | |

**Table 3. 10: Detection probabilities based on two counts of 10 minutes with a fixed 50m count radius at Block F points in mixed woodland, clearfell, conifers and young broad-leaved regeneration. Figures in bold indicate detection probabilities or differences in probabilities of greater than 0.5. *(i)* is the difference between a fixed 50m count radius and an unlimited radius for 10 minute counts. (ii) is the difference between the 10 minute and five minute counts with a fixed radius of 50m.**

| Species | Mixed | | | Clearfell | | | Conifers | | | Broad-leaved Regeneration | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F3 | *(i)* | *(ii)* | F4 | *(i)* | *(ii)* | F5 | *(i)* | *(ii)* | F6 | *(i)* | *(ii)* | F7 | *(i)* | *(ii)* |
| Chaffinch | **1.00** | | | **0.78** | +0.22 | | **1.00** | | -0.11 | **1.00** | | | **0.78** | | |
| Willow warbler | **0.78** | | -0.22 | **0.78** | +0.22 | | 0.33 | +0.44 | | **1.00** | | | **1.00** | | |
| Wren | **1.00** | | | **1.00** | | | 0.00 | **+0.67** | | **1.00** | | | **1.00** | | |
| Blue tit | 0.33 | | | **0.56** | +0.22 | -0.22 | 0.00 | | | 0.00 | | | **0.78** | | |
| Blackbird | 0.33 | | -0.33 | 0.33 | +0.33 | | 0.00 | | | 0.33 | | | 0.33 | | |
| Robin | **1.00** | | -0.22 | **0.67** | | | **0.89** | | | 0.33 | | | **1.00** | | |
| Treecreeper | **0.78** | | | **0.67** | | | 0.00 | | | 0.33 | | | 0.00 | | |
| Garden warbler | 0.00 | | | 0.00 | | | 0.00 | | | **0.89** | | -0.11 | **1.00** | | |
| Great tit | 0.33 | | -0.33 | 0.00 | | | 0.00 | | | **0.56** | | | 0.33 | | |
| Siskin | 0.33 | | | 0.33 | | | 0.33 | | | 0.00 | | | 0.00 | | |
| Chiffchaff | 0.33 | | | 0.00 | | | 0.00 | | | **0.78** | | | 0.33 | +0.33 | |
| Song thrush | 0.33 | +0.44 | | 0.00 | **+0.56** | | 0.00 | **+1.00** | | **0.67** | +0.33 | | **1.00** | | |
| Blackcap | 0.00 | | | 0.00 | | | 0.00 | | | **0.56** | | -0.22 | **0.78** | | |
| Greenfinch | 0.00 | | | 0.00 | | | 0.00 | | | 0.33 | | | 0.33 | | |
| Whitethroat | 0.00 | | | 0.00 | | | 0.00 | | | 0.33 | | -0.33 | 0.33 | | |
| Wood warbler | **1.00** | | | **0.78** | +0.11 | | 0.33 | +0.33 | | 0.33 | | | 0.00 | | |
| Coal tit | **0.89** | +0.11 | -0.11 | 0.33 | +0.44 | | **1.00** | | | 0.00 | | | 0.00 | | |
| Dunnock | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Goldcrest | **0.67** | +0.33 | | 0.00 | **+0.67** | | **1.00** | | | 0.00 | | | 0.00 | **+1.00** | |
| Long-tailed tit | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Pied flycatcher | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Lesser Redpoll | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Redstart | 0.00 | | | 0.00 | **+0.67** | | 0.33 | | | 0.00 | | | 0.00 | | |
| Spotted flycatcher | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | | 0.00 | | |
| Tree Pipit | 0.00 | | | 0.33 | +0.33 | -0.33 | 0.00 | | | 0.00 | | | 0.00 | | |

Table 3.11 shows that only around half of the species actually recorded in the bird counts had a mean detection rate of greater than 0.5 at points where they actually were present. Where all probabilities of less than 0.5 were excluded from the calculation of the mean, blackcap, blackbird, chiffchaff and great tit also had detection probabilities of greater than 0.5. These second average probabilities are only more meaningful if it is reasonable to assume that an infrequent occurrence at a point is a false positive due to erroneous identification or a transient individual.

**Table 3. 11: Mean probability of detecting species accurately across the habitats found in the study area in 10 minute counts with a 50m restricted radius. Figures in bold indicate detection probabilities of greater than 0.5. *(i)* No probabilities have been excluded from the calculations. *(ii)* All probabilities of less than 0.5 have been excluded from the calculations.**

| Species | Detection Probability | |
|---|---|---|
| | *(i)* | *(ii)* |
| Chaffinch | **0.96** | **0.96** |
| Wren | **0.90** | **0.96** |
| Willow warbler | **0.85** | **0.95** |
| Robin | **0.79** | **0.76** |
| Wood warbler | **0.79** | **0.80** |
| Goldcrest | **0.75** | **0.67** |
| Blue tit | **0.69** | **0.72** |
| Coal tit | **0.67** | **0.68** |
| Treecreeper | **0.64** | **0.64** |
| Song thrush | **0.58** | **0.89** |
| Garden warbler | **0.57** | **0.71** |
| Redstart | **0.56** | 0.48 |
| Spotted flycatcher | **0.56** | 0.28 |
| Blackcap | 0.49 | **0.67** |
| Blackbird | 0.42 | **0.52** |
| Chiffchaff | 0.41 | **0.67** |
| Great tit | 0.40 | **0.56** |
| Siskin | 0.33 | 0.00 |
| Greenfinch | 0.33 | 0.00 |
| Whitethroat | 0.33 | 0.00 |
| Long-tailed tit | 0.33 | 0.00 |
| Pied flycatcher | 0.33 | 0.00 |
| Lesser Redpoll | 0.33 | 0.00 |
| Tree Pipit | 0.33 | 0.00 |
| Dunnock | 0.20 | 0.00 |
| Bullfinch | 0.07 | 0.00 |

## 3.5 Discussion

Variations in the total numbers of different species counted with time of year (days since the start of the field season) may represent genuine variation in numbers present, or variation in the detectability of these species. Pied flycatchers, garden warblers and willow warblers are migrant species and the initial increase in the numbers of these counted with days may partially be due to gradual arrival into the study area of returning migrants. However, another cause of the variation in numbers of different bird species counted with time is likely to be due to changes in detectability. Most of the bird registrations were through bird song and calls. Song output varies with time of year because the roles that it is fulfilling vary over time. For example, it has been suggested that male song output in the great tit has a direct relationship with female fertility, being greatest several weeks before the fertile period (Mace, 1987). Furthermore singing and foraging are mutually exclusive activities in the great tit (Kacelnik, 1979), which has implications for the bird time budgets when nestlings are being fed.

The finding that minimum temperature was the most consistently significant weather variable in the Poisson models agrees with earlier studies which have found relationships between air temperature and song output (for example, Garson and Hunter, 1979; Gottlander, 1987). The result for the siskin is more typical of the general direction of relationship found in these earlier studies with numbers counted increasing with minimum temperature. The sensitivity of the body weight of small passerines to changes in air temperature (Baldwin and Kendeigh, 1938) may be one explanation for this relationship. Bird song is energetically expensive and under cooler conditions less energy may be available for singing behaviour (Ydenberg and Houston, 1986; Gottlander, 1987; Strain and Mumme, 1988). However, a negative relationship between minimum temperature and song output and hence detectability of the birds could be due to the effect of temperature on the mobility of invertebrate prey. Invertebrates are likely to be more active in warmer temperatures and it may therefore be more profitable for birds to forage rather than sing in these circumstances (Kacelnik, 1979; Avery and

Krebs, 1984). Wood warblers and blue tits both feed on invertebrates. Although siskins also do so, seeds may form a larger part of their diet.

Thorpe (1961) found that many birds sing less when the weather is cloudy and dull. The result for the coal tit (Figure 3.7) and the analysis of variance results for sample points L1 and L2 (Tables 3.5 and 3.6) support this result. Since the interaction between cloudiness and time of day is significant, some of the variation in output with time of day is likely to relate to how bright conditions were. Relationships between the degree of illumination and onset of bird song in the morning are known to exist, for example, for the song thrush (Higgins, 1979).

It is important to understand how the observed relationships between the numbers of birds counted and time and weather parameters may introduce biases into the bird counts. Although counts were avoided during extremes of temperature and windiness it is still possible to detect effects of these variables in the bird data. This would suggest that some species are highly sensitive to these conditions. In addition, for the blue tit it was the conditions on the day preceding the count that were significant. No account of these was taken in planning fieldwork, and arguably more account should be taken of this in future studies. It is also possible that not all weather effects were detected in the RSPB dataset due to the distance between the study site and the location of the weather station. No weather data were actually available for Inversnaid.

The Poisson models used abundance data. When this was reduced to presence or absence level in the Binomial models all of the time and weather variables were no longer significant and significant models were only produced for three species. Thus at a presence and absence level there is no longer any evidence that the bird counts were being biased by the timing of the count or prevailing weather conditions. However, sample block was only significant in one of the models and year was no longer significant at all. Thus some interesting variation may also be being eliminated from the models since the block effect may be partly due to habitat variation as well as differing weather conditions on the day of the count.

Any biases due to weather and time of year effects are also likely to be reduced by using combinations of counts from different parts of the sample period to construct a final dataset. Two was the maximum number of counts per point identified as being feasible in this study given the number of fieldwork hours available and the spatial coverage which it was desirable to achieve. However, since for practical reasons points within each sample block always had to be counted in the same order, any bias due to the effect of time of day would remain.

Figures 3.8 to 3.15 all demonstrate that two counts per sample point were inadequate to give a complete measure of species richness. This agrees with the findings of Anderson and Ohmart (1981) who suggested the need for more than three counts per point to calculate species richness using a circular plot method. Some form of jack-knifing or rarefaction may be advantageous to obtain a more realistic estimate of the number of species (see for example methods in Heltshe and Forrester, 1983). Species richness can still be compared between points where sample effort is constant. For example a comparison of the species accumulation curves for point L1 and L2 imply greater species richness at point

L1 than point L2. However, the confidence bands for the two points overlap, and this distinction may not be identified based on two counts per point. Thus it is not really valid to model species richness with only two counts per sample point.

In terms of count duration the results agree with Fuller and Langslows' (1984) study. They recommended 10 minutes as the maximum count length under British conditions and stated that five minute counts may often be adequate. Tables 3.7–3.11 all suggest that the majority of birds were counted within the first five minutes of the count. The relatively short count period also has the advantage that it incurs a lower risk of double counting birds and allows time for a greater number of independent counts than a longer count period would (Dawson, 1981; Morrison *et al*., 1981; Fuller and Langslow, 1984).

Differences between results for a restricted count radius relative to an unlimited radius were marked, especially for certain species (notably song thrush, blackbird and wren). These species all tend to have particularly loud songs, which therefore carry over long distances. They also often have larger territory sizes than many of the other species. Using an unlimited count radius could be dangerous given the fine grain of habitat variation in the study area. Where a species was only recorded beyond the 50m count radius, there is no evidence that it was in fact using the habitat measured at the sample point.

The probability of detecting individual species appears to vary between habitats. This may be because a species detected at low frequency is in fact a transient, not actually using the habitat in which it has been recorded. However, these cases cannot be distinguished from those where a species does use the habitat but is less detectable than in alternative habitats where it is also present. Species will be more readily detectable where they occur in greater abundance, since obviously there will be more of them to see or hear. Individual birds may also be stimulated to sing more if surrounded by other individuals of the same species. For example, Garson, (1980b) showed that not all wren songs were spontaneous, but also included reply songs within 10 seconds of a song by a neighbour. In addition birds may be easier to see and hear in some habitats because of differences in vegetation density and sound attenuation (Catchpole and Slater, 1995). These factors could all contribute to the marked variations in detectability between different sample points observed for such species as the garden warbler (Tables 3.9 and 3.10).

The mean detection probability of each species across all of the control sample points of Blocks F and L (Table 3.11), gives a useful indication of how completely two counts per sample point are likely to represent the distribution of each species in the study area. The first measure assumes that all registrations are true positives, there are no incorrect identifications of species and none of the birds recorded were transients. The second measure assumes that all birds recorded with a probability of less than 0.5 at any sample point were in fact false positives. The true situation is likely to lie at an indeterminate point between these two extremes.

A sample effort of two counts per point is adequate to determine the distribution of some but not all of the species recorded in the bird counts. Those species in the top half of Table 3.11 (chaffinch to garden warbler) were consistently recorded at over 50% of sample points where they were present. Below this point in the table the mean detection probability was 50% or less. The data is likely to give an incomplete estimate of the distribution of these species. The pied flycatcher is a possible exception. None of the control points included areas of bird boxes, the factor which is most likely to account for the strong block effect in the pied flycatcher models from the RSPB data (Table 3.3).

## 3.6 Conclusion

Although time and weather conditions in which counts were carried out were restricted to a narrow band, there is still evidence that these parameters influenced the abundance of birds recorded and species richness. These influences included effects of time of day of the count, time of year, temperature and cloud cover. They can be interpreted in terms of their influences on bird behaviour and sound attenuation and hence on the detectability of different bird species. In some cases bird counts may be affected by conditions on the preceding day, which were not taken into account at all when planning the sampling. When data is reduced to presence and absence level most of these biases are lost. Using combinations of two counts per point will further eliminate these biases. The remaining biases to be considered are the effect of observer in the RSPB data and time of day in all cases. Since there was no overlap between observers and years, it is impossible to separate completely observer from annual effects in the time series.

The majority of bird species were recorded within the first five minutes of the counts and counts of longer than 10 minutes would have been unnecessary. Likewise in most cases a restricted counting band of 50m did not greatly reduce the probability of detecting species present at a sample point and may be important to avoid including species only using a neighbouring habitat. Two counts per sample point were insufficient to determine species richness adequately at sample points in the study area. It was sufficient to record the distribution of approximately half of the species recorded in the counts.

# Chapter 4: Multivariate models of woodland bird distributions for East Loch Lomond and the Central Scotland Forest.

## 4.1 Introduction

The aim of this section of the study was to build multivariate models to describe the woodland bird distributions of the East Loch Lomond (ELL) and Central Scotland Forest (CSF) study sites. The key theoretical principle underlying this approach was that of the ecological niche. It has been argued that multiple habitat measurements can be used to characterise the ecological niche of a species (James, 1971; Brown, 1984).

Early studies using this approach concentrated on local habitat variables as important determinants of bird distributions (for example, James and Wamer, 1982). However, it is increasingly being argued that factors operating at a wider spatial scale in the environment may also be important, especially as declines in populations have occurred concurrent with increasing habitat fragmentation (Léscourret and Genard, 1994, Scheck *et al*., 1995; Bellamy *et al*., 1996b). Thus it is an interesting question as to whether habitat based models predicting species occurrence can be improved by the addition of landscape scale variables.

A common approach to studying area and isolation effects on woodland birds has been derived from the theory of Island Biogeography of MacArthur and Wilson (1967). They suggested that larger islands held more species due to lower population extinction rates and that more isolated islands have lower colonization rates. Such species-area relationships have been studied for birds where woodland patches are viewed as habitat islands in a hostile matrix (Moore and Hooper, 1975; Helliwell, 1976; Galli *et al*., 1976; Ambuel and Temple, 1983; Howe, 1984; Opdam *et al*., 1984; Opdam *et al*., 1985; Askins *et al*., 1987; Blake and Karr, 1987; Ford, 1987; McCollin, 1993; Haila *et al*., 1993; Bellamy *et al*., 1996a). However, woodland patches are less isolated than the true islands considered in the original MacArthur and Wilson (1967) theory (Martin, 1980; Gilbert, 1980). As shown in Chapter 2 interspecific differences occur in how birds view habitat connectivity. Defining discreet woodland patches in a way which would be applicable to all of the species studied is not feasible.

This study therefore took the approach of modelling species individually in relation to local habitat variables and additional variables at a wider spatial scale. There was no basis for assuming that species-variable relationships would be linear. Consequently a more flexible generalized additive modelling (GAM) approach was adopted.

Generalized Additive Modelling is a non-parametric approach which uses smoothing techniques to allow the data to define the form of the relationship. This means that a range of different curves can be fitted which may more accurately reflect the true relationship between the response variable and the predictor (Hastie and Tibshirani, 1990; Austin, 1999). Ecological theory often predicts a non-linear relationship. For example, niche theory predicts at least a curvilinear relationship with environmental predictors (Austin and Meyers, 1996).

However, GAMs have only been applied in ecological studies relatively recently and the earliest studies modelled vegetation (for example, Yee and Mitchell, 1991). Lately GAMs have also been successfully applied to model bird species (for example, Fewster *et al*., 2000; Pearce and Ferrier, 2001).

However, the GAM approach is still a static modelling technique relating bird distributions to their present environment (Guisan and Zimmermann, 2000). On the other hand, a key reason for studying bird-habitat associations is for prediction (Fielding and Haworth, 1995). This information is especially pertinent where landscape change is expected, as with the on-going management being carried out by the Forestry Commission at East Loch Lomond. This study also therefore aimed to test the generality of the models built by looking at their ability to predict distributions between the two study sites and inter-annually at Loch Lomond.

Thus this part of the study addressed the following questions: (1) What is the relative importance of habitat and landscape parameters as determinants of avian population distributions in woodland? (2) Can the inclusion of landscape and fragmentation related variables improve the models? (3) How general are these models for predicting bird distributions for the same site in different years, and for different sites?

# 4.2 Method

## *4.2.1 Study Sites*

The study sites were described in Chapter 1 (Section 1.3).

## *4.2.2 Sample Design for East Loch Lomond*

The sample design for East Loch Lomond was described in detail in Section 3.2.1. Sample points for bird point counts were marked with tape during April 1998 and could be located using written directions and a sighting compass. Tapes were placed where possible on broad-leaved trees or around a root of a conifer tree so that they would be likely to remain even when conifers were felled. This strategy proved very effective and the majority of tapes were still in place for the 2000 field season. Missing tapes were replaced during April 2000. Although these replacement tapes may not have been in precisely the same position as the original sample point, the detailed written directions ensured only minimal errors.

## *4.2.3 Sample Design for the Central Scotland Forest*

During April 1999 a total of 267 sample points were established throughout approximately 62 separate woodland blocks within the Central Scotland Forest. Woodlands sampled ranged in size from 0.14ha to 302ha with a median patch size of 9.79ha. Sample points were at least 150m apart and, where possible, at least 50m from habitat edges. However, the 50m rule was violated quite frequently due to the configuration of many of the woodlands. The aim was for the sample effort to be proportional to woodland area in each case, and there was a relationship between the number of points in a woodland and woodland area. Unfortunately strict proportionality of sample effort to area was impossible to achieve. A single sample point in small woodlands could cover the whole woodland area, whereas complete coverage in larger woodlands was not feasible. Thus small woodlands may have been over sampled and large woodlands under sampled with respect to their areas.

As at East Loch Lomond sample points were marked with tape that could be relocated using written directions and a sighting compass. Points were organised into 22 sampling blocks, where one block could be sampled per day. Individual blocks consisted of one to seven separate woodlands and between eight to 17 sample points.

### *4.2.4 Bird Count Methodology*

Bird counts were carried out at East Loch Lomond during 1998 and 2000 and in the Central Scotland Forest during 1999. In each year the sampling period commenced on 30th April or 1st May and ended on the 30th June or the 3rd July. Any extension into July only occurred if poor weather had prevented counts being carried out at an earlier date. Counts were generally avoided during strong wind, during light to heavy precipitation, when visibility was obscured due to fog, and under conditions of extreme temperature. Two counts were performed at each point, firstly during May and secondly during June or the beginning of July. The bird count methodology employed was described in detail in Section 3.2.2.

### *4.2.5 Habitat Measurements*

Habitat measurements were made using a method adapted from the circular plot technique of James (1971). At East Loch Lomond sampling was carried out over a 20m radius circle centred on the sample point. A smaller radius circle of only 10m was sampled for the Central Scotland Forest points during 1999. This was for practical reasons since there were more points and the study area was more extensive leading to greater journey times. In addition, access for fieldwork could only be gained for limited time periods for some of the woodlands. A smaller sample area will only have affected the accuracy of the data for a minority of points where habitat was more heterogeneous such that some of the variation may not have been included within a 10m radius circle. In other respects the methodology employed for gathering habitat data was the same for East Loch Lomond and the CSF.

To ensure that all measurements were made within the appropriate sample area, a ranging pole was placed at the centre of the circle at the position used by the observer for the bird counts. A second stick was then held at arms length. Where the length of this stick appeared the same length as the 1.5m mark on the ranging pole, the observer was standing at the edge of the circle. The accuracy of this technique was verified by measuring with a tape measure the radius for a proportion of both the 10m and 20m radius circles. It was assumed that the habitat sampled was representative of the wider habitat area used by birds counted from that point.

All trees within the sample area were identified to species level and counted within specific diameter breast height (dbh) categories (<7cm, 7-16cm, 16-24cm, 24-30cm and >30cm). Each stem of a multi-stemmed tree was therefore counted separately. In addition the total numbers of individual broad-leaved and coniferous trees of greater than seven centimetres dbh were counted. Standing dead trees (snags) were counted for each dbh category for broad-leaved and coniferous categories. The proportion of trees within different height categories (<10m, 10-15m and >15m) was estimated. It was not possible to measure heights with greater precision using clinometer readings and trigonometry because of the unevenness of the terrain over much of the East Loch Lomond study site. Tests of repeatability of such measures revealed large discrepancies in height estimates.

Measurements of the shrub layer, canopy and ground cover were made along two transects across the circle. The direction of the first transect was determined at random and the second transect was then placed at right angles to the first. All stems of less than seven centimetres dbh encountered within an arm span either side of the transect line were identified to species level and assigned to a height category (<2m, 2-4m and 4-10m). For every fourth step (ELL) or every second step (CSF) along the transects, the presence or absence of ground cover and canopy cover was recorded using a sighting tube of 3.5cm diameter held at arms length. This gave 20 ground and canopy cover readings for calculating percentage covers.

A more detailed description of ground cover was obtained by recording the presence or absence of broad categories of cover types at every fourth (ELL) or second (CSF) step for an armspan width either side of the transects. This included moss, grass, herbaceous vegetation, litter, brash, ferns and tree seedlings. Heather, bilberry, bramble and bracken were quantified separately. The number of times each ground cover component was recorded as present was used as an index of its percentage cover.

Broad-leaved and coniferous dead wood lying on the ground was quantified using a scoring system for each time it was encountered along transects. For this purpose only wood of a thickness greater than seven centimetres was counted. Below this thickness it was quantified as part of the litter or brash component of ground cover. Care was taken to avoid double counting wood which crossed both transect lines when located near the centre of the sample circle. Dead wood on the ground can take a wider variety of forms than when it is present as snags. For example, it may be present as tree stumps, logs, branches and fallen trees. A simple count would apply the same weight to a relatively small log, as to a whole fallen tree and would therefore not give a realistic measure of the quantity of dead wood present. The scoring system given in Table 4.1 was devised as a way to avoid this bias.

**Table 4. 1: Scoring system for dead wood on the ground.**

| Score | Description |
|---|---|
| 1 - 4 | Individual logs and tree stumps |
| 7 | Small fallen trees |
| 12 | Large fallen trees |

A final score was obtained by summing the total score for the two transects. Although a subjective scale, repeat measures separated by a three week interval of dead wood for the same transects of the points of Block F at East Loch Lomond during 1998, suggested that ratings were assigned consistently.

To characterise the physical environment, the dominant slope angle was measured using a clinometer, and aspect was recorded in degrees. The presence of bogs, fens and flushes was also recorded. The presence of nest boxes, footpaths and exclosure fences was recorded for the full 50m area of the bird count.

At a small number of sample points regeneration was too dense to count all trees of less than seven centimetres dbh. In these cases a proportion of the area was counted and the results extrapolated for the whole circle. Extrapolation also had to be employed for estimates of numbers of trees in all dbh categories for two of the East Loch Lomond sample points (B6 and O2), due to the extreme density (both sites) combined with very uneven topography (site O2). In these cases a third of the area was counted. Habitat was relatively homogeneous for the entire circle in all cases, so that the area counted will have accurately represented the habitat present.

Habitat measurements were completed between 29th April and 7th July in 1998 and 2000 (ELL) and 1999 (CSF). Measurements were only repeated at East Loch Lomond in 2000 for 36 sample points where the habitat had changed significantly since the 1998 field season.

### *4.2.6 Landscape Measurements*

The locations of all sample points were identified within ArcView 3.2 Geographical Information System (GIS). Buffers of distances of 50m, 100m, 200m, 500m, 1000m, 2500m and 5000m were then created for each point. The areas of broad-leaved, coniferous and mixed woodland within each buffer distance of each point were then tabulated. These values were summed to give total woodland areas for different areas around sample points. In addition the length of different habitat boundaries and woodland edge within the buffer areas of each point was calculated.

## 4.3 Data Analysis

### *4.3.1 Descriptive statistics of study sites for each bird count year*

Patch Analyst 2.2 within ArcView GIS was used to calculate median patch size, edge density, mean patch fractal dimension and area weighted mean-patch fractal dimension for the ELL98, ELL00 and CSF99 landscapes. This gave an indication of the differences in woodland fragmentation between the different sites and years. The maximum scale of variables used for model building was a 5000m radius from each sample point. Consequently this scale was used to define the landscape area for which statistics were calculated. Since the area sampled varied between Loch Lomond and the Central Scotland Forest study sites, only statistics which were independent of total landscape area and therefore were comparable between sites, were computed.

A patch was defined as an area of woodland unconnected to other areas of woodland. No differentiation was made for variations in woodland type or inter-patch distance. As discussed in Chapter 2 patches within home-range gap crossing abilities of birds may not be perceived as separate entities, but this may vary interspecifically. Edge density was the total edge in metres divided by the total landscape area in hectares and so gave the amount of edge relative to the landscape area. Mean patch fractal dimension gave a measure of shape complexity which falls between one and two with a higher value indicative of more complex shapes (McGarigal and Marks, 1994). When this measure is area weighted an adjustment is made for shape size to take account of the fact that larger patches tend to be more complex than smaller patches. It was measured on the same scale as the unweighted statistic (McGarigal and Marks, 1994).

For a 100m and 5000m radius around sample points, the percentage cover of broad-leaved, coniferous and mixed woodland was calculated. In addition, the percentage of open and wooded habitat was determined. For a scale of 100m, the percentage of points at which broad-leaved, coniferous and mixed habitat were present were also determined. The difference between 1998 and 2000 at ELL in percentage cover of woodland (broad-leaved, coniferous and mixed) and open habitat for a radius of 100m and 5000m around sample points, and percentage presence of each general woodland type at a radius of 100m around sample points, was also calculated.

### *4.3.2 Investigation of the correlation structure of variables used in model building*

A Spearman Rank correlation matrix was calculated for ELL98, ELL00 and CSF99 for all variables used in model construction. A non-parametric approach was used since not all variables were normally distributed. Where a large number of correlation tests are carried out, a proportion of results are likely to be significant purely due to chance (Bibby *et al.*, 1989; Bibby *et al.*, 1992). However the significance of the correlation coefficients was not considered. Coefficients were used to avoid multicollinearity problems in model building, and for interpreting patterns of cross-prediction between sites and years.

### *4.3.3 Model Selection*

Based on the conclusions from Chapter 3, the data modelled for both East Loch Lomond and the CSF was 10 minute count data for a 50m restricted radius. Abundance data for each species was reduced to presence/ absence level at each sample point, and modelled using generalized additive modelling (GAM) in S-Plus 2000. GAM is a more flexible modelling approach than generalized linear modelling (GLM) where the linear term is replaced by a smoothing function allowing any shape to be fitted for each predictor, from a straight line through a range of increasingly complex non-parametric curves (Fewster *et al.*, 2000). The covariates were habitat variables measured in the field, and landscape measurements generated using tabulation within a geographical information system (GIS). These included both continuous and categorical variables.

Models were fitted using a logistic link function and assuming a binomial error distribution, which is appropriate for modelling data where the dependent variable takes the value of zero (absent) or one (present) (McCullagh and Nelder, 1989; Hastie and Tibshirani, 1990). For a binomial distribution the dispersion parameter is assumed to be one. However, calculation of the empirical scale parameter (Residual Deviance/ Degrees of Freedom) suggested that some of the fitted models suffered from over or under dispersion. Replacing the binomial assumption with the quasi-likelihood can circumvent this difficulty.

A proportion of the East Loch Lomond models were rebuilt using the quasi-likelihood technique where the data was allowed to specify the error structure, however there was very little difference in the selection of variables included in the models. It has previously been suggested that quite large deviations from the assumed variance only have a very small effect on GLMs (McCullagh and Nelder, 1989; Parker, 1999). This may also apply to GAMs though this requires further investigation. Since the models in this study were predominantly made up of linear terms with a small number of non-linear parameters a decision was made to use the binomial error structure.

Models were constructed using a forward stepwise selection procedure. Continuous variables were fitted as smoothing splines (piecewise cubic polynomials) with between one and four degrees of freedom. A spline with one degree of freedom produces a straight line. With larger numbers of degrees of freedom an increasingly complex curve is fitted. The shape of the curve is determined by the data. The maximum number of splines that could be fitted for each variable was restricted to four to reduce the risk of over fitting (Anderson *et al.*, 1994). A range of smoothing techniques are available; however the method chosen has little effect on the final curve fitted (Fewster *et al.*, 2000). Consequently alternative smoothers were not considered.

In the model building procedure the variable selected at each stage was the one explaining the most variance per degree of freedom used. This selection was made manually. However, the number of splines associated with each variable selected was determined automatically based on Akaike's Information Criterion (AIC) (Akaike, 1974; Hastie and Tibshirani, 1990). Selection continued until no more variables were significant at the 0.05 significance level, or until a maximum of approximately 10 (ELL) or 13 (CSF) degrees of freedom had been utilised. This upper limit was established to avoid over-defining the models and was determined by the sample size (Harrell *et al.*, 1996). The significance test was a likelihood ratio test based on the F statistic. Models were compared with and without the additional variable and the significance of the change in residual deviance was measured. To avoid multicollinearity problems, variables were not selected where they had a Spearman Rank correlation coefficient of at least 0.8 with parameters already in the model. Models were fitted using a maximum likelihood method (Hastie and Tibshirani, 1990). Where no non-linear terms were significant in the final model, the model quoted is a GLM.

To take account of deviation from a 50:50 ratio of presence and absence in the data for certain species, weights were included in the models. These were calculated such that the total weight allocated to presence data was equal to that for the absence points.

### 4.3.4 Model Evaluation

Diagnostic plots were used to identify points with high residual and leverage values. Where outliers were identified the model was rebuilt omitting those points so that their effect on the model could be discerned. Where the points appeared to be having only a limited effect on the model they were included in the final model. However in some cases the absence of a few points affected the significance of some of the parameters in the model. In these cases, as found by Parker (1999), removing some of the variables generally resolved the leverage and residual problems and all points were included in the final models.

Models were tested using cross-validation (Fielding and Bell, 1997). Data was partitioned into 10 (ELL) or 12 (CSF) even sized blocks and the model rebuilt omitting one block at a time. These models were used to predict the response at the omitted sample points. A value, $D^2$, was calculated to measure the overall fit of the model. The formula for this value is given in Equation 2.1. To take account of the number of parameters in the model, an adjustment of the $D^2$ was calculated using an adaptation of Weisberg's (1980) adjusted $R^2$ statistic. This is explained in Section 2.3.1 and Section 3.3.3.1 and the formula is given in Equation 2.2. Note that where models are being used to predict presence and absence, the $D^2$ and adjusted $D^2$ measures cannot be directly equated with the $R^2$ and adjusted $R^2$ in a gaussian glm with an identity link function. A point may have high residual variation associated with it and yet correctly predict presence or absence.

Thus model performances were also evaluated using nonparametric Receiver Operator Characteristic (ROC) curves (Hanley and McNeil, 1983; Beck and Schultz, 1986; Zweig and Campbell, 1993). These consist of a plot of sensitivity (the conditional probability that a point is correctly classified) against one minus the specificity (the conditional probability that a point is not correctly classified). An example is shown in Figure 4.1. The overall accuracy of different models can then be compared using the area under the curve (AUC). This takes a value between 0.5 and 1.0 where a value of 0.5 indicates that the model is predicting no better than random and a value of 1.0 indicates perfect prediction.

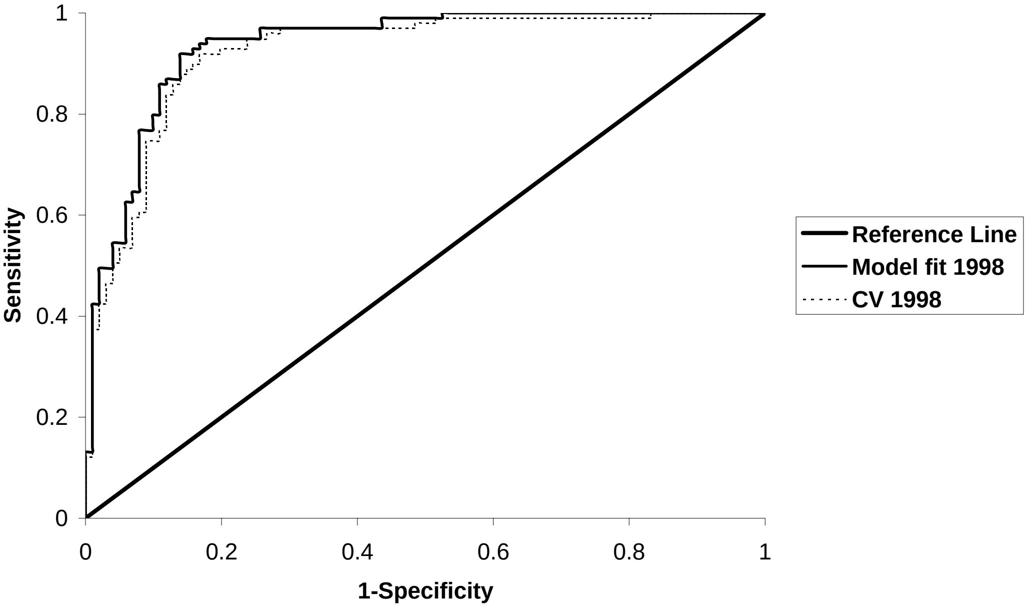

**Figure 4. 1: Example Receiver Operating Characteristics (ROC) plot for the East Loch Lomond 1998 generalized additive model for the coal tit. The reference line indicates the plot which would be expected where the model was performing as random.**

The significance of the AUC was tested using a standard critical ratio test as recommended by Beck and Schultz (1986). The formula for this test is given in Equation 4.1, where W is the area under the ROC curve and $SE_w$ is the standard error of the AUC.

$$z = (W - 0.5) / SE_w \qquad \textit{Equation 4.1}$$

The z score tests the null hypothesis that the AUC is not significantly different from 0.5, the value that would be obtained if the model was predicting presence or absence randomly. Swets (1988) suggested that AUC values between 0.7 and 0.9 indicate models with useful application, while those of greater than 0.9 have high accuracy.

ROC plots are a threshold independent measure of model performance. Consequently they are less susceptible to bias due to uneven prevalence of presence and absence points in the data than alternative commonly employed measures of model performance such as Cohen's Kappa (Zweig and Campbell, 1993; Manel *et al*., 2001). However, a threshold dependent cross-tabulation was also carried out since this provided clarity in mapping predicted bird distributions. Three different threshold criteria were evaluated. Firstly a cut point of 0.5 was utilised, such as is often employed in studies involving cross-tabulations (for example, López and Moro, 1997). Additional thresholds (T) were determined based on Equations 4.2 and 4.3 (Mahoney and Atkinson, 2001).

$$T = \min(abs(sensitivity - specificity)) \qquad \textit{Equation 4.2}$$

$$T = \min(sqrt((1 - sensitivity)^2 + (1 - specificity)^2)) \qquad \textit{Equation 4.3}$$

The highest percentages of correctly predicted points were consistently obtained with the threshold defined by Equation 4.2. Consequently these cross-tabulations are quoted in the results tables.

Mann-Whitney tests were performed to compare the habitat and landscape characteristics of points which were correctly and incorrectly classified by the models. However, where multiple tests are carried out there is a risk that a proportion of significant results will be spurious due to chance (Bibby *et al.*, 1989; Bibby *et al.*, 1992). Thus these results were only used to give a description of differences occurring between correctly classified and misclassified points based on the 10 most significant variables differentiating the classes, in each case.

### *4.3.5 Model Application*

The models built using the East Loch Lomond data for 1998 were used to predict bird distributions at the same points for 2000 and for the Central Scotland Forest sample points for 1999. Likewise the CSF models were used to predict distributions at East Loch Lomond in both 1998 and 2000. The accuracy of these predictions was evaluated using the ROC plot and cross-tabulation methodology described in Section 4.3.4. These predictions were possible because equivalent variables had been measured for both the East Loch Lomond and the Central Scotland Forest sample points. However, the area of the circular plot within which habitat measurements were made was smaller for the CSF points. Thus it was necessary to scale down the East Loch Lomond measurements for predictions based on the CSF models. Likewise the CSF habitat variables had to be extrapolated for a larger area in order to apply the East Loch Lomond models. These adjustments made the assumption that the habitat was relatively homogeneous over a 20m radius around sample points at both East Loch Lomond and the CSF.

Models for each species for the CSF and for East Loch Lomond in 2000 were rebuilt using only those variables significant in the East Loch Lomond models for 1998 for the appropriate species. Conversely models were rebuilt for each species for East Loch Lomond in 1998 and 2000 based solely on the variables significant in the equivalent CSF models. The predictive power of these models was also tested using ROC plots and cross-tabulation. This made it possible to identify any bird-habitat relationships that were consistent between years and across sites.

To identify which variables explained most variation across all of the models, variables were grouped into general categories including local habitat variables, landscape variables and indirect parameters (slope and aspect). The proportion of variance accounted for by each group of variables was calculated and compared with the proportion of variables available for selection from each category. The percentage of variables significant when models were rebuilt for other sites and years were also calculated.

The relationship between the predictive power of the models and bird prevalence was assessed by plotting percentage presence for the original modelled data against the AUC values for the original data, and for the models built for the different sites and years using only variables selected in the original model. Curves were fitted to these plots using linear and polynomial terms as appropriate. This was to investigate whether the predictive accuracy of models was affected by deviations from a 50:50 ratio of presence and absence sample points in the data.

### *4.3.6 Calculation of an index of habitat occupancy*

Birds were divided into ubiquitous (robin, wren), coniferous (goldcrest, coal tit and siskin) and broad-leaved species (all other modelled species) based on the habitat associations indicated by the GLM and GAM models. An index of habitat occupancy was calculated for each species by subtracting the percentage of sample points at which each species was present from the percentage of points at which the general woodland type within which it would most commonly occur was present within a 100m radius of the points. This index gave a positive value where the percentage of times when habitat was present was greater than the percentage habitat occupancy by a species, and a negative value where percentage bird presence exceeded the frequency of occurrence of suitable woodland habitat based on general woodland categories.

## 4.4 Results

### *4.4.1 Bird distributions*

The most widely distributed species for both the ELL and CSF study areas was the chaffinch occurring at between 94% and 99% of sample points in all years.

There was too little variation in its occurrence for it to be meaningful to model this species. A total of 15 bird species were modelled, of which three were only modelled at ELL (redstart, wood warbler and siskin) and one was only modelled for the CSF (blackcap). This was due to the very low occurrence of these species at the CSF and ELL respectively (Table 4.2). The robin was the most widely distributed of the modelled species, for all sites and years. Other generally widely distributed species were the wren and willow warbler, although the precise ranking in the percentage of sample points at which these were present does show slight variation between sites and years (Table 4.2).

The main differences in species distributions between 1998 and 2000 at ELL occurred for the wood warbler, siskin and garden warbler. The number of sample points at which these species occurred declined considerably between 1998 and 2000. However, the differences in percentage presence were much greater between ELL 1998 and CSF 1999 than for ELL in the two sample years 1998 and 2000. The blue tit, great tit, blackbird and blackcap all occurred with greater frequency in the CSF compared with at ELL (Table 4.2).

Local habitat variables accounted for most of the explained variance in the models. As Table 4.3 shows, these variables accounted for 71.1% at ELL98 and 84.8% at CSF99, of variance explained. Birds could be classified as occurring in different habitat types based on the habitat variables in the models (Tables 4.4-4.18). There were three species favouring coniferous habitat (goldcrest, coal tit and siskin) (Tables 4.4-4.6). The robin and the wren occurred in both broad-leaved and coniferous habitat (Tables 4.7 and 4.8). The remaining species all favoured broad-leaved habitat with the treecreeper, wood warbler and redstart preferring woodland with less secondary growth present (Tables 4.9-4.18). A key to codes used in Tables 4.4-4.18 is given in Table 4.19.

**Table 4. 2: Percentage presence of the ubiquitous, coniferous and broad-leaved modelled species for ELL98, ELL00 and CSF99. The change in percentage presence between 1998 and 2000 for Loch Lomond is given in the column headed 'Diff.' Figures in bold indicate changes in percentage presence at ELL of at least 15 (an arbitrary cut point to highlight the species showing the greatest magnitude of change in % presence).**

| Habitat | Species | ELL | | | CSF |
|---|---|---|---|---|---|
| | | 1998 | 2000 | Diff. | 1999 |
| **Ubiquitous** | Robin | 80.50 | 92.00 | 11.50 | 91.01 |
| | Wren | 68.00 | 57.00 | -11.00 | 79.03 |
| **Coniferous** | Goldcrest | 58.50 | 50.50 | -8.00 | 39.33 |
| | Coal tit | 49.50 | 51.00 | 1.50 | 38.58 |
| | Siskin | 25.50 | 6.00 | **-19.50** | 0.75 |
| **Broad-leaved** | Willow warbler | 59.00 | 53.00 | -6.00 | 61.80 |
| | Treecreeper | 51.50 | 46.50 | -5.00 | 56.18 |
| | Wood warbler | 49.00 | 30.50 | **-18.50** | 2.25 |
| | Blue tit | 44.50 | 51.50 | 7.00 | 86.14 |
| | Garden warbler | 23.50 | 7.50 | **-16.00** | 17.60 |
| | Song thrush | 23.12 | 25.13 | 2.01 | 23.22 |
| | Great tit | 20.00 | 18.50 | -1.50 | 38.58 |
| | Blackbird | 17.00 | 18.50 | 1.50 | 74.53 |
| | Redstart | 15.50 | 21.50 | 6.00 | 0.75 |
| | Blackcap | 3.50 | 7.00 | 3.50 | 19.85 |

**Table 4. 3: The overall percentage variance explained by different general categories of variables where total variance explained was summed across all species modelled for each general variable category (a) and the percentage occurrence of variables from these categories (b) for the ELL98 and CSF99 models. The column (a)-(b) is the difference between the overall percentage variance explained and the proportion of variables present across all species modelled for each site for each general variable category. The largest differences (arbitrarily defined as those over five) are highlighted in bold italics. Figures in bold are total % variance and % variable occurrence in the models for the local and landscape variables.**

| Variable Categories | | ELL98 | | | CSF99 | | |
|---|---|---|---|---|---|---|---|
| | | a | b | (a)-(b) | a | b | (a)-(b) |
| **Local** | Ground cover | 7.49 | 9.57 | -2.08 | 18.80 | 8.54 | ***10.26*** |
| | Local habitat structure | 5.68 | 3.72 | 1.96 | 5.70 | 2.44 | 3.26 |
| | Tree species richness/ diversity measures | 0.99 | 1.60 | -0.61 | 0.62 | 1.22 | -0.60 |
| | BL general variables | 7.36 | 6.38 | 0.97 | 8.24 | 4.88 | 3.37 |
| | CF general variables | 22.88 | 5.32 | ***17.56*** | 7.58 | 4.07 | 3.51 |
| | BL species variables | 9.25 | 16.49 | ***-7.24*** | 28.17 | 34.55 | ***-6.38*** |
| | CF species variables | 10.57 | 9.57 | 0.99 | 7.26 | 8.13 | -0.87 |
| | Area 0-100m radius | 3.29 | 4.26 | -0.96 | 0.71 | 3.25 | -2.54 |
| | Edge 0-100m radius | 3.56 | 7.45 | -3.89 | 5.06 | 5.69 | -0.63 |
| | Ratio area/edge 0-100m radius | 0.00 | 1.06 | -1.06 | 1.98 | 0.81 | 1.17 |
| | PA 1,2 or 3ha continuous woodland | 0.00 | 1.60 | -1.60 | 0.65 | 1.22 | -0.57 |
| | | **71.08** | **67.02** | | **84.77** | **74.80** | |
| **Landscape** | Area 200-5000m radius | 9.36 | 10.64 | -1.27 | 9.48 | 8.13 | 1.35 |
| | Edge 200-5000m radius | 17.34 | 18.62 | -1.28 | 5.49 | 14.23 | ***-8.74*** |
| | Ratio area/edge 200-5000m radius | 0.00 | 2.66 | -2.66 | 0.35 | 2.03 | -1.69 |
| | | **26.70** | **31.91** | | **15.32** | **24.39** | |
| **Indirect** | Slope/ aspect | 1.92 | 1.06 | 0.86 | 0.00 | 0.81 | -0.81 |

**Table 4. 4: Generalized additive models (A) and evaluation (B) for the goldcrest for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.**

### (i) ELL98

### (A) Model

| Variable | East Loch Lomond | | | | Central Scotland Forest | |
|---|---|---|---|---|---|---|
| | 1998 | | 2000 | | 1999 | |
| | DF | F | DF | F | DF | F |
| No. CF Trees (dbh 16-24 cm) | 0.15 | 559.47 *** + | 1.03 | 14.14 *** + | 0.94 | 33.81 *** + |
| BL Edge (500 m radius) (km) | 0.82 | 117.84 *** - | 0.98 | 0.22 | 1.02 | 9.33 ** - |
| No. Pine (dbh <7 cm) | 0.83 | 55.28 *** + | 0.99 | 0.23 | 0.96 | 10.21 ** + |
| Area M (500 m radius) (ha) | 0.94 | 44.06 *** + | 1.78 | 5.38 ** ╮ | 1.02 | 0.06 |
| Area WD (200 m radius) (ha) | 4.81 | 12.62 *** ╭ | 4.02 | 3.23 ** ╯ | 3.92 | 3.22 ** ╭ |
| **Null** | **200.00** | | **200.00** | | **267.00** | |
| **Residual** | **190.19** | | **190.26** | | **258.03** | |
| **Adj. $D^2$** | **0.86** | | **0.49** | | **0.20** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |  |
| ELL | 1998 | Fit | Absent | 83 | 41.50 | **82** | **98.8** | 1 | 1.2 |  |  |  |
|  |  |  | Present | 117 | 58.50 | 3 | 2.6 | **114** | **97.4** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **98.10** | 0.99 ± 0.00 | *** |
|  |  | CV | Absent | 83 | 41.50 | **78** | **94.0** | 5 | 6.0 |  |  |  |
|  |  |  | Present | 117 | 58.50 | 10 | 8.5 | **107** | **91.5** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **92.75** | 0.98 ± 0.01 | *** |
|  | 2000 | Fit 1 | Absent | 99 | 49.50 | **89** | **89.9** | 10 | 10.1 |  |  |  |
|  |  |  | Present | 101 | 50.50 | 20 | 19.8 | **81** | **80.2** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **85.05** | 0.86 ± 0.03 | *** |
|  |  | Fit 2 | Absent | 99 | 49.50 | **92** | **92.9** | 7 | 7.1 |  |  |  |
|  |  |  | Present | 101 | 50.50 | 17 | 16.8 | **84** | **83.2** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **88.05** | 0.92 ± 0.02 | *** |
| CSF | 1999 | Fit 1 | Absent | 162 | 60.67 | **122** | **75.3** | 40 | 24.7 |  |  |  |
|  |  |  | Present | 105 | 39.33 | 43 | 41.0 | **62** | **59.0** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **67.15** | 0.75 ± 0.03 | *** |
|  |  | Fit 2 | Absent | 162 | 60.67 | **130** | **80.2** | 32 | 19.8 |  |  |  |
|  |  |  | Present | 105 | 39.33 | 32 | 30.5 | **73** | **69.5** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **74.85** | 0.80 ± 0.03 | *** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest |  |  |  | East Loch Lomond |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 1999 |  |  |  | 1998 |  |  |  | 2000 |  |  |  |
|  | DF | F |  |  | DF | F |  |  | DF | F |  |  |
| No. CF Trees (dbh >7 cm) | 1.00 | 36.51 | *** | + | 0.87 | 182.00 | *** | + | 0.86 | 56.88 | *** | + |
| BL Edge (100 m radius) (km) | 1.00 | 18.70 | *** | - | 1.04 | 5.69 | * | - | 1.02 | 1.51 |  |  |
| No. Pine (dbh >30 cm) | 1.01 | 15.11 | *** | + | 1.01 | 5.62 | * | + | 0.84 | 1.42 |  |  |
| CF Edge (100 m radius) (km) | 1.00 | 6.26 | * | + | 1.01 | 2.19 |  |  | 1.00 | 0.10 |  |  |
| No. Sycamore (dbh 24-30 cm) | 1.00 | 10.85 | *** | - |  |  |  |  |  |  |  |  |
| No. BL Snags (dbh 7-16 cm) | 0.99 | 18.71 | *** | - | 1.01 | 0.44 |  |  | 1.00 | 0.35 |  |  |
| % Fern cover (not bracken) | 3.95 | 8.64 | *** | ∿ | 3.83 | 2.00 |  |  | 3.81 | 0.74 |  |  |
| No. Gean (dbh <7 cm) | 1.00 | 9.19 | ** | - |  |  |  |  |  |  |  |  |
| No. Lime (dbh <7 cm) | 1.00 | 8.22 | ** | - |  |  |  |  |  |  |  |  |
| Fallen dead BL rating | 1.00 | 6.54 | ** | + | 1.01 | 2.71 |  |  | 0.99 | 0.44 |  |  |
| **Null** | **267.00** |  |  |  | **200.00** |  |  |  | **200.00** |  |  |  |
| **Residual** | **253.05** |  |  |  | **189.17** |  |  |  | **189.19** |  |  |  |
| **Adj. $D^2$** | **0.40** |  |  |  | **0.69** |  |  |  | **0.47** |  |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |
| CSF | 1999 | Fit | Absent | 162 | 60.67 | **146** | **90.1** | 16 | 9.9 |  |  |
|  |  |  | Present | 105 | 39.33 | 27 | 25.7 | **78** | **74.3** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **82.20** | 0.89 ± 0.02 *** |
|  |  | CV | Absent | 162 | 60.67 | **125** | **77.2** | 37 | 22.8 |  |  |
|  |  |  | Present | 105 | 39.33 | 20 | 19.0 | **85** | **81.0** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **79.10** | 0.86 ± 0.02 *** |
| ELL | 1998 | Fit 1 | Absent | 83 | 41.50 | **75** | **90.4** | 8 | 9.6 |  |  |
|  |  |  | Present | 117 | 58.50 | 17 | 14.5 | **100** | **85.5** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **87.95** | 0.94 ± 0.02 *** |
|  |  | Fit 2 | Absent | 83 | 41.50 | **79** | **95.2** | 4 | 4.8 |  |  |
|  |  |  | Present | 117 | 58.50 | 11 | 9.4 | **106** | **90.6** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **92.90** | 0.97 ± 0.01 *** |
|  | 2000 | Fit 1 | Absent | 99 | 49.50 | **85** | **85.9** | 14 | 14.1 |  |  |
|  |  |  | Present | 101 | 50.50 | 22 | 21.8 | **79** | **78.2** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **82.05** | 0.86 ± 0.03 *** |
|  |  | Fit 2 | Absent | 99 | 49.50 | **90** | **90.9** | 9 | 9.1 |  |  |
|  |  |  | Present | 101 | 50.50 | 17 | 16.8 | **84** | **83.2** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **87.05** | 0.92 ± 0.02 *** |

## Table 4. 5: Generalized additive and generalized linear models (A) and evaluation (B) for the coal tit for (i) the ELL98 GAM and its rebuild for ELL00 and CSF99 and (ii) the CSF99 GLM and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond |  |  |  | Central Scotland Forest |  |
|---|---|---|---|---|---|---|
|  | 1998 |  | 2000 |  | 1999 |  |
|  | DF | F | DF | F | DF | F |
| No. CF Trees (dbh >30 cm) | 1.05 | 14.14 *** + | 0.95 | 14.95 *** + | 1.16 | 21.37 *** + |
| Area M (2500m radius) (ha) | 3.99 | 7.42 *** ◞ | 3.81 | 1.85 | 4.00 | 0.86 |
| No. Birch (dbh 7-16 cm) | 0.99 | 10.76 *** + | 1.00 | 0.04 | 0.99 | 1.17 |
| No. Spruce (dbh >30 cm) | 0.98 | 13.28 *** + | 0.98 | 6.87 ** + | 1.00 | 0.07 |
| Area BL (100 m radius) (ha) | 0.99 | 6.59 ** - | 1.00 | 0.39 | 1.20 | 3.46 * - |
| No. Hazel (dbh >7 cm) | 1.17 | 6.48 ** - | 1.00 | 4.38 * - | 1.00 | 0.83 |
| **Null** | **200.00** |  | **200.00** |  | **267.00** |  |
| **Residual** | **190.01** |  | **190.19** |  | **257.00** |  |
| **Adj. $D^2$** | **0.53** |  | **0.22** |  | **0.12** |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points No. | Sample Points % | Points predicted as Absent No. | Absent % | Points predicted as Present No. | Present % | Total % correct | ROC AUC ± SE |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ELL | 1998 | Fit | Absent | 101 | 50.50 | **87** | **86.1** | 14 | 13.9 | | |
| | | | Present | 99 | 49.50 | 8 | 8.1 | **91** | **91.9** | | |
| | | | Total | 200 | | | | | | **89.00** | 0.94 ± 0.02 *** |
| | | CV | Absent | 101 | 50.50 | **87** | **86.1** | 14 | 13.9 | | |
| | | | Present | 99 | 49.50 | 12 | 12.1 | **87** | **87.9** | | |
| | | | Total | 200 | | | | | | **87.00** | 0.92 ± 0.02 *** |
| | 2000 | Fit 1 | Absent | 98 | 49.00 | **73** | **74.5** | 25 | 25.5 | | |
| | | | Present | 102 | 51.00 | 25 | 24.5 | **77** | **75.5** | | |
| | | | Total | 200 | | | | | | **75.00** | 0.78 ± 0.03 *** |
| | | Fit 2 | Absent | 98 | 49.00 | **79** | **80.6** | 19 | 19.4 | | |
| | | | Present | 102 | 51.00 | 28 | 27.5 | **74** | **72.5** | | |
| | | | Total | 200 | | | | | | **76.55** | 0.81 ± 0.03 *** |
| CSF | 1999 | Fit 1 | Absent | 164 | 61.42 | **106** | **64.6** | 58 | 35.4 | | |
| | | | Present | 103 | 38.58 | 44 | 42.7 | **59** | **57.3** | | |
| | | | Total | 267 | | | | | | **60.95** | 0.63 ± 0.03 *** |
| | | Fit 2 | Absent | 164 | 61.42 | **118** | **72.0** | 46 | 28.0 | | |
| | | | Present | 103 | 38.58 | 35 | 34.0 | **68** | **66.0** | | |
| | | | Total | 267 | | | | | | **69.00** | 0.75 ± 0.03 *** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest 1999 DF | Central Scotland Forest 1999 F | East Loch Lomond 1998 DF | East Loch Lomond 1998 F | East Loch Lomond 2000 DF | East Loch Lomond 2000 F |
|---|---|---|---|---|---|---|
| Fallen dead CF rating | 1.00 | 15.97 *** + | 1.00 | 0.40 | 1.00 | 0.64 |
| No. CF (dbh 16-24 cm) | 1.00 | 9.85 ** + | 1.00 | 12.15 *** + | 1.00 | 27.07 *** + |
| No. Lime (dbh <7 cm) | 1.00 | 16.93 *** + | | | | |
| % Litter cover | 1.00 | 7.27 ** + | 1.00 | 3.21 | 1.00 | 0.13 |
| M-CF (100 m radius) (km) | 1.00 | 7.26 ** + | 1.00 | 2.53 | 1.00 | 1.29 |
| No. Lime (dbh >7 cm) | 1.00 | 8.22 ** - | | | | |
| No. BL Snags (dbh >7 cm) | 1.00 | 5.53 * - | 1.00 | 0.00 | 1.00 | 1.43 |
| No. Hazel (dbh <7 cm) | 1.00 | 5.19 * + | 1.00 | 0.38 | 1.00 | 0.20 |
| Area WD (5000m radius) (ha) | 1.00 | 4.27 * - | 1.00 | 2.82 | 1.00 | 1.32 |
| **Null** | **267.00** | | **200.00** | | **200.00** | |
| **Residual** | **257.00** | | **192.00** | | **192.00** | |
| **Adj. $D^2$** | **0.27** | | **0.29** | | **0.20** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |
| CSF | 1999 | Fit | Absent | 164 | 61.42 | **122** | **74.4** | 42 | 25.6 |  |  |
|  |  |  | Present | 103 | 38.58 | 24 | 23.3 | **79** | **76.7** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **75.55** | 0.84 ± 0.03 *** |
|  |  | CV | Absent | 164 | 61.42 | **130** | **79.3** | 34 | 20.7 |  |  |
|  |  |  | Present | 103 | 38.58 | 34 | 33.0 | **69** | **67.0** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **73.15** | 0.79 ± 0.03 *** |
| ELL | 1998 | Fit 1 | Absent | 101 | 50.50 | **79** | **78.2** | 22 | 21.8 |  |  |
|  |  |  | Present | 99 | 49.50 | 12 | 12.1 | **87** | **87.9** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **83.05** | 0.84 ± 0.03 *** |
|  |  | Fit 2 | Absent | 101 | 50.50 | **85** | **84.2** | 16 | 15.8 |  |  |
|  |  |  | Present | 99 | 49.50 | 15 | 15.2 | **84** | **84.8** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **84.50** | 0.88 ± 0.03 *** |
|  | 2000 | Fit 1 | Absent | 98 | 49.00 | **63** | **64.3** | 35 | 35.7 |  |  |
|  |  |  | Present | 102 | 51.00 | 26 | 25.5 | **76** | **74.5** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **69.40** | 0.72 ± 0.04 *** |
|  |  | Fit 2 | Absent | 98 | 49.00 | **86** | **87.8** | 12 | 12.2 |  |  |
|  |  |  | Present | 102 | 51.00 | 33 | 32.4 | **69** | **67.6** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **77.70** | 0.80 ± 0.03 *** |

## Table 4. 6: Generalized linear model (A) and evaluation (B) for the siskin for the ELL98 model and its rebuild for ELL00.

## (A) Model

| Variable | East Loch Lomond |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
|  | 1998 |  |  |  | 2000 |  |  |  |
|  | DF | F |  |  | DF | F |  |  |
| No. CF Trees (dbh >7 cm) | 1.00 | 19.57 | *** | + | 1.00 | 6.26 | ** | + |
| WD Edge (2500m radius) (km) | 1.00 | 14.34 | *** | + | 1.00 | 3.91 | * | + |
| No. BL Trees (dbh <7 cm) | 1.00 | 12.67 | *** | - | 1.00 | 2.56 |  |  |
| No. CF Snags (dbh <7 cm) | 1.00 | 7.13 | ** | - | 1.00 | 2.64 |  |  |
| % Bare ground | 1.00 | 4.81 | * | - | 1.00 | 6.88 | ** | - |
| Tree Species Richness | 1.00 | 12.09 | *** | + | 1.00 | 16.67 | *** | + |
| BL-CF (500 m radius) (km) | 1.00 | 10.40 | *** | - | 1.00 | 0.00 |  |  |
| % Fern cover (not bracken) | 1.00 | 5.15 | * | - | 1.00 | 0.88 |  |  |
| **Null** | **200.00** |  |  |  | **200.00** |  |  |  |
| **Residual** | **191.00** |  |  |  | **191.00** |  |  |  |
| **Adj. $D^2$** | **0.26** |  |  |  | **0.15** |  |  |  |

### (B) Evaluation

| Location | Year | Model | Observed status | Sample Points No. | Sample Points % | Points predicted as Absent No. | Absent % | Points predicted as Present No. | Present % | Total % correct | ROC AUC ± SE | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ELL | 1998 | Fit | Absent | 149 | 74.50 | **104** | **69.8** | 45 | 30.2 | | | |
| | | | Present | 51 | 25.50 | 8 | 15.7 | **43** | **84.3** | | | |
| | | | Total | 200 | | | | | | **77.05** | 0.84 ± 0.03 | *** |
| | | CV | Absent | 149 | 74.50 | **111** | **74.5** | 38 | 25.5 | | | |
| | | | Present | 51 | 25.50 | 13 | 25.5 | **38** | **74.5** | | | |
| | | | Total | 200 | | | | | | **74.50** | 0.79 ± 0.04 | *** |
| | 2000 | Fit 1 | Absent | 188 | 94.00 | **145** | **77.1** | 43 | 22.9 | | | |
| | | | Present | 12 | 6.00 | 4 | 33.3 | **8** | **66.7** | | | |
| | | | Total | 200 | | | | | | **71.90** | 0.67 ± 0.09 | * |
| | | Fit 2 | Absent | 188 | 94.00 | **125** | **66.5** | 63 | 33.5 | | | |
| | | | Present | 12 | 6.00 | 3 | 25.0 | **9** | **75.0** | | | |
| | | | Total | 200 | | | | | | **70.75** | 0.75 ± 0.05 | *** |

## Table 4. 7: Generalized additive models (A) and evaluation (B) for the robin for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.

### (i) ELL98

### (A) Model

| Variable | East Loch Lomond | | | | | | | | Central Scotland Forest | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1998 | | | | 2000 | | | | 1999 | | | |
| | DF | F | | | DF | F | | | DF | F | | |
| CF Edge (50 m radius) (km) | 1.24 | 18.43 | *** | + | 1.00 | 0.60 | | | 0.99 | 0.94 | | |
| M Edge (1000m radius) (km) | 1.00 | 11.38 | *** | + | 1.00 | 0.54 | | | 1.01 | 10.32 | *** | + |
| No. BL Snags (dbh <7 cm) | 1.24 | 8.47 | ** | + | 1.08 | 8.07 | ** | + | 1.01 | 0.57 | | |
| Fallen dead CF rating | 1.00 | 16.93 | *** | - | 1.00 | 1.05 | | | 0.92 | 3.95 | * | - |
| No. CF Trees (dbh 24-30 cm) | 1.00 | 10.77 | *** | + | 0.97 | 28.98 | *** | + | 0.97 | 5.47 | * | + |
| No. Alder (dbh <7 cm) | 4.00 | 6.86 | *** | ╮ | 3.59 | 3.01 | * | ╭ | 3.62 | 2.59 | * | ╯ |
| **Null** | **200.00** | | | | **200.00** | | | | **200.00** | | | |
| **Residual** | **190.00** | | | | **190.40** | | | | **257.36** | | | |
| **Adj. $D^2$** | **0.34** | | | | **0.18** | | | | **0.04** | | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |  |
| ELL | 1998 | Fit | Absent | 39 | 19.50 | **35** | **89.7** | 4 | 10.3 |  |  |  |
|  |  |  | Present | 161 | 80.50 | 43 | 26.7 | **118** | **73.3** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **81.50** | 0.85 ± 0.03 | *** |
|  |  | CV | Absent | 39 | 19.50 | **34** | **87.2** | 5 | 12.8 |  |  |  |
|  |  |  | Present | 161 | 80.50 | 51 | 31.7 | **110** | **68.3** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **77.75** | 0.80 ± 0.03 | *** |
|  | 2000 | Fit 1 | Absent | 16 | 8.00 | **10** | **62.5** | 6 | 37.5 |  |  |  |
|  |  |  | Present | 184 | 92.00 | 61 | 33.2 | **123** | **66.8** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **64.65** | 0.62 ± 0.08 |  |
|  |  | Fit 2 | Absent | 16 | 8.00 | **13** | **81.3** | 3 | 18.8 |  |  |  |
|  |  |  | Present | 184 | 92.00 | 75 | 40.8 | **109** | **59.2** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **70.25** | 0.77 ± 0.05 | *** |
| CSF | 1999 | Fit 1 | Absent | 24 | 8.99 | **14** | **58.3** | 10 | 41.7 |  |  |  |
|  |  |  | Present | 243 | 91.01 | 104 | 42.8 | **139** | **57.2** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **57.75** | 0.59 ± 0.06 |  |
|  |  | Fit 2 | Absent | 24 | 8.99 | **15** | **62.5** | 9 | 37.5 |  |  |  |
|  |  |  | Present | 243 | 91.01 | 89 | 36.6 | **154** | **63.4** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **62.95** | 0.65 ± 0.05 | ** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest |  |  |  | East Loch Lomond |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 1999 |  |  |  | 1998 |  |  |  | 2000 |  |  |  |
|  | DF | F |  |  | DF | F |  |  | DF | F |  |  |
| % Grass cover | 0.98 | 46.50 | *** | - | 1.01 | 2.81 |  |  | 1.06 | 9.29 | ** | - |
| No. Willow (dbh >7 cm) | 1.09 | 27.78 | *** | + |  |  |  |  |  |  |  |  |
| No. CF (dbh 7-16 cm) | 0.99 | 16.15 | *** | + | 1.00 | 1.70 |  |  | 1.12 | 16.04 | *** | + |
| No. Ash (dbh 24-30 cm) | 0.99 | 12.58 | *** | + | 1.00 | 1.14 |  |  | 1.10 | 2.86 |  |  |
| No. BL Trees (dbh 16-24 cm) | 3.95 | 17.26 | *** | ∿ | 3.80 | 2.98 | * | ⌒ | 3.88 | 7.55 | *** | ∿ |
| No. Beech (dbh <7 cm) | 0.99 | 12.38 | *** | + | 1.00 | 0.33 |  |  | 1.00 | 1.45 |  |  |
| No. Hazel (dbh >7 cm) | 1.00 | 6.13 | * | + | 1.01 | 1.25 |  |  | 1.04 | 15.64 | *** | + |
| % Heather cover | 0.95 | 12.78 | *** | + | 1.00 | 1.03 |  |  | 0.99 | 2.16 |  |  |
| No. BL (dbh <7 cm) | 0.98 | 20.27 | *** | + | 1.01 | 1.37 |  |  | 1.07 | 5.06 | * | + |
| **Null** | **267.00** |  |  |  | **200.00** |  |  |  | **200.00** |  |  |  |
| **Residual** | **254.05** |  |  |  | **188.20** |  |  |  | **188.12** |  |  |  |
| **Adj. $D^2$** | **0.55** |  |  |  | **0.03** |  |  |  | **0.27** |  |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| CSF | 1999 | Fit | Absent | 24 | 8.99 | **24** | **100.0** | 0 | 0.0 | | |
| | | | Present | 243 | 91.01 | 39 | 16.0 | **204** | **84.0** | | |
| | | | Total | 267 | | | | | | **92.00** | 0.93 ± 0.02 *** |
| | | CV | Absent | 24 | 8.99 | **20** | **83.3** | 4 | 16.7 | | |
| | | | Present | 243 | 91.01 | 46 | 18.9 | **197** | **81.1** | | |
| | | | Total | 267 | | | | | | **82.20** | 0.88 ± 0.03 *** |
| ELL | 1998 | Fit 1 | Absent | 39 | 19.50 | **20** | **51.3** | 19 | 48.7 | | |
| | | | Present | 161 | 80.50 | 57 | 35.4 | **104** | **64.6** | | |
| | | | Total | 200 | | | | | | **57.95** | 0.57 ± 0.05 |
| | | Fit 2 | Absent | 39 | 19.50 | **27** | **69.2** | 12 | 30.8 | | |
| | | | Present | 161 | 80.50 | 52 | 32.3 | **109** | **67.7** | | |
| | | | Total | 200 | | | | | | **68.45** | 0.69 ± 0.05 *** |
| | 2000 | Fit 1 | Absent | 16 | 8.00 | **14** | **87.5** | 2 | 12.5 | | |
| | | | Present | 184 | 92.00 | 60 | 32.6 | **124** | **67.4** | | |
| | | | Total | 200 | | | | | | **77.45** | 0.72 ± 0.07 ** |
| | | Fit 2 | Absent | 16 | 8.00 | **12** | **75.0** | 4 | 25.0 | | |
| | | | Present | 184 | 92.00 | 35 | 19.0 | **149** | **81.0** | | |
| | | | Total | 200 | | | | | | **78.00** | 0.84 ± 0.04 *** |

**Table 4. 8: Generalized linear models (A) and evaluation (B) for the wren for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.**

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond | | | | | | | | Central Scotland Forest | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1998 | | | | 2000 | | | | 1999 | |
| | DF | F | | | DF | F | | | DF | F |
| No. Spruce (dbh 16-24 cm) | 1.00 | 30.46 | *** | - | 1.00 | 7.04 | ** | - | 1.00 | 0.01 |
| Slope angle (degrees) | 1.00 | 8.96 | ** | - | 1.00 | 4.06 | * | - | 1.00 | 0.10 |
| WD Edge (200 m radius) (km) | 1.00 | 7.21 | ** | + | 1.00 | 13.34 | *** | + | 1.00 | 1.55 |
| M-CF (50 m radius) (km) | 1.00 | 9.83 | ** | + | 1.00 | 0.22 | | | 1.00 | 0.73 |
| CF Edge (5000m radius) (km) | 1.00 | 11.04 | *** | + | 1.00 | 0.30 | | | 1.00 | 0.88 |
| No. Trees (4-10 m) | 1.00 | 5.49 | * | - | 1.00 | 1.06 | | | 1.00 | 0.66 |
| **Null** | **200.00** | | | | **200.00** | | | | **267.00** | |
| **Residual** | **193.00** | | | | **193.00** | | | | **260.00** | |
| **Adj. $D^2$** | **0.29** | | | | **0.14** | | | | **-0.01** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± | SE |  |
| ELL | 1998 | Fit | Absent | 64 | 32.00 | **49** | **76.6** | 15 | 23.4 |  |  |  |  |
|  |  |  | Present | 136 | 68.00 | 35 | 25.7 | **101** | **74.3** |  |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **75.45** | 0.85 ± | 0.03 | *** |
|  |  | CV | Absent | 64 | 32.00 | **49** | **76.6** | 15 | 23.4 |  |  |  |  |
|  |  |  | Present | 136 | 68.00 | 39 | 28.7 | **97** | **71.3** |  |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **73.95** | 0.80 ± | 0.03 | *** |
|  | 2000 | Fit 1 | Absent | 86 | 43.00 | **58** | **67.4** | 28 | 32.6 |  |  |  |  |
|  |  |  | Present | 114 | 57.00 | 29 | 25.4 | **85** | **74.6** |  |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **71.00** | 0.74 ± | 0.04 | *** |
|  |  | Fit 2 | Absent | 86 | 43.00 | **68** | **79.1** | 18 | 20.9 |  |  |  |  |
|  |  |  | Present | 114 | 57.00 | 40 | 35.1 | **74** | **64.9** |  |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **72.00** | 0.77 ± | 0.03 | *** |
| CSF | 1999 | Fit 1 | Absent | 56 | 20.97 | **31** | **55.4** | 25 | 44.6 |  |  |  |  |
|  |  |  | Present | 211 | 79.03 | 95 | 45.0 | **116** | **55.0** |  |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **55.20** | 0.54 ± | 0.04 |  |
|  |  | Fit 2 | Absent | 56 | 20.97 | **29** | **51.8** | 27 | 48.2 |  |  |  |  |
|  |  |  | Present | 211 | 79.03 | 83 | 39.3 | **128** | **60.7** |  |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **56.25** | 0.58 ± | 0.04 |  |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest |  |  |  | East Loch Lomond |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 1999 |  |  |  | 1998 |  |  |  | 2000 |  |  |  |
|  | DF | F |  |  | DF | F |  |  | DF | F |  |  |
| No. BL Snags (dbh 24-30 cm) | 1.00 | 10.49 | *** | + | 1.00 | 3.60 | * | - | 1.00 | 1.24 |  |  |
| No. Trees (<2 m) | 1.00 | 15.86 | *** | + | 1.00 | 0.26 |  |  | 1.00 | 0.03 |  |  |
| % Water cover | 1.00 | 20.33 | *** | + | 1.00 | 1.03 |  |  | 1.00 | 8.85 | ** | + |
| No. BL Snags (dbh 16-24 cm) | 1.00 | 7.97 | ** | + | 1.00 | 3.49 |  |  | 1.00 | 0.00 |  |  |
| BL-M (500 m radius) (km) | 1.00 | 14.56 | *** | + | 1.00 | 0.01 |  |  | 1.00 | 0.58 |  |  |
| Area BL (500 m radius) (ha) | 1.00 | 24.49 | *** | - | 1.00 | 3.51 |  |  | 1.00 | 3.77 | * | + |
| % Bracken cover | 1.00 | 16.27 | *** | + | 1.00 | 0.07 |  |  | 1.00 | 2.28 |  |  |
| No. Willow (dbh <7 cm) | 1.00 | 11.98 | *** | - |  |  |  |  |  |  |  |  |
| No. Larch (dbh 16-24 cm) | 1.00 | 9.95 | ** | - | 1.00 | 0.00 |  |  | 1.00 | 0.73 |  |  |
| P/A Bogs, fens or flushes | 1.00 | 7.45 | ** | P>A | 1.00 | 1.33 |  |  | 1.00 | 0.07 |  |  |
| % Bramble cover | 1.00 | 4.47 | * | + | 1.00 | 1.45 |  |  | 1.00 | 0.60 |  |  |
| **Null** | **267.00** |  |  |  | **200.00** |  |  |  | **200.00** |  |  |  |
| **Residual** | **255.00** |  |  |  | **189.00** |  |  |  | **189.00** |  |  |  |
| **Adj. $D^2$** | **0.29** |  |  |  | **0.06** |  |  |  | **0.07** |  |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |  |
| CSF | 1999 | Fit | Absent | 56 | 20.97 | **46** | **82.1** | 10 | 17.9 |  |  |  |
|  |  |  | Present | 211 | 79.03 | 59 | 28.0 | **152** | **72.0** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **77.05** | 0.84 ± 0.03 | *** |
|  |  | CV | Absent | 56 | 20.97 | **47** | **83.9** | 9 | 16.1 |  |  |  |
|  |  |  | Present | 211 | 79.03 | 63 | 29.9 | **148** | **70.1** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **77.00** | 0.81 ± 0.03 | *** |
| ELL | 1998 | Fit 1 | Absent | 64 | 32.00 | **30** | **46.9** | 34 | 53.1 |  |  |  |
|  |  |  | Present | 136 | 68.00 | 36 | 26.5 | **100** | **73.5** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **60.20** | 0.60 ± 0.04 | ** |
|  |  | Fit 2 | Absent | 64 | 32.00 | **39** | **60.9** | 25 | 39.1 |  |  |  |
|  |  |  | Present | 136 | 68.00 | 36 | 26.5 | **100** | **73.5** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **67.20** | 0.70 ± 0.04 | *** |
|  | 2000 | Fit 1 | Absent | 86 | 43.00 | **60** | **69.8** | 26 | 30.2 |  |  |  |
|  |  |  | Present | 114 | 57.00 | 55 | 48.2 | **59** | **51.8** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **60.80** | 0.62 ± 0.04 | ** |
|  |  | Fit 2 | Absent | 86 | 43.00 | **72** | **83.7** | 14 | 16.3 |  |  |  |
|  |  |  | Present | 114 | 57.00 | 56 | 49.1 | **58** | **50.9** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **67.30** | 0.71 ± 0.04 | *** |

## Table 4. 9: Generalized additive and generalized linear models (A) and evaluation (B) for the song thrush for (i) the ELL98 GAM and its rebuild for ELL00 and CSF99 and (ii) the CSF99 GLM and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond |  |  |  |  |  |  |  | Central Scotland Forest |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 1998 |  |  |  | 2000 |  |  |  | 1999 |  |  |  |
|  | DF | F |  |  | DF | F |  |  | DF | F |  |  |
| BL-CF (500 m radius) (km) | 1.20 | 15.06 | *** | + | 1.00 | 2.08 |  |  | 1.00 | 1.44 |  |  |
| % Fern cover (not bracken) | 1.20 | 12.28 | *** | - | 1.00 | 0.26 |  |  | 1.00 | 0.05 |  |  |
| No. BL Trees (dbh 7-16 cm) | 1.18 | 26.01 | *** | + | 0.97 | 2.33 |  |  | 0.99 | 0.48 |  |  |
| % Bare ground | 1.01 | 9.25 | ** | - | 0.99 | 1.77 |  |  | 1.00 | 0.02 |  |  |
| No. Birch (dbh 24-30 cm) | 0.99 | 11.92 | *** | - | 1.01 | 7.36 | ** | - | 1.00 | 0.67 |  |  |
| No. Hazel (dbh <7 cm) | 1.19 | 11.14 | *** | - | 1.07 | 8.51 | ** | - | 0.98 | 1.61 |  |  |
| Area WD (5000m radius) (ha) | 3.97 | 4.80 | *** | + | 3.88 | 0.77 |  |  | 3.92 | 2.49 | * | ∪ |
| **Null** | **199.00** |  |  |  | **199.00** |  |  |  | **267.00** |  |  |  |
| **Residual** | **188.03** |  |  |  | **188.12** |  |  |  | **256.08** |  |  |  |
| **Adj. $D^2$** | **0.28** |  |  |  | **0.06** |  |  |  | **0.00** |  |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |
| ELL | 1998 | Fit | Absent | 153 | 76.88 | **115** | **75.2** | 38 | 24.8 |  |  |
|  |  |  | Present | 46 | 23.12 | 12 | 26.1 | **34** | **73.9** |  |  |
|  |  |  | Total | 199 |  |  |  |  |  | **74.55** | 0.84 ± 0.03 *** |
|  |  | CV | Absent | 153 | 76.88 | **117** | **76.5** | 36 | 23.5 |  |  |
|  |  |  | Present | 46 | 23.12 | 16 | 34.8 | **30** | **65.2** |  |  |
|  |  |  | Total | 199 |  |  |  |  |  | **70.85** | 0.77 ± 0.04 *** |
|  | 2000 | Fit 1 | Absent | 149 | 74.87 | **94** | **63.1** | 55 | 36.9 |  |  |
|  |  |  | Present | 50 | 25.13 | 16 | 32.0 | **34** | **68.0** |  |  |
|  |  |  | Total | 199 |  |  |  |  |  | **65.55** | 0.67 ± 0.04 *** |
|  |  | Fit 2 | Absent | 149 | 74.87 | **94** | **63.1** | 55 | 36.9 |  |  |
|  |  |  | Present | 50 | 25.13 | 14 | 28.0 | **36** | **72.0** |  |  |
|  |  |  | Total | 199 |  |  |  |  |  | **67.55** | 0.72 ± 0.04 *** |
| CSF | 1999 | Fit 1 | Absent | 205 | 76.78 | **87** | **42.4** | 118 | 57.6 |  |  |
|  |  |  | Present | 62 | 23.22 | 26 | 41.9 | **36** | **58.1** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **50.25** | 0.48 ± 0.04 |
|  |  | Fit 2 | Absent | 205 | 76.78 | **118** | **57.6** | 87 | 42.4 |  |  |
|  |  |  | Present | 62 | 23.22 | 22 | 35.5 | **40** | **64.5** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **61.05** | 0.64 ± 0.04 ** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest |  |  | East Loch Lomond |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  | 1999 |  |  | 1998 |  |  | 2000 |  |  |
|  | DF | F |  | DF | F |  | DF | F |  |
| No. Larch (dbh <7 cm) | 1.00 | 16.11 *** | + | 1.00 | 0.03 |  | 1.00 | 1.98 |  |
| No. Larch (dbh 24-30 cm) | 1.00 | 18.70 *** | - | 1.00 | 0.25 |  | 1.00 | 0.52 |  |
| M Edge (50 m radius) (km) | 1.00 | 18.59 *** | - | 1.00 | 2.29 |  | 1.00 | 2.50 |  |
| % Reeds cover | 1.00 | 18.18 *** | - | 1.00 | 3.70 * | - | 1.00 | 1.46 |  |
| M-CF (1000m radius) (km) | 1.00 | 10.00 ** | + | 1.00 | 0.03 |  | 1.00 | 5.84 * | - |
| No. Alder (dbh 16-24 cm) | 1.00 | 11.19 *** | - | 1.00 | 1.61 |  | 1.00 | 0.40 |  |
| P/A 2 ha continuous wood | 1.00 | 11.44 *** | P>A | 1.00 | 1.39 |  | 1.00 | 18.16 *** | P>A |
| No. Ash (dbh 24-30 cm) | 1.00 | 9.65 ** | - | 1.00 | 2.04 |  | 1.00 | 0.12 |  |
| No. Yew (dbh >7 cm) | 1.00 | 8.24 ** | - |  |  |  |  |  |  |
| P/A Old coppice | 1.00 | 10.58 *** | P<A | 1.00 | 0.07 |  | 1.00 | 0.26 |  |
| Wood area/edge ratio 50m | 1.00 | 10.67 *** | + | 1.00 | 1.23 |  | 1.00 | 17.12 *** | - |
| No. Trees (4-10 m) | 1.00 | 8.80 ** | - | 1.00 | 0.13 |  | 1.00 | 0.31 |  |
| **Null** | **267.00** |  |  | **200.00** |  |  | **200.00** |  |  |
| **Residual** | **254.00** |  |  | **188.00** |  |  | **188.00** |  |  |
| **Adj. $D^2$** | **0.27** |  |  | **0.00** |  |  | **0.12** |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| CSF | 1999 | Fit | Absent | 205 | 76.78 | **155** | **75.6** | 50 | 24.4 | | |
| | | | Present | 62 | 23.22 | 15 | 24.2 | **47** | **75.8** | | |
| | | | Total | 267 | | | | | | **75.70** | 0.83 ± 0.03 *** |
| | | CV | Absent | 205 | 76.78 | **146** | **71.2** | 59 | 28.8 | | |
| | | | Present | 62 | 23.22 | 11 | 17.7 | **51** | **82.3** | | |
| | | | Total | 267 | | | | | | **76.75** | 0.80 ± 0.03 *** |
| ELL | 1998 | Fit 1 | Absent | 154 | 77.00 | **88** | **57.1** | 66 | 42.9 | | |
| | | | Present | 46 | 23.00 | 18 | 39.1 | **28** | **60.9** | | |
| | | | Total | 200 | | | | | | **59.00** | 0.56 ± 0.05 |
| | | Fit 2 | Absent | 154 | 77.00 | **91** | **59.1** | 63 | 40.9 | | |
| | | | Present | 46 | 23.00 | 16 | 34.8 | **30** | **65.2** | | |
| | | | Total | 200 | | | | | | **62.15** | 0.63 ± 0.04 ** |
| | 2000 | Fit 1 | Absent | 150 | 75.00 | **86** | **57.3** | 64 | 42.7 | | |
| | | | Present | 50 | 25.00 | 21 | 42.0 | **29** | **58.0** | | |
| | | | Total | 200 | | | | | | **57.65** | 0.53 ± 0.05 |
| | | Fit 2 | Absent | 150 | 75.00 | **100** | **66.7** | 50 | 33.3 | | |
| | | | Present | 50 | 25.00 | 15 | 30.0 | **35** | **70.0** | | |
| | | | Total | 200 | | | | | | **68.35** | 0.72 ± 0.04 *** |

## Table 4. 10: Generalized additive models (A) and evaluation (B) for the garden warbler for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond | | | | Central Scotland Forest | |
|---|---|---|---|---|---|---|
| | 1998 | | 2000 | | 1999 | |
| | DF | F | DF | F | DF | F |
| No. CF Trees (dbh >7 cm) | 0.96 | 37.31 *** - | 1.00 | 96.39 *** - | 0.99 | 3.51 |
| BL-CF (200 m radius) (km) | 1.10 | 15.64 *** + | 1.01 | 3.58 | 1.00 | 0.03 |
| M Edge (2500m radius) (km) | 1.05 | 21.01 *** - | 1.00 | 0.00 | 1.00 | 2.55 |
| No. Birch (dbh <7 cm) | 1.00 | 6.33 ** + | 1.09 | 16.85 *** + | 1.00 | 7.34 ** - |
| No. Holly (dbh <7 cm) | 1.02 | 6.26 ** - | 1.00 | 12.56 *** - | 1.00 | 2.28 |
| % Brash cover | 3.43 | 6.46 *** ⌒ | 3.89 | 9.80 *** ⌒ | 3.56 | 3.74 ** ⌒ |
| **Null** | **200.00** | | **200.00** | | **267.00** | |
| **Residual** | **190.57** | | **190.11** | | **257.44** | |
| **Adj. $D^2$** | **0.38** | | **0.43** | | **0.05** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |
| ELL | 1998 | Fit | Absent | 153 | 76.50 | **124** | **81.0** | 29 | 19.0 |  |  |
|  |  |  | Present | 47 | 23.50 | 6 | 12.8 | **41** | **87.2** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **84.10** | 0.88 ± 0.03 *** |
|  |  | CV | Absent | 153 | 76.50 | **116** | **75.8** | 37 | 24.2 |  |  |
|  |  |  | Present | 47 | 23.50 | 7 | 14.9 | **40** | **85.1** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **80.45** | 0.84 ± 0.03 *** |
|  | 2000 | Fit 1 | Absent | 185 | 92.50 | **160** | **86.5** | 25 | 13.5 |  |  |
|  |  |  | Present | 15 | 7.50 | 5 | 33.3 | **10** | **66.7** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **76.60** | 0.77 ± 0.07 *** |
|  |  | Fit 2 | Absent | 185 | 92.50 | **142** | **76.8** | 43 | 23.2 |  |  |
|  |  |  | Present | 15 | 7.50 | 3 | 20.0 | **12** | **80.0** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **78.40** | 0.84 ± 0.04 *** |
| CSF | 1999 | Fit 1 | Absent | 220 | 82.40 | **124** | **56.4** | 96 | 43.6 |  |  |
|  |  |  | Present | 47 | 17.60 | 21 | 44.7 | **26** | **55.3** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **55.85** | 0.53 ± 0.05 |
|  |  | Fit 2 | Absent | 220 | 82.40 | **136** | **61.8** | 84 | 38.2 |  |  |
|  |  |  | Present | 47 | 17.60 | 17 | 36.2 | **30** | **63.8** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **62.80** | 0.67 ± 0.04 *** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest |  | East Loch Lomond |  |  |  |
|---|---|---|---|---|---|---|
|  | 1999 |  | 1998 |  | 2000 |  |
|  | DF | F | DF | F | DF | F |
| No. Rowan (dbh 7-16 cm) | 0.99 | 15.87 *** - | 0.99 | 2.67 | 1.00 | 1.43 |
| No. Pine (dbh >7 cm) | 0.98 | 24.88 *** - | 1.00 | 0.04 | 0.95 | 5.60 * + |
| No. Birch (dbh 7-16 cm) | 0.99 | 11.76 *** - | 1.00 | 0.01 | 1.00 | 2.43 |
| No. Beech (dbh 7-16 cm) | 0.99 | 18.16 *** - | 0.99 | 0.63 | 0.99 | 2.71 |
| Wood area/edge ratio 50m | 0.97 | 24.77 *** - | 1.00 | 1.35 | 1.00 | 0.73 |
| M Edge (100 m radius) (km) | 0.99 | 12.37 *** + | 1.00 | 0.67 | 0.92 | 13.19 *** - |
| No. CF Snags (dbh <7 cm) | 0.98 | 15.42 *** - | 0.99 | 4.47 * - | 1.00 | 0.07 |
| No. CF Snags (dbh 7-16 cm) | 0.98 | 14.68 *** + | 1.00 | 0.30 | 0.94 | 11.43 *** - |
| No. Elm (dbh 16-24 cm) | 0.99 | 14.26 *** - | 0.99 | 1.61 | 1.00 | 2.23 |
| % Herb cover | 3.93 | 9.44 *** ∿ | 3.83 | 1.60 | 3.81 | 8.10 *** ∩ |
| **Null** | **267.00** |  | **200.00** |  | **200.00** |  |
| **Residual** | **253.07** |  | **186.17** |  | **186.19** |  |
| **Adj. $D^2$** | **0.35** |  | **0.12** |  | **0.42** |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points No. | Sample Points % | Predicted Absent No. | Predicted Absent % | Predicted Present No. | Predicted Present % | Total % correct | ROC AUC ± SE |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CSF | 1999 | Fit | Absent | 220 | 82.40 | **181** | **82.3** | 39 | 17.7 | | |
| | | | Present | 47 | 17.60 | 10 | 21.3 | **37** | **78.7** | | |
| | | | Total | 267 | | | | | | **80.50** | 0.89 ± 0.02 *** |
| | | CV | Absent | 220 | 82.40 | **150** | **68.2** | 70 | 31.8 | | |
| | | | Present | 47 | 17.60 | 12 | 25.5 | **35** | **74.5** | | |
| | | | Total | 267 | | | | | | **71.35** | 0.79 ± 0.04 *** |
| ELL | 1998 | Fit 1 | Absent | 153 | 76.50 | **90** | **58.8** | 63 | 41.2 | | |
| | | | Present | 47 | 23.50 | 11 | 23.4 | **36** | **76.6** | | |
| | | | Total | 200 | | | | | | **67.70** | 0.67 ± 0.04 *** |
| | | Fit 2 | Absent | 153 | 76.50 | **114** | **74.5** | 39 | 25.5 | | |
| | | | Present | 47 | 23.50 | 13 | 27.7 | **34** | **72.3** | | |
| | | | Total | 200 | | | | | | **73.40** | 0.77 ± 0.04 *** |
| | 2000 | Fit 1 | Absent | 185 | 92.50 | **110** | **59.5** | 75 | 40.5 | | |
| | | | Present | 15 | 7.50 | 5 | 33.3 | **10** | **66.7** | | |
| | | | Total | 200 | | | | | | **63.10** | 0.66 ± 0.05 ** |
| | | Fit 2 | Absent | 185 | 92.50 | **145** | **78.4** | 40 | 21.6 | | |
| | | | Present | 15 | 7.50 | 1 | 6.7 | **14** | **93.3** | | |
| | | | Total | 200 | | | | | | **85.85** | 0.89 ± 0.03 *** |

## Table 4. 11: Generalized linear models (A) and evaluation (B) for the treecreeper for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond 1998 DF | F | | | East Loch Lomond 2000 DF | F | | | Central Scotland Forest 1999 DF | F |
|---|---|---|---|---|---|---|---|---|---|---|
| No. BL Trees (dbh >30 cm) | 1.00 | 17.53 | *** | + | 1.00 | 11.18 | *** | + | 1.00 | 2.33 |
| No. Birch (dbh >7 cm) | 1.00 | 4.18 | * | + | 1.00 | 0.54 | | | 1.00 | 0.03 |
| No. Spruce (dbh 16-24 cm) | 1.00 | 13.00 | *** | - | 1.00 | 1.17 | | | 1.00 | 1.51 |
| BL-CF (100 m radius) (km) | 1.00 | 4.10 | * | + | 1.00 | 1.16 | | | 1.00 | 0.00 |
| No. Hazel (dbh >7 cm) | 1.00 | 5.13 | * | - | 1.00 | 0.00 | | | 1.00 | 0.22 |
| % Brash cover | 1.00 | 4.53 | * | - | 1.00 | 1.96 | | | 1.00 | 0.67 |
| **Null** | **200.00** | | | | **200.00** | | | | **267.00** | |
| **Residual** | **193.00** | | | | **193.00** | | | | **260.00** | |
| **Adj. $D^2$** | **0.42** | | | | **0.12** | | | | **-0.01** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| ELL | 1998 | Fit | Absent | 97 | 48.50 | **87** | **89.7** | 10 | 10.3 | | |
| | | | Present | 103 | 51.50 | 16 | 15.5 | **87** | **84.5** | | |
| | | | Total | 200 | | | | | | **87.10** | 0.91 ± 0.02 *** |
| | | CV | Absent | 97 | 48.50 | **83** | **85.6** | 14 | 14.4 | | |
| | | | Present | 103 | 51.50 | 19 | 18.4 | **84** | **81.6** | | |
| | | | Total | 200 | | | | | | **83.60** | 0.88 ± 0.02 *** |
| | 2000 | Fit 1 | Absent | 107 | 53.50 | **82** | **76.6** | 25 | 23.4 | | |
| | | | Present | 93 | 46.50 | 25 | 26.9 | **68** | **73.1** | | |
| | | | Total | 200 | | | | | | **74.85** | 0.73 ± 0.04 *** |
| | | Fit 2 | Absent | 107 | 53.50 | **81** | **75.7** | 26 | 24.3 | | |
| | | | Present | 93 | 46.50 | 23 | 24.7 | **70** | **75.3** | | |
| | | | Total | 200 | | | | | | **75.50** | 0.77 ± 0.03 *** |
| CSF | 1999 | Fit 1 | Absent | 117 | 43.82 | **64** | **54.7** | 53 | 45.3 | | |
| | | | Present | 150 | 56.18 | 58 | 38.7 | **92** | **61.3** | | |
| | | | Total | 267 | | | | | | **58.00** | 0.56 ± 0.04 |
| | | Fit 2 | Absent | 117 | 43.82 | **71** | **60.7** | 46 | 39.3 | | |
| | | | Present | 150 | 56.18 | 59 | 39.3 | **91** | **60.7** | | |
| | | | Total | 267 | | | | | | **60.70** | 0.60 ± 0.04 ** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest | | | | East Loch Lomond | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1999 | | | | 1998 | | | | 2000 | | | |
| | DF | F | | | DF | F | | | DF | F | | |
| No. Willow (dbh 24-30 cm) | 1.00 | 13.71 | *** | - | | | | | | | | |
| S-W Tree diversity | 1.00 | 9.63 | ** | + | 1.00 | 11.62 | *** | + | 1.00 | 10.80 | *** | + |
| P/A Bird boxes | 1.00 | 7.67 | ** | P>A | 1.00 | 1.60 | | | 1.00 | 7.78 | ** | P>A |
| P/A Bogs, fens or flushes | 1.00 | 10.22 | ** | P>A | 1.00 | 0.27 | | | 1.00 | 0.01 | | |
| No. Trees <10 m | 1.00 | 16.27 | *** | - | 1.00 | 0.41 | | | 1.00 | 5.09 | * | + |
| No. Gean (dbh <7 cm) | 1.00 | 11.16 | *** | + | | | | | | | | |
| No. Gorse (dbh <7 cm) | 1.00 | 7.47 | ** | + | | | | | | | | |
| % Litter cover | 1.00 | 7.76 | ** | + | 1.00 | 1.06 | | | 1.00 | 0.10 | | |
| No. Pine (dbh >7 cm) | 1.00 | 10.12 | ** | - | 1.00 | 2.99 | | | 1.00 | 3.92 | * | - |
| P/A Footpaths | 1.00 | 6.91 | ** | P<A | 1.00 | 4.27 | * | P<A | 1.00 | 0.36 | | |
| No. Elm (dbh <7 cm) | 1.00 | 5.79 | * | - | | | | | | | | |
| Wood area/edge ratio 5000m | 1.00 | 5.39 | * | - | 1.00 | 0.21 | | | 1.00 | 4.15 | * | + |
| **Null** | **267.00** | | | | **200.00** | | | | **200.00** | | | |
| **Residual** | **254.00** | | | | **191.00** | | | | **191.00** | | | |
| **Adj. $D^2$** | **0.22** | | | | **0.08** | | | | **0.10** | | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |
| CSF | 1999 | Fit | Absent | 117 | 43.82 | **86** | **73.5** | 31 | 26.5 |  |  |
|  |  |  | Present | 150 | 56.18 | 34 | 22.7 | **116** | **77.3** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **75.40** | 0.82 ± 0.03 *** |
|  |  | CV | Absent | 117 | 43.82 | **89** | **76.1** | 28 | 23.9 |  |  |
|  |  |  | Present | 150 | 56.18 | 50 | 33.3 | **100** | **66.7** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **71.40** | 0.77 ± 0.03 *** |
| ELL | 1998 | Fit 1 | Absent | 97 | 48.50 | **60** | **61.9** | 37 | 38.1 |  |  |
|  |  |  | Present | 103 | 51.50 | 47 | 45.6 | **56** | **54.4** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **58.15** | 0.60 ± 0.04 ** |
|  |  | Fit 2 | Absent | 97 | 48.50 | **71** | **73.2** | 26 | 26.8 |  |  |
|  |  |  | Present | 103 | 51.50 | 35 | 34.0 | **68** | **66.0** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **69.60** | 0.73 ± 0.04 *** |
|  | 2000 | Fit 1 | Absent | 107 | 53.50 | **60** | **56.1** | 47 | 43.9 |  |  |
|  |  |  | Present | 93 | 46.50 | 39 | 41.9 | **54** | **58.1** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **57.10** | 0.58 ± 0.04 * |
|  |  | Fit 2 | Absent | 107 | 53.50 | **75** | **70.1** | 32 | 29.9 |  |  |
|  |  |  | Present | 93 | 46.50 | 29 | 31.2 | **64** | **68.8** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **69.45** | 0.75 ± 0.03 *** |

## Table 4. 12: Generalized additive models (A) and evaluation (B) for the blackbird for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond |  |  |  | Central Scotland Forest |  |
|---|---|---|---|---|---|---|
|  | 1998 |  | 2000 |  | 1999 |  |
|  | DF | F | DF | F | DF | F |
| Area BL (500 m radius) (ha) | 0.98 | 23.37 *** + | 1.00 | 0.06 | 1.00 | 0.00 |
| Area CF (5000 m radius) (ha) | 0.75 | 16.78 *** - | 1.00 | 1.57 | 1.00 | 1.49 |
| No. Pine (dbh 24-30 cm) | 2.04 | 19.03 *** - | 3.80 | 2.34 | 3.86 | 1.64 |
| No. Rowan (dbh <7 cm) | 0.51 | 49.36 *** + | 1.00 | 0.06 | 1.01 | 1.81 |
| No. Trees (2-4 m) | 2.18 | 7.81 *** - | 1.01 | 3.86 * + | 1.00 | 0.04 |
| No. Trees (<2 m) | 1.05 | 8.42 *** - | 1.00 | 0.08 | 1.00 | 0.05 |
| M Edge (200 m radius) (km) | 0.72 | 4.55 * - | 1.00 | 0.00 | 1.03 | 0.18 |
| No. CF Snags (dbh 16-24 cm) | 1.89 | 8.07 *** - | 3.97 | 0.57 | 0.99 | 1.18 |
| **Null** | **200.00** |  | **200.00** |  | **267.00** |  |
| **Residual** | **184.73** |  | **185.22** |  | **255.14** |  |
| **Adj. $D^2$** | **0.34** |  | **0.00** |  | **-0.01** |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points No. | Sample Points % | Predicted Absent No. | Predicted Absent % | Predicted Present No. | Predicted Present % | Total % correct | ROC AUC ± SE |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ELL | 1998 | Fit | Absent | 166 | 83.00 | **130** | **78.3** | 36 | 21.7 | | |
| | | | Present | 34 | 17.00 | 4 | 11.8 | **30** | **88.2** | | |
| | | | Total | 200 | | | | | | **83.25** | 0.89 ± 0.02 *** |
| | | CV | Absent | 166 | 83.00 | **124** | **74.7** | 42 | 25.3 | | |
| | | | Present | 34 | 17.00 | 6 | 17.6 | **28** | **82.4** | | |
| | | | Total | 200 | | | | | | **78.55** | 0.81 ± 0.04 *** |
| | 2000 | Fit 1 | Absent | 163 | 81.50 | **71** | **43.6** | 92 | 56.4 | | |
| | | | Present | 37 | 18.50 | 17 | 45.9 | **20** | **54.1** | | |
| | | | Total | 200 | | | | | | **48.85** | 0.47 ± 0.05 |
| | | Fit 2 | Absent | 163 | 81.50 | **134** | **82.2** | 29 | 17.8 | | |
| | | | Present | 37 | 18.50 | 21 | 56.8 | **16** | **43.2** | | |
| | | | Total | 200 | | | | | | **62.70** | 0.63 ± 0.05 ** |
| CSF | 1999 | Fit 1 | Absent | 68 | 25.47 | **31** | **45.6** | 37 | 54.4 | | |
| | | | Present | 199 | 74.53 | 83 | 41.7 | **116** | **58.3** | | |
| | | | Total | 267 | | | | | | **51.95** | 0.49 ± 0.04 |
| | | Fit 2 | Absent | 68 | 25.47 | **45** | **66.2** | 23 | 33.8 | | |
| | | | Present | 199 | 74.53 | 111 | 55.8 | **88** | **44.2** | | |
| | | | Total | 267 | | | | | | **55.20** | 0.57 ± 0.04 * |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest 1999 DF | F | | East Loch Lomond 1998 DF | F | | East Loch Lomond 2000 DF | F | |
|---|---|---|---|---|---|---|---|---|---|
| % Rhododendron (2-4 m) | 3.46 | 12.98 *** | ◞ | 3.80 | 1.95 | | 3.83 | 2.10 | |
| No. Ash (dbh >30 cm) | 1.25 | 11.58 *** | + | 1.00 | 0.18 | | 1.00 | 5.87 * | - |
| No. CF Snags (dbh <7 cm) | 0.91 | 23.88 *** | + | 1.00 | 0.33 | | 0.99 | 1.63 | |
| M-CF (5000m radius) (km) | 0.97 | 18.50 *** | - | 1.00 | 1.92 | | 0.98 | 7.11 ** | - |
| No. Beech (dbh >30 cm) | 0.92 | 13.91 *** | - | 1.00 | 0.19 | | 1.00 | 3.37 | |
| CF Edge (1000m radius) (km) | 0.94 | 9.37 ** | - | 1.02 | 7.48 ** | - | 1.00 | 0.57 | |
| No. Blackthorn (dbh <7 cm) | 1.00 | 7.63 ** | + | | | | | | |
| No. Rowan (dbh 16-24 cm) | 1.00 | 6.69 ** | - | 1.00 | 0.29 | | 1.01 | 1.23 | |
| No. Willow (dbh 7-16 cm) | 1.01 | 4.86 * | + | | | | | | |
| **Null** | **267.00** | | | **200.00** | | | **200.00** | | |
| **Residual** | **254.54** | | | **189.20** | | | **189.17** | | |
| **Adj. $D^2$** | **0.22** | | | **0.03** | | | **0.05** | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| CSF | 1999 | Fit | Absent | 68 | 25.47 | **50** | **73.5** | 18 | 26.5 | | |
| | | | Present | 199 | 74.53 | 64 | 32.2 | **135** | **67.8** | | |
| | | | Total | 267 | | | | | | **70.65** | 0.80 ± 0.03 *** |
| | | CV | Absent | 68 | 25.47 | **41** | **60.3** | 27 | 39.7 | | |
| | | | Present | 199 | 74.53 | 49 | 24.6 | **150** | **75.4** | | |
| | | | Total | 267 | | | | | | **67.85** | 0.74 ± 0.03 *** |
| ELL | 1998 | Fit 1 | Absent | 166 | 83.00 | **65** | **39.2** | 101 | 60.8 | | |
| | | | Present | 34 | 17.00 | 15 | 44.1 | **19** | **55.9** | | |
| | | | Total | 200 | | | | | | **47.55** | 0.45 ± 0.05 |
| | | Fit 2 | Absent | 166 | 83.00 | **116** | **69.9** | 50 | 30.1 | | |
| | | | Present | 34 | 17.00 | 12 | 35.3 | **22** | **64.7** | | |
| | | | Total | 200 | | | | | | **67.30** | 0.68 ± 0.05 *** |
| | 2000 | Fit 1 | Absent | 163 | 81.50 | **73** | **44.8** | 90 | 55.2 | | |
| | | | Present | 37 | 18.50 | 15 | 40.5 | **22** | **59.5** | | |
| | | | Total | 200 | | | | | | **52.15** | 0.50 ± 0.05 |
| | | Fit 2 | Absent | 163 | 81.50 | 96 | 58.9 | 67 | 41.1 | | |
| | | | Present | 37 | 18.50 | 8 | 21.6 | 29 | 78.4 | | |
| | | | Total | 200 | | | | | | **68.65** | 0.67 ± 0.04 *** |

## Table 4. 13: Generalized additive and generalized linear models (A) and evaluation (B) for the willow warbler for (i) the ELL98 GAM and its rebuild for ELL00 and CSF99 and (ii) the CSF99 GLM and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond | | | | Central Scotland Forest | |
|---|---|---|---|---|---|---|
| | 1998 | | 2000 | | 1999 | |
| | DF | F | DF | F | DF | F |
| Area CF (500 m radius) (ha) | 0.82 | 71.47 *** - | 0.94 | 15.12 *** - | 1.97 | 4.47 ** ╯ |
| WD Edge (50 m radius) (km) | 0.95 | 14.87 *** + | 0.99 | 2.93 | 1.00 | 0.05 |
| No. CF Snags (dbh <7 cm) | 0.83 | 24.93 *** - | 1.00 | 0.15 | 1.00 | 0.30 |
| No. Larch (dbh 7-16 cm) | 3.76 | 8.52 *** ╯ | 3.81 | 0.41 | 3.74 | 1.50 |
| CF Edge (5000m radius) (km) | 1.09 | 11.52 *** + | 1.08 | 0.44 | 1.33 | 7.46 ** ╭ |
| % Seedlings cover | 0.99 | 10.04 ** + | 1.00 | 0.02 | 1.00 | 0.11 |
| **Null** | **200.00** | | **200.00** | | **267.00** | |
| **Residual** | **190.12** | | **190.09** | | **255.88** | |
| **Adj. $D^2$** | **0.48** | | **0.09** | | **0.04** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± | SE | |
| ELL | 1998 | Fit | Absent | 82 | 41.00 | **73** | **89.0** | 9 | 11.0 | | | | |
| | | | Present | 118 | 59.00 | 18 | 15.3 | **100** | **84.7** | | | | |
| | | | Total | 200 | | | | | | **86.85** | 0.92 ± | 0.02 | *** |
| | | CV | Absent | 82 | 41.00 | **70** | **85.4** | 12 | 14.6 | | | | |
| | | | Present | 118 | 59.00 | 21 | 17.8 | **97** | **82.2** | | | | |
| | | | Total | 200 | | | | | | **83.80** | 0.89 ± | 0.02 | *** |
| | 2000 | Fit 1 | Absent | 94 | 47.00 | **57** | **60.6** | 37 | 39.4 | | | | |
| | | | Present | 106 | 53.00 | 37 | 34.9 | **69** | **65.1** | | | | |
| | | | Total | 200 | | | | | | **62.85** | 0.68 ± | 0.04 | *** |
| | | Fit 2 | Absent | 94 | 47.00 | **64** | **68.1** | 30 | 31.9 | | | | |
| | | | Present | 106 | 53.00 | 33 | 31.1 | **73** | **68.9** | | | | |
| | | | Total | 200 | | | | | | **68.50** | 0.74 ± | 0.03 | *** |
| CSF | 1999 | Fit 1 | Absent | 102 | 38.20 | **58** | **56.9** | 44 | 43.1 | | | | |
| | | | Present | 165 | 61.80 | 75 | 45.5 | **90** | **54.5** | | | | |
| | | | Total | 267 | | | | | | **55.70** | 0.55 ± | 0.04 | |
| | | Fit 2 | Absent | 102 | 38.20 | **61** | **59.8** | 41 | 40.2 | | | | |
| | | | Present | 165 | 61.80 | 46 | 27.9 | **119** | **72.1** | | | | |
| | | | Total | 267 | | | | | | **65.95** | 0.71 ± | 0.03 | *** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest | | | | East Loch Lomond | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1999 | | | | 1998 | | | | 2000 | | | |
| | DF | F | | | DF | F | | | DF | F | | |
| No. Birch (dbh <7 cm) | 1.00 | 12.87 | *** | + | 1.00 | 7.42 | ** | + | 1.00 | 3.85 | * | + |
| No. Trees (4-10 m) | 1.00 | 19.97 | *** | - | 1.00 | 4.57 | * | - | 1.00 | 2.82 | | |
| No. Sycamore (dbh <7 cm) | 1.00 | 11.40 | *** | - | 1.00 | 1.01 | | | 1.00 | 0.19 | | |
| No. Beech (dbh <7 cm) | 1.00 | 14.80 | *** | + | 1.00 | 0.79 | | | 1.00 | 0.75 | | |
| No. Trees (2-4 m) | 1.00 | 13.31 | *** | - | 1.00 | 0.12 | | | 1.00 | 0.70 | | |
| No. Beech (dbh >30 cm) | 1.00 | 7.74 | ** | - | 1.00 | 4.13 | * | - | 1.00 | 2.36 | | |
| M-CF (2500m radius) (km) | 1.00 | 10.41 | *** | - | 1.00 | 11.10 | *** | - | 1.00 | 22.45 | *** | - |
| P/A Water | 1.00 | 7.88 | ** | P<A | 1.00 | 2.72 | | | 1.00 | 0.84 | | |
| % Bracken cover | 1.00 | 6.85 | ** | + | 1.00 | 10.13 | ** | + | 1.00 | 0.40 | | |
| **Null** | **267.00** | | | | **200.00** | | | | **200.00** | | | |
| **Residual** | **257.00** | | | | **190.00** | | | | **190.00** | | | |
| **Adj. $D^2$** | **0.25** | | | | **0.19** | | | | **0.10** | | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| CSF | 1999 | Fit | Absent | 102 | 38.20 | **77** | **75.5** | 25 | 24.5 | | |
| | | | Present | 165 | 61.80 | 44 | 26.7 | **121** | **73.3** | | |
| | | | Total | 267 | | | | | | **74.40** | 0.82 ± 0.03 *** |
| | | CV | Absent | 102 | 38.20 | **75** | **73.5** | 27 | 26.5 | | |
| | | | Present | 165 | 61.80 | 44 | 26.7 | **121** | **73.3** | | |
| | | | Total | 267 | | | | | | **73.40** | 0.79 ± 0.03 *** |
| ELL | 1998 | Fit 1 | Absent | 82 | 41.00 | **64** | **78.0** | 18 | 22.0 | | |
| | | | Present | 118 | 59.00 | 47 | 39.8 | **71** | **60.2** | | |
| | | | Total | 200 | | | | | | **69.10** | 0.72 ± 0.04 *** |
| | | Fit 2 | Absent | 82 | 41.00 | **66** | **80.5** | 16 | 19.5 | | |
| | | | Present | 118 | 59.00 | 33 | 28.0 | **85** | **72.0** | | |
| | | | Total | 200 | | | | | | **76.25** | 0.80 ± 0.03 *** |
| | 2000 | Fit 1 | Absent | 94 | 47.00 | **64** | **68.1** | 30 | 31.9 | | |
| | | | Present | 106 | 53.00 | 40 | 37.7 | **66** | **62.3** | | |
| | | | Total | 200 | | | | | | **65.20** | 0.69 ± 0.04 *** |
| | | Fit 2 | Absent | 94 | 47.00 | **63** | **67.0** | 31 | 33.0 | | |
| | | | Present | 106 | 53.00 | 33 | 31.1 | **73** | **68.9** | | |
| | | | Total | 200 | | | | | | **67.95** | 0.74 ± 0.04 *** |

## Table 4. 14: Generalized additive and generalized linear models (A) and evaluation (B) for the great tit for (i) the ELL98 GAM and its rebuild for ELL00 and CSF99 and (ii) the CSF99 GLM and its rebuild for ELL98 and ELL00.

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond | | | | Central Scotland Forest | |
|---|---|---|---|---|---|---|
| | 1998 | | 2000 | | 1999 | |
| | DF | F | DF | F | DF | F |
| No. CF Trees (dbh >7 cm) | 3.82 | 5.15 *** ╮ | 3.56 | 1.10 | 3.90 | 5.17 *** ↘ |
| No. Hazel (dbh >7 cm) | 1.00 | 17.87 *** + | 1.00 | 0.94 | 1.00 | 4.47 * - |
| Area BL (100 m radius) (ha) | 0.99 | 19.24 *** + | 0.98 | 19.16 *** + | 1.00 | 0.07 |
| No. CF Snags (dbh 16-24 cm) | 1.01 | 8.22 ** - | 0.99 | 7.09 ** - | 1.00 | 0.19 |
| BL Edge (500 m radius) (km) | 0.99 | 7.83 ** + | 1.01 | 3.36 | 1.00 | 0.00 |
| **Null** | **200.00** | | **200.00** | | **267.00** | |
| **Residual** | **191.18** | | **191.44** | | **258.10** | |
| **Adj. $D^2$** | **0.40** | | **0.19** | | **0.04** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE | |
| ELL | 1998 | Fit | Absent | 160 | 80.00 | **125** | **78.1** | 35 | 21.9 | | | |
| | | | Present | 40 | 20.00 | 2 | 5.0 | **38** | **95.0** | | | |
| | | | Total | 200 | | | | | | **86.55** | 0.88 ± 0.02 | *** |
| | | CV | Absent | 160 | 80.00 | **120** | **75.0** | 40 | 25.0 | | | |
| | | | Present | 40 | 20.00 | 5 | 12.5 | **35** | **87.5** | | | |
| | | | Total | 200 | | | | | | **81.25** | 0.85 ± 0.03 | *** |
| | 2000 | Fit 1 | Absent | 163 | 81.50 | **110** | **67.5** | 53 | 32.5 | | | |
| | | | Present | 37 | 18.50 | 8 | 21.6 | **29** | **78.4** | | | |
| | | | Total | 200 | | | | | | **72.95** | 0.72 ± 0.04 | *** |
| | | Fit 2 | Absent | 163 | 81.50 | **107** | **65.6** | 56 | 34.4 | | | |
| | | | Present | 37 | 18.50 | 6 | 16.2 | **31** | **83.8** | | | |
| | | | Total | 200 | | | | | | **74.70** | 0.80 ± 0.04 | *** |
| CSF | 1999 | Fit 1 | Absent | 164 | 61.42 | **78** | **47.6** | 86 | 52.4 | | | |
| | | | Present | 103 | 38.58 | 34 | 33.0 | **69** | **67.0** | | | |
| | | | Total | 267 | | | | | | **57.30** | 0.55 ± 0.04 | |
| | | Fit 2 | Absent | 164 | 61.42 | **88** | **53.7** | 76 | 46.3 | | | |
| | | | Present | 103 | 38.58 | 32 | 31.1 | **71** | **68.9** | | | |
| | | | Total | 267 | | | | | | **61.30** | 0.62 ± 0.03 | *** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest | | | | East Loch Lomond | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1999 | | | | 1998 | | | | 2000 | | | |
| | DF | F | | | DF | F | | | DF | F | | |
| No. CF Snags (dbh >7 cm) | 1.00 | 6.17 | * | - | 1.00 | 0.09 | | | 1.00 | 0.55 | | |
| No. CF Trees (dbh >7 cm) | 1.00 | 13.67 | *** | - | 1.00 | 8.12 | ** | - | 1.00 | 0.00 | | |
| No. Rowan (dbh <7 cm) | 1.00 | 7.16 | ** | - | 1.00 | 1.83 | | | 1.00 | 0.03 | | |
| Area CF (1000m radius) (ha) | 1.00 | 10.82 | *** | + | 1.00 | 10.92 | *** | - | 1.00 | 0.34 | | |
| BL Edge (100 m radius) (km) | 1.00 | 12.26 | *** | + | 1.00 | 1.47 | | | 1.00 | 5.65 | * | + |
| No. Hazel (dbh >7 cm) | 1.00 | 6.43 | * | - | 1.00 | 4.54 | * | + | 1.00 | 0.85 | | |
| No. Elder (dbh <7 cm) | 1.00 | 8.93 | ** | - | 1.00 | 2.08 | | | 1.00 | 1.55 | | |
| % Grass cover | 1.00 | 8.27 | ** | - | 1.00 | 0.14 | | | 1.00 | 15.58 | *** | + |
| No. Rose (dbh <7 cm) | 1.00 | 5.83 | * | - | | | | | | | | |
| % Litter cover | 1.00 | 4.08 | * | - | 1.00 | 2.00 | | | 1.00 | 0.83 | | |
| **Null** | **267.00** | | | | **200.00** | | | | **200.00** | | | |
| **Residual** | **256.00** | | | | **190.00** | | | | **190.00** | | | |
| **Adj. $D^2$** | **0.15** | | | | **0.33** | | | | **0.18** | | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |  |
| CSF | 1999 | Fit | Absent | 164 | 61.42 | **120** | **73.2** | 44 | 26.8 |  |  |  |
|  |  |  | Present | 103 | 38.58 | 35 | 34.0 | **68** | **66.0** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **69.60** | 0.76 ± 0.03 | *** |
|  |  | CV | Absent | 164 | 61.42 | **116** | **70.7** | 48 | 29.3 |  |  |  |
|  |  |  | Present | 103 | 38.58 | 37 | 35.9 | **66** | **64.1** |  |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **67.40** | 0.71 ± 0.03 | *** |
| ELL | 1998 | Fit 1 | Absent | 160 | 80.00 | **85** | **53.1** | 75 | 46.9 |  |  |  |
|  |  |  | Present | 40 | 20.00 | 11 | 27.5 | **29** | **72.5** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **62.80** | 0.63 ± 0.04 | ** |
|  |  | Fit 2 | Absent | 160 | 80.00 | **113** | **70.6** | 47 | 29.4 |  |  |  |
|  |  |  | Present | 40 | 20.00 | 3 | 7.5 | **37** | **92.5** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **81.55** | 0.85 ± 0.03 | *** |
|  | 2000 | Fit 1 | Absent | 163 | 81.50 | **115** | **70.6** | 48 | 29.4 |  |  |  |
|  |  |  | Present | 37 | 18.50 | 17 | 45.9 | **20** | **54.1** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **62.35** | 0.63 ± 0.05 | ** |
|  |  | Fit 2 | Absent | 163 | 81.50 | **120** | **73.6** | 43 | 26.4 |  |  |  |
|  |  |  | Present | 37 | 18.50 | 8 | 21.6 | **29** | **78.4** |  |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **76.00** | 0.79 ± 0.04 | *** |

**Table 4. 15: Generalized additive models (A) and evaluation (B) for the blue tit for (i) the ELL98 model and its rebuild for ELL00 and CSF99 and (ii) the CSF99 model and its rebuild for ELL98 and ELL00.**

## (i) ELL98

## (A) Model

| Variable | East Loch Lomond |  |  |  |  |  |  |  | Central Scotland Forest |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 1998 |  |  |  | 2000 |  |  |  | 1999 |  |  |  |
|  | DF | F |  |  | DF | F |  |  | DF | F |  |  |
| No. CF Trees (dbh >7 cm) | 0.90 | 58.83 | *** | - | 1.00 | 7.15 | ** | - | 0.96 | 15.98 | *** | - |
| CF Edge (1000m radius) (km) | 0.98 | 8.79 | ** | - | 1.01 | 11.41 | *** | - | 1.14 | 0.72 |  |  |
| % Canopy cover | 3.82 | 5.00 | *** | ◞ | 3.98 | 3.78 | ** | ∩ | 3.79 | 1.96 |  |  |
| No. Spruce (dbh >30 cm) | 0.99 | 12.86 | *** | - | 1.00 | 0.45 |  |  | 1.00 | 0.09 |  |  |
| Aspect | 3.93 | 4.16 | ** | Cat | 4.00 | 0.67 |  |  | 3.96 | 1.93 |  |  |
| **Null** | **200.00** |  |  |  | **200.00** |  |  |  | **267.00** |  |  |  |
| **Residual** | **188.18** |  |  |  | **188.00** |  |  |  | **255.07** |  |  |  |
| **Adj. $D^2$** | **0.48** |  |  |  | **0.23** |  |  |  | **0.07** |  |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points |  | Points predicted as |  |  |  | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | Absent |  | Present |  |  |  |
|  |  |  |  | No. | % | No. | % | No. | % |  | AUC ± SE |
| ELL | 1998 | Fit | Absent | 111 | 55.50 | **95** | **85.6** | 16 | 14.4 |  |  |
|  |  |  | Present | 89 | 44.50 | 14 | 15.7 | **75** | **84.3** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **84.95** | 0.93 ± 0.02 *** |
|  |  | CV | Absent | 111 | 55.50 | **89** | **80.2** | 22 | 19.8 |  |  |
|  |  |  | Present | 89 | 44.50 | 16 | 18.0 | **73** | **82.0** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **81.10** | 0.89 ± 0.02 *** |
|  | 2000 | Fit 1 | Absent | 97 | 48.50 | **71** | **73.2** | 26 | 26.8 |  |  |
|  |  |  | Present | 103 | 51.50 | 25 | 24.3 | **78** | **75.7** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **74.45** | 0.77 ± 0.03 *** |
|  |  | Fit 2 | Absent | 97 | 48.50 | **76** | **78.4** | 21 | 21.6 |  |  |
|  |  |  | Present | 103 | 51.50 | 25 | 24.3 | **78** | **75.7** |  |  |
|  |  |  | Total | 200 |  |  |  |  |  | **77.05** | 0.84 ± 0.03 *** |
| CSF | 1999 | Fit 1 | Absent | 37 | 13.86 | **20** | **54.1** | 17 | 45.9 |  |  |
|  |  |  | Present | 230 | 86.14 | 89 | 38.7 | **141** | **61.3** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **57.70** | 0.61 ± 0.05 * |
|  |  | Fit 2 | Absent | 37 | 13.86 | **27** | **73.0** | 10 | 27.0 |  |  |
|  |  |  | Present | 230 | 86.14 | 82 | 35.7 | **148** | **64.3** |  |  |
|  |  |  | Total | 267 |  |  |  |  |  | **68.65** | 0.73 ± 0.05 *** |

## (ii) CSF99

## (A) Model

| Variable | Central Scotland Forest |  |  | East Loch Lomond |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  | 1999 |  |  | 1998 |  |  | 2000 |  |  |
|  | DF | F |  | DF | F |  | DF | F |  |
| No. Elder (dbh <7 cm) | 1.03 | 28.84 | *** + | 1.00 | 0.04 |  | 1.00 | 0.55 |  |
| Area WD (5000m radius) (ha) | 4.08 | 20.59 | *** ~ | 4.05 | 3.61 | ** ~ | 3.98 | 1.03 |  |
| No. Oak (dbh >7cm) | 1.06 | 19.43 | *** + | 1.28 | 13.22 | *** + | 1.00 | 2.35 |  |
| Area BL (2500m radius) (ha) | 1.23 | 23.62 | *** - | 0.97 | 2.18 |  | 0.99 | 0.81 |  |
| Area CF (50 m radius) (ha) | 1.08 | 13.30 | *** - | 0.98 | 16.03 | *** - | 0.99 | 20.98 | *** - |
| P/A Footpaths | 0.92 | 9.73 | ** P<A | 0.99 | 2.00 |  | 1.00 | 0.02 |  |
| No. Lime (dbh >7 cm) | 1.03 | 8.26 | ** + |  |  |  |  |  |  |
| No. Larch (dbh 24-30 cm) | 4.00 | 7.12 | *** ∩ | 4.03 | 1.01 |  | 3.98 | 1.03 |  |
| **Null** | **267.00** |  |  | **200.00** |  |  | **200.00** |  |  |
| **Residual** | **252.16** |  |  | **186.17** |  |  | **186.03** |  |  |
| **Adj. $D^2$** | **0.35** |  |  | **0.38** |  |  | **0.16** |  |  |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| CSF | 1999 | Fit | Absent | 37 | 13.86 | **32** | **86.5** | 5 | 13.5 | | |
| | | | Present | 230 | 86.14 | 63 | 27.4 | **167** | **72.6** | | |
| | | | Total | 267 | | | | | | **79.55** | 0.86 ± 0.03 *** |
| | | CV | Absent | 37 | 13.86 | **30** | **81.1** | 7 | 18.9 | | |
| | | | Present | 230 | 86.14 | 77 | 33.5 | **153** | **66.5** | | |
| | | | Total | 267 | | | | | | **73.80** | 0.78 ± 0.04 *** |
| ELL | 1998 | Fit 1 | Absent | 111 | 55.50 | **34** | **30.6** | 77 | 69.4 | | |
| | | | Present | 89 | 44.50 | 34 | 38.2 | **55** | **61.8** | | |
| | | | Total | 200 | | | | | | **46.20** | 0.40 ± 0.04 |
| | | Fit 2 | Absent | 111 | 55.50 | **96** | **86.5** | 15 | 13.5 | | |
| | | | Present | 89 | 44.50 | 18 | 20.2 | **71** | **79.8** | | |
| | | | Total | 200 | | | | | | **83.15** | 0.90 ± 0.02 *** |
| | 2000 | Fit 1 | Absent | 97 | 48.50 | **50** | **51.5** | 47 | 48.5 | | |
| | | | Present | 103 | 51.50 | 50 | 48.5 | **53** | **51.5** | | |
| | | | Total | 200 | | | | | | **51.50** | 0.49 ± 0.04 |
| | | Fit 2 | Absent | 97 | 48.50 | **71** | **73.2** | 26 | 26.8 | | |
| | | | Present | 103 | 51.50 | 21 | 20.4 | **82** | **79.6** | | |
| | | | Total | 200 | | | | | | **76.40** | 0.81 ± 0.03 *** |

## Table 4. 16: Generalized additive model (A) and evaluation (B) for the blackcap for the CSF99 model and its rebuild for ELL98 and ELL00.

## (A) Model

| Variable | Central Scotland Forest | | East Loch Lomond | | | |
|---|---|---|---|---|---|---|
| | 1999 | | 1998 | | 2000 | |
| | DF | F | DF | F | DF | F |
| Fallen dead CF rating | 3.14 | 9.89 *** ╮ | 3.57 | 17.19 *** ╮ | 3.69 | 15.64 *** ╮ |
| BL Edge (50 m radius) (km) | 1.01 | 14.12 *** - | 1.00 | 17.75 *** + | 0.97 | 8.40 ** + |
| Area WD (2500m radius) (ha) | 0.98 | 24.48 *** - | 1.00 | 0.02 | 1.00 | 0.20 |
| No. Ash (dbh >30 cm) | 0.99 | 7.72 ** - | 1.00 | 10.36 ** - | 0.99 | 8.80 ** - |
| No. BL Snags (dbh 7-16 cm) | 1.00 | 10.70 *** + | 1.02 | 1.59 | 0.92 | 10.23 ** - |
| M Edge (2500m radius) (km) | 3.60 | 8.80 *** ∩ | 3.84 | 4.69 *** ∿ | 3.78 | 7.91 *** ∿ |
| **Null** | **267.00** | | **200.00** | | **200.00** | |
| **Residual** | **254.92** | | **187.44** | | **187.43** | |
| **Adj. $D^2$** | **0.21** | | **0.32** | | **0.26** | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| CSF | 1999 | Fit | Absent | 214 | 80.15 | **139** | **65.0** | 75 | 35.0 | | |
| | | | Present | 53 | 19.85 | 10 | 18.9 | **43** | **81.1** | | |
| | | | Total | 267 | | | | | | **73.05** | 0.79 ± 0.03 *** |
| | | CV | Absent | 214 | 80.15 | **144** | **67.3** | 70 | 32.7 | | |
| | | | Present | 53 | 19.85 | 19 | 35.8 | **34** | **64.2** | | |
| | | | Total | 267 | | | | | | **65.75** | 0.72 ± 0.04 *** |
| ELL | 1998 | Fit 1 | Absent | 193 | 96.50 | **141** | **73.1** | 52 | 26.9 | | |
| | | | Present | 7 | 3.50 | 3 | 42.9 | **4** | **57.1** | | |
| | | | Total | 200 | | | | | | **65.10** | 0.60 ± 0.11 |
| | | Fit 2 | Absent | 193 | 96.50 | **158** | **81.9** | 35 | 18.1 | | |
| | | | Present | 7 | 3.50 | 1 | 14.3 | **6** | **85.7** | | |
| | | | Total | 200 | | | | | | **83.80** | 0.88 ± 0.03 *** |
| | 2000 | Fit 1 | Absent | 186 | 93.00 | **111** | **59.7** | 75 | 40.3 | | |
| | | | Present | 14 | 7.00 | 7 | 50.0 | **7** | **50.0** | | |
| | | | Total | 200 | | | | | | **54.85** | 0.56 ± 0.06 |
| | | Fit 2 | Absent | 186 | 93.00 | **145** | **78.0** | 41 | 22.0 | | |
| | | | Present | 14 | 7.00 | 2 | 14.3 | **12** | **85.7** | | |
| | | | Total | 200 | | | | | | **81.85** | 0.85 ± 0.04 *** |

## Table 4. 17: Generalized additive model (A) and evaluation (B) for the wood warbler for the ELL98model and its rebuild for ELL00.

## (A) Model

| Variable | East Loch Lomond | | | | | |
|---|---|---|---|---|---|---|
| | 1998 | | | 2000 | | |
| | DF | F | | DF | F | |
| No.BL Trees (dbh > 30cm) | 1.02 | 10.92 *** | + | 1.01 | 28.56 *** | + |
| No. BL Trees (dbh >7 cm) | 1.00 | 10.44 *** | + | 1.00 | 1.11 | |
| P/A Old coppice | 1.01 | 8.87 ** | P>A | 1.00 | 3.59 | |
| No. Larch (dbh >30 cm) | 1.00 | 6.55 ** | + | 1.00 | 3.55 | |
| Area M (100 m radius) (ha) | 1.21 | 4.86 * | ⌣ | 1.08 | 1.24 | |
| **Null** | **200.00** | | | **200.00** | | |
| **Residual** | **193.77** | | | **193.92** | | |
| **Adj. $D^2$** | **0.37** | | | **0.24** | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± | SE | |
| ELL | 1998 | Fit | Absent | 102 | 51.00 | **83** | **81.4** | 19 | 18.6 | | | | |
| | | | Present | 98 | 49.00 | 9 | 9.2 | **89** | **90.8** | | | | |
| | | | Total | 200 | | | | | | **86.10** | 0.89 ± | 0.03 | *** |
| | | CV | Absent | 102 | 51.00 | **81** | **79.4** | 21 | 20.6 | | | | |
| | | | Present | 98 | 49.00 | 12 | 12.2 | **86** | **87.8** | | | | |
| | | | Total | 200 | | | | | | **83.60** | 0.87 ± | 0.03 | *** |
| | 2000 | Fit 1 | Absent | 139 | 69.50 | **106** | **76.3** | 33 | 23.7 | | | | |
| | | | Present | 61 | 30.50 | 14 | 23.0 | **47** | **77.0** | | | | |
| | | | Total | 200 | | | | | | **76.65** | 0.80 ± | 0.03 | *** |
| | | Fit 2 | Absent | 139 | 69.50 | **100** | **71.9** | 39 | 28.1 | | | | |
| | | | Present | 61 | 30.50 | 8 | 13.1 | **53** | **86.9** | | | | |
| | | | Total | 200 | | | | | | **79.40** | 0.82 ± | 0.03 | *** |

## Table 4. 18: Generalized additive model (A) and evaluation (B) for the redstart for the ELL98 model and its rebuild for ELL00.

## (A) Model

| Variable | East Loch Lomond | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1998 | | | | 2000 | | | |
| | DF | F | | | DF | F | | |
| No. CF Trees (dbh 16-24 cm) | 1.01 | 11.12 | *** | - | 1.23 | 22.35 | *** | - |
| WD Edge (1000m radius) (km) | 1.00 | 17.79 | *** | - | 1.00 | 0.39 | | |
| No. Alder (dbh <7 cm) | 0.98 | 13.24 | *** | - | 1.00 | 5.08 | * | + |
| M-CF (500 m radius) (km) | 3.87 | 12.51 | *** | ∪ | 3.94 | 2.45 | * | ◝ |
| % Canopy cover | 1.00 | 22.79 | *** | + | 1.03 | 8.40 | ** | + |
| % Ground cover | 0.95 | 14.02 | *** | + | 0.98 | 6.32 | ** | + |
| No. BL Snags (dbh >7 cm) | 1.00 | 5.27 | * | - | 1.00 | 0.70 | | |
| **Null** | **200.00** | | | | **200.00** | | | |
| **Residual** | **189.13** | | | | **189.06** | | | |
| **Adj. $D^2$** | **0.42** | | | | **0.30** | | | |

## (B) Evaluation

| Location | Year | Model | Observed status | Sample Points | | Points predicted as | | | | Total % correct | ROC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Absent | | Present | | | |
| | | | | No. | % | No. | % | No. | % | | AUC ± SE |
| ELL | 1998 | Fit | Absent | 169 | 84.50 | **148** | **87.6** | 21 | 12.4 | | |
| | | | Present | 31 | 15.50 | 5 | 16.1 | **26** | **83.9** | | |
| | | | Total | 200 | | | | | | **85.75** | 0.90 ± 0.02 *** |
| | | CV | Absent | 169 | 84.50 | **134** | **79.3** | 35 | 20.7 | | |
| | | | Present | 31 | 15.50 | 6 | 19.4 | **25** | **80.6** | | |
| | | | Total | 200 | | | | | | **79.95** | 0.83 ± 0.04 *** |
| | 2000 | Fit 1 | Absent | 157 | 78.50 | **100** | **63.7** | 57 | 36.3 | | |
| | | | Present | 43 | 21.50 | 11 | 25.6 | **32** | **74.4** | | |
| | | | Total | 200 | | | | | | **69.05** | 0.71 ± 0.04 *** |
| | | Fit 2 | Absent | 157 | 78.50 | **131** | **83.4** | 26 | 16.6 | | |
| | | | Present | 43 | 21.50 | 11 | 25.6 | **32** | **74.4** | | |
| | | | Total | 200 | | | | | | **78.90** | 0.85 ± 0.03 *** |

## Table 4. 19: Definition of codes used in Tables 4.4 to 4.18 (GLM and GAM models of woodland bird distributions in relation to habitat and landscape parameters).

| Table | Code | Definition |
|---|---|---|
| **Model Tables** | BL | Broad-leaved woodland |
| | CF | Coniferous woodland |
| | M | Mixed broad-leaved and coniferous woodland |
| | WD | Total woodland |
| | S-W | Shannon-Wiener diversity index |
| | dbh | Diameter breast height |
| | DF | Degrees of freedom |
| | P/A | Presence and absence categorical variable |
| | P<A | Presence less than absence |
| | P>A | Presence greater than absence |
| | Cat | Categorical variable with more than two categories |
| | + | Positive direction of relationship |
| | - | Negative direction of relationship |
| | ↘ | Curve indicating the shape of a relationship |
| | Null | Null degrees of freedom |
| | Residual | Residual degrees of freedom |
| | Adj. $D^2$ | Adjusted $D^2$ |
| **Evaluation Tables** | ROC | Receiver Operator Characteristic |
| | AUC | Area under the ROC curve |
| | SE | Standard error |
| | CV | Cross-validated result |
| | Fit | The original model |
| | Fit 1 | Cross-tabulation of direct predictions from the original model |
| | Fit 2 | Cross-tabulations of models rebuilt for other sites and years using only variables selected in the original model |
| **Model and Evaluation Tables** | *** | Significant at $p \leq 0.001$ |
| | ** | Significant at $p \leq 0.01$ |
| | * | Significant at $p \leq 0.05$ |

### *4.4.2 Habitat and landscape structure*

#### 4.4.2.1 Landscape structure at a scale of up to 100m from sample points

At a 100m radius scale from sample points, the amount of open area increased from 14.5% to 22.3% between 1998 and 2000 at ELL. By comparison, 34.1% of the area was open habitat for the CSF in 1999 (Table 4.20). Habitat distribution between broad-leaved, coniferous and mixed classes also differed between sites and years. ELL98 had a higher percentage of coniferous habitat (48.2%) than the CSF (30.7%), although the percentage conifer cover decreased by 4.8% at Loch Lomond between 1998 and 2000 (Table 4.21).

The pattern of a higher percentage of broad-leaved habitat relative to coniferous habitat at the CSF was also evident when the measure used was the percentage presence or absence of each habitat type within a 100m radius of each sample point. For ELL, although the percentage cover of broad-leaved woodland was lower within a 100m radius from each sample point, the proportion of points at which it was present was similar to the proportion at which coniferous habitat was present (66% broad-leaved presence in both years compared with 66% and 57% coniferous woodland presence for ELL98 and ELL00 respectively) (Table 4.22).

**Table 4. 20: The percentage cover of broad-leaved (BL), coniferous (CF), mixed (M), wooded (Wood) and open habitat (Open) for a total area based on a 100m and a 5000m radius around sample points for ELL98, ELL00 and CSF99. Diff. is the change in percentage cover between 1998 and 2000 at Loch Lomond.**

| Location | Year | % Landscape Cover | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 100m Radius | | | | | 5000m Radius | | | | |
| | | BL | CF | M | Wood | Open | BL | CF | M | Wood | Open |
| ELL | 1998 | 36.86 | 41.25 | 7.41 | 85.53 | 14.47 | 5.96 | 10.08 | 1.30 | 17.33 | 82.67 |
| | 2000 | 38.30 | 33.81 | 5.64 | 77.75 | 22.25 | 6.00 | 9.50 | 1.23 | 16.73 | 83.27 |
| | **Diff.** | **1.44** | **-7.45** | **-1.78** | **-7.78** | **7.78** | **0.04** | **-0.58** | **-0.06** | **-0.60** | **0.60** |
| CSF | 1999 | 41.99 | 20.24 | 3.72 | 65.95 | 34.05 | 6.10 | 4.88 | 0.92 | 11.89 | 88.11 |

**Table 4. 21: The total amount of broad-leaved (BL), coniferous (CF), mixed (M), broad-leaved and mixed (BL+M) and coniferous and mixed (CF+M) woodland as a percentage of total woodland cover for an area based on 100m and 5000m radii around sample points at ELL98, ELL00 and CSF99. Diff. is the change in percentage cover between 1998 and 2000 at Loch Lomond.**

| Location | Year | % Woodland Cover | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 100m Radius | | | | | 5000m Radius | | | | |
| | | BL | CF | M | BL+M | CF+M | BL | CF | M | BL+M | CF+M |
| ELL | 1998 | 43.10 | 48.23 | 8.67 | 51.77 | 56.90 | 34.38 | 58.14 | 7.47 | 41.86 | 65.62 |
| | 2000 | 49.26 | 43.48 | 7.25 | 56.52 | 50.74 | 35.85 | 56.77 | 7.37 | 43.23 | 64.15 |
| | **Diff.** | **6.17** | **-4.75** | **-1.42** | **4.75** | **-6.17** | **1.47** | **-1.37** | **-0.10** | **1.37** | **-1.47** |
| CSF | 1999 | 63.67 | 30.69 | 5.64 | 69.31 | 36.33 | 51.27 | 41.01 | 7.73 | 58.99 | 48.73 |

**Table 4. 22: The percentage of sample points with broad-leaved (BL), coniferous (CF), mixed (M), broad-leaved and mixed (BL+M) and coniferous and mixed (CF+M) habitat present within a 100m radius for ELL98, ELL00 and CSF99. Diff. is the change in percentage presence between 1998 and 2000 at Loch Lomond.**

| Location | Year | % Sample points with habitat present | | | | |
|---|---|---|---|---|---|---|
| | | BL | CF | M | BL+M | CF+M |
| ELL | 1998 | 66.00 | 66.00 | 32.00 | 73.00 | 73.00 |
| | 2000 | 66.00 | 57.00 | 28.50 | 73.00 | 66.50 |
| | **Diff.** | **0.00** | **-9.00** | **-3.50** | **0.00** | **-6.50** |
| CSF | 1999 | 80.15 | 35.96 | 7.12 | 80.90 | 41.20 |

### 4.4.2.2 Landscape structure at a scale of up to 5000m from sample points

The percentage cover of broad-leaved woodland was greater at a scale of 100m than at 5000m for ELL in 1998 and 2000 and for the CSF in 1999. However, coniferous woodland occurred at lower percentage covers locally (within 100m radii) than in the wider landscape (5000m radii) (Table 4.21). Changes in cover between ELL98 and ELL00 were all between 0 and 1.5% at a scale of 5000m (Table 4.20 and 4.21). Although there was still a higher percentage cover of broad-leaved woodland relative to coniferous woodland in the CSF compared with at Loch Lomond, the overall differences in cover between the ELL and CSF study sites were less when measured at a scale of 5000m. Woodland cover was around five percent higher at East Loch Lomond in both years, than in the CSF99 (Table 4.20).

Median patch size decreased and edge density increased between 1998 and 2000 at Loch Lomond. However the median patch size was still lower and edge density was correspondingly higher for the CSF. Both measures of patch fractal dimension were virtually identical for Loch Lomond in 1998 and 2000, and were nearer to one than two. The mean patch fractal dimension was higher for the CSF (Table 4.23) though only marginally so when area weighted.

**Table 4. 23: Landscape metrics for East Loch Lomond (1998 and 2000) and for the Central Scotland Forest (1999). MedPS is median patch size; ED is edge density; MPFD is mean patch fractal dimension and AWMPFD is area-weighted mean patch fractal dimension. For detailed definitions of the metrics see Section 4.3.1.**

| Location | Year | MedPS | ED | MPFD | AWMPFD |
|---|---|---|---|---|---|
| East Loch Lomond | 1998 | 1.16 | 119.35 | 1.37 | 1.33 |
| | 2000 | 0.94 | 124.59 | 1.36 | 1.33 |
| Central Scotland Forest | 1999 | 0.63 | 233.95 | 1.46 | 1.37 |

### 4.4.2.3 Correlation structure of variables in the models

The correlation structure of variables was very similar between ELL98 and ELL00, but not between Loch Lomond and the CSF. For Loch Lomond general categories of broad-leaved woodland could be identified within the correlation structure of the habitat variables. Likewise coniferous habitat variables were often correlated significantly with each other. Generally broad-leaved and coniferous associated variables were negatively (often significantly) correlated with each other.

At Loch Lomond the broad-leaved area and edge variables mostly occurred in the models up to a scale of 500m. They were mostly positively correlated with general broad-leaved and oak habitat variables and negatively correlated with coniferous variables. Conifer edge and area variables occurred at a wider range of scales in the models and were significantly positively correlated with coniferous habitat variables and significantly negatively correlated with broad-leaved habitat variables. The mixed area and edge variables showed more variation in their patterns of correlation with habitat variables depending on scale. Wood area and edge variables were significantly positively correlated with coniferous habitat variables and negatively correlated with broad-leaved habitat variables.

Significant positive correlations occurred between area and edge variables of the same broad woodland type (coniferous, broad-leaved, mixed or all woodland) across scales, with some reduction in the correlation coefficients and loss of significance at 2500m and 5000m.

Habitat variables at the CSF were mostly less correlated interspecifically than those at ELL and it was not possible to identify the different general woodland types within them. Species which would form sub-dominant components of other woodland types were largely uncorrelated with other variables. Coniferous woodland species and brash variables were more significantly positively correlated with each other. Thus the correlation structure of conifer variables was more comparable between the CSF and ELL, than that of the broad-leaved variables.

Broad-leaved edge and area variables were mostly not significantly correlated with habitat variables at the CSF. However, the pattern of correlations with habitat variables for coniferous and mixed area and edge variables was similar in the CSF to that found at Loch Lomond, though with fewer significant correlations. Wood edge and area variables at the CSF were not significantly positively correlated with conifer habitat variables. The correlation between area and edge variables of different scales had some similarity in pattern to that found at Loch Lomond. The key differences were the occurrence of significant negative correlations between broad-leaved and mixed area and edge variables in the CSF, but not at Loch Lomond. Similarly, although broad-leaved and coniferous edge and area variables were significantly negatively correlated at both sites, the coefficients tended to be higher at Loch Lomond. Edge and area conifer variables were less correlated with woodland area variables in the CSF. Selected correlation matrices are given in Appendix 2.

### *4.4.3 Species occurrence in relation to habitat area*

#### 4.4.3.1 Coniferous species

Goldcrest occurrence was approximately proportional to the incidence of coniferous habitat around sample points for all sites and years. This also applied for the coal tit, except in 1998 at East Loch Lomond when the amount of coniferous habitat was 16.5% greater than percentage coal tit presence (Table 4.24). Siskin occurrence was not proportional to the area of coniferous and mixed woodland. The percentage occurrence of coniferous habitat was between approximately 35% and 50% greater than percentage occupancy for all sites and years.

#### 4.4.3.2 Broad-leaved species

Some association between the occurrence of broad-leaved habitat and percentage occurrence may be present for the willow warbler, blue tit and blackbird. For the remaining species, the occurrence of broad-leaved habitat generally exceeded percentage presence. The percentage presence for the willow warbler was relatively proportional to the occurrence of broad-leaved habitat within 100m of sample points for ELL98, but not for ELL00 and CSF99. Blue tit and blackbird occurrence was proportional to broad-leaved woodland frequency of occurrence around sample points at 100m for the CSF in 1999 (Table 4.24). In all other cases broad-leaved habitat occurrence exceeded bird species occurrence (Table 4.24).

**Table 4. 24: Index of habitat occupancy for all modelled species for ELL98, ELL00 and CSF99. A positive value indicates habitat availability greater than occupancy and a negative value indicates bird presence exceeding available habitat of the type within which the species most commonly occurs. Figures in bold indicate index values between -10 and +10.**

| Habitat | Species | ELL | | CSF |
|---|---|---|---|---|
| | | 1998 | 2000 | 1999 |
| **Ubiquitous** | Robin | 19.50 | **6.50** | **8.99** |
| | Wren | 32.00 | 41.50 | 20.97 |
| **Coniferous** | Goldcrest | **7.50** | **6.50** | **-3.37** |
| | Coal tit | 16.50 | **6.00** | **-2.62** |
| | Siskin | 40.50 | 51.00 | 35.21 |
| **Broad-leaved** | Willow warbler | **7.00** | 13.00 | 18.35 |
| | Treecreeper | 14.50 | 19.50 | 23.97 |
| | Wood warbler | 17.00 | 35.50 | 77.90 |
| | Blue tit | 21.50 | 14.50 | **-5.99** |
| | Garden warbler | 42.50 | 58.50 | 62.55 |
| | Song thrush | 42.88 | 40.87 | 56.93 |
| | Great tit | 46.00 | 47.50 | 41.57 |
| | Blackbird | 49.00 | 47.50 | **5.62** |
| | Redstart | 50.50 | 44.50 | 79.40 |
| | Blackcap | 62.50 | 59.00 | 60.30 |

### *4.4.4 Evidence for fragmentation effects*

Variables which may be indicative of fragmentation effects include, area/edge ratio measures, woodland area variables from 200m to 5000m in scale, edge measures from 50m to 5000m, and presence or absence of two hectares of continuous woodland around sample points.

Ratio variables were only selected for three species (song thrush, garden warbler and treecreeper) in the CSF99 models and not for any of the ELL98 models (Tables 4.9, 4.10 and 4.11). The ratio variable was at a scale of 50m for the song thrush and the garden warbler and at a 5000m scale for the treecreeper. The direction of relationship was negative for the treecreeper and garden warbler and positive for the song thrush. The only significant relationships for the ratio variables when models were rebuilt for Loch Lomond based on the CSF99 variables occurred for ELL00 for the treecreeper and song thrush. In both cases the direction of the relationship was reversed compared with the original model for CSF99.

Parameters expected to be affected most severely by habitat fragmentation accounted for 30.3% and 23.0% of variation overall in the ELL98 and CSF99 models respectively (Table 4.3). The majority of models included one or more of these fragmentation sensitive variables (Tables 4.4-4.18). Woodland composition (greater than 100m from sample points) and edge variables (at all scales) accounted for approximately equal amounts of variation overall in the CSF99 models. By contrast a higher percentage of variation was accounted for overall by edge variables (all scales) than by area variables (>100m from points) in the ELL98 models (Table 4.3).

A total of nine species (goldcrest (Table 4.4), coal tit (Table 4.5), wren (Table 4.8), song thrush (Table 4.9), blackbird (Table 4.12), willow warbler (Table 4.13), great tit (Table 4.14), blue tit (Table 4.15) and blackcap (Table 4.16)) had area variables at a scale greater than 100m in the models. These variables accounted for approximately equal proportions of variation in the ELL98 and CSF99 models (Table 4.3). Whereas area variables in the models at a scale of up to 100m radius always indicated habitat preference (positive relationship) or aversion (negative relationship) to the dominant habitat type in which you would expect the species to occur, this did not always apply at scales of over 100m radius. For example, the great tit in the ELL98 model had a positive relationship with broad-leaved woodland within 100m of sample points. In the CSF99 model it had a positive relationship with coniferous woodland within 1000m of sample points (Table 4.14).

Only one of the modelled species (wood warbler) had no edge variables in any of the selected models (Table 4.17). Edge variables were slightly more prevalent in the ELL98 than in the CSF99 models, and explained overall a higher proportion of variation (Table 4.3). For the ELL98 models, where edge variables were significant in the models re-built for ELL00 and CSF99 using the ELL98 selected variables, the direction of the predicted relationship, if not the precise form of the relationship was always the same. This did not always apply for the edge variables in the models rebuilt for ELL98 and ELL00 based on the variables selected in the CSF99 models (Tables 4.4-4.18).

There was more evidence of broad-leaved woodland edge providing suitable habitat than coniferous woodland edge. Results indicated that wrens, garden warblers, blackbirds, willow warblers and great tits all favoured broad-leaved edge (Tables 4.8, 4.10, 4.12, 4.13 and 4.14), while the coal tit, siskin and goldcrest avoided it (Tables 4.4, 4.5 and 4.6). The robin and willow warbler favoured coniferous woodland edges (Tables 4.7 and 4.13). The goldcrest also had a positive relationship with coniferous edge, but only in the CSF99 model (Table 4.4). Species avoiding coniferous woodland edge were predominantly those where the models indicated positive associations with broad-leaved variables (wren, song thrush, treecreeper, blackbird, blue tit, blackcap and redstart,) (Tables 4.8, 4.9, 4.11, 4.12, 4.15, 4.16 and 4.18). However the coal tit also appeared to avoid coniferous edge (Table 4.5).

Presence or absence of two hectares of continuous woodland around sample points was significant only for the song thrush in the CSF99 model (Table 4.9). In this model song thrushes were present more often where there were two hectares of continuous habitat present, relative to when this was absent (Figure 4.2).

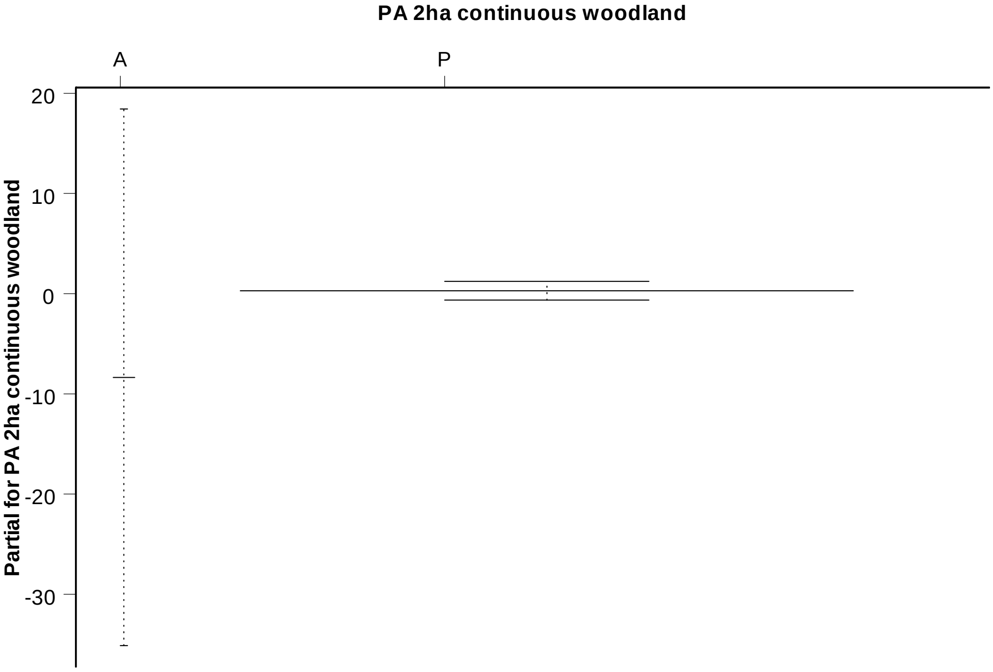

**Figure 4. 2: Partial fit for the presence or absence (PA) of two hectares of continuous woodland around sample points for the GLM given in Table 4.9 (ii, A) for the song thrush for CSF99. Dashed lines indicate the standard error. On the x-axis A represents absence points and P represents presence points.**

This variable was not significant in the model built for ELL98 using the variables selected for CSF99. However it was significant when the same variables were used to build a model for the ELL00 data. Again song thrushes preferred two hectares of continuous habitat to be present (Figure 4.3).

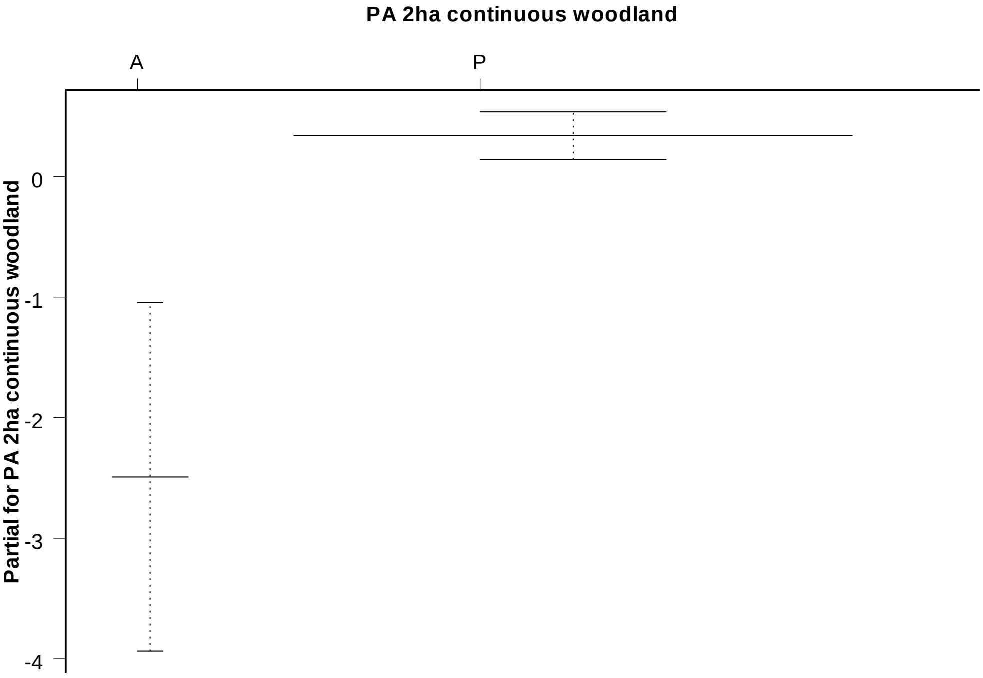

**Figure 4. 3: Partial fit for the presence or absence (PA) of two hectares of continuous woodland around sample points for the GLM given in Table 4.9 (ii, A) for the song thrush at East Loch Lomond in 2000. Variables included in the model were those selected for the song thrush for CSF99. Dashed lines indicate the standard error. On the x-axis A represents absence points and P represents presence points.**

## *4.4.5 Model Evaluation*

### 4.4.5.1 Model predictive power

The majority of both ELL98 and CSF99 models were either generalized linear models or, generalized additive models with predominantly linear terms. Fewer non-linear relationships were identified in the CSF99 models than in the ELL98 models. In both cases the non-linear variables covered a range of types and were recorded at a range of scales. Usually variables which were non-linear in the initial model were also non-linear where the same variables were used to model different sites and years, though the form of the relationship was not always the same (Tables 4.4-4.18).

The percentage variance explained by the models was generally greater for ELL98 than for the CSF99. For the ELL98 the Adjusted $D^2$ ranged from 0.26 (siskin) to 0.87 (goldcrest). By comparison the range for the CSF99 models was from 0.15 (great tit) to 0.55 (robin) (Table 4.25).

**Table 4. 25: Adjusted $D^2$ values for the ELL98 and CSF99 models for each species, and for the models built for ELL00 and CSF99 based on the variables selected in the ELL98 models, and for ELL98 and ELL00 based on the variables selected in the CSF99 models.**

| Species | ELL 1998 Model | | | CSF 1999 Model | | |
|---|---|---|---|---|---|---|
| | ELL | | CSF | CSF | ELL | |
| | 1998 | 2000 | 1999 | 1999 | 1998 | 2000 |
| Goldcrest | 0.86 | 0.49 | 0.20 | 0.40 | 0.69 | 0.47 |
| Coal tit | 0.53 | 0.22 | 0.12 | 0.27 | 0.29 | 0.20 |
| Blue tit | 0.48 | 0.23 | 0.07 | 0.35 | 0.38 | 0.16 |
| Willow warbler | 0.48 | 0.09 | 0.04 | 0.25 | 0.19 | 0.10 |
| Treecreeper | 0.42 | 0.12 | -0.01 | 0.22 | 0.08 | 0.10 |
| Great tit | 0.40 | 0.19 | 0.04 | 0.15 | 0.33 | 0.18 |
| Garden warbler | 0.38 | 0.43 | 0.05 | 0.35 | 0.12 | 0.42 |
| Blackbird | 0.34 | 0.00 | -0.01 | 0.22 | 0.03 | 0.05 |
| Robin | 0.34 | 0.18 | 0.04 | 0.55 | 0.03 | 0.27 |
| Wren | 0.29 | 0.14 | -0.01 | 0.29 | 0.06 | 0.07 |
| Song thrush | 0.28 | 0.06 | 0.00 | 0.27 | 0.00 | 0.12 |
| Redstart | 0.42 | 0.30 | | | | |
| Wood warbler | 0.37 | 0.24 | | | | |
| Siskin | 0.26 | 0.15 | | | | |
| Blackcap | | | | 0.21 | 0.32 | 0.26 |

The mis-classified points of all of the models were generally distributed relatively evenly between absence and presence categories (Tables 4.4-4.18). Mann-

Whitney analysis comparing points which were correctly and incorrectly classified by the models suggested that mis-classified points tended to have higher values for mixed habitat variables than did correctly classified points. This applied to the willow warbler, wren and goldcrest amongst others. Edge variables at a range of scales also occurred with higher values in many groups of mis-classified points. For example the false presence points for the garden warbler tended to have higher values for several edge variables than the correctly predicted presence points. False presence points were also often high in alder variables at ELL (for example coal tit and siskin) and willow and water cover variables for the CSF99 (for example goldcrest).

### 4.4.5.2 Model cross-predictions between sites and years

When models were built for ELL00 based only on the variables selected for the ELL98 models for each species, the variance explained was less in every case except the garden warbler. Adjusted $D^2$ values for these models ranged from 0.00 (blackbird) to 0.49 (goldcrest). The variance explained in the ELL00 equivalent models was not proportional to that of the original ELL98 models. The drop in the percentage variance explained was even greater when the same variables were used to build models for the CSF99, ranging from -0.01 (wren, blackbird and treecreeper) to 0.20 (goldcrest). When models were built for each species for ELL98 and ELL00 based on the variables selected in the CSF99 models the percentage variance explained increased in some cases and decreased in others. In both years at ELL the goldcrest model built using the variables selected for the CSF99, had the highest explained variance (Tables 4.4-4.18 and Table 4.25).

The Adjusted $D^2$ and ROC AUC values were significantly positively correlated for both the ELL98 models (Kendall's tau b=0.869, df=11, $p<0.001$) and CSF99 models (Kendall's tau b=0.953, df=13, $p<0.001$). The AUC is more directly comparable between ELL and the CSF because it is less influenced by the differences in total habitat and landscape variance which exist between the two study areas.

In all cases the AUCs for the cross-validated (CV) models were slightly lower than for the models built using the complete data set (Tables 4.4-4.18). However the CV model AUCs were strongly positively linearly related to the 'complete data' AUCs. Similarly where the models were evaluated for other sites and years the AUCs derived from a direct prediction based on the original model were slightly lower than those where the model was re-fit for the different data sets (Tables 4.4-4.18). There was also a positive linear relationship between the AUC values based on the two different prediction methods. All figures quoted below are for the 'complete data' models and the direct prediction from these models across sites and years. These are summarized in Table 4.26.

AUC values indicate that all of the models built for ELL98 and CSF99 perform significantly better than random (0.001 significance level) for the year and site in which the data was collected. All of these models had AUC values >0.7 and so could be classed as having 'useful application' (Swets, 1988). Five of the models for the ELL98 species (goldcrest, coal tit, blue tit, willow warbler and treecreeper) and one of the models for the CSF99 species (song thrush) had AUC values greater than 0.9 and so could be classed as having 'high accuracy' (Table 4.26).

**Table 4. 26: Area under the curve (AUC) values and their standard error (SE) derived from ROC plots for ELL98 and CSF99 models. Cross-validated AUC values for these models are not quoted. The AUC values for ELL 2000 and CSF 1999 based on the ELL 1998 models and for ELL 1998 and ELL2000 based on the CSF 1999 models are directly predicted from the initial models without re-parameterization. AUC values ≥ 0.7 (after Swets, 1988) are given in bold. Significance levels are indicated as *** = p ≤ 0.001, ** = p ≤ 0.01 and * = p ≤ 0.05.**

| Species | East Loch Lomond 1998 Model | | | Central Scotland Forest 1999 Model | | |
|---|---|---|---|---|---|---|
| | ELL 1998 | ELL 2000 | CSF 1999 | CSF 1999 | ELL 1998 | ELL 2000 |
| | AUC ± SE | AUC ± SE | AUC ± SE | AUC ± SE | AUC ± SE | AUC ± SE |
| Goldcrest | **0.99** ± 0.00 *** | **0.86** ± 0.03 *** | **0.75** ± 0.03 *** | **0.89** ± 0.02 *** | **0.94** ± 0.02 *** | **0.86** ± 0.03 *** |
| Coal tit | **0.94** ± 0.02 *** | **0.78** ± 0.03 *** | 0.63 ± 0.03 *** | **0.84** ± 0.03 *** | **0.84** ± 0.03 *** | **0.72** ± 0.04 *** |
| Blue tit | **0.93** ± 0.02 *** | **0.77** ± 0.03 *** | 0.61 ± 0.05 * | **0.86** ± 0.03 *** | 0.40 ± 0.04 | 0.49 ± 0.04 |
| Willow warbler | **0.92** ± 0.02 *** | 0.68 ± 0.04 *** | 0.55 ± 0.04 | **0.82** ± 0.03 *** | **0.72** ± 0.04 *** | 0.69 ± 0.04 *** |
| Treecreeper | **0.91** ± 0.02 *** | **0.73** ± 0.04 *** | 0.56 ± 0.04 | **0.82** ± 0.03 *** | 0.60 ± 0.04 ** | 0.58 ± 0.04 * |
| Blackbird | **0.89** ± 0.02 *** | 0.47 ± 0.05 | 0.49 ± 0.04 | **0.80** ± 0.03 *** | 0.45 ± 0.05 | 0.50 ± 0.05 |
| Great tit | **0.88** ± 0.02 *** | **0.72** ± 0.04 *** | 0.55 ± 0.04 | **0.76** ± 0.03 *** | 0.63 ± 0.04 ** | 0.63 ± 0.05 ** |
| Garden warbler | **0.88** ± 0.03 *** | **0.77** ± 0.07 *** | 0.53 ± 0.05 | **0.89** ± 0.02 *** | 0.67 ± 0.04 *** | 0.66 ± 0.05 ** |
| Wren | **0.85** ± 0.03 *** | **0.74** ± 0.04 *** | 0.54 ± 0.04 | **0.84** ± 0.03 *** | 0.60 ± 0.04 ** | 0.62 ± 0.04 ** |
| Robin | **0.85** ± 0.03 *** | 0.62 ± 0.08 | 0.59 ± 0.06 | **0.93** ± 0.02 *** | 0.57 ± 0.05 | **0.72** ± 0.07 ** |
| Song thrush | **0.84** ± 0.03 *** | 0.67 ± 0.04 *** | 0.48 ± 0.04 | **0.83** ± 0.03 *** | 0.56 ± 0.05 | 0.53 ± 0.05 |
| Redstart | **0.90** ± 0.02 *** | **0.71** ± 0.04 *** | | | | |
| Wood warbler | **0.89** ± 0.03 *** | **0.80** ± 0.03 *** | | | | |
| Siskin | **0.84** ± 0.03 *** | 0.67 ± 0.09 * | | | | |
| Blackcap | | | | **0.79** ± 0.03 *** | 0.60 ± 0.11 | 0.56 ± 0.06 |

When the ELL98 models were used to predict the bird distributions for ELL00 they performed significantly better than random for all species at a significance level of 0.001, except for the siskin (significant only at level 0.05) and the blackbird and robin (non-significant). All of the predicted results significant at the 0.001 level had useful application except for those for the willow warbler and the song thrush based on the Swets (1988) criterion of an AUC value greater than 0.7. The ELL98 models predicted the bird distributions for the CSF99 significantly better than random for three species (goldcrest, coal tit ($p \leq 0.001$) and blue tit ($p \leq 0.05$). Of these three species the AUC for the goldcrest was over 0.7 and so had useful application (Swets, 1988) (Table 4.26).

The CSF99 models directly predicted the distributions of seven species (goldcrest, coal tit, willow warbler, garden warbler, ($p \leq 0.001$) treecreeper, great tit, and wren ($p \leq 0.01$)) significantly better than random for ELL98. Of these the goldcrest, coal tit and willow warbler predictions had useful application. They predicted bird distributions better than random for eight species for ELL00. These were the same seven species as were predicted better than random for ELL98 (goldcrest, coal tit, willow warbler ($p \leq 0.001$), great tit, garden warbler, wren ($p \leq 0.01$) and treecreeper ($p \leq 0.05$) and also the robin ($p \leq 0.01$)). The goldcrest, coal tit and the robin predictions had useful application for ELL00. Overall the most precise models with the highest accuracy in cross-prediction between sites and years were built for the goldcrest and the coal tit (Tables 4.4 and 4.5). The CSF99 model performed better than the ELL98 model in cross-prediction between sites (Table 4.26).

When the models were rebuilt for ELL00 and CSF99 using only the variables selected in the ELL98 models, a higher percentage of variables were significant for ELL00 than for CSF99. General coniferous variables were significant more often than general broad-leaved variables in rebuilt models and species specific broad-leaved variables were significant more often than conifer species variables (Table 4.27). Overall a higher proportion of variables were significant for ELL00 than for ELL98 when the CSF99 model variables were used to model these two data sets. This especially applied to the habitat variables in the local habitat structure, general broad-leaved variables, coniferous species and the edge categories (Table 4.27).

**Table 4. 27: Percentage significance of variables from different general categories for the models built for ELL00 and CSF99 based on the variables selected for ELL98, and for the models built for ELL98 and ELL00 based on the variables selected for CSF99. Results for categories in italics must be treated with caution because there were fewer than five variables in these categories for at least one inter site or inter year comparison leading to mis-leading extremes in the percentage significance of variables in the rebuilt models. Figures in bold highlight categories where at least 50% of variables were significant in rebuilt models.**

| Variable Categories | | ELL98 Re-built for | | CSF99 Re-built for | |
|---|---|---|---|---|---|
| | | ELL00 | CSF99 | ELL98 | ELL00 |
| **Local** | Ground cover | 33.33 | 33.33 | 19.05 | 28.57 |
| | Local habitat structure | **50.00** | 0.00 | 14.29 | 28.57 |
| | *Tree species richness/ diversity measures* | **100.00** | 0.00 | **100.00** | **100.00** |
| | BL general variables | 33.33 | 33.33 | 28.57 | 42.86 |
| | CF general variables | **75.00** | **55.56** | **50.00** | **50.00** |
| | BL species variables | **72.73** | 25.00 | 12.82 | 12.82 |
| | CF species variables | 25.00 | 14.29 | 12.50 | 25.00 |
| | *Area 0-100m radius* | **50.00** | **50.00** | **100.00** | **100.00** |
| | *Edge 0-100m radius* | 0.00 | 0.00 | 28.57 | 42.86 |
| | *Ratio area/edge 0-100m radius* | 0.00 | 0.00 | 0.00 | **50.00** |
| | *PA 1,2 or 3ha continuous woodland* | 0.00 | 0.00 | 0.00 | **100.00** |
| **Landscape** | Area 200-5000m radius | **57.14** | 42.86 | 33.33 | 16.67 |
| | Edge 200-5000m radius | 26.67 | 27.27 | **50.00** | **66.67** |
| | *Ratio area/edge 200-5000m radius* | 0.00 | 0.00 | 0.00 | **100.00** |
| **Indirect parameters** | *Slope/ aspect* | **50.00** | 0.00 | 0.00 | 0.00 |

The data range sampled was very similar for most variables for ELL98 and ELL00. More differences in range sampled occurred between ELL and the CSF99. With few exceptions, the data range sampled was similar for variables which were significant across sites and years. However, differences in the range sampled were not always present for those variables which were non-significant or had inconsistent directions of significant relationships, across sites and years. Inconsistencies in the direction of significant relationships occurred in seven cases when the ELL98 models were rebuilt for ELL00 and CSF99, and in 16 cases when the CSF99 models were rebuilt for ELL98 and ELL00. These included local through to landscape scale variables with relatively equal frequency (Tables 4.4-4.18).

When the AUC value was plotted against bird prevalence, there was a slight decline in AUC at lower and higher prevalence for ELL98, and no significant trend for CSF99. However, there was a curvi-linear relationship between bird prevalence in the initial model and the AUC value of predictions derived from these models for different sites and years. Where the relative number of presence to absence points deviated from a 50:50 ratio in the initial model the predictive accuracy, as measured through the AUC, was lower when these models were used to predict bird distributions at different sites and years (Figures 4.4 and 4.5).

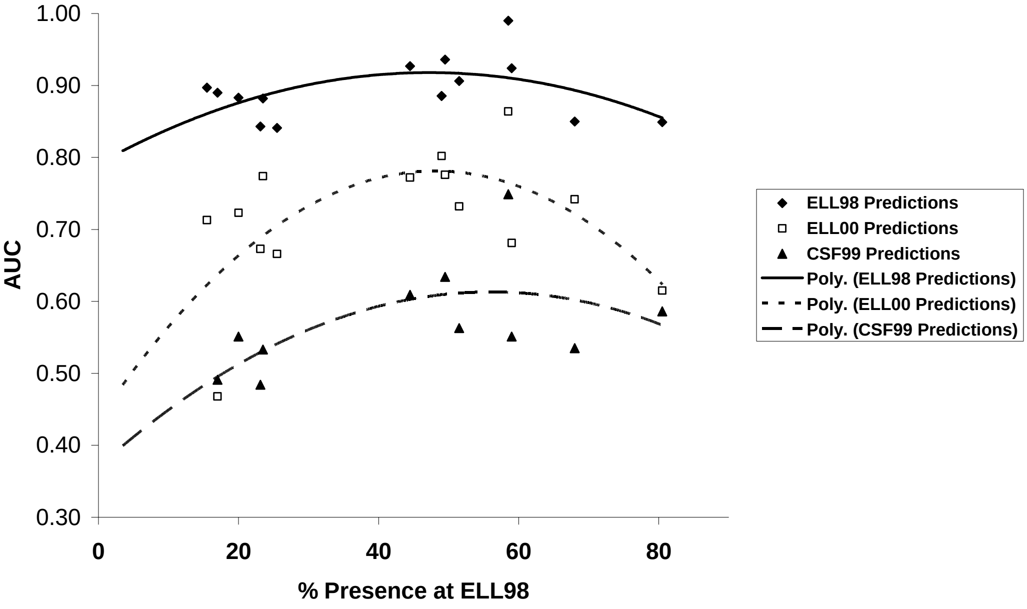

**Figure 4. 4: AUC values in relation to percentage presence of birds at ELL in 1998 for ELL98 and for cross-predictions for ELL00 and CSF99. Each graph point represents one species model. Curves fitted are for illustrative purposes only.**

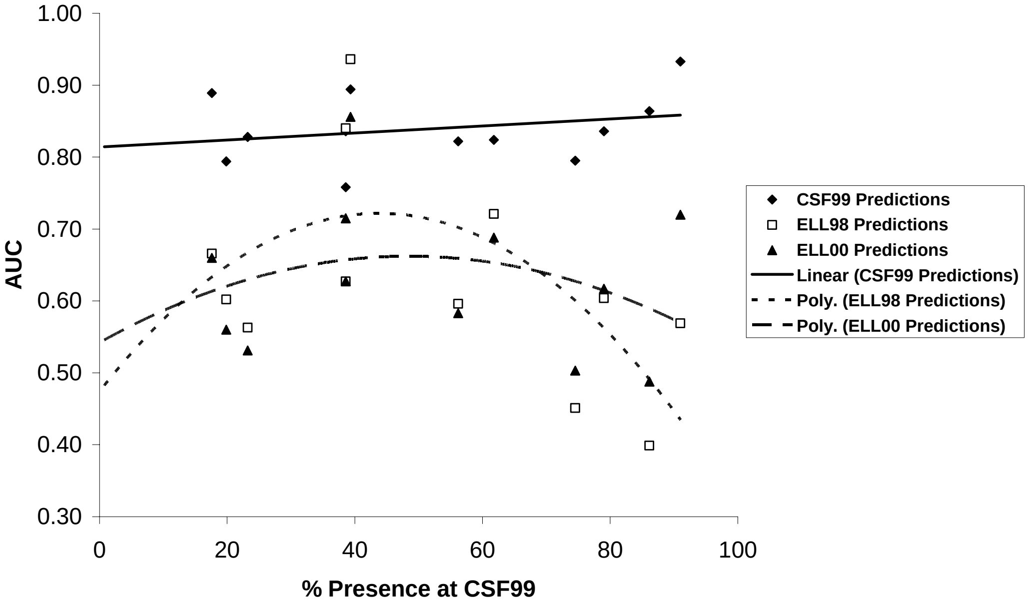

**Figure 4. 5: AUC values in relation to percentage presence of birds at CSF in 1999 for CSF99 and for cross-predictions for ELL98 and ELL00. Each graph point represents one species model. Curves fitted are for illustrative purposes only.**

## 4.5 Discussion

### *4.5.1 Bird habitat associations*

As with previous studies of woodland birds (Arnold, 1983; Hinsley *et al*., 1995) habitat variables within a territory scale accounted for most of the explained variation in the models for all species. These bird habitat associations were in agreement with the results of earlier studies (for example, Lack and Venables, 1939; Simms, 1971; Fuller, 1982). They can largely be interpreted in terms of bird feeding strategy and nesting requirements. Thus the three species which favoured conifers (goldcrest, coal tit and siskin) all have adaptations for feeding which are more efficient in this habitat (Snow, 1954; Klopfer and Ganzhorn, 1985; Peck, 1989). Similarly the species found in broad-leaved habitat were adapted for feeding and nesting in either shrubby or more open broad-leaved woodland. For example, the blackbird, wren, garden warbler and blackcap all nest and feed in the shrub layer (Armstrong, 1955; Williamson, 1969; Simms, 1971; Edington and Edington, 1972; Mason, 1976; Fuller and Moreton, 1987).

#### 4.5.1.1 Bird feeding behaviour

The great tit and the blue tit which both feed on insects and leaf-eating caterpillars in the breeding season (Lack, 1971; Krebs *et al*., 1972) occurred especially in high canopy broad-leaved woodlands, generally with little secondary growth. The song thrush which often feeds on the ground (Mitchell, 1981) and so favours a rich shrub layer (Simms, 1971) had a negative relationship with percentage bare ground in the ELL98 model (Table 4.9). Both the wren and treecreeper probe bark crevices for food (Armstrong, 1955; Norberg, 1979). This explains the positive relationship with broad-leaved snags in the CSF99 model for the wren (Table 4.8), and the positive relationship with mature broad-leaved trees in the ELL98 model for the treecreeper (Table 4.11). Both of these often have bark crevices and loose bark behind which insects could be found. The correctly classified points for the redstart all fell within oak woodland with little or no shrub layer. An open habitat is necessary because the redstart catches insects on the wing (Lack and Venables, 1939).

#### 4.5.1.2 Bird nesting behaviour

Woodland birds can be subdivided based on their nesting location into ground nesters, shrub layer nesters and species nesting higher up in the trees. The ground nesters were the wood warbler, robin and willow warbler. These species either had positive relationships with ground layer variables in the models (for example heather cover for the robin in the CSF99 model, Table 4.7) or the points where the species was correctly predicted as present had significantly more grass cover than those where the species was correctly predicted as absent (the ELL98 model for the wood warbler and the CSF99 model for the willow warbler, Tables 4.17 and 4.13).

For the shrub-nesting species, shrub variables occurred in the models or characterised the different groups of points subdivided by the models. For example both the ELL98 and CSF99 garden warbler models were dominated by tree variables of low diameter breast height, which are characteristic of shrub layers (Table 4.10). By contrast shrub variables did not occur in the CSF99 model for the blackcap (Table 4.16) but did have significantly higher values for presence points than for absence points. These results also agree with Mason (1976) who found that blackcaps often favour elder for nesting. For the wren, a positive relationship was found with the presence of water and bogs, fens and flushes in the CSF model (Table 4.8). This may also relate to nesting requirements, since wet material is required for building the domed nests (Armstrong, 1955). Positive associations between wren occurrence and damp conditions have been found in previous studies (Williamson, 1969; Creegan, 1996).

The hole and tree-nesting species included the blue tit, great tit, redstart, treecreeper, coal tit, siskin and goldcrest. All of these species showed associations with quite mature broad-leaved or coniferous trees depending on their habitat preference. Although the coal tit is a hole nester, it can also nest in crevices, on the ground or in log piles (Moss, 1978). This may account for the positive relationship found for the coal tit with fallen dead conifers in the CSF99 model (Table 4.5).

Nest boxes suitable for the blue tit, great tit and redstart were provided quite extensively at Loch Lomond and in small areas of the CSF. Although nestbox presence or absence was available for selection, it did not occur in any of the models for these species. However, the type of habitat identified as suitable in the tit and redstart models was that in which a lot of the boxes were placed. The absence of bird box as a model variable could be due to the fact that some also occurred in habitat which was more optimal for other species such as the pied flycatcher. Also, boxes cannot have been the sole nesting sites for these species since they also occurred outwith the areas with boxes. Interspecific competition for boxes may also have occurred, again leading to a mismatch between box presence and the presence of a particular species. Nest site requirements of the blue and great tits do overlap leading to the potential for competition (Minot and Perrins, 1986).

## *4.5.2 Evidence for effects of habitat fragmentation on bird distributions*

Habitat fragmentation was evident in both the Loch Lomond and CSF study sites, from territory scale upwards. It increased at Loch Lomond between 1998 and 2000 due to the management programme for the area involving conifer felling. Overall habitat fragmentation was greater for the CSF with a greater extent of open area at territory scale and a lower median patch size and correspondingly higher edge density in the landscape as a whole.

### 4.5.2.1 Woodland area effects

Fragmentation will inevitably lead to population decline purely due to a reduction in the spatial extent of suitable habitat. However, population declines greater than that which would be expected due to the reduction in habitat area, are indicative of fragmentation effects in excess of those due to pure habitat loss (Andrén, 1994) and these require additional explanation. Comparisons of bird distribution with the availability of broad habitat categories gave some indication of which species may show fragmentation effects greater than those due to habitat loss alone. However, the habitat occupancy index was very simplistic looking at habitat presence (not area) within only broad categories within 100m which was assumed to represent territory scale. The GLM and GAM models indicate that birds may be responding to woodland areas at a range of scales making an index of habitat occupancy difficult to calculate.

The broad categories used were based on the general preferences for broad-leaved or coniferous habitat derived from the models. Of the coniferous species, the goldcrest occurrence matched conifer habitat availability sufficiently closely that it was unlikely that population declines would exceed those predicted by pure loss of habitat area. With the exception of the result for 1998 at ELL, this also applied for the coal tit. The siskin population in all sites and years and the coal tit population in 1998 at ELL appeared to be under-saturated in terms of habitat availability. Where this applies in all years it could indicate that not all of the general habitat class was in fact ‘suitable’, and so the index of habitat occupancy cannot be used to determine fragmentation effects above those relating to habitat loss.

Since the broad-leaved habitat was generally more heterogeneous than the coniferous woodland, the general index of habitat occupancy had useful application for fewer species. Of these species there may be evidence for additional fragmentation effects for the willow warbler, blue tit, and blackbird. Where percentage species presence matched habitat availability at one site but not the other, there are two plausible explanations. Firstly the disparity could be due to differences between sites in habitat suitability within the general broad-leaved habitat category. Secondly it could indicate fragmentation effects over and above those due to habitat loss. A habitat suitability explanation is more likely where the proportion of habitat available matched for the CSF (the more fragmented study area) but not for Loch Lomond in either year. This applies for the blackbird and blue tit.

Definitive evidence for a minimum area effect cannot be obtained where data is being analysed by sample point rather than by separate woodlands. However, there are some indications that this factor may be important for some species. The strongest evidence for a minimum area effect was obtained for the song thrush where the presence of at least two hectares of contiguous woodland around each point was significant in the CSF99 model (Table 4.9). When the variables selected for the CSF99 model were used to build models for Loch Lomond, this variable was also significant for 2000, although not in 1998. As habitat becomes more fragmented it is more likely that a minimum habitat area will not be present around each sample point. This is more likely to apply in the CSF where habitat was more fragmented than at East Loch Lomond. Habitat was more fragmented at East Loch Lomond in 2000 than in 1998, and this may partly account for why this variable was significant in the later year but not the earlier one.

Minimum habitat area may be important because below a certain size insufficient resources may be present for breeding (Moore and Hooper, 1975; Galli *et al.*, 1976). However, Avery and Leslie (1990) suggested that there is no evidence for any British woodland bird species requiring a minimum area much greater than their territory size. This may still be true for the song thrush. Nevertheless, it was one of the largest species modelled and its territory size requirements are larger than most other modelled species. Previous studies, such as Moore and Hooper

(1975) and Hinsley *et al*. (1995) have also suggested that the song thrush is sensitive to woodland area.

Minimum area effects may not occur because individuals utilize none contiguous blocks of woodland within their territories (Howe, 1984; Andrén, 1994). The song thrush result suggests that this is not generally happening for this species in the CSF study area. This is not what might be expected for this species given that the Chapter 2 results indicate that the number of separate woodland patches in the CSF landscape decreases exponentially with increasing gap crossing distance and the song thrush would be predicted to have a quite a high willingness to cross gaps based on its large mass if the hypothesis suggested in Section 2.5.2 applies. Song thrushes will utilise resources in open grassland areas during the breeding season (Mitchell, 1981) suggesting that it will cross gaps in the woodland cover. However, the song thrush population, based on the proportion of sample points at which it was present (23.2%) was quite low and it is possible that the population was occupying only the most optimal territories which required less gap crossing and so had lower costs in terms of energetics and predation risk.

Woodland area around each sample point is significant at different scales in some of the models for ELL98 and the CSF99. For example, area of woodland at a scale of 5000m had a significant positive relationship in the blue tit CSF99 model (Table 4.15) and song thrush ELL98 model (Table 4.9) which could indicate sensitivity to habitat loss. This agrees with the area sensitivity suggested by Hinsley *et al*. (1995) for these species. However, the relationships with woodland area are generally hard to interpret because area variables are correlated across scales and between woodland type categories and inconsistencies occur in some cases in the directions of relationships between sites and years.

### 4.5.2.2 Edge effects

Edge variables were the most prevalent of all fragmentation related parameters in the models. They occurred in both the CSF99 and the ELL98 models. However, their frequency of occurrence was slightly greater in the ELL98 models, especially at a scale of greater than 100m from sample points. This was despite the fact that the CSF study area was more fragmented than the ELL one and so the opposite trend might have been expected, especially as predator related edge processes are often more intense in agricultural landscapes than in logged areas (Andrén, 1992; Bayne and Hobson, 1997; Chalfoun *et al*., 2002). Jackdaws, jays, magpies and hooded crows all occurred in the study area (pers. obs.) and have been implicated in increased nest predation at habitat edges (Møller, 1988; Andrén, 1992).

It may be that as the CSF was more fragmented, the differences between edge and interior habitat were less pronounced than at East Loch Lomond. Edge effects can extend over different distances from the habitat perimeter. For example, Chen *et al*. (1995) identified microhabitat changes extending from the woodland edge to over 240m within the woodland. Likewise Paton (1994) found that effects of enhanced nest predation and parasitism extended for 50m into woodlands from the edge. In some cases entire woodland fragments within the CSF may effectively have been edge habitat.

This may account for why edge/area ratio variables were only selected as significant in CSF99 models, not for the ELL98 models. Some of these ratio variables were significantly correlated with edge variables. However, they were not measuring exactly the same thing. For example, the positive significance of the edge/area ratio for the song thrush at a scale of 50m (Table 4.9) indicates not only an aversion for edge habitat, at this scale, but an actual preference for interior habitat. This is in keeping with its preference for the presence of two hectares of continuous habitat around each point.

The directions of the relationships of the edge variables in the CSF99 models were less consistent when these variables were used to model the ELL data than vice versa. These inconsistencies may be due to different characteristics of the habitat edges in the CSF and ELL study areas. All of the edge variables were pure length measurements and therefore were descriptive of the habitat characteristics in only a very general way. However, edge habitats do differ between logged and agricultural landscapes. Blake and Karr (1987) found that woodlots in agricultural landscapes were often sharply delineated. However, new forest management practices often lead to more transitional vegetation along edges in logged landscapes (Avery and Leslie, 1990; Forestry Commission, 2001).

Many of the broad-leaved bird species showed positive relationships with broad-leaved, mixed or general woodland edge and negative relationships with coniferous woodland edge. Similarly coniferous edge variables were either not significant or had a positive relationship and broad-leaved edge a negative relationship for coniferous bird species. The negative relationships with edge of a habitat type within which a species rarely, if ever, occurred are probably coincidental with a general aversion to that broad habitat type. The positive edge relationships, especially for the broad-leaved and ubiquitous species were more likely to be indicative of an actual edge effect.

These broad-leaved species included the willow warbler, great tit, wren, garden warbler and blackcap. These species all benefit from the presence of shrubby vegetation (Colquhoun and Morley, 1943; Armstrong, 1955; Edington and Edington, 1972; Moss, 1978; Fuller, 1982; Hinsley *et al*., 1996a). Denser shrub layers often occur at woodland edges, possibly due to greater light penetration (Forman and Godron, 1986; Fuller and Whittington, 1987). Previous positive associations with woodland edge have been found for many of these species including the willow warbler (Cody, 1985; Bryant *et al*., 1993), great tit (Bellamy *et al*., 2000), wren (Hinsley *et al*., 1996b) and blackcap (Moore and Hooper, 1975) and these have generally been interpreted as being due to the shrub layer development at the edge.

There is some ambiguity involved in the blackcap relationship with broad-leaved woodland edge (Table 4.16). The form of the relationship was positive at Loch Lomond for both 1998 and 2000 and this is logically interpretable as being due to the benefits of good shrub development for the blackcap. The disparity between Loch Lomond and the CSF cannot be accounted for by differences in the correlation structure between sites. Possibly landscape differences in nest predation at the woodland edge may be affecting the blackcap population more in the CSF than at ELL. Edge related nest predation has been found to be higher in agricultural landscapes (Andrén, 1992).

However, the broad-leaved species, the blackbird, song thrush and redstart all showed negative relationships with general or mixed woodland edge. This is understandable for the redstart which prefers open canopy woodland without dense shrub development (Williamson, 1972) due to its flycatching feeding technique. Furthermore woodland edge at the 1000m scale found in the redstart models (Table 4.18) is positively correlated with large conifer blocks which the redstart also avoids.

The same argument does not apply for the blackbird and song thrush which generally benefit from a good shrub layer (Simms, 1971; Williamson, 1974; Fuller, 1982), and so might be expected to favour woodland edges. Hinsley *et al.*, (1995) and Hinsley *et al.* (1996a) found that blackbird presence was in fact related to woodland perimeter. Paradis *et al.* (2000) found that nest failure rate of blackbirds and song thrushes increased with corvid density and numerous studies have found elevated nest predation rates at woodland edges (for example, Gates and Gysel, 1978; Askins *et al.*, 1987; Paton, 1994).

It is unlikely that corvids would be preying on thrush and blackbird nests, but not on some of the other woodland bird species nests. Some interspecific difference in predation rate is likely to relate to degree of nest crypsis. For example wren nests tend to be particularly well concealed and so should suffer less predation (Armstrong, 1956; Garson, 1980a). However, it is possible that the balance of positive effects from greater shrub development versus negative effects from increased predation varies interspecifically. The relative usage of different habitat areas can also be influenced by population density. Both the blackbird and song thrush were less abundant than many of the other woodland species. Also, some species may be able to assess more accurately predation risk. Though depressed breeding has been found due to predation in birds (Geer, 1978; Paradis *et al.*, 2000) these studies do not actually measure predator risk assessment by birds, and cannot separate this from a population saturation effect.

Of the coniferous or ubiquitous woodland species the robin, siskin and goldcrest all had positive relationships with woodland edge in at least one of the models. For the goldcrest the positive relationship with coniferous edge occurred in the CSF99 model and was never significant at East Loch Lomond (Table 4.4). No earlier studies have suggested that goldcrests particularly favour woodland edges and there are no obvious habitat benefits to explain such a relationship. Sample points were at least 50m from habitat edges in all cases except where this was impossible due to habitat configuration. This occurred more often in the CSF than at Loch Lomond. Similarly there were more sample points at the CSF relative to Loch Lomond where conifer edge occurred more extensively within 100m of the sample point, the scale of the conifer edge variable in the CSF99 model. This meant that conifer edge was more strongly correlated with conifer area in the CSF than at Loch Lomond. Thus the relationship of goldcrests with conifer edge in the CSF could be coincidental on the correlation between conifer edge and area at this site.

The positive association between siskins at woodland edges was present only at Loch Lomond at a scale of 2500m (Table 4.6). Siskins feed on conifer seeds, and it is conceivable that the densities of these were higher at woodland edges. However, as with the goldcrests this relationship could be slightly spurious, due to the correlation structure of the variables. At Loch Lomond woodland edge at 2500m was strongly positively correlated with large blocks of conifer woodland which would have provided good siskin habitat. The correlation coefficient for woodland edge and conifer blocks was lower for the CSF.

A direct explanation of the relationship between occurrence and conifer edge at 50m is more likely for the robin (Table, 4.7). Robins benefit from the development of a shrub layer which provides suitable nesting sites and a greater abundance of invertebrate food (Lack and Venables, 1939; Williamson, 1972; Bellamy *et al*., 2000). Shrub development can occur along conifer edges (Avery and Leslie, 1990) and is more likely in a Forestry Commission managed area than for many of the woodlots in the agricultural CSF landscape. This may account for why this variable was significant only at Loch Lomond.

Edges also occurred between different types of woodland habitat. Up to a scale of 500m around sample points the effects of these variables were generally positive for the model for which they were selected and none significant when the model was rebuilt for different sites and years. Thus positive effects were observed for the wren, treecreeper, coal tit, garden warbler and song thrush. These boundaries were likely to have greater structural complexity and possibly insect diversity which would be advantageous in terms of nest site provision and food availability.

Increased productivity has long been recognised along the junction between neighbouring habitat types (Leopold, 1936) (in Yahner, 1988). The relationships at a scale greater than 500m from sample points only occurred for three species (willow warbler, blackbird and song thrush) in the CSF models and were less consistent in direction. It is possible that these relationships were spurious due to the correlation of the edge variables with other parameters which the species either avoided (negative relationships) or preferred (positive relationships).

## *4.5.3 Evaluation of the modelling techniques*

### 4.5.3.1 Use of GAM versus GLM modelling

Most of the relationships identified in the data were linear and so could have been modelled using generalized linear modelling (GLM). However, it is only because a generalized additive modelling (GAM) approach was used that it is possible to rule out the widespread occurrence of non-linear relationships in the data. GAM allows the investigation of the presence of more complex relationships (Hastie and Tibshirani, 1990). Linear relationships are more likely to occur over relatively short variable gradients (Greig-Smith, 1983). It is therefore more likely that these are what were present in both the ELL and CSF sites.

### 4.5.3.2 Model predictive power

Explained variation was generally higher for the ELL98 models than for the CSF99 models. This was most likely due to the overall presence of more variation in the CSF than the ELL landscape. Unmeasured parameters are likely to be important in accounting for some of the unexplained variation at both sites

(Siffczyk *et al*., 2001). Such parameters can be hard to identify since non-random variations in avian distributions can occur in apparently quite uniform woodland habitats where birds are responding to very subtle variations in habitat quality (Fuller, 1995).

Additional variation could also have been accounted for through the use of interaction terms such as those employed by Siffczyk *et al*. (2001). No interaction terms were considered because the modelling technique would not have supported the additional variables which this would have generated. Such variables also often have high degrees of multicollinearity (Kim and Kohout, 1975), which affects the assessment of the significance of each variable in a model (Wetherill, 1986; Buckland *et al*., 1997). An approach based on an understanding of each species ecology, would have been the only way in which interactions could have been incorporated (Gates *et al*., 1994). This information was not available for all of the species modelled, especially with regard to landscape and fragmentation effects.

There is a longer history of studies relating woodland bird distributions to local scale habitat variations, than those considering wider spatial effects. Consequently, methods for defining local habitat variables are better developed than those for wider spatial effects. Based on the relative degrees of habitat fragmentation for the CSF compared with Loch Lomond, it would have been reasonable to expect variables at a scale greater than 100m to explain more variation in the CSF than in the ELL models. In fact the opposite occurred. This does not necessarily mean that birds were being less affected by fragmentation at this scale in the CSF relative to Loch Lomond. It is more likely that other landscape measures would have better accounted for the effects of fragmentation on bird distributions, as suggested by Watson (2002).

Defining suitable landscape metrics is complicated by the issue of spatial autocorrelation. Data was defined for sample points which were all at least 150m to 200m apart. Measurements at this scale should have been relatively independent, although points closer together in the landscape may have had a higher probability of possessing similar habitat characteristics than those further apart (Augustin *et al*., 1996). This effect will have been lessened in instances where discontinuities between woodland types were quite sharp. Such discontinuities occurred at ELL between coniferous and broad-leaved habitat and within some of the CSF woodland blocks. However, points from different woodland blocks in the CSF were often more dissimilar than those from a single block. Autocorrelation problems are likely to be even more pronounced when measurements are based on wider circle radii from sample points, since these inevitably overlap to increasing degrees as the scale is increased.

This leads to problems of pseudoreplication because where points are autocorrelated they do not each contribute a full degree of freedom to the dataset, affecting the assessment of the significance of variables in the models (Hurlbert, 1984; Legendre, 1993; Fielding and Bell, 1997). Spatial data violates the independence assumptions of both GLM (McCullagh and Nelder, 1989) and GAM (Hastie and Tibshirani, 1990) modelling approaches. The modelling carried out here should ideally be refined to take account of this factor, possibly through some form of autologistic modelling such as that carried out by Augustin *et al.* (1996). They used data based on grid squares and presence in one square was allowed to depend on presence in neighbouring squares. Augustin *et al's* (1996) methodology could not be directly transferred to this study because the fragmented nature of the woodland meant that the numbers of neighbouring points for different neighbourhood sizes was not constant. Biases would also arise due to a lack of data for the surrounding area for points occurring at the edge of the study sites. An alternative approach is the incorporation into the models of structure functions describing the autocorrelation present in the data (Legendre, 1993; Smith, 1994).

Despite the disparity in variance explained between ELL and the CSF, the models when assessed by the area under the ROC curve, and the misclassification rate of bird distributions all performed significantly better than random and had useful application as defined by Swets (1988). Total elimination of misclassification is an unrealistic goal since some will inevitably arise due to data gathering limitations, and a failure to take account of all ecological processes relevant to each species (Fielding and Bell, 1997). Some of these, such as population processes operating outwith the period of data collection, are hard to model using a static modelling approach like GLM or GAM (Guisan and Zimmermann, 2000).

However, where patterns can be identified within groups of mis-classified points, this information could potentially be used to improve model accuracy. For example, Mann-Whitney tests identified that mis-classified points especially occurred in mixed habitat and at edges. More detailed edge measurements could help to reduce the mis-classification due to this parameter. The mixed habitat often included broad-leaved species such as willow in the CSF and alder at ELL. These species are characteristic of wetter areas. In the CSF, patches of willow occurred within coniferous woodlands. Likewise at Loch Lomond, alder formed a large component of the broad-leaved woodland which occurred along the streams within conifer plantations. Thus the models were generally insensitive to the habitat variation concurrent with moister areas, especially streams.

#### 4.5.3.3 Cross-prediction of models

The ELL98 models cross-predicted with higher accuracy for ELL00 than for CSF99. Similarly when models were rebuilt for ELL00 and CSF99 using only the variables selected for ELL98, a higher percentage of these variables were significant in the ELL00 models compared with the CSF99 models. This can be accounted for based on the greater similarity between the ELL98 and ELL00 landscapes relative to the ELL98 and CSF99 landscapes. Both GLM and GAM modelling approaches are static, relating species distributions to their current environment (Guisan and Zimmermann, 2000). The variable gradients being sampled and the correlation structure of the variables were more similar for ELL in 1998 and 2000, than for the CSF99 and this affects the extrapolation of results between sites. Where different sections of a gradient are being sampled the form of the relationship may differ (Buckland and Elston, 1993). Similarly a species may actually be responding to a parameter correlated with a variable in the initial model, and not the variable itself (Smith, 1994). Where this correlation is absent in a different site or year, the variable is unlikely to be significant and so will not have predictive value (Gates *et al*., 1994).

Differences in the correlation structure between sites can account for changes in direction in species-variable relationships. For example, in the blue tit model for the CSF99 site the area of woodland at a scale of 5000m has positive significance. When the variables significant in the CSF99 model were used to model the blue tit for ELL98, the form of the relationship was negative (Table 4.15). The blue tit generally prefers broad-leaved over coniferous habitat. In the CSF99 data woodland area at 5000m was positively correlated with broad-leaved variables, whereas in the ELL98 data it was positively correlated with coniferous variables. Thus it is likely that the woodland variable was really a proxy for broad-leaved habitat selection in the CSF99 model and coniferous habitat aversion in the ELL98 model.

When the CSF99 models were cross-predicted for Loch Lomond in 1998 and 2000, predictive accuracy was greater for 2000 than for 1998. Between 1998 and 2000 the main habitat and landscape changes at Loch Lomond were due to conifer felling. Thus overall less coniferous habitat was available and habitat fragmentation had increased. This made the resemblance between the CSF and Loch Lomond study sites more similar and was reflected in slightly greater similarity in gradients sampled and variable correlation structure.

Perfect cross-prediction will only occur where the variables in the models are indicative of causative rather than simply correlative relationships; where all appropriate parameters to which birds are responding have been included in the models; and where the species are in equilibrium with the environment (Wiens, 1976; Gates *et al*., 1994; Guisan and Zimmermann, 2000; Merrill, 2002). In this study some of the relationships were more obviously correlative than causative and the presence of unexplained variation indicated that not all parameters to which the birds were responding had been included in the models. There are also various factors which could have meant that species were not in equilibrium with the environment.

Management was very active at Loch Lomond within and between field seasons, and there will have been disturbance associated with this. Disturbance can lead to disequilibrium between populations and their environments (Begon and Mortimer, 1986). For example, time lags can occur in the response to habitat change due to deforestation (Lack, 1933). This may be partly due to individuals showing fidelity to natal sites irrespective of habitat changes (Austin, 1949; Blake and Karr, 1987). However, this varies with species and while it has been observed for some woodland species such as the great tit (Kluijver, 1951), wren (Armstrong, 1956) and blackbird (Snow, 1956), Bellamy *et al.* (2000) found that site fidelity was not a major factor determining woodland bird distributions.

Species will also not be at equilibrium where the population is under or over saturated. Where the population is low, only the most optimal habitats should be occupied. As the population increases birds will occupy less optimal habitat and ultimately there may be a pool of sexually mature ‘floaters’ which are unable to breed due to insufficient resources (Orians and Willson, 1964; Brown and Orians, 1970; Orians and Wittenberger, 1991).

Presence and absence data is not a direct measure of the breeding population, so it is was not possible to categorically determine habitat saturation. Some of the birds recorded may have been transients or non-breeding floaters and these could not be distinguished from the true breeding population. However, there was some indication of interspecific differences in habitat saturation where large population fluctuations occurred between years at Loch Lomond (as for the siskin, garden warbler and wood warbler) and where species presence was proportional to habitat availability in some but not all cases, as discussed in Section 4.5.2.1.

Differences also occurred interspecifically in the accuracy with which models cross-predicted between sites and years. Overall the most accurate models for predicting between sites and years were built for the goldcrest and the coal tit (Tables 4.4 and 4.5). These species both favoured conifers and had general conifer variables in both the ELL98 and CSF99 models. Analysis of the proportions of variables from different categories significant in models re-built for different sites and years indicates a consistent high percentage of significance for variables from the general conifer category. More specific species variables were significant less often in cross-prediction, especially between sites. Further analysis could be carried out to investigate whether more general variables could be substituted in the initial models. This may sacrifice some precision in predictions for the initial model, but achieve higher predictive accuracy when transferred to other sites and years.

The relationship between percentage presence in the initial model and the accuracy of predictions for different sites and years (as assessed by the ROC

AUC) indicates that the most accurate models were derived from an approximately 50:50 ratio of presence and absence points in the initial model. ROC however is a threshold independent measure (Fielding and Bell, 1997). Where the ratio deviated from a 50:50 presence absence split, weighting was applied. The implications of weighting models which are then used to predict distributions at different sites and years have to my knowledge, not been investigated. However this could be having a negative effect on predictive accuracy. Further work could be carried out to compare the cross-predictive accuracy of unweighted and weighted models built for ELL98 and CSF99.

Based on these results, data for logistic modelling where the models are to be used for distribution predictions for other sites and years, should ideally have an equal number of presence and absence points. This may require data collection over larger areas and selecting only a proportion of points for modelling. This inevitably creates other modelling considerations of avoiding biases due to modelling only part of the data. It also omits much of the variation in absence points for rare species where the need for predictive models of conservation application is greatest.

## 4.6 Conclusion

To conclude, the largest proportion of variation in the models was accounted for by local habitat variation. This agreed with earlier studies of bird-habitat association for these species and could be explained in terms of feeding and nesting requirements. Additional variation in all of the models was accounted for by landscape variables and by fragmentation related parameters, especially edge effects. These can mostly be accounted for by processes which may vary in intensity with fragmentation, but which are actually operating at a local scale. The main evidence of an effect of woodland area was found for the song thrush where the presence of two hectares of continuous woodland was a significant predictor in the CSF99 model.

All of the ELL98 and CSF99 models predicted bird distributions significantly better than random and had useful application as defined by Swets (1988). The generalized additive and generalized linear modelling approaches were therefore useful for identifying patterns in bird distributions. Mis-classified points were often those associated with edge and mixed habitat, especially areas of broad-leaved woodland in moist areas, such as along streams, in conifers.

The most accurate cross-predictions were derived for ELL00 based on the ELL98 models. Predictions between sites were generally less accurate, although the CSF99 model predicted the Loch Lomond data better for 2000 than for 1998. These patterns could be explained in terms of differences in correlation structure and gradient sampled for the variables in the models. In addition no interaction terms were considered and in some cases birds may have been responding to variables correlated with those actually in the model. Interspecific differences in cross-predictive accuracy of models may also depend on differences in population saturation and the generality of the variables in the original model.

# Chapter 5: Predictions of bird distribution changes at East Loch Lomond over the next 50 years.

## 5.1 Introduction

Woodlands and forests cover more than a quarter of the Loch Lomond and the Trossachs National Park. They therefore have an important role to play in fulfilling the natural, cultural, recreational and economic aims of a Scottish National Park, in a sustainable manner (The National Park Authority, 2003). To this end a Local Forestry Framework has been established by the National Park Committee, the Forestry Commission and Scottish Natural Heritage. If implemented, this framework will involve the restructuring of existing coniferous woodlands and their restoration to native woodland where they are Plantations on Ancient Woodland Sites (PAWS). It will also involve improved management and expansion of existing semi-natural woodlands.

The majority of the East Loch Lomond study site is owned by the Forestry Commission and management is under way to replace the coniferous plantations with native broad-leaved woodland. An understanding of the implications of this management for the bird communities will be valuable in terms of contributing to fulfilling each of the four aims of the National Park described in Section 1.4.1. Thus, woodland birds contribute to the biodiversity of the woodlands and their presence therefore enhances the natural value of the landscape. Their continued presence is especially important as declines have been reported for many woodland species and they are one of the government's indicators of sustainability (Gregory *et al*., 2003). In addition birds can be seen as a 'flagship' group holding much popular appeal with the general public. Thus their continued presence will bring important social benefits through the enjoyment which they give people.

An understanding of how the bird communities will be affected by the woodland management is therefore important. The aim of this section of the study was to demonstrate the potential to use the bird models developed in Chapter 4 to predict changes in the woodland bird distributions. Since the Forestry Commission's plan is for complete recovery to broad-leaved woodland by 2050, bird distributions were projected for this time scale. Specifically the following questions were addressed: (1) How are bird distributions likely to change over the next 50 years? (2) What degree of confidence can be placed in the accuracy of these predictions? (3) How could the modelling be improved to increase the accuracy of predicted distributional changes of the woodland birds?

## 5.2 Method and Data Analysis

### *5.2.1 Species selection for distribution projections*

Species were selected for forward projection of their distributions based on the cross-prediction results for ELL00 of the ELL98 GLM and GAM models given in Section 4.4.5.2. There were nine species for which the ELL98 models had 'useful application' as defined by Swets (1988) when directly used to predict the ELL00 data. These species (wren, goldcrest, coal tit, blue tit, treecreeper, great tit, garden warbler, redstart and wood warbler) all had AUC values of at least 0.7 for direct predictions of the ELL00 data using the ELL98 models (Table 4.26).

In addition there were four species for which the CSF99 models had useful application based on the Swets (1988) criterion when directly used to predict distributions at Loch Lomond. These were the goldcrest, coal tit, willow warbler and robin. The AUC values exceeded 0.7 in cross-prediction for both ELL98 and ELL00 for the goldcrest and coal tit. However, this value was only exceeded for ELL98 for the willow warbler and for ELL00 for the robin (Table 4.26).

### *5.2.2 Construction of future scenarios*

A list of variables present in the nine ELL98 models and four CSF99 models selected for use in distribution projections was compiled. The ELL00 data was taken as a baseline dataset since this was the most up to date information available for Loch Lomond. Three classes of variable were identified for which predicted future datasets needed to be compiled. These were physical parameters; area and edge variables derived from ArcView GIS; and habitat measurements originally derived in the field from the circular plot method (after James, 1971). The physical parameters were slope and aspect. It was assumed that these would remain constant within the time scale being modelled.

Scenarios were constructed for 2025 and for 2050, a time scale sufficient to allow for reasonable tree growth based on Forestry Commission production forecast tables (Hamilton and Christie, 1971). The management plan for the East Loch Lomond area also suggested that it should be fully restocked by 2050. Since natural regeneration can be very unpredictable (Thompson *et al.*, 2003) two scenarios were modelled for each year. One scenario, assumed no regeneration with new woodland being purely derived from replanting. Information on areas for replanting was available. It was assumed that sufficient grazing management was carried out to allow these areas to become established. The second scenario included new planting, but also allowed for regeneration.

Proximity to a seed source is likely to enhance the probability of regeneration occurring (Forestry Commission, 2003). Therefore regeneration was modelled as proceeding outwards from woodland edges, a pattern which has been observed in other studies (Seddon, 1971; Sauer, 1988, Rogers, 1989). Such studies have suggested disparate rates of spread at woodland margins with estimates ranging from an average of 0.6m per year (Wardle, 1980; Rogers, 1989) to around two metres per year (Alexander, 1969). No rates of regeneration at woodland edges could be found for Scotland and a fairly conservative estimate of one metre per year was decided upon for modelling purposes.

Landscapes were constructed within ArcView GIS to fit each of the scenarios. There were three stages involved in their construction. Firstly the Forestry Commission felling plan was used to identify which conifer areas required removing for each year. Although such plans are not always completely adhered to (pers. obs.), this represented the most accurate information available. Secondly, areas of replanting were added for the appropriate years. Replanting was counted as new woodland once it was 10 years old. Thirdly a buffer technique was used to add regeneration proceeding away from woodland edges. Management information was only available for the East Loch Lomond area. The areas of coniferous, mixed and broad-leaved woodland were modelled as undergoing no change outwith this area.

Once the landscapes had been constructed, area and edge measurements could be generated for the buffer distances around sample points established for the bird counts in 1998 and 2000 (50m, 100m, 200m, 500m, 1000m, 2500m and 5000m) as described in Section 4.2.6. Descriptive statistics of the proportion of open habitat and wooded habitat (broad-leaved, coniferous and mixed) within 100m of sample points were also calculated for each scenario so that a graph of habitat change under the no regeneration and regeneration scenarios could be produced.

The GIS maps were used to compile a list of the general habitat types present at each point for each scenario in each year, and the age of the woodland at the point. Tree diameter breast height measurements were then determined based on what was present in 2000 modified for felling, replanting or regeneration. Standard regeneration measurements were derived from early regeneration points present in 1998 and 2000. Tree growth was projected forwards using production forecast tables for each species (Hamilton and Christie, 1971). Ground and canopy cover variables and habitat structure variables (numbers of trees in different height categories) were predicted based on regression relationships with tree diameter breast height variables.

### *5.2.3 Predictions of future bird distributions*

Once datasets had been constructed for the 2025 and 2050 scenarios, they were used to predict bird distributions based on the ELL98 and CSF99 models of Section 4.4.1. Because no bird data was available against which predictions could be compared in a ROC plot, Equation 4.2 could not be applied to determine an appropriate cut point for defining presence and absence. Consequently a cut point of 0.5 was employed. Results from Section 4.3.4 suggest that this performs only slightly less accurately than the cut point determined by Equation 4.2. The total number of predicted presence points were summed for each species for each scenario and plotted to show total predicted distribution changes.

## 5.3 Results

### *5.3.1 Description of habitat changes under different scenarios*

Maps showing the East Loch Lomond landscape in 1998 and 2000 are given in Figures 5.1 and 5.2 respectively. The constructed landscapes for 2025 and 2050 showing changing areas of broad-leaved, coniferous and mixed woodland are given in Figures 5.3 and 5.4 (2025 and 2050 respectively, assuming no regeneration) and Figures 5.5 and 5.6 (2025 and 2050 respectively, assuming regeneration).

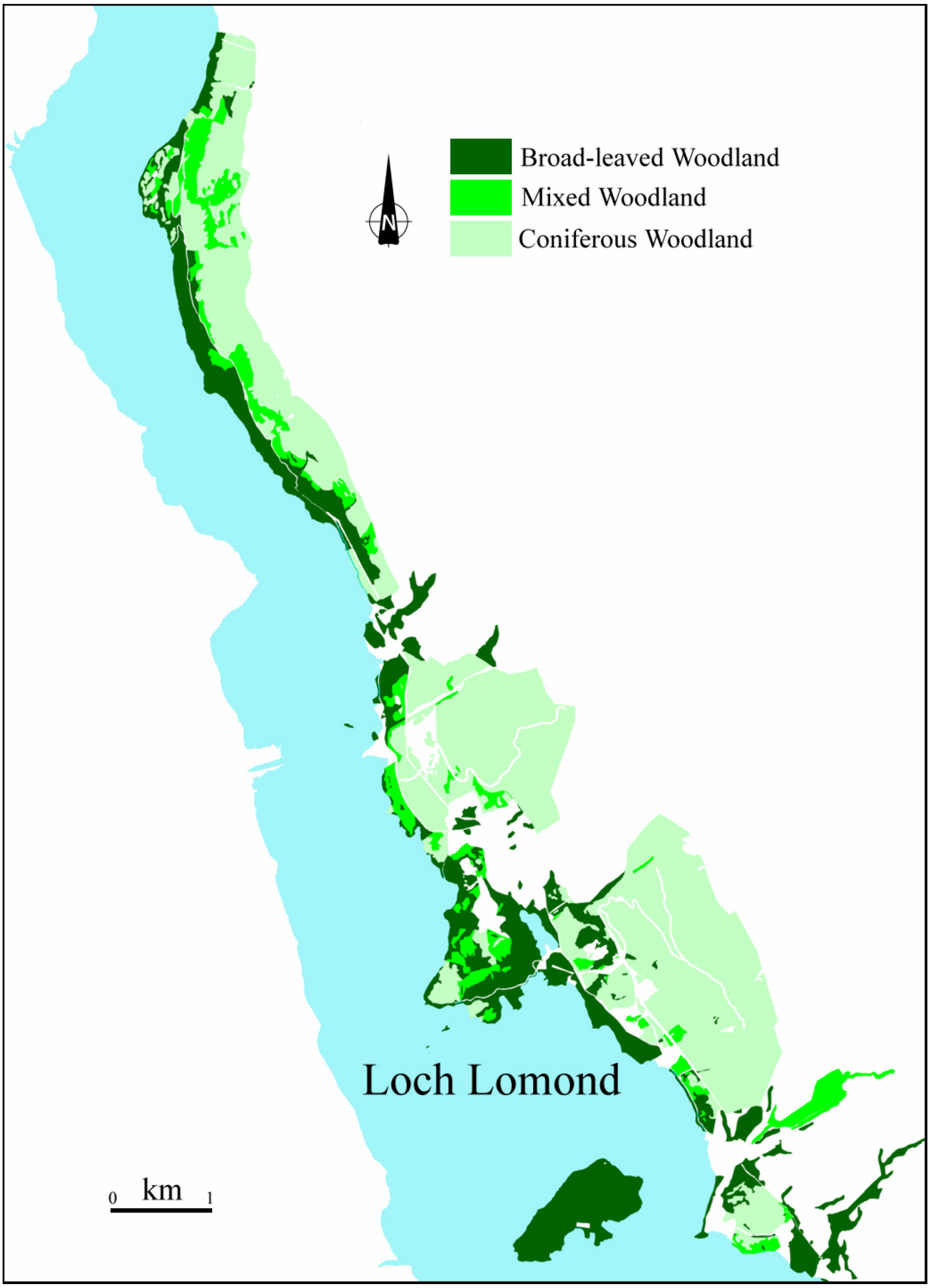

Figure 5. 1: The distribution of broad-leaved, coniferous and mixed habitat in the area owned by the Forestry Commission at East Loch Lomond in 1998.

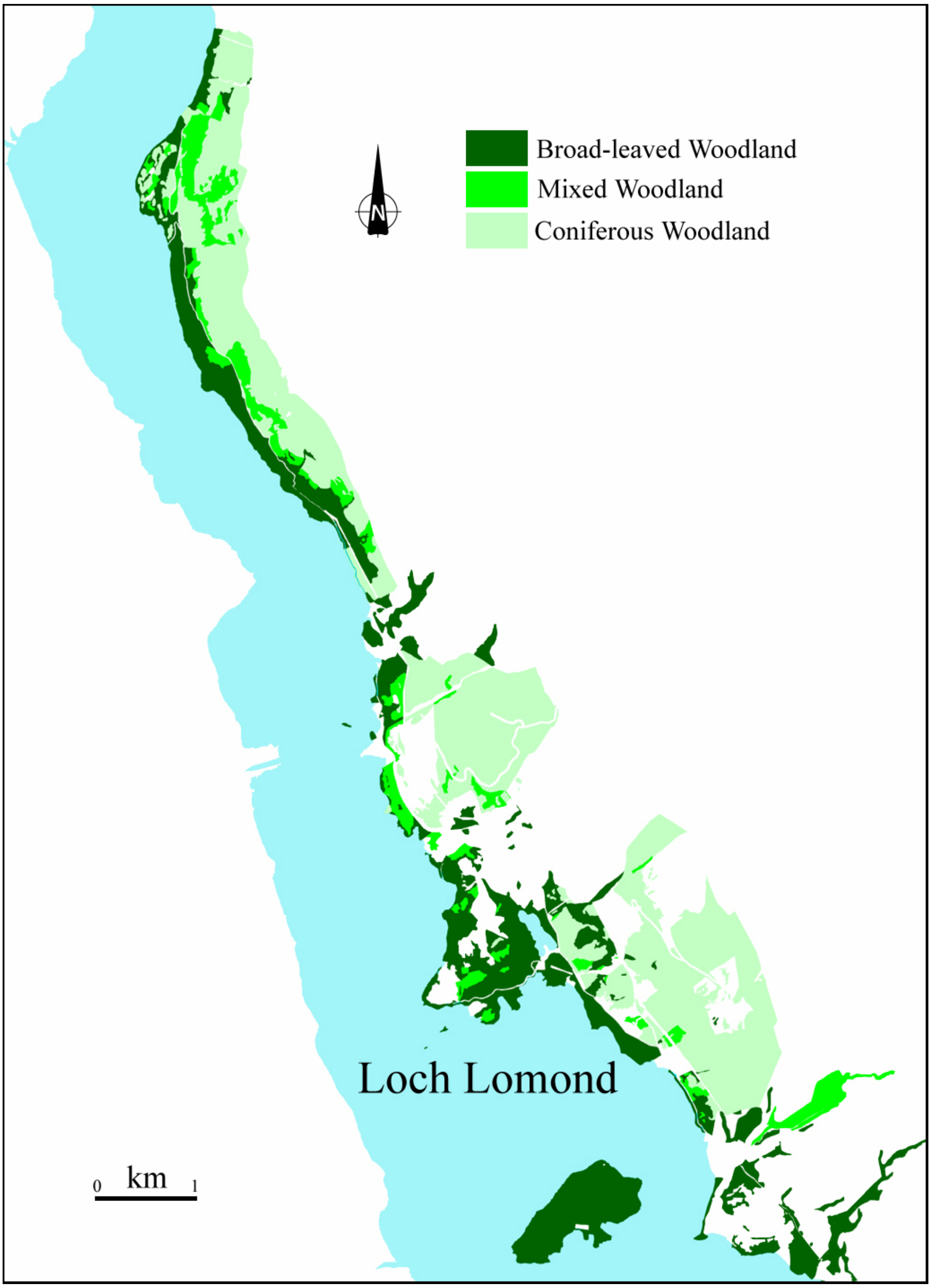

**Figure 5. 2: The distribution of broad-leaved, coniferous and mixed habitat in the area owned by the Forestry Commission at East Loch Lomond in 2000.**

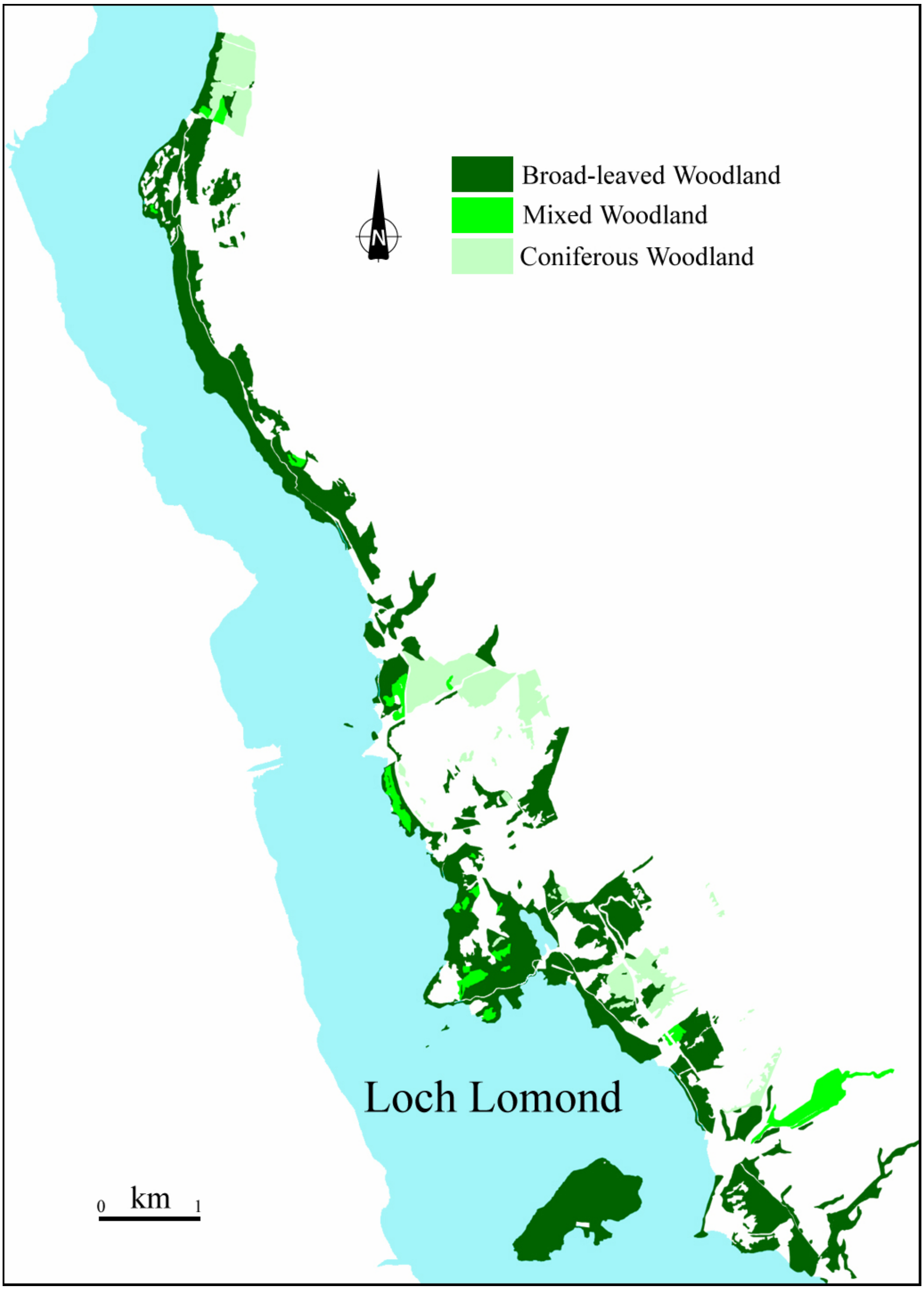

**Figure 5. 3: The predicted distribution of broad-leaved, coniferous and mixed habitat in the area owned by the Forestry Commission at East Loch Lomond in 2025, assuming no natural regeneration.**

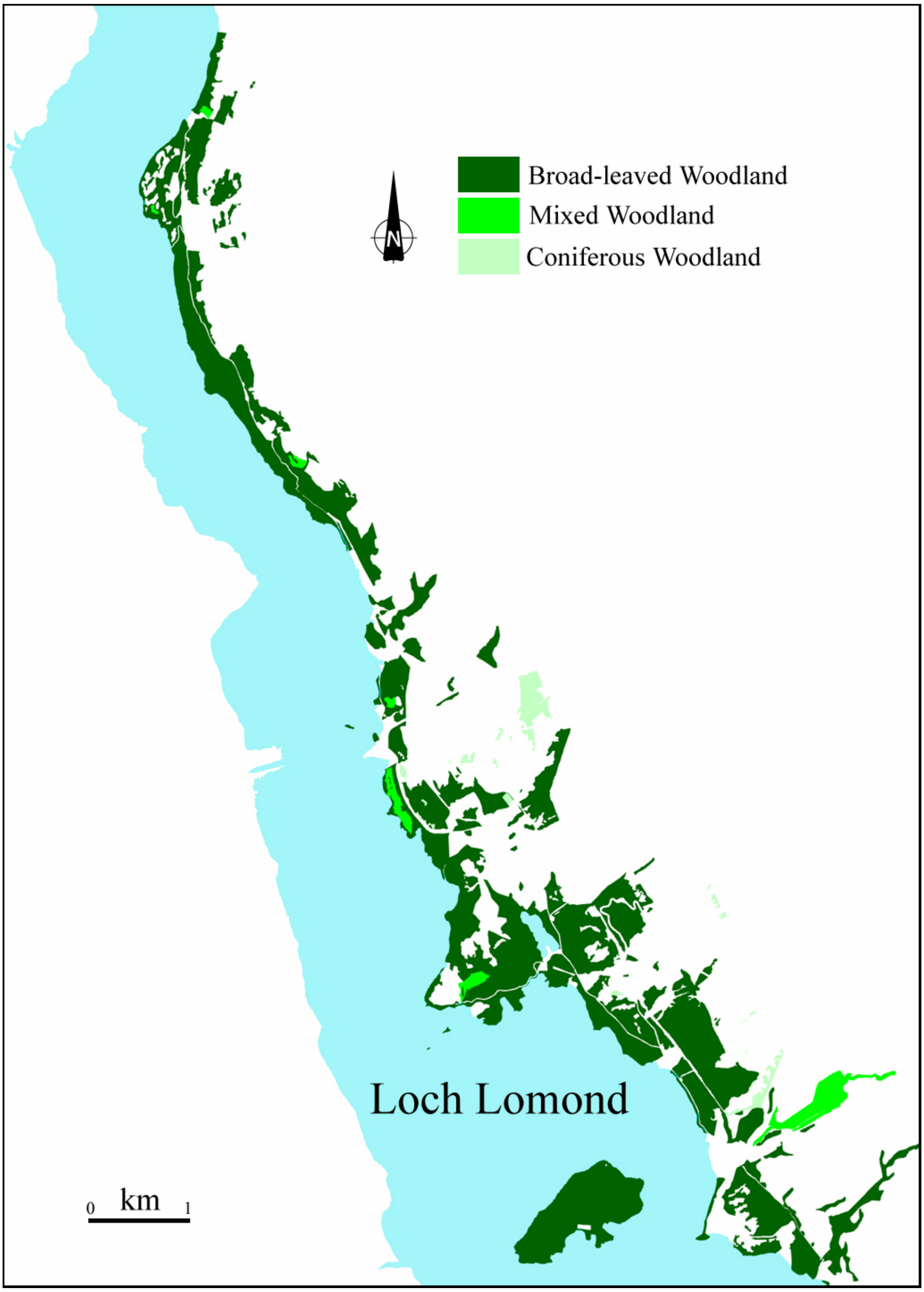

**Figure 5. 4: The predicted distribution of broad-leaved, coniferous and mixed habitat in the area owned by the Forestry Commission at East Loch Lomond in 2050, assuming no natural regeneration.**

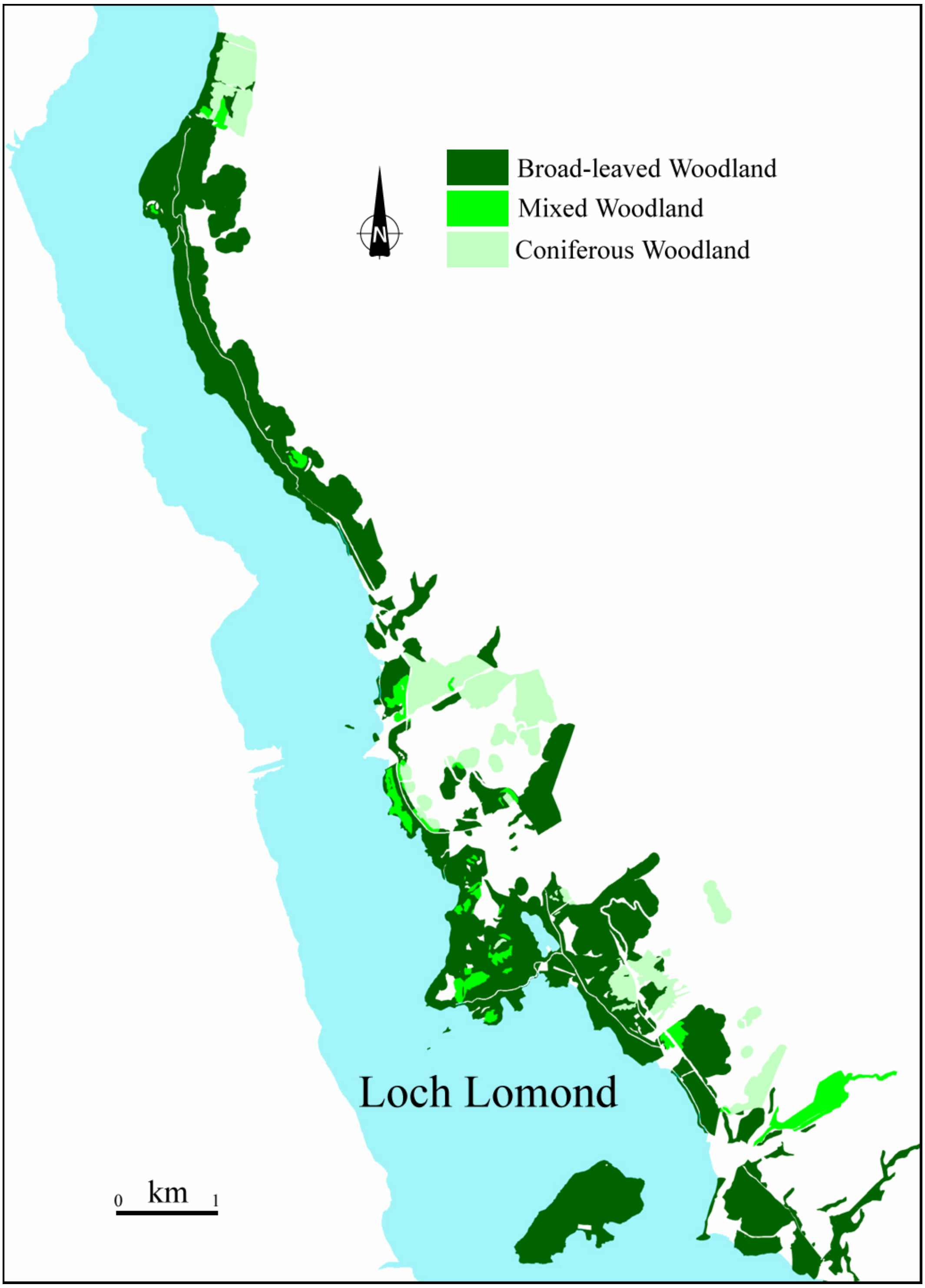

**Figure 5. 5: The predicted distribution of broad-leaved, coniferous and mixed habitat in the area owned by the Forestry Commission at East Loch Lomond in 2025, assuming natural regeneration at a rate of one metre per year.**

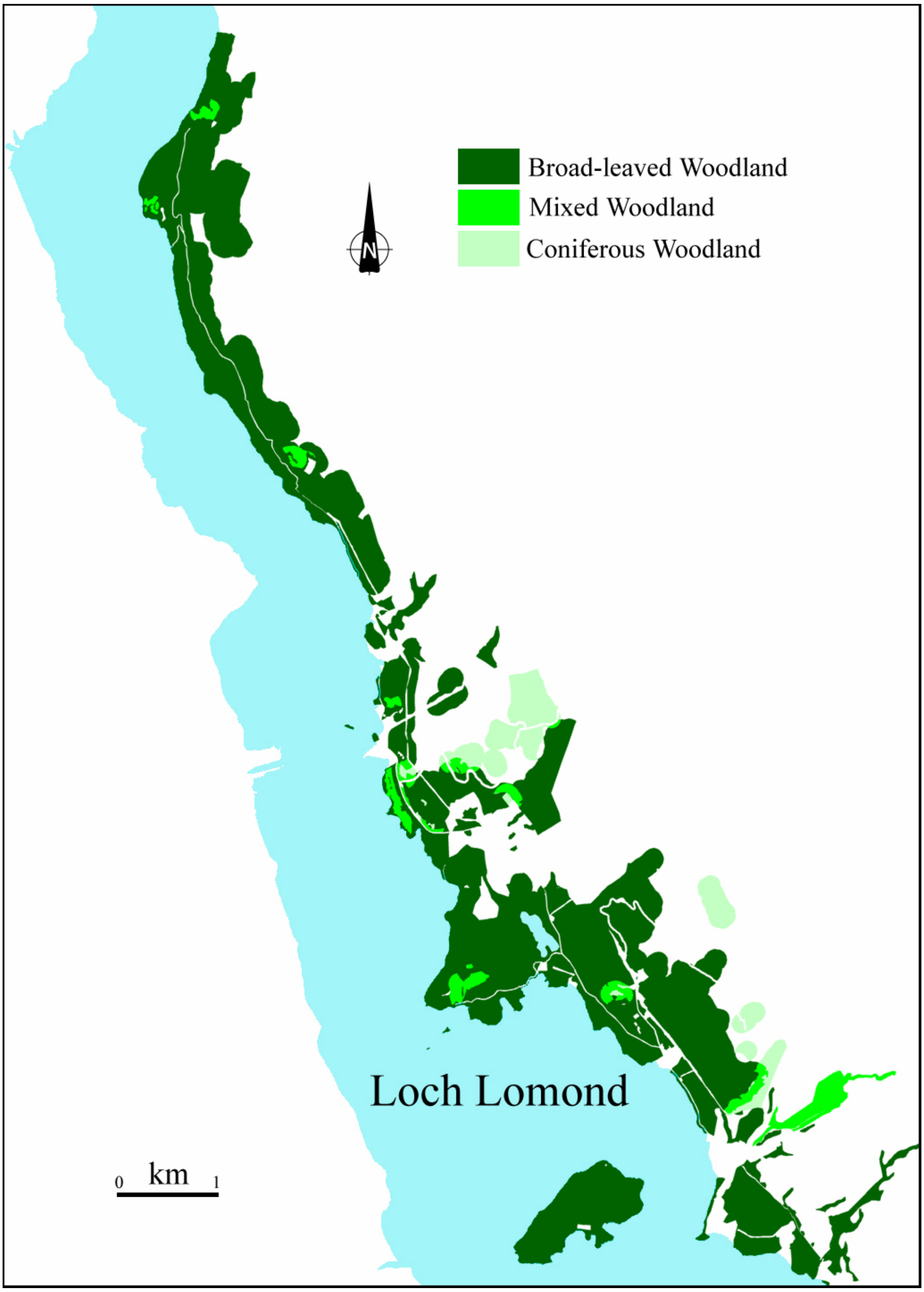

**Figure 5. 6: The predicted distribution of broad-leaved, coniferous and mixed habitat in the area owned by the Forestry Commission at East Loch Lomond in 2050, assuming natural regeneration at a rate of one metre per year.**

The main differences between the 'no regeneration' and 'regeneration' scenarios at a scale of 100m from sample points (territory scale) occurred for the percentage cover of broad-leaved woodland and open habitat. In both cases the percentage cover of mixed and coniferous habitat declined and levelled off at around five percent cover. The percentage cover of conifers declined steeply from around 40% to less than 10% between 2000 and 2025. The rise in the percentage cover of broad-leaved woodland was steeper and reached a higher maximum by 2050 under the 'regeneration' scenario than under the 'no regeneration' scenario. The proportion of open habitat increased more steeply between 2000 and 2025 for the 'no regeneration' scenario and was still predicted to be greater in 2050 than under the 'regeneration' scenario (Figure 5.7).

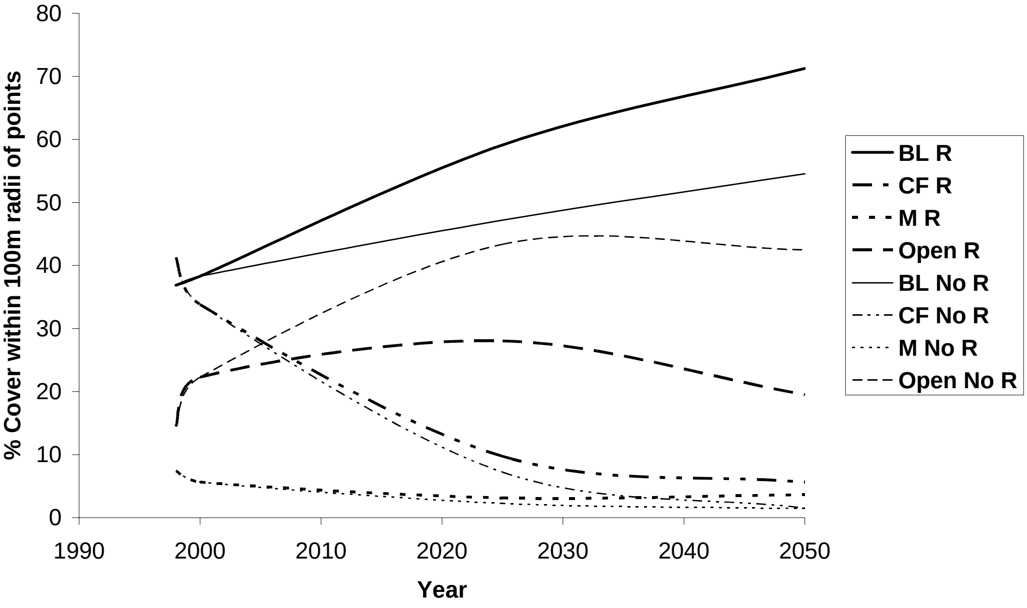

**Figure 5. 7: The predicted change in percentage cover of broad-leaved, (BL), coniferous (CF), mixed (M) and open (Open) habitat at a scale of 100m radii around sample points for the 'regeneration' (R) and 'no regeneration' (No R) scenarios. Lines are smoothed between the actual cover in 2000 and the predicted covers for 2025 and 2050 under each scenario.**

### *5.3.2 Population distribution projections for the ELL98 models*

Distribution declines were predicted for the ubiquitous (wren) (Figure 5.8) and coniferous woodland species (goldcrest and coal tit) (Figures 5.9 and 5.10). Conversely, increases of between 10% and 60% were predicted for the broad-leaved species (great tit, garden warbler, treecreeper, wood warbler, blue tit, and redstart) (Figures 5.11-5.16 and Table 5.1).

The predicted rate and magnitude of decline was less for the wren than for the two coniferous species (Figures, 5.8, 5.9 and 5.10 and Table 5.1) which showed similar patterns when projected into the future. In both cases the distribution was predicted to decline until around 2025 and then level off. At all times the projection for 'regeneration' lay slightly above that for 'no regeneration'. The magnitude of the predicted distribution decline was virtually identical for both species. By contrast the wren population declined less in the 'no regeneration' scenario than in the 'regeneration' scenario. It showed a stable distribution after 2000 under conditions of no regeneration.

The predicted distribution increases for the broad-leaved species showed different patterns interspecifically. For the great tit and the garden warbler the predicted rise was greatest between 2000 and 2025 and then levelled off between 2025 and 2050 (Figures 5.11 and 5.12). The other broad-leaved species all showed steadier raises in percentage distribution between 2000 and 2050 for at least one of the 'no regeneration' or 'regeneration' scenarios. The greatest overall percentage increase in distribution was predicted for the great tit (53-59%), with the smallest increase expected for the redstart (12-17%). Predicted increases for other species were all around 30-35% with the exception of the ‘no regeneration’ scenario for the wood warbler and treecreeper where an increase of only 10-15% was predicted (Table 5.1). Population predictions were higher for the scenario with regeneration for the, great tit, treecreeper and wood warbler (Figures 5.11, 5.13 and 5.14). There was no real difference in predicted distribution changes between the ‘no regeneration’ and ‘regeneration’ scenarios for the garden warbler and the blue tit (Figures 5.12 and 5.15), while the redstart distribution increased more under ‘no regeneration’ conditions (Figure 5.16).

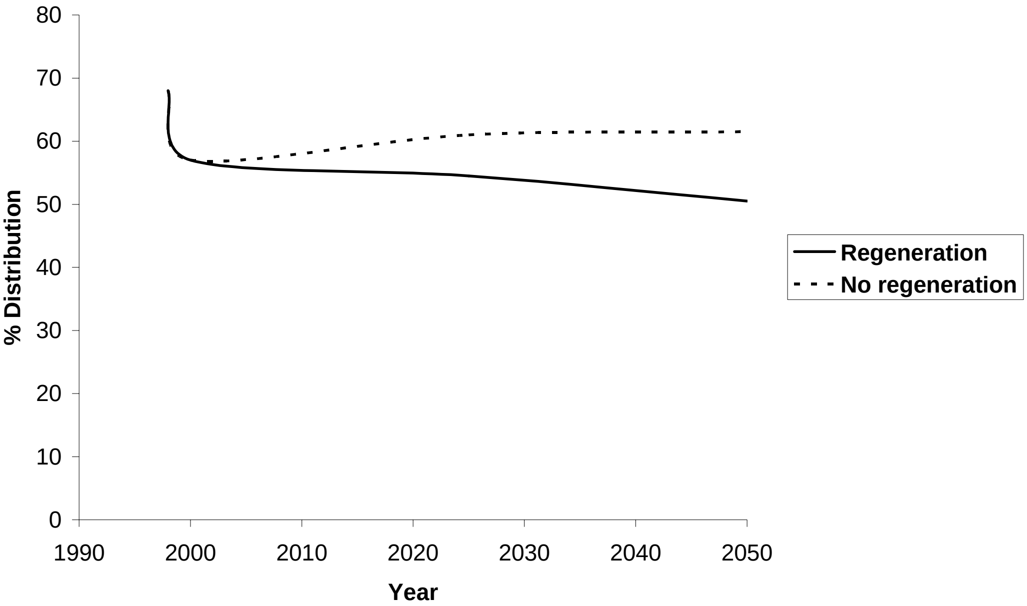

**Figure 5. 8: Predicted distribution changes over the next 50 years for the wren for the ‘regeneration’ and ‘no regeneration’ scenarios based on the ELL98 model. Lines are smoothed between the actual % points occupied in 1998 and 2000 and the predicted % occupied in 2025 and 2050 under each scenario.**

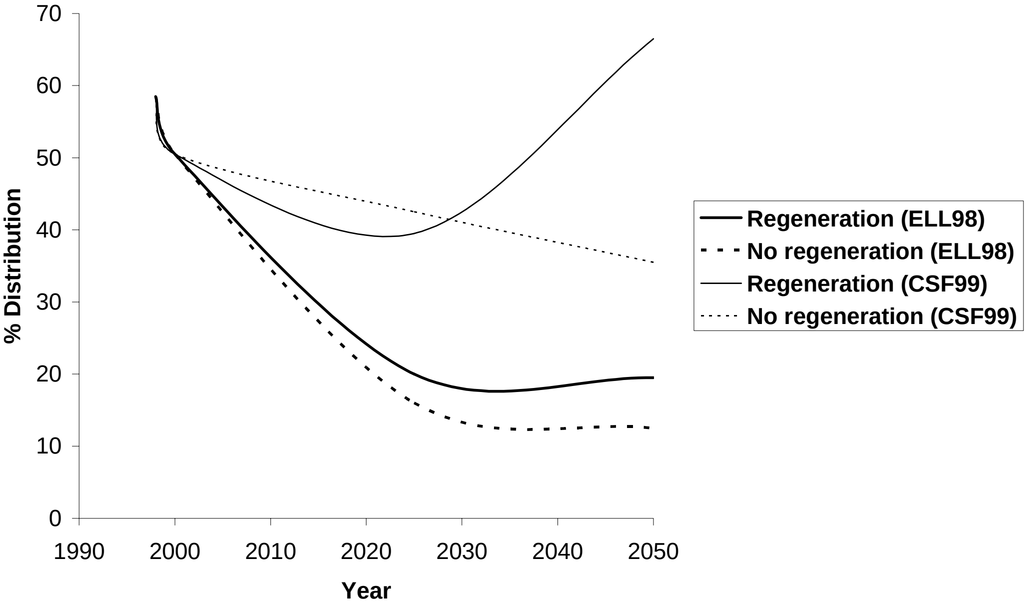

**Figure 5. 9: Predicted distribution changes over the next 50 years for the goldcrest for the 'regeneration' and 'no regeneration' scenarios based on the ELL98 and CSF99 models.**

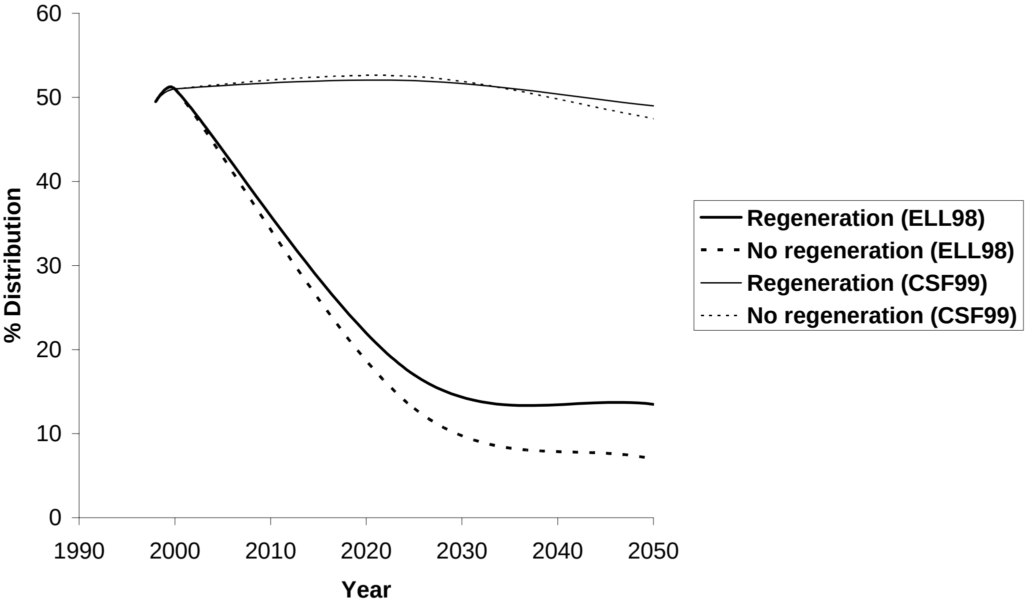

**Figure 5. 10: Predicted distribution changes over the next 50 years for the coal tit for the 'regeneration' and 'no regeneration' scenarios based on the ELL98 and CSF99 models.**

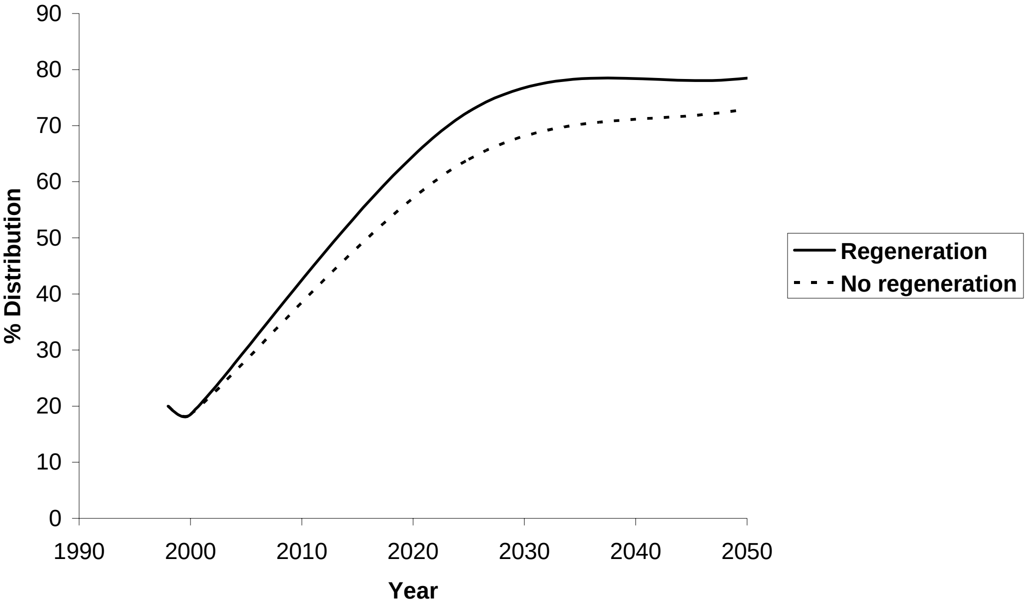

Figure 5. 11: Predicted distribution changes over the next 50 years for the great tit for the 'regeneration' and 'no regeneration' scenarios based on the ELL98 model.

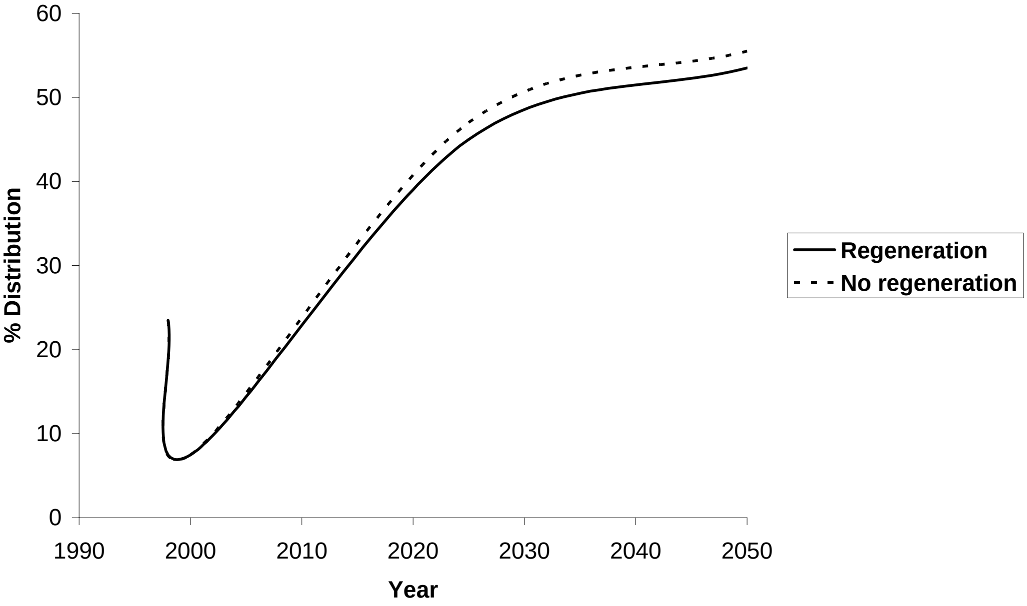

Figure 5. 12: Predicted distribution changes over the next 50 years for the garden warbler for the 'regeneration' and 'no regeneration' scenarios based on the ELL98 model.

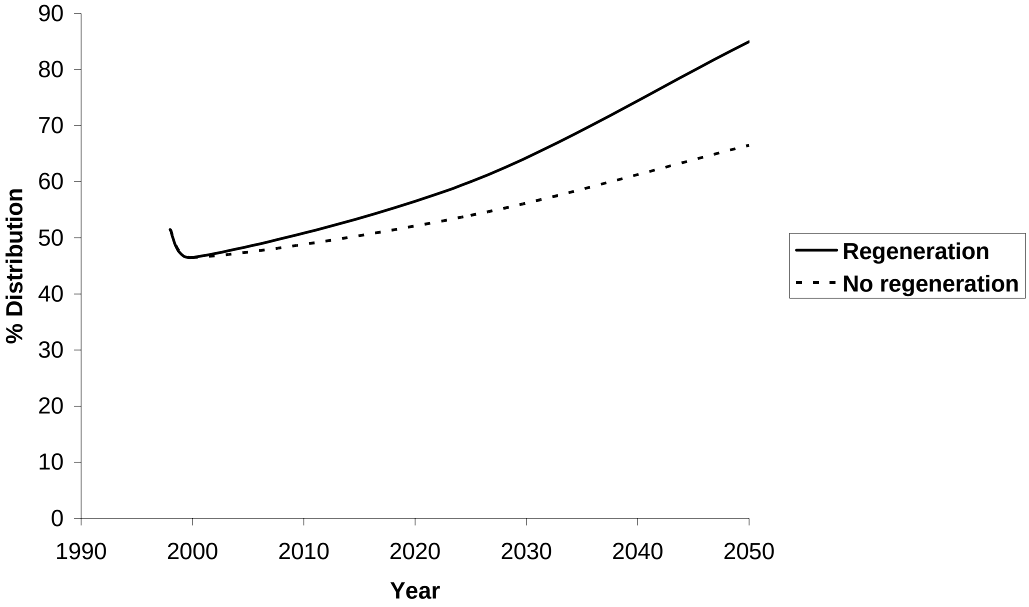

Figure 5. 13: Predicted distribution changes over the next 50 years for the treecreeper for the ‘regeneration’ and ‘no regeneration’ scenarios based on the ELL98 model.

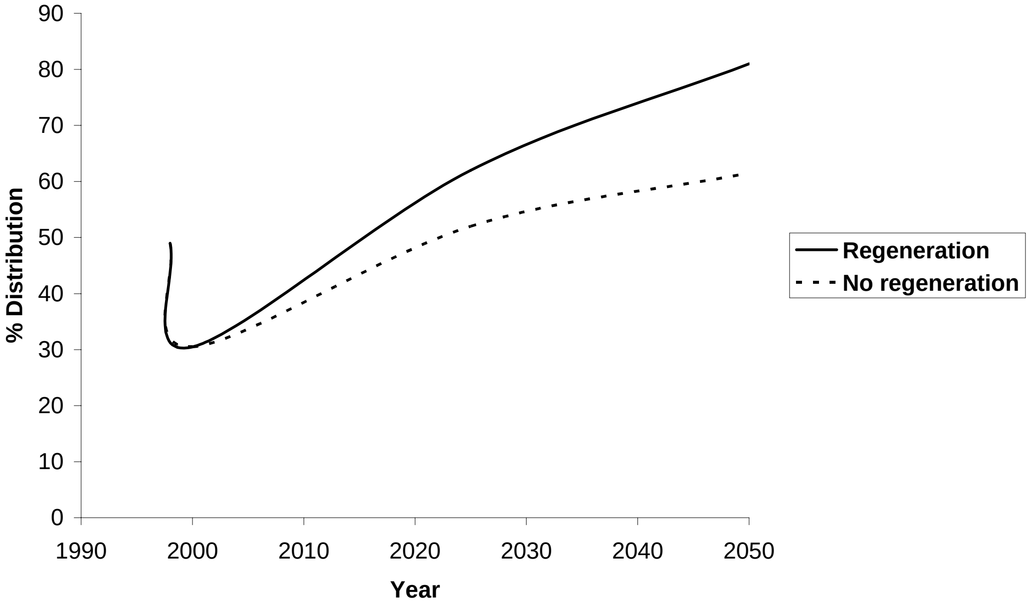

Figure 5. 14: Predicted distribution changes over the next 50 years for the wood warbler for the ‘regeneration’ and ‘no regeneration’ scenarios based on the ELL98 model.

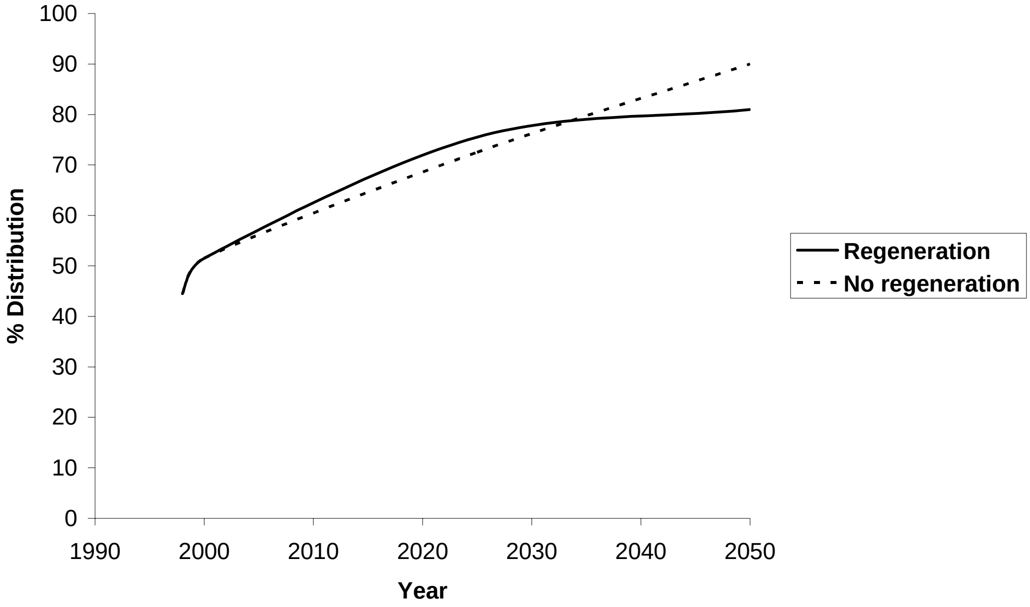

**Figure 5. 15: Predicted distribution changes over the next 50 years for the blue tit for the ‘regeneration’ and ‘no regeneration’ scenarios based on the ELL98 model.**

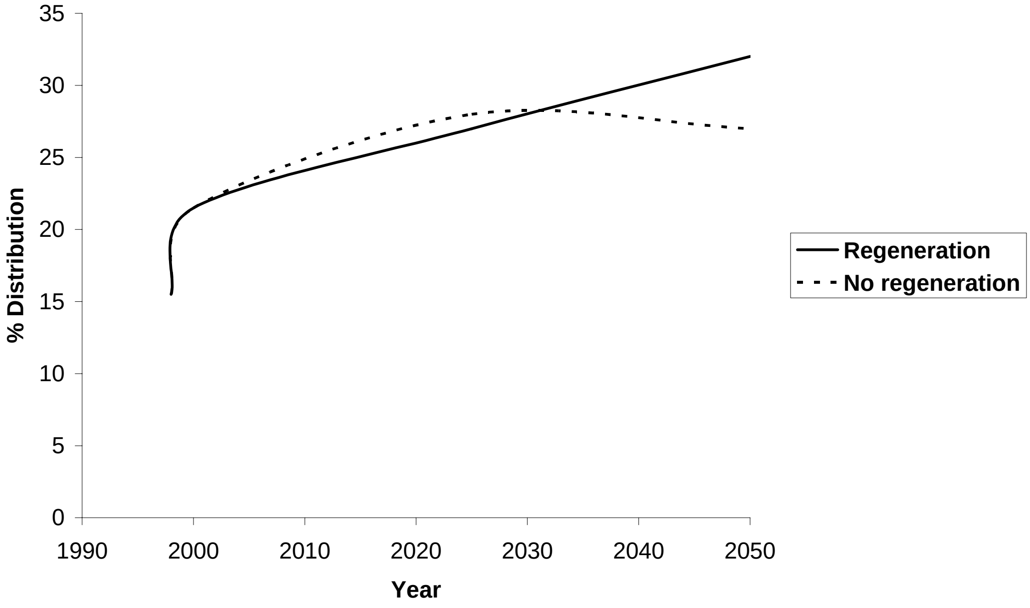

**Figure 5. 16: Predicted distribution changes over the next 50 years for the redstart for the ‘regeneration’ and ‘no regeneration’ scenarios based on the ELL98 model.**

**Table 5. 1: Predicted percentage change in distribution for the ubiquitous, coniferous and broad-leaved species based on the ELL98 models. 'R' is the 'regeneration' scenario and 'No R' is the 'no regeneration' scenario. 'Diff 1' is the difference in percentage distribution between the 'regeneration' and 'no regeneration' scenarios for 2025 and 2050 for each species. 'Diff 2' is the change in percentage difference in distribution predicted between 1998 and 2050 for each species for each scenario.**

| Habitat | Species | Scenario | Year | | | | **Diff 2** |
|---|---|---|---|---|---|---|---|
| | | | 1998 | 2000 | 2025 | 2050 | |
| **Ubiquitous** | Wren | R | 68.0 | 57.0 | 54.5 | 50.5 | **-17.5** |
| | | No R | 68.0 | 57.0 | 61.0 | 61.5 | **-6.5** |
| | | **Diff 1** | | | **-6.5** | **-11.0** | |
| **Coniferous** | Goldcrest | R | 58.5 | 50.5 | 20.0 | 19.5 | **-39.0** |
| | | No R | 58.5 | 50.5 | 16.0 | 12.5 | **-46.0** |
| | | **Diff 1** | | | **4.0** | **7.0** | |
| | Coal tit | R | 49.5 | 51.0 | 17.0 | 13.5 | **-36.0** |
| | | No R | 49.5 | 51.0 | 13.0 | 7.0 | **-42.5** |
| | | **Diff 1** | | | **4.0** | **6.5** | |
| **Broad-leaved** | Treecreeper | R | 51.5 | 46.5 | 60.0 | 85.0 | **33.5** |
| | | No R | 51.5 | 46.5 | 54.0 | 66.5 | **15.0** |
| | | **Diff 1** | | | **6.0** | **18.5** | |
| | Wood warbler | R | 49.0 | 30.5 | 62.0 | 81.0 | **32.0** |
| | | No R | 49.0 | 30.5 | 52.0 | 61.5 | **12.5** |
| | | **Diff 1** | | | **10.0** | **19.5** | |
| | Blue tit | R | 44.5 | 51.5 | 75.5 | 81.0 | **36.5** |
| | | No R | 44.5 | 51.5 | 72.5 | 90.0 | **45.5** |
| | | **Diff 1** | | | **3.0** | **-9.0** | |
| | Garden warbler | R | 23.5 | 7.5 | 45.0 | 53.5 | **30.0** |
| | | No R | 23.5 | 7.5 | 47.0 | 55.5 | **32.0** |
| | | **Diff 1** | | | **-2.0** | **-2.0** | |
| | Great tit | R | 20.0 | 18.5 | 72.5 | 78.5 | **58.5** |
| | | No R | 20.0 | 18.5 | 64.0 | 73.0 | **53.0** |
| | | **Diff 1** | | | **8.5** | **5.5** | |
| | Redstart | R | 15.5 | 21.5 | 27.0 | 32.0 | **16.5** |
| | | No R | 15.5 | 21.5 | 28.0 | 27.0 | **11.5** |
| | | **Diff 1** | | | **-1.0** | **5.0** | |

### *5.3.3 Population distribution projections for the CSF99 models*

None of the predicted distribution patterns from the CSF99 models for the coal tit or the goldcrest matched those predicted from the ELL98 models. The goldcrest was predicted to show a steady decline under conditions of no regeneration and to decline until 2025 and then increase sharply under conditions of regeneration.

The coal tit was predicted to show little change in overall distributional extent for both scenarios (Figures 5.9 and 5.10 and Table 5.2).

**Table 5. 2: Predicted percentage change in distribution for the ubiquitous, coniferous and broad-leaved species based on the CSF99 models. 'R' is the 'regeneration' scenario and 'No R' is the 'no regeneration' scenario. 'Diff 1' is the difference in percentage distribution between the 'regeneration' and 'no regeneration' scenarios for 2025 and 2050 for each species. 'Diff 2' is the change in percentage difference in distribution predicted between 1998 and 2050 for each species for each scenario**

| Habitat | Species | Scenario | Year | | | | **Diff 2** |
|---|---|---|---|---|---|---|---|
| | | | 1998 | 2000 | 2025 | 2050 | |
| **Ubiquitous** | Robin | R | 80.5 | 92.0 | 60.5 | 92.5 | **12.0** |
| | | No R | 80.5 | 92.0 | 65.5 | 57.5 | **-23.0** |
| | | **Diff 1** | | | **-5.0** | **35.0** | |
| **Coniferous** | Goldcrest | R | 58.5 | 50.5 | 39.5 | 66.5 | **8.0** |
| | | No R | 58.5 | 50.5 | 42.5 | 35.5 | **-23.0** |
| | | **Diff 1** | | | **-3.0** | **31.0** | |
| | Coal tit | R | 49.5 | 51.0 | 52.0 | 49.0 | **-0.5** |
| | | No R | 49.5 | 51.0 | 52.5 | 47.5 | **-2.0** |
| | | **Diff 1** | | | **-0.5** | **1.5** | |
| **Broad-leaved** | Willow warbler | R | 59.0 | 53.0 | 100.0 | 100.0 | **41.0** |
| | | No R | 59.0 | 53.0 | 100.0 | 100.0 | **41.0** |
| | | **Diff 1** | | | **0.0** | **0.0** | |

For the broad-leaved species (the willow warbler) the predicted pattern was identical for 'regeneration' and 'no regeneration' scenarios. It followed the same predicted pattern as the garden warbler and great tit based on the ELL98 models. The population was expected to increase until 2025 and then to level off (Figure 5.17). The pattern for the robin diverged more between the two regeneration scenarios. Irrespective of regeneration the distribution was predicted to decline between 2000 and 2025. This decline was predicted to continue without regeneration. However under conditions of regeneration the distribution was predicted to rise back to levels comparable with those in 2000 (Figure 5.18).

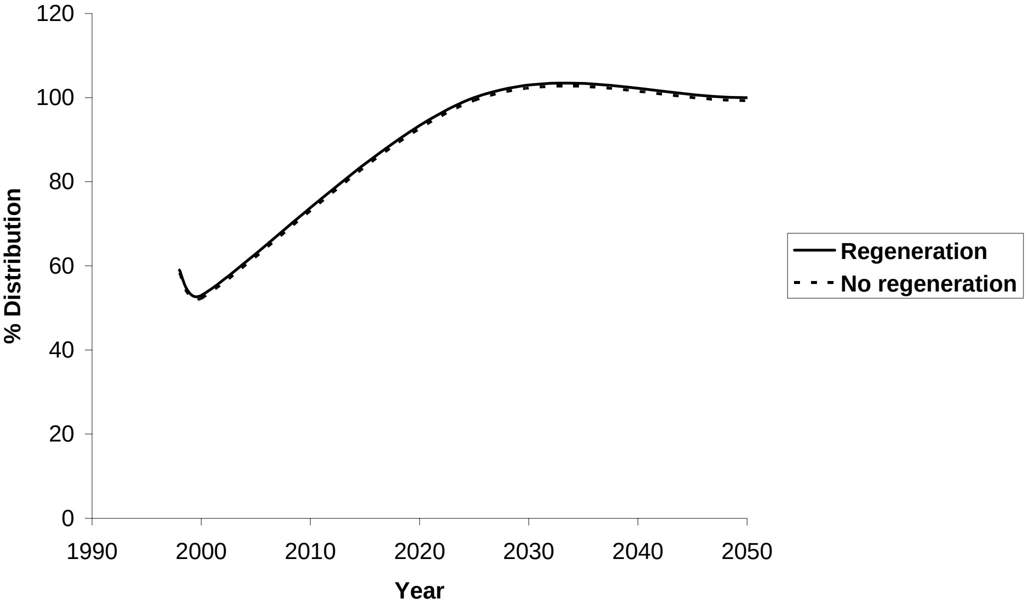

**Figure 5. 17: Predicted distribution changes over the next 50 years for the willow warbler for the 'regeneration' and 'no regeneration' scenarios based on the CSF99 model.**

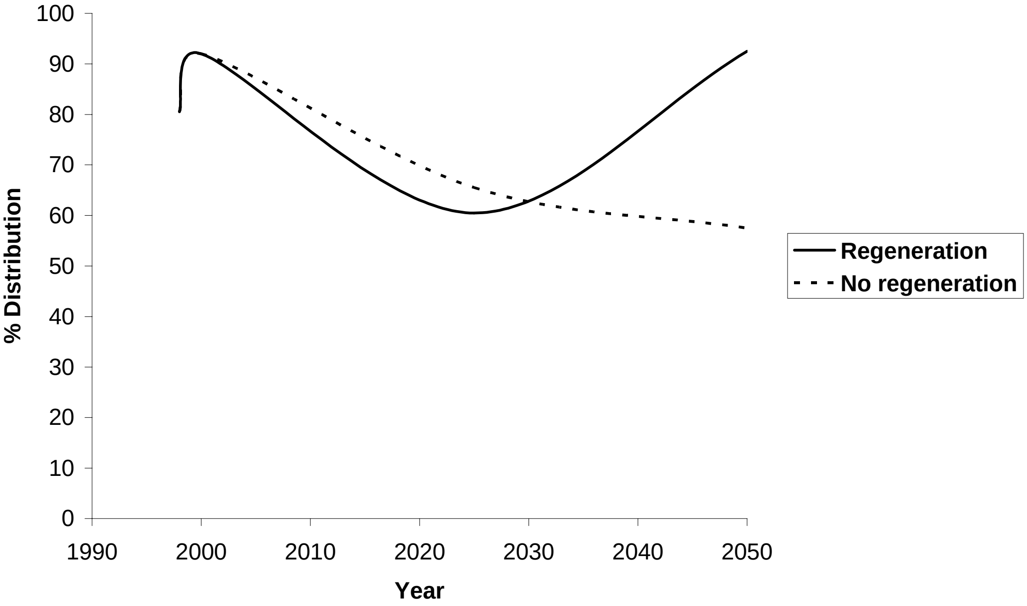

**Figure 5. 18: Predicted distribution changes over the next 50 years for the robin for the 'regeneration' and 'no regeneration' scenarios based on the CSF99 model.**

## 5.4 Discussion

### *5.4.1 Predicted changes in bird distributions in relation to habitat change*

#### 5.4.1.1 Predictions from the ELL98 Models

The predicted changes in the extent of bird distributions based on the ELL98 models are explicable in terms of the changes in the extent of broad-leaved and coniferous habitat which should occur under the Forestry Commission Management plan for East Loch Lomond. Conifer felling will lead to a reduction in the extent of conifers and the distribution of the coniferous species (goldcrest and coal tit) are predicted to decline in a manner mirroring the pattern of decline in conifer area at a territory scale. Similarly the distributions of broad-leaved species are predicted to increase due to the planting of broad-leaved woodland and natural regeneration where this is included in the scenario. The population change for the ubiquitous species, the wren, was less pronounced. The model predicts its presence in both broad-leaved and coniferous habitat and, as one habitat type declined it would be able to compensate by using new broad-leaved habitat.

The interspecific differences in distribution projections for the broad-leaved species will depend on the different shapes of the response curves for individual parameters in the models and the manner in which these individual variables are predicted to change over time. For example, the great tit and garden warbler were both predicted to show greater distribution increases during the first 25 years, the period of greatest decline in conifer cover. The models for these species have a negative relationship with conifers, explaining a high proportion of the variation.

The differences between the ‘no regeneration’ and ‘regeneration’ scenarios were relatively small in most cases for the projections based on the ELL98 models. Where there was a difference, the distribution was predicted to be higher for the ‘regeneration’ scenario than for the ‘no regeneration’ scenario in more cases. This direction of difference is more intuitive because for woodland species, benefits should accrue more from a greater extent of wooded relative to open habitat. Some of this regeneration will have included pine regeneration, which could account for the greater distributional extent predicted for the goldcrest but not for the coal tit under the ‘regeneration’ scenario compared with the ‘no regeneration’ scenario. Pine was present in the goldcrest, but not the coal tit model.

The results for the redstart showed a greater distribution predicted after 50 years for the ‘no regeneration’ scenario compared with the ‘regeneration’ scenario. This could be because new regeneration is shrubbier than mature woodland and the redstart requires open woodland for its feeding habit (Lack and Venables, 1939). The ELL98 model predicted points with open woodland with little or no shrub layer as suitable for redstarts.

Overall, the differences between the two modelled scenarios were probably not larger because for a large proportion of the sample points there was no difference in habitat change with scenario. Approximately half of the sample points were set up in broad-leaved woodland in 1998 and this was predicted to remain as broad-leaved woodland under the management plan and will have shown no habitat differences between scenarios. Of the points in coniferous and clearfell areas, some were in areas of replanting, which again were predicted as being the same for both ‘regeneration’ and ‘no regeneration’ scenarios. In any year, only a fraction of the remaining points would have been predicted as regenerating and so will have been different for the two scenarios. This fraction of points regenerating in each year will have been quite small because the regeneration rate selected was quite conservative.

### 5.4.1.2 Predictions from the CSF99 Models

The distribution predictions for the coniferous species (the coal tit and goldcrest) based on the CSF99 models showed very different patterns compared with those predicted by the ELL98 models. These patterns of, little change irrespective of scenario (coal tit), distribution increases (goldcrest in the ‘regeneration’ scenario) or relatively shallow rates of decline (goldcrest in the ‘no regeneration’ scenario), are less plausible than the predictions based on the ELL98 models given the extent to which conifers will decline over the next 50 years at Loch Lomond. One problem could be the presence of habitat parameters in the CSF which feature in the models for these species, but which are absent at East Loch Lomond. For example lime was present in the CSF woodlands but not at Loch Lomond, but occurred in both the goldcrest and coal tit CSF models (Tables 4.4 and 4.5).

All of the variables in the CSF99 models for the robin and the willow warbler were also present at Loch Lomond. The predicted patterns for these species are more readily interpretable than those for the coal tit and goldcrest. Thus the willow warbler was predicted to increase following a similar pattern to the garden warbler and great tit based on the ELL98 models. The robin was predicted to decline gradually under the ‘no regeneration’ scenario, probably due to the loss of the coniferous habitat which it utilized at Loch Lomond in 1998 and 2000. Under the ‘regeneration’ scenario the decline in distribution was reversed after the first 25 years because the model predicts that it will move into the newly regenerating broad-leaved habitat. Since the future distributions of these two species were only projected based on the CSF99 models, no comparison of predicted distribution patterns from the ELL98 models could be made.

### *5.4.2 Evaluation of the distribution projections*

Since modelling was carried out in two stages there are two components to consider when considering how much confidence can be placed in the predicted patterns of change of bird distribution under the Forestry Commission management plan for East Loch Lomond. Firstly the predictive value of the models built to relate bird distributions to the ELL98 and CSF99 environments need to be considered when projected for a different time and site. Secondly, the methodology used to model landscape change needs to be evaluated.

#### 5.4.2.1 Predictive value of the bird-habitat models

GLM and GAM models are static empirical modelling approaches (Guisan and Zimmermann, 2000) which were used to relate bird distributions to their present environment at Loch Lomond or the Central Scotland Forest. Such models only have predictive value for the future where generality exists in the bird-habitat associations in the models (James and McCulloch, 1985; Fielding and Haworth, 1995).

Models were only used for predicting distributions where results from Chapter 4 indicated some generality in the bird-habitat associations recorded. Thus, all of the models used for predicting future distributions of each species had useful application (an AUC value of at least 0.7, Swets, 1988) when directly used to predict distributions for East Loch Lomond in 2000. Furthermore, an ecological interpretation in relation to bird nesting and feeding requirements could be applied for many of the variables in the models. In these cases it was more likely that the bird was responding to the parameter measured rather than to a different factor which was correlated with this parameter (Bibby *et al*., 1989). Where such correlations are not constant between sites and years the predictive value of a model is less (Gates *et al*., 1994).

However, in some cases relationships in the models may have been correlative, especially for variables at landscape scale. The ELL98 models generally cross predicted with higher accuracy for ELL00 than did the CSF99 models at least in part because of the greater similarity in correlation structure of variables between years at the same site, than between different sites. With time the correlation structure of the variables at Loch Lomond will change as conifers are removed and other management is carried out. This was found within the datasets constructed for 2025 and 2050, though the regression methodology employed for projecting ground vegetation changes may have held the correlation structure of these variables artificially more constant then may actually occur. Similarity in correlation structure for the same site over time is still likely to be greater than between sites. This may mean that greater confidence can be placed in the distribution projections from the ELL98 models relative to those from the CSF99 models.

Unexplained variation existed in all of the models for the year and site for which they were constructed. Similarly a proportion of points were mis-classified by the models. It would be reasonable to expect that the mis-classification rate for future distributions will at least be equal to and probably greater than the rate found when the models were used to predict distributions at East Loch Lomond in 2000. However confidence intervals cannot be readily constructed.

#### 5.4.2.2 Evaluation of the methodology of landscape scenario construction

Time limitations dictated that the method used to model future landscape scenarios was a relatively simplistic empirical approach. It was largely based on the use of yield tables, which represent a very early form of static mathematical modelling (Garcia, 2001). Empirical models can provide quite accurate site specific quantitative information for forest management (Landsberg, 2003) and they are still employed in numerous studies modelling forest growth (for example, Amaro and Reed, 2001; Fang and Gertner, 2001; Cummings *et al*., 2001). However, model value is very dependent on the accuracy of the input data (Porte and Bartelink, 2002; Landsberg, 2003).

Input data was particularly sparse with regards to natural regeneration. For the ‘regeneration’ scenario a constant regeneration rate proceeding away from woodland edges was assumed. However, since regeneration rates vary depending on the presence of seed-bearing trees, soil type, felling regime, ground flora and grazing pressure (Thompson *et al*., 2003) rates of regeneration are unlikely to be constant throughout the study site. Proper consideration of this aspect would have required detailed vegetation and soil surveys like those carried out by Broome *et al.* (2004) for Ross Wood and Ptarmigan Wood. This could be combined with information on grazing control. Both deer and goats occur at East Loch Lomond, and can greatly influence regeneration rates (Pigott, 1983; Peterken and Jones, 1989; Bibby *et al*., 1989). Control through a combination of culling and fencing is therefore an important management consideration where natural regeneration is being encouraged (Thompson *et al*., 2003).

Although the majority of the explained variation in the models was accounted for by local scale variables, (Section 4.4.1 Table 4.3), some model parameters were at scales of 2500m-5000m. The area and edge measurements at these scales may be inaccurate in the future scenarios where changes occur in the woodland cover outside the East Loch Lomond study area. To take account of this, additional information on the management planned in surrounding woodland would need to be considered. This area is still within the Loch Lomond and the Trossachs National Park and as such is likely to undergo restructuring of the conifer plantations and expansion of native broad-leaved areas (The National Park Authority, 2003).

In addition, no account was taken of possible climate effects. These may vary within site due to the range in elevation present, and over time due to climate change. Temperature decreases and rainfall increases with increasing altitude

(Harrison and Dunn, 1993). Similarly there is evidence that winters are becoming milder and summers drier in Scotland (Harrison *et al*., 1999). These factors have been related to the length of the growing season in Scotland (Harrison and Harrison, 1988). Thus by not including these parameters in modelling future landscapes, the predictive accuracy of the models will be reduced (Guisan and Zimmermann, 2000; Landsberg, 2003).

Climate data could potentially be incorporated into an empirical model to improve its predictive accuracy for future scenarios. However, for more realistic scenarios it may be necessary to develop more mechanistic models (Garcia, 2001; Landsberg, 2003). This is a more dynamic approach in which processes are actually modelled. Mechanistic models and modelling environments for growth in different forest types have been developed, for example REGROW (Mou and Fahey, 1993), SYMFOR (Phillips and van Gardingen, 2004) and the Simile modelling environment (Muetzelfeldt and Taylor, 2004). Some of these models are actually hybrid models (Landsberg, 2003) incorporating both empirical and mechanistic components. These models can combine the advantages of both the process-based and empirical approaches (Porte and Bartelink, 2002; Landsberg, 2003). For example, an empirical aspect may be necessary to convert model outputs to the diameter breast height measurements required for the bird-habitat models (Landsberg, 2003).

Such dynamic forest models are a relatively recent phenomenon (Garcia, 2001) and some aspects such as recruitment sub-models are still not very effectively modelled (Porte and Bartelink, 2002). Care also needs to be taken to avoid making models too complex so that they are difficult to test (Pakeman *et al*., 1995). However, as sensitivity analyses are carried out (Wallach and Genard, 1998) and data gathered from forestry experiments used to improve model parameterizations (Reed *et al*., 2001) the predictive accuracy of these models should improve.

Ultimately the optimal approach would be to directly predict changes in bird distribution using process-based models which incorporate both landscape changes and the responses of birds to these changes. The presence of a bird in a particular habitat area depends on the extent to which the habitat meets the requirements of the individual for reproduction and survival, the effects of competition from other species and individuals and the dispersal ability of the bird. Few species have been studied in sufficient detail to construct a dynamic process based model to predict their responses to landscape change over time (Guisan and Zimmermann, 2000). For woodland birds the most significant attempts at this type of modelling have probably been carried out for the nuthatch (for example, Verboom *et al*., 1991). In many cases data is especially lacking with regard to dispersal. There is clear potential for combining the understanding gained through static GLM and GAM models with information derived from gap crossing work, such as that described in Chapter 2 to work towards the construction of dynamic bird-habitat models for predicting changes in bird distributions over time.

## 5.5 Conclusion

Predicted trends based on the ELL98 models suggest that the distributions of coniferous species will decline and broad-leaved species will increase in line with the changing relative extents of coniferous and broad-leaved woodland. Ubiquitous species like the wren are likely to vary in the proportions of broad-leaved and coniferous habitat occupied and so show less change in total spatial extent though the actual habitat areas occupied will change. The patterns predicted based on the CSF99 models are less readily interpretable, especially for the coniferous species and indicate some problems in transferring models between sites for predictive purposes.

Models were only used for forward projection where there was some evidence of generality when cross predicted for ELL00. However, some of the relationships in the models may well have been only correlative and as the correlation structure of variables changes over time this will have implications for predictive accuracy. However, there is no satisfactory method for obtaining confidence intervals for the distribution predictions.

Improvements could be made to the methodology employed for modelling landscape change were more time available. Detailed vegetation and soil data along with climate data could be gathered for the area. Applying this within a combined mechanistic and empirical framework may produce a more realistic and detailed picture of how the landscape is likely to change at Loch Lomond. Ultimately sufficient data may be compiled to allow a process-based approach, modelling dynamic responses of bird populations to changes in their habitat distribution.

# Chapter 6: Overall Conclusion

This thesis used two approaches (experimental and observational) to investigate the effects which habitat fragmentation may have on woodland birds. Such an understanding is particularly important given that habitat fragmentation is increasing and has been implicated in recent declines in populations of woodland birds (Bellamy *et al.*, 2000). The results from both methodologies indicate that habitat fragmentation does affect the distributions of many woodland bird species and these findings have practical application for directing management both within the study areas and in a more general context.

For the experimental study it was hypothesised that bird willingness to cross gaps would decrease with increasing gap distance and that these declines would vary interspecifically in relation to bird morphology. Sufficient data was obtained for analysis for only four species. However, data on bird dispersal is generally sparse since it is difficult to collect. The playback methodology is a new approach and a lot of work had to be carried out adapting it so that it could be employed where the conifer density made it impossible to locate individual birds prior to playback. This study demonstrated that dispersal behaviour at a home-range scale can be investigated using an attractant to draw birds across gaps. Further adaptations of the methodology could yield more interesting and useful results in terms of management guidelines.

Bird willingness to cross gaps decreased with increasing distance for each species recorded. However, clear interspecific differences existed with maximum gap crossing distances under playback varying from 150m (chaffinch) to 46m (goldcrest). Larger species with bigger wings responded more readily across gaps relative to though woodland. It was hypothesised that these species would be less manoeuvrable in woodlands and better adapted to flight in open areas making them more likely to be able to evade a predator.

The observational study had three sections to it. In Chapter 3 the point count data were analysed to identify which species were being recorded with high consistency and so could be modelled in relation to habitat and landscape parameters with a high degree of confidence. This modelling was then described in Chapter 4 and the models were examined to determine their ability to accurately predict bird distributions for the same site in different years and for different sites. The models which had useful application in cross-prediction were then used to predict future bird distribution changes for 50 years at East Loch Lomond (Chapter 5).

Results from Chapter 3 indicated that the numbers of birds counted did vary with observer, prevailing weather conditions and timing of the count and that different species varied in their sensitivity to these parameters. These differences are likely to be due to variations in song output, since most registrations were based on birds' songs and calls. Studies routinely avoid bird counts during extreme weather conditions on the day of the count; however no account is taken of the conditions on the day preceding the count. This study indicated that some attention should be played to this factor especially where actual abundance data is being used for analysis. An effect of weather conditions on the day preceding the count on numbers of birds counted has not to my knowledge been previously observed.

Time and weather biases could be eliminated from the data by reducing it to presence and absence level. In addition, there was relatively little difference in numbers counted based on counts of five versus ten minutes duration. A sample period of ten minutes should have been adequate to record most species present while minimising the risk of double counting individuals. However two counts per sample point were inadequate to assess species richness. The number of fieldwork hours available meant that two counts per point was the maximum feasible in this study. Therefore bird species richness was not adequately recorded and so this was not analysed in Chapter 4.

Species which were recorded with high consistency based on two counts per sample point were modelled using generalized linear and generalized additive modelling. The predictors were variables ranging from habitat to landscape scale (up to 5000m from points) and included parameters sensitive to habitat fragmentation. Local habitat variables accounted for around 70-85% of explained variation in the models. These variables could largely be interpreted in terms of bird feeding and nesting behaviour. However, around 15-25% of explained variation was accounted for by variables occurring at a landscape scale. Therefore the bird-habitat association models could be improved by the inclusion of variables measured at a landscape scale. Fragmentation related variables also featured in most models, especially edge variables with both negative and positive effects observed. Positive effects could be due to greater availability of food and nesting sites at edges while negative effects may relate to enhanced predation rates which have been observed at edges.

Generalized linear modelling (GLM) has often been used to model bird distributions (for example, Osborne and Tigar, 1992; Fielding and Haworth, 1995; Buckland *et al.*, 1996; Bellamy *et al.*, 1998; Eaton *et al.*, 2001; Brotons *et al.*, 2004). Fewer studies have employed generalized additive modelling (GAM) (for example, Fewster *et al.*, 2000; Pearce and Ferrier, 2001). It is not always realistic to assume that relationships will be linear. The GAM approach employed here meant that it was possible to state with confidence that where linear relationships arose, they were genuine since the data itself defined the form of the relationship.

The models all had good predictive power for the data for which they were built. Receiver Operator Characteristic (ROC) AUC values ranged from 0.84-0.99 for the species modelled for ELL98 and from 0.76-0.93 for the CSF99. In many cases they also had useful application (Swets, 1988) for predicting bird distributions for the same site in different years. Fewer instances of useful predictions for distributions in a different site arose probably because of differences in the correlation structure of the variables and in portions of the variable gradient sampled.

Where models had useful application for ELL00, predictions of distribution changes over the next 50 years at East Loch Lomond were logical in terms of the changes in extent of broad-leaved and coniferous woodland which should occur. Thus broad-leaved species were predicted to increase and coniferous species to decrease in distribution. This especially applies to the ELL98 more than for the CSF99 models. However, if the criteria for evaluating the predictions is simply that they make sense based on knowledge of species ecologies, then it could be argued that the complex modelling exercise was unnecessary to predict management outcomes. A key advantage to the modelling was that as well as a general indicator of overall population change it was also possible to map this change. Further modelling work such as that suggested in Chapter 5 will lead to higher degrees of confidence in such maps in the future.

The East Loch Lomond study site was in a dynamic state with coniferous habitat being removed to make way for broad-leaved habitat. This meant that in the short term the woodland cover was becoming more fragmented and the negative effect of this on the woodland birds was observed in population declines of especially coniferous favouring species, between 1998 and 2000. Some of these declines will almost certainly have been purely due to a habitat loss effect. However, the high occurrence of edge variables in the models and the experimental work indicating interspecific differences in willingness to cross gaps indicates that these additional fragmentation effects should definitely be considered when investigating possible causes of population declines in woodland birds.

Overall, this study contributes towards more effective management and therefore conservation of woodland birds in three main ways. Firstly the results can be used to produce general conservation guidelines of wider application outwith the areas studied. Such guidelines especially follow from the experimental work which strongly demonstrated the value of collecting data on actual dispersal behaviour. For example, the maximum gap crossing distance recorded for the species most reluctant to cross gaps (the goldcrest) was 46m. This value exceeds the 30m recommended gap distance for woodland blocks to be considered as part of a Forest Habitat Network under Forestry Commission guidelines (Forestry Commission, 2001). The current scientific basis for this recommendation is sparse and this finding provides justification for it for woodland birds, especially as the goldcrest is the smallest European bird. If the hypothesis relating morphology and gap crossing has credence, this guideline may be more widely applicable.

Secondly, the study has increased our understanding of bird habitat and landscape relationships. Although statistical modelling is an empirical approach it can be used to suggest hypotheses so that limited research resources can be more effectively targeted. For example, the models suggested that a minimum area of two hectares of continuous woodland cover was important for the song thrush and it was hypothesised that this may indicate a minimum area requirement for this species. This should be tested further, especially as the song thrush is on the red list of species of particular conservation concern.

Thirdly the results can be used to predict the probable outcomes of different management. Chapter 5 illustrated how this may be applied for East Loch Lomond. Were comparable information compiled for the Central Scotland Forest a similar predictive exercise could be carried out. Predictions can be compared with management aims and where these are unlikely to be fulfilled changes can be implemented at an early stage.

The approach employed in this study was species-centred. However, because of the range of species studied, general trends could also be observed which gives the results value outwith the confines of the two study areas. Taken as a whole it demonstrates the value of a combined experimental and observational approach for generating data of merit for conservation management. Ultimately the data could be linked more closely together in joint empirical and process orientated models to generate more detailed predictions of effects of different management strategies. Such output could also generate a clearer picture of why many woodland bird species are declining and so help in reversing this trend.

# References

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716-723.

Alexander, R. R. (1969) Seedfall and establishment of Engelmann spruce in clearcut openings: a case history. *USDA Forest Research Paper RM-53*

Alverson, W. S., Waller, D. M., and Solheim, S. L. (1988) Forests too deer: edge effects in Northern Wisconsin. *Conservation Biology* **2**, 348-358.

Amaro, A. and Reed, D. D. (2001) Forest re-measurements and modeling strategies. In: Rennolls, K. Proceedings of a IUFRO 4.11 conference: Forest Biometry, Modelling and Information Systems held at the University of Greenwich, June 2001, http://cms1.gre.ac.uk/conferences/iufro/proceedings/themes.htm, Accessed on 10th March, 2004.

Ambuel, B. and Temple, S. A. (1983) Area-dependent changes in the bird communities and vegetation of Southern Wisconsin forests. *Ecology* **64**, 1057-1068.

Anderson, B. W. and Ohmart, R. D. (1981) Comparisons of avian census results using variable distance transect and variable circular plot techniques. *Studies in Avian Biology* **6**, 186-192.

Anderson, D. R., Burnham, K. P., and White, G. C. (1994) AIC model selection in overdispersed capture-recapture data. *Ecology* **75**, 1780-1793.

Anderson, M. L. (1967) *A history of Scottish forestry*. Nelson, London.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355-366.

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

Andrén, H., Angelstam, P., Lindström, E., and Wildén, P. (1985) Differences in predation pressure in relation to habitat fragmentation: an experiment. *Oikos* **45**, 273-277.

Armstrong, E. A. (1955) *The Wren*. Collins, London.

Armstrong, E. A. (1956) Territory in the wren, *Troglodytes troglodytes*. *Ibis* **98**, 430-437.

Arnold, G. W. (1983) The influence of ditch and hedgerow structure, length of hedgerows, and area of woodland and garden on bird numbers on farmland. *Journal of Applied Ecology* **20**, 731-750.

Askins, R. A., Philbrick, M. J., and Sugeno, D. S. (1987) Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* **39**, 129-152.

Augustin, N. H., Mugglestone, M. A., and Buckland, S. T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* **33**, 339-347.

Austin, M. P. (1999) The potential contribution of vegetation ecology to biodiversity research. *Ecography* **22**, 465-484.

Austin, M. P. and Meyers, J. A. (1996) Current approaches to modelling the environmental niche of eucalypts: implications for management of forest biodiversity. *Forest Ecology and Management* **85**, 95-106.

Austin, O. L. (1949) Site tenacity, a behaviour trait of the common tern (*Sterna hirundo* Linn.). *Bird-Banding* **20**, 1-39.

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

Avery, M. I. and Krebs, J. R. (1984) Temperature and foraging success of great tits *Parus major*, hunting for spiders. *Ibis* **126**, 33-38.

Baldwin, S. P. and Kendeigh, S. C. (1938) Variations in the weights of birds. *Auk* **55**, 416-467.

Balmford, A., Thomas, A. L. R., and Jones, I. L. (1993) Aerodynamics and the evolution of long tails in birds. *Nature* **361**, 628-630.

Bayne, E. M. and Hobson, K. A. (1997) Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* **11**, 1418-1429.

Beck, R. J. and Schultz, E. K. (1986) The use of Relative Operating Characteristic (ROC) Curves in test performance evaluation. *Arch Pathol Lab Med* **110**, 13-20.

Begon, M. and Mortimer, M. (1986) *Population Ecology - a unified study of animals and plants*. 2nd edn. Blackwell Scientific Publications, Oxford.

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

Bellamy, P. E., Hinsley, S. A., and Newton, I. (1996a) Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology* **33**, 249-262.

Bellamy, P. E., Hinsley, S. A., and Newton, I. (1996b) Local extinctions and recolonisations of passerine bird populations in small woods. *Oecologia* **108**, 64-71.

Bellamy, P. E., Rothery, P., Hinsley, S. A., and Newton, I. (2000) Variation in the relationship between numbers of breeding pairs and woodland area for passerines in fragmented habitat. *Ecography* **23**, 130-138.

Bender, D. J., Contreras, T. A., and Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**, 517-533.

Berg, Å. (1997) Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. *Bird Study* **44**, 355-366.

Best, L. B. (1981) Seasonal changes in detection of individual bird species. *Studies in Avian Biology* **6**, 252-261.

Bibby, C. J., Bain, C. G., and Burgess, D. J. (1989) Bird communities of highland birchwoods. *Bird Study* **36**, 123-133.

Bibby, C. J., Burgess, N. D., and Hill, D. A. (1992) *Bird Census Techniques*. Academic Press Limited, London.

Blake, J. G. and Karr, J. R. (1987) Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* **68**, 1724-1734.

Blondel, J., Ferry, C., and Frochot, B. (1981) Point counts with unlimited distance. *Studies in Avian Biology* **6**, 414-420.

Bolger, D. T., Scott, T. A., and Rotenberry, J. T. (1997) Breeding bird abundance in an urbanizing landscape in coastal Southern California. *Conservation Biology* **11**, 406-421.

British Ornithologists' Union (2002) The British List: Bird Species recorded in Great Britain. http://www.bou.org.uk/recbrlst.html. Accessed on 11th January 2005.

Broome, A., Clare, J., Ray, D., and Humphrey, J. (2004) *Using an Ecological Site Classification at the landscape scale to guide the restoration of Atlantic Oakwoods within the Ben Lomond National Memorial Park*. Woodland Ecology Branch, Forest Research Northern Research Station, Roslin.

Brotons, L., Thuiller, W., Araujo, M. B., and Hirzel, A. H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* **27**, 437-448.

Brown, J. H. (1984) On the relationship between abundance and distribution of species. *American Naturalist* **124**, 255-279.

Brown, J. L. and Orians, G. H. (1970) Spacing patterns in mobile animals. *Annual Review of Ecology and Systematics* **1**, 239-262.

Bryant, D. M., Bell, M. V., Hentry, C. J., and Newton, S. F. (1993) Birds . In: Corbett, L., Dix, N. J., Bryant, D. M., McLusky, D. S., Elliott, B. J., and Tranter, N. L. *Central Scotland, Land - Wildlife - People,* pp 57-75, Forth Naturalist and Historian, Stirling.

Buckland, S. T., Burnham, K. P., and Augustin, N. H. (1997) Model selection, an integral part of inference. *Biometrics* **53**, 603-618.

Buckland, S. T. and Elston, D. A. (1993) Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* **30**, 478-495.

Buckland, S. T., Elston, D. A., and Beaney, S. J. (1996) Predicting distributional change, with application to bird distribution in northeast Scotland. *Global Ecology and Biogeography Letters* **5**, 66-84.

Calmaestra, R. G. and Moreno, E. (2001) A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in passeriformes. *Ardea* **89**, 407-416.

Catchpole, C. K. and Slater, P. J. B. (1995) *Bird Song - Biological themes and variation*. Cambridge University Press, Cambridge .

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

Chen, J., Franklin, J. F., and Spies, T. A. (1995) Growing season microclimate gradients for clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* **5**, 74-86.

Cody, M. L. (1985) *Habitat Selection in Birds*. Academic Press, San Diego.

Colquhoun, M. K. and Morley, A. (1943) Vertical zonation in woodland bird communities. *Journal of Animal Ecology* **12**, 75-81.

Cousens, J. E. (1963) Variation in some diagnostic characters of the sessile and pedunculate oaks and their hybrids in Scotland. *Watsonia* **5**, 273-286.

Creegan, H. (1996) An examination of how the time budgets of singing male wrens in Mine Wood change with overnight temperature, time of year and day. Unpublished B.Sc. (Hons) Thesis in the Department of Biological and Molecular Sciences, University of Stirling.

Cresswell, W. (1993) Escape responses by redshanks *Tringa totanus*, on attack by avian predators. *Animal Behaviour* **46**, 609-611.

CSCT (1995) *The Central Scotland Forest Strategy*. Central Scotland Countryside Trust, Shotts.

CSCT (2001) *Central Scotland Countryside Trust Annual Report 1999/ 2000*. Central Scotland Countryside Trust, Shotts.

Cummings, W., Jones, E., Reed, D., and Drummer, T. (2001) Frontier function analysis to estimate the maximum relative growth rate of red pine (*Pinus resinosa*, Ait.) in Northern Michigan . In: Rennolls, K. Proceedings of a IUFRO 4.11 conference: Forest Biometry, Modelling and Information Systems held at the University of Greenwich, June 2001, http://cms1.gre.ac.uk/conferences/iufro/proceedings/themes.htm, Accessed on 10th March, 2004.

Curio, E. (1978) The adaptive significance of avian mobbing I. Teleonomic hypotheses and predictions. *Zeitschrift fur Tierpsychologie* **48**, 175-183.

Curio, E. and Regelmann, K (1985) The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Zeitschrift fur Tierpsychologie* **69**, 3-18.

Dawson, D. G. (1981) Counting birds for a relative measure (index) of density. *Studies in Avian Biology* **6**, 12-16.

Desrochers, A. and Hannon, S. J. (1997) Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* **11**, 1204-1210.

Dooling, R. J. (1982) Auditory perception in birds. In: Kroodsma, D. E. and Miller, E. H. *Acoustic communication in birds, Volume 1 Production, perception and design features of sound*, pp 95-130, Academic Press, London.

Eaton, M. A., Stoate, C., Whittingham, M. J., and Bradbury, R. B. (2001) Determinants of whitethroat *Sylvia communis* distribution in different agricultural landscapes. In: Chamberlain, D. and Wilson, A. Proceedings of the 2002 Annual IALE (UK) Conference held at the University of East Anglia, 10 - 13 September 2002, pp 300-304 IALE, UK.

Edington, J. M. and Edington, M. A. (1972) Spatial patterns and habitat partition in the breeding birds of an upland wood. *Journal of Animal Ecology* **41**, 331-359.

Elkie, P., Rempel, R., and Carr, A. (1999) *Patch Analyst User's Manual*. Ontario Ministry of Natural Resources, Northwest Science and Technology, Thunder Bay, Ontario.

Emlen, J. T. (1971) Population densities of birds derived from transect counts. *Auk* **88**, 323-342.

Fang, S. and Gertner, G. (2001) Analysis of parameters of two growth models estimated using Bayesian methods and nonlinear regression . In: Rennolls, K. Proceedings of a IUFRO 4.11 conference: Forest Biometry, Modelling and Information Systems held at the University of Greenwich, June 2001, http://cms1.gre.ac.uk/conferences/iufro/proceedings/themes.htm, Accessed on 10th March, 2004.

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

Fielding, A. H. and Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* **24**, 38-49.

Fielding, A. H. and Haworth, P. F. (1995) Testing the generality of bird habitat models. *Conservation Biology* **9**, 1466-1481.

Ford, H. A. (1987) Bird communities on habitat islands in England. *Bird Study* **34**, 205-218.

Forestry Commission (2001) Forestry Commission guidance note 20 December 2001: Forest Habitat Networks. www.forestry.gov.uk/pdf/gnote.pdf/$FILE/gnote.pdf, Accessed on 2nd February 2004.

Forestry Commission (2003) *The Forestry Commission in Scotland Corporate Plan 2003-2004*. Forestry Commission, Edinburgh.

Forman, R. T. and Godron, M. (1986) *Landscape Ecology*. John Wiley and Sons, New York.

Fuller, R. J. (1982) *Bird Habitats in Britain*. T & A D Poyser, Calton.

Fuller, R. J. (1995) *Bird life of woodland and forest*. Cambridge University Press, Cambridge.

Fuller, R. J. (2001) Spatial differences in habitat selection and occupancy by woodland bird species in Europe: a neglected aspect of bird-habitat relationships. In: Chamberlain, D. and Wilson, A. Proceedings of the 2002 Annual IALE (UK) Conference held at the University of East Anglia, 10 - 13 September 2002, pp 101-111 IALE, UK.

Fuller, R. J. and Langslow, D. R. (1984) Estimating numbers of birds by point counts: how long should counts last? *Bird Study* **31**, 195-202.

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

Galli, A. E., Leck, C. F., and Forman, R. T. T. (1976) Avian distribution patterns in forest islands of different sizes in Central New Jersey. *Auk* **93**, 356-364.

Garcia, O. (2001) On bridging the gap between tree-level and stand-level models. In: Rennolls, K. Proceedings of a IUFRO 4.11 conference: Forest Biometry, Modelling and Information Systems held at the University of Greenwich, June 2001, http://cms1.gre.ac.uk/conferences/iufro/proceedings/themes.htm, Accessed on 10th March, 2004.

Garson, P. J (1980a) The breeding ecology of the wren in Britain. *Bird Study* **27**, 63-72.

Garson, P. J. (1980b) Male behaviour and female choice: mate selection in the wren? *Animal Behaviour* **28**, 491-502.

Garson, P. J. and Hunter, M. L. (1979) Effects of temperature and time of year on the singing behaviour of wrens *Troglodytes troglodytes*, and great tits *Parus major*. *Ibis* **121**, 481-487.

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

Gates, S., Gibbons, D. W., Lack, P. C., and Fuller, R. J. (1994) Declining farmland bird species: modelling geographical patterns of abundance in Britain . In: Edwards, P. E., May, R. M., and Webb, N. *Large-scale ecology and conservation biology*, pp 153-177, Blackwell Scientific Publications, Oxford.

Geer, T. A. (1978) Effects of nesting sparrowhawks on nesting tits. *Condor* **80**, 419-422.

Gehlbach, F. R. and Leverett, J. S. (1995) Mobbing of Eastern screech-owls: predatory cues, risk to mobbers and degree of threat . *Condor* **97**, 831-834.

Gibbons, D. W., Hill, D., and Sutherland, W. J. (1996) Birds . In: Sutherland, W. J. *Ecological Census Techniques: A handbook*, pp 227-259, Cambridge University Press, Cambridge.

Gilbert, F. S. (1980) The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography* **7**, 209-235.

Gottlander, K. (1987) Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca*: causes and consequences. *Animal Behaviour* **35**, 1037-1043.

Granholme, S. L. (1983) Bias in density estimates due to movement of birds. *Condor* **85**, 243-248.

Gregory, R. D., Eaton, M. A., Noble, D. G., Robinson, J. A., Parsons, M., Baker, H., Austin, G., and Hilton, G. M. (2003) *The state of the UK's birds 2002*. The RSPB, BTO, WWT & JNCC, Sandy.

Greig-Smith, P. (1983) *Quantitative plant ecology*. 3rd edn. Blackwell Scientific Publications, Oxford.

Grubb, T. C. Jr. and Doherty, P. F. Jr. (1999) On home-range gap crossing. *Auk* **116**, 618-628.

Guisan, A. and Zimmermann, N. E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.

Haas, C. A. (1995) Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* **9**, 845-854.

Haila, Y., Hanski, I. K., and Raivio, S. (1993) Turnover of breeding birds in small forest fragments: the "sampling" colonization hypothesis corroborated. *Ecology* **74**, 714-725.

Hamilton, G. J. and Christie, J. M. (1971) *Forest Management Tables (Metric), Forestry Commission Booklet No. 34.* HMSO, London.

Hanley, J. A. and McNeil, B. J. (1983) A method of comparing the areas under Receiver Operating Characteristic Curves derived from the same cases. *Radiology* **148**, 839-843.

Harrell, F. E., Lee, K. L., and Mark, D. B. (1996) Multivariable prognostic models: Issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. *Statistics in Medicine* **15**, 361-387.

Harrison, A. R. and Dunn, R. (1993) Problems of sampling the landscape. In: Haines-Young, R., Green, D. R., and Cousins, S. H. *Landscape Ecology and Geographic Information Systems*, pp 101-109, Taylor and Francis, London.

Harrison, S. J. and Harrison, D. J. (1988) The effect of elevation on the climatically determined growing season in the Ochil Hills. *Scottish Geographical Magazine* **104**, 108-115.

Harrison, S. J., Winterbottom, S. J., and Sheppard, C. (1999) The potential effects of climate change on the Scottish tourist industry. *Tourism Management* **20**, 203-211.

Hartley, M. J. and Hunter, M. L. Jr. (1998) A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conservation Biology* **12**, 465-469.

Haskell, D. G. (1995) A re-evaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* **5**, 1316-1318.

Hastie, T. J. and Tibshirani, R. J. (1990) *Generalized Additive Models*. Chapman and Hall, London.

Helliwell, D. R. (1976) The effect of size and isolation on the conservation value of wooded sites in Britain. *Journal of Biogeography* **3**, 407-416.

Heltshe, J. F. and Forrester, N. E. (1983) The jackknife estimate of species richness. *Biometrics* **39**, 1-11.

Higgins, R. McR. (1979) Temperature-related variation in the duration of morning song of the song thrush *Turdus ericetorium*. *Ibis* **121**, 333-335.

Hinde, R. A. (1952) The behaviour of the great tit (*Parus major*) and some related species. *Behaviour Supplement* **2**, 1-201.

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

Hinsley, S. A., Pakeman, R., Bellamy, P. E., and Newton, I. (1996b) Influences of habitat fragmentation on bird species distributions and regional population sizes. *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**, 307-313.

HMSO (1994) *Sustainable Forestry: The UK Programme*. HMSO, London.

Howard, R. and Moore, A. (1990) *A complete checklist of birds of the world*. 3rd edn. Academic Press Limited.

Howe, R. W. (1984) Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. *Ecology* **65**, 1585-1601.

Huhta, E., Aho, T., Jantti, A., Suorsa, P., Kuitunen, M., Nikula, A., and Hakkarainen, H. (2004) Forest fragmentation increases nest predation in the Eurasian treecreeper. *Conservation Biology* **18**, 148-155.

Huhta, E., Jokimaki, J., and Helle, P. (1998) Predation on artificial nests in a forest dominated landscape - the effects of nest type, patch size and edge structure. *Ecography* **21**, 464-471.

Hurd, C. R. (1996) Interspecific attraction to the mobbing calls of Black-capped Chickadees (*Parus atricapillus*). *Behavioral Ecology and Sociobiology* **38**, 287-292.

Hurlbert, S. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187-211.

Hutto, R. L., Pletschet, S. M., and Hendricks, P. (1986) A fixed-radius point count method for nonbreeding and breeding season use. *Auk* **103**, 593-602.

James, F. C. (1971) Ordinations of habitat relationships among breeding birds. *Wilson Bulletin* **83**, 215-236.

James, F. C. and McCulloch, C. E. (1985) Data analysis and the design of experiments in ornithology. *Current Ornithology* **2**, 1-63.

James, F. C. and Wamer, N. O. (1982) Relationships between temperate forest bird communities and vegetation structure. *Ecology* **63**, 159-171.

Johnstone, I. (1998) Territory structure of the Robin *Erithacus rubecula* outside the breeding season. *Ibis* **140**, 244-251.

Kacelnik, A. (1979) The foraging efficiency of great tits (*Parus major*) in relation to light intensity. *Animal Behaviour* **27**, 237-241.

Kim, J-O. and Kohout, F. J. (1975) Multiple regression analysis: subprogram regression. In: Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K., and Bent, D. H. *SPSS - Statistical Package for the Social Sciences*, 2nd edn. pp 320-367, McGraw Hill, New York.

Kirby, K. (1995) *Rebuilding the English countryside: habitat fragmentation and wildlife corridors as issues in practical conservation.* English Nature, Peterborough.

Klopfer, P. H. and Ganzhorn, J. U. (1985) Habitat selection: behavioural aspects. In: Cody, M. L. *Habitat selection in birds* , pp 435-453, Academic Press, San Diego.

Kluijver, H. N. (1951) The population ecology of the great tit, *Parus m. major* L. *Ardea* **29**, 1-135.

Klump, G. M. and Shalter, M. D. (1984) Acoustic behaviour of birds and mammals in the predator context. *Zeitschrift fur Tierpsychologie* **66**, 189-226.

Knox, A. G., Collinson, M., Helbig, A. J., Parkin, D. T., and Sangster, G. (2002) Taxonomic recommendations for British birds. *Ibis* **144**, 707-710.

Krebs, J. R., MacRoberts, M. H., and Cullen, J. M. (1972) Flocking and feeding in the great tit *Parus major*, an experimental study. *Ibis* **114**, 507-530.

Kroodsma, D. E. (1986) Design of song playback experiments. *Auk* **103**, 640-642.

Lack, D. (1933) Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. *Journal of Animal Ecology* **2**, 239-262.

Lack, D. (1971) *Ecological isolation in birds*. Blackwell Scientific Publications, Oxford.

Lack, D. and Venables, L. S. V. (1939) The habitat distribution of British woodland birds. *Journal of Animal Ecology* **8**, 39-71.

Landsberg, J. (2003) Physiology in forest models: history and the future. *FBMIS* **1**, 49-63.

Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**, 1659-1673.

Léscourret, F. and Genard, M. (1994) Habitat, landscape and bird composition in mountain forest fragments. *Journal of Environmental Management* **40**, 317-328.

Lima, S. L. and Dill, L. M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.

López, G. and Moro, M. J. (1997) Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. *Journal of Applied Ecology* **34**, 1257-1272.

MacArthur, R. H. and Wilson, E. O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Mace, R. (1987) The dawn chorus in the great tit (*Parus major*) is directly related to female fertility. *Nature* **330**, 745-746.

Mahoney, D. and Atkinson, B. (2001) Shar archive (roc.shar) of functions to calculate plots associated with Sensitivity and Specificity, along with pairwise comparisons of the area under the curve in S-Plus. http://www.mayo.edu/hsr/Sfunc.html, Accessed on 8th October 2002.

Manel, S., Williams, H. C., and Ormerod, S. J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**, 921-931.

Margules, C., Higgs, A. J., and Rafe, R. W. (1982) Modern biogeographic theory - are there any lessons for nature reserve design. *Biological Conservation* **24**, 115-128.

Marler, P. (1955) Characteristics of some animal calls. *Nature* **176**, 6-8.

Martin, T. E. (1980) Diversity and abundance of spring migratory birds using habitat islands on the Great Plains. *Condor* **82**, 430-439.

Martin, T. E. (1988) Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* **69**, 74-84.

Mason, C. F. (1976) Breeding biology of the *Sylvia* warblers. *Bird Study* **23**, 213-232.

Matthysen, E., Adriaensen, F., and Dhondt, A. A. (1995) Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* **72**, 375-381.

McCollin, D. (1993) Avian distribution patterns in a fragmented wooded landscape (North Humberside, UK): the role of between-patch and within-patch structure. *Global Ecology and Biogeography Letters* **3**, 48-62.

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

McColm, F. (1999) An experiment to investigate whether Scottish woodland birds will cross habitat gaps using food as an attractant. Unpublished dissertation submitted as part of the degree of MSc in Environmental Management in the Department of Environmental Sciences, University of Stirling.

McCullagh, P. and Nelder, J. A. (1989) *Generalized Linear Models*. 2nd edn. Chapman and Hall, London.

McGarigal, K. and Marks, B. J. (1994) *Fragstats spatial pattern analysis program for quantifying landscape structure: Version 2.0.* Forest Science Department, Oregon State University, Corvallis.

McPhillimy, D. and Stiven, R. (1998) *A native woodland action plan for the Central Scotland Forest*. CSCT, Shotts.

Merrill, E.(2002) Density dependent habitat selection of forest birds in the Bighorn Mountains of Wyoming. Presentation given at the 2002 Annual IALE (UK) Conference, held at the University of East Anglia 10th-13th September, 2002.

Minot, E. O. and Perrins, C. M. (1986) Interspecific interference competition - nest sites for blue and great tits. *Journal of Animal Ecology* **55**, 331-350.

Mitchell, J. (1981) The breeding bird communities of Balloch Park Loch Lomondside. *Loch Lomond Bird Report* **10**, 8-14.

Møller, A. (1988) Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. *Oikos* **53**, 215-221.

Moore, N. W. and Hooper, M. D. (1975) On the number of bird species in British woods. *Biological Conservation* **8**, 239-250.

Morrison, M. L., Mannan, R. W., and Dorsey, G. L. (1981) Effects of number of circular plots on estimates of avian density and species richness. *Studies in Avian Biology* **6**, 405-408.

Moss, D. (1978) Song-bird populations in forestry plantations. *Quarterly Journal of Forestry* **72**, 5-14.

Mou, P. and Fahey, T. J. (1993) REGROW: A computer model simulating the early successional process of a disturbed northern hardwood ecosystem. *Journal of Applied Ecology* **30**, 676-688.

Muetzelfeldt, R. and Taylor, J. (2004) Developing forest models in the Simile visual modelling environment. http://www.ierm.ed.ac.uk/simile/documents/iufro3.pdf, Accessed on 12th March 2004.

Newton, I. (1986) *The sparrowhawk*. Poyser, Calton, U.K.

Newton, I. and Marquiss, M. (1982) Food, predation and breeding season in sparrowhawks (*Accipiter nisus*). *Journal of Zoology, London* **197**, 221-240.

Norberg, U. M. (1979) Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest and the treecreeper in relation to locomotor pattern and feeding station selection. *Philosophical Transactions of the Royal Society of London B* **287**, 131-165.

Norberg, U. M. (1995) How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology* **9**, 48-54.

O’Connor, R. J. (1980) The effects of census date on the results of intensive Common Bird Census surveys. *Bird Study* **27**, 126-136.

O'Connor, R. J. and Hicks, R. K. (1980) The influence of weather conditions on the detection of birds during Common Birds Census fieldwork. *Bird Study* **27**, 137-151.

Opdam, P. (1978) Feeding ecology of a sparrowhawk population (*Accipiter nisus*). *Ardea* **66**, 137-155.

Opdam, P., Foppen, R Reijnen R., and Schotman, A. (1994) The landscape ecological approach in bird conservation: integrating the metapopulation concept into spatial planning. *Ibis (Suppl 1)* **137**, 139-146.

Opdam, P., Rijsdijk, G., and Hustings, F. (1985) Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* **34**, 333-352.

Opdam, P., Van Dorp, D., and Ter Braak, C. J. F. (1984) The effect of isolation on the number of woodland birds in small woods in the Netherlands. *Journal of Biogeography* **11**, 473-478.

Orians, G. H. and Willson, M. F. (1964) Interspecific territories of birds. *Ecology* **45**, 736-745.

Orians, G. H. and Wittenberger, J. F. (1991) Spatial and temporal scales in habitat selection. *American Naturalist (Supplement 1)* **137**, 29-49.

Osborne, P. E. and Tigar, B. J. (1992) Interpreting bird atlas data using logistic models: an example from Lesotho, Southern Africa. *Journal of Applied Ecology* **29**, 55-62.

Pakeman, E. J., Hill, M. O., and Marrs, R. H. (1995) Modelling vegetation succession after bracken control. *Journal of Environmental Management* **43**, 29-39.

Paradis, E., Baillie, S. R., Sutherland, W. J., Dudley, C., Crick, H. Q. P., and Gregory, R. D. (2000) Large-scale spatial variation in the breeding performance of song thrushes *Turdus philomelos* and blackbirds *T-merula* in Britain. *Journal of Applied Ecology* **37**, 73-87.

Paradis, E., Baillie, S. R., Sutherland, W. J., and Gregory, R. D. (1998) Patterns of natal and breeding dispersal in birds . *Journal of Animal Ecology* **67**, 518-536.

Parker, V. (1999) The use of logistic regression in modelling the distributions of bird species in Swaziland. *South African Journal of Zoology* **34**, 39-47.

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

Pearce, J. and Ferrier, S. (2001) The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation* **98**, 33-43.

Peck, K. M. (1989) Tree species preferences shown by foraging birds in forest plantations in Northern England. *Biological Conservation* **48**, 41-57.

Perkins, A. C. (1998) *Native woodland initiative field survey - Report on selection of woods for management*. Heritage Woodlands, Fife.

Peterken, G. F. and Jones, E. W. (1989) Forty years of change in Lady Park Wood: the young-growth stands. *Journal of Ecology* **77**, 401-429.

Phillips, P. D. and van Gardingen, P. R. (2004) The SYMFOR framework for modelling the effects of silviculture on the growth and yield of tropical forests. In: Rennolls, K. Proceedings of a IUFRO 4.11 conference: Forest Biometry, Modelling and Information Systems held at the University of Greenwich, June 2001, http://cms1.gre.ac.uk/conferences/iufro/proceedings/themes.htm, Accessed on 10th March, 2004.

Pigott, C. D. (1983) Regeneration of oak-birch woodland following exclusion of sheep. *Journal of Ecology* **71**, 629-646.

Porte, A. and Bartelink, H. H. (2002) Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling* **150**, 141-188.

Rayner, J. M. V. (1979) A new approach to animal flight mechanics. *Journal of Experimental Biology* **80**, 17-54.

Reed, D., Tomé, M., Araújo, M. C., and Jones, E. (2001) A re-examination of potential modifier dimensional growth models. In: Rennolls, K. Proceedings of a IUFRO 4.11 conference: Forest Biometry, Modelling and Information Systems held at the University of Greenwich, June 2001, http://cms1.gre.ac.uk/conferences/iufro/proceedings/themes.htm, Accessed on 10th March, 2004.

Richards, D. B. (1981) Estimation of distance of singing conspecifics by the Carolina wren. *Auk* **98**, 127-133.

Robinson, S. K., Thompson, F. R., Donovan, T. M., Whitehead, D. R., and Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**, 1987-1990.

Rogers, G. M. (1989) Beech and conifer forest interactions in Moawhango Ecological Region, North Island, New Zealand. *New Zealand Journal of Ecology* **12**, 47-61.

Rudebeck, G. (1950) The choice of prey and modes of hunting of predatory birds with special reference to their selective effect . *Oikos* **2**, 65-88.

Saab, V. (1999) Importance of scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* **9**, 135-151.

Sauer, J. D. (1988) *The dynamics of geographic patterning in seed plant species*. University of California, California.

Scheck, J., Lertzman, K., Nyberg, B., and Page, R. (1995) Effects of patch size on birds in old-growth montane forest. *Conservation Biology* **9**, 1072-1084.

Schmiegelow, F. K. A. and Monkkonen, M. (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* **12**, 375-389.

Scott, J. M. and Ramsey, F. L. (1981) Length of count period as a possible source of bias in estimating bird densities. *Studies in Avian Biology* **6**, 409-413.

Seddon, B. (1971) *Introduction to Biogeography*. Duckworth, London.

Shalter, M. D. and Schleidt, W. M. (1977) The ability of barn owls, *Tyto alba*, to discriminate and localize avian alarm calls. *Ibis* **119**, 22-27.

Shaw, G. (1976) The breeding bird community of the hillside oakwoods of Loch Lomondside. *The Western Naturalist* **5**, 41-52.

Siffczyk, C., Orell, M., and Nikula, A. (2001) Nest site selection of Siberian Tits *Parus cinctus* at different landscape levels. In: Chamberlain, D. and Wilson, A. Proceedings of the 2002 Annual IALE (UK) Conference held at the University of East Anglia, 10 - 13 September 2002, pp 81-86, IALE, UK.

Simms, E. (1971) *Woodland Birds*. Collins, London.

Small, M. F. and Hunter, M. L. (1988) Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* **76**, 62-64.

Smith, J. M. and Graves, H. B. (1978) Some factors influencing mobbing behavior in barn swallows (*Hirundo rustica*). *Behavioural Biology* **23**, 355-372.

Smith, P. A. (1994) Autocorrelation in logistic regression modelling of species distributions. *Global Ecology and Biogeography Letters* **4**, 47-61.

SNH (1993) *National Countryside Monitoring Scheme, Scotland, Central*, Scottish Natural Heritage, Edinburgh.

Snow, D. W. (1954) The habitats of Eurasian Tits (*Parus* species). *Ibis* **96**, 565-585.

Snow, D. W. (1956) Territory in the blackbird, *Turdus merula*. *Ibis* **98**, 438-447.

Strain, J. G. and Mumme, R. L. (1988) Effects of food supplementation, song playback, and temperature on vocal territorial behaviour of Carolina wrens. *Auk* **105**, 11-16.

Swets, J. A. (1988) Measuring the accuracy of diagnostic systems. *Science* **240**, 1285-1293.

Tatner, P. and Bryant, O. M. (1986) Flight cost of a small passerine measured using doubly labelled water: implications for energetic studies. *Auk* **103**, 169-180.

The National Park Authority (2003) *Loch Lomond and The Trossachs Local Woodland and Forestry Framework*. Report prepared by Eamonn Wall and Co. Consultants for Loch Lomond and the Trossachs National Park Authority, Forestry Commission Scotland and Scottish National Heritage. National Park Authority, Balloch.

Thompson, R., Humphrey, J., Harmer, R., and Ferris, R. (2003) *Restoration of Native Woodlands on Ancient Woodland Sites, Forestry Commission Practice Guide*. Forestry Commission, Edinburgh.

Thorpe, W. H. (1961) *Bird Song - The biology of vocal communications and expressions*. Cambridge University Press, Cambridge.

Tittensor, R. M. (1970) History of the Loch Lomond oakwoods. *Scottish Forestry* **24**, 100-118.

Tittensor, R. M. and Steele, R. C. (1971) Plant communities of the Loch Lomond oakwoods. *Journal of Ecology* **59**, 561-582.

Verboom, J., Schotman, A., Opdam, P., and Metz, A. J. (1991) European nuthatch metapopulations in a fragmented agricultural landscape. *Oikos* **61**, 149-156.

Verner, J. (1985) Assessment of counting techniques. *Current Ornithology* **2**, 247-302.

Vieth, W., Curio, E., and Ernst, U. (1980) The adaptive significance of avian mobbing III. Cultural transmission of enemy recognition in blackbirds: cross-species tutoring and properties of learning. *Animal Behaviour* **28**, 1217-1229.

Wallach, D. and Genard, M. (1998) Effect of uncertainty in input and parameter values on model prediction error. *Ecological Modelling* **105**, 337-345.

Wardle, P. (1980) Ecology and distribution of silver beech (*Nothofagus menziesii*) in the Paringa district, South Westland, New Zealand. *New Zealand Journal of Ecology* **3**, 23-34.

Watson, J.(2002) The effect of landscape metrics on bird diversity in fragmented littoral forests of southeastern Madagascar. Presentation given at the 2002 Annual IALE (UK) Conference, held at the University of East Anglia 10th-13th September, 2002.

Weisberg, S. (1980) *Applied Linear Regression* . Wiley, New York.

Wetherill, G. B. (1986) *Regression analysis with applications. Monographs on statistics and applied probability 27.* Chapman and Hall, London.

Wiens, J. A. (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**, 81-120.

Wiens, J. A., Crawford, C. S., and Gosz, J. R. (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* **45**, 421-427.

Wilcove, D. S. (1985) Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**, 1211-1214.

Williamson, K. (1969) Bird communities in woodland habitats in Wester Ross, Scotland. *Quarterly Journal of Forestry* **63**, 305-328.

Williamson, K. (1972) Breeding birds of Ariundle oakwood forest nature reserve. *Quarterly Journal of Forestry* **66**, 243-255.

Williamson, K. (1974) Oak wood breeding bird communities in the Loch Lomond National Nature Reserve. *Quarterly Journal of Forestry* **68**, 9-28.

With, K. A. (1997) The application of neutral landscape models in conservation biology. *Conservation Biology* **11**, 1069-1080.

With, K. A, Gardner, R. H., and Turner, M. G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**, 151-169.

Yahner, R. H. (1988) Changes in wildlife communities near edges. *Conservation Biology* **2**, 333-339.

Ydenberg, R. C. and Houston, A. I. (1986) Optimal trade-offs between competing behavioural demands in the great tit. *Animal Behaviour* **34**, 1041-1050.

Yee, T. W. and Mitchell, N. D. (1991) Generalized additive models in plant ecology. *Journal of Vegetation Science* **2**, 587-602.

Zimmermann, U. and Curio, E. (1988) Two conflicting needs affecting predator mobbing by great tits, *Parus major*. *Animal Behaviour* **36**, 926-932.

Zweig, M. H. and Campbell, G. (1993) Receiver-Operating Characteristic (ROC) Plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry* **39**, 561-577.

# Appendices

## Appendix 1: List of bird species referred to in the thesis giving common and scientific names. Nomenclature is that used by the British Ornithologists' Union (2002) following Knox *et al* (2002). English names are as in Howard and Moore (1990).

| Species | |
|---|---|
| Common name | Scientific name |
| Sparrowhawk | *Accipiter nisus* |
| Great Spotted Woodpecker | *Dendrocopos major* |
| Tree Pipit | *Anthus trivialis* |
| Wren | *Troglodytes troglodytes* |
| Dunnock | *Prunella modularis* |
| Robin | *Erithacus rubecula* |
| Redstart | *Phoenicurus phoenicurus* |
| Blackbird | *Turdus merula* |
| Song Thrush | *Turdus philomelos* |
| Mistle Thrush | *Turdus viscivorus* |
| Blackcap | *Sylvia atricapilla* |
| Garden Warbler | *Sylvia borin* |
| Whitethroat | *Sylvia communis* |
| Wood Warbler | *Phylloscopus sibilatrix* |
| Chiffchaff | *Phylloscopus collybita* |
| Willow Warbler | *Phylloscopus trochilus* |
| Goldcrest | *Regulus regulus* |
| Spotted Flycatcher | *Muscicapa striata* |
| Pied Flycatcher | *Ficedula hypoleuca* |
| Long-tailed Tit | *Aegithalos caudatus* |
| Coal Tit | *Parus ater* |
| Blue Tit | *Parus caeruleus* |
| Great Tit | *Parus major* |
| Nuthatch | *Sitta europaea* |
| Treecreeper | *Certhia familiaris* |
| Jay | *Garrulus glandarius* |
| Magpie | *Pica pica* |
| Jackdaw | *Corvus monedula* |
| Hooded Crow | *Corvus cornix* |
| Chaffinch | *Fringilla coelebs* |
| Greenfinch | *Carduelis chloris* |
| Siskin | *Carduelis spinus* |
| Lesser Redpoll | *Carduelis cabaret* |
| Bullfinch | *Pyrrhula pyrrhula* |

**Appendix 2: Summary of important correlations at ELL98 (i) and CSF99 (ii). In all cases the correlation structure for ELL00 was very similar to that for ELL98, so figures are not included. Correlations over 0.3 are given in bold and over 0.8 are in italics. Tables include; (A) correlations of broad-leaved (BL) and coniferous (CF) general habitat variables for the diameter breast height categories 1 (<7cm dbh), 2 (7-16 cm dbh), 3 (16-24 cm dbh), 4 (24 – 30 cm dbh), 5 (>30 cm dbh) and non-specified (>7 cm dbh); (B) Correlations of broad-leaved related habitat variables; (C) Correlations of coniferous related habitat variables; (D) Correlations between the numbers of broad-leaved trees (BL) and coniferous trees (CF) greater than 7cm dbh and habitat area and edge variables from 50 to 5000m in scale (M = Mixed broad-leaved and coniferous woodland, WD = woodland of any type and O indicates the woodland borders an open non-wooded habitat); (E) Correlations between area and edge variables from 50m to 5000m scale for broad-leaved, coniferous, mixed and general wooded habitats.**

## (A) Correlations of general broad-leaved and coniferous habitat variables

### (i) ELL98

| | BL | BL1 | BL2 | BL3 | BL4 | BL5 | CF | CF1 | CF2 | CF3 | CF4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BL1 | **0.633** | | | | | | | | | | |
| BL2 | ***0.897*** | **0.738** | | | | | | | | | |
| BL3 | ***0.860*** | **0.431** | **0.653** | | | | | | | | |
| BL4 | **0.708** | 0.274 | **0.436** | **0.787** | | | | | | | |
| BL5 | **0.613** | 0.259 | **0.350** | **0.637** | **0.771** | | | | | | |
| CF | **-0.517** | **-0.303** | **-0.330** | **-0.524** | **-0.621** | **-0.728** | | | | | |
| CF1 | -0.250 | -0.056 | -0.079 | **-0.315** | **-0.444** | **-0.566** | **0.785** | | | | |
| CF2 | **-0.457** | -0.267 | -0.276 | **-0.470** | **-0.580** | **-0.693** | ***0.973*** | ***0.816*** | | | |
| CF3 | **-0.535** | **-0.332** | **-0.353** | **-0.548** | **-0.642** | **-0.743** | ***0.973*** | **0.750** | ***0.951*** | | |
| CF4 | **-0.555** | **-0.366** | **-0.385** | **-0.559** | **-0.616** | **-0.686** | ***0.862*** | **0.565** | ***0.804*** | ***0.873*** | |
| CF5 | **-0.493** | **-0.337** | **-0.355** | **-0.456** | **-0.496** | **-0.620** | **0.740** | **0.514** | **0.677** | **0.726** | ***0.867*** |

### (ii) CSF99

| | BL | BL1 | BL2 | BL3 | BL4 | BL5 | CF | CF1 | CF2 | CF3 | CF4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BL1 | 0.185 | | | | | | | | | | |
| BL2 | ***0.889*** | 0.273 | | | | | | | | | |
| BL3 | **0.628** | 0.016 | **0.374** | | | | | | | | |
| BL4 | 0.169 | -0.142 | -0.105 | **0.301** | | | | | | | |
| BL5 | -0.112 | -0.189 | **-0.317** | -0.087 | **0.327** | | | | | | |
| CF | **-0.317** | -0.146 | -0.204 | -0.245 | -0.241 | -0.277 | | | | | |
| CF1 | -0.213 | 0.022 | -0.145 | -0.136 | -0.110 | -0.146 | **0.442** | | | | |
| CF2 | -0.190 | -0.071 | -0.080 | -0.150 | -0.232 | -0.299 | **0.747** | **0.553** | | | |
| CF3 | **-0.303** | -0.141 | -0.204 | -0.247 | -0.245 | -0.264 | ***0.871*** | **0.411** | **0.707** | | |
| CF4 | -0.280 | -0.147 | -0.225 | -0.161 | -0.098 | -0.158 | **0.656** | 0.065 | 0.290 | **0.582** | |
| CF5 | -0.292 | -0.131 | -0.230 | -0.208 | -0.061 | -0.076 | **0.576** | 0.054 | 0.081 | **0.398** | **0.616** |

## (B) Correlations of broad-leaved related habitat variables

### (i) ELL98

| Variable | AL | AS | BI | BL | BLSnag | HA | HZ | OA | RO | TSR |
|---|---|---|---|---|---|---|---|---|---|---|
| AS | 0.284 | | | | | | | | | |
| BI | 0.025 | 0.099 | | | | | | | | |
| BL | **0.482** | 0.286 | **0.584** | | | | | | | |
| BLSnag | **0.372** | 0.179 | 0.185 | **0.523** | | | | | | |
| HA | **0.454** | 0.292 | -0.096 | **0.333** | 0.199 | | | | | |
| HZ | **0.507** | **0.368** | 0.054 | **0.446** | 0.276 | **0.427** | | | | |
| OA | 0.090 | 0.094 | 0.170 | **0.520** | **0.422** | 0.001 | 0.134 | | | |
| RO | -0.001 | 0.219 | 0.278 | 0.222 | 0.010 | -0.019 | -0.043 | -0.044 | | |
| TSR | **0.366** | **0.376** | **0.527** | **0.557** | 0.288 | 0.232 | **0.345** | 0.240 | **0.440** | |
| Ground | **0.379** | 0.208 | 0.140 | **0.538** | 0.224 | 0.287 | **0.327** | **0.455** | 0.048 | **0.318** |

All tree variables are for >7cm dbh. AL = Alder, AS = Ash, BI = Birch, BL = Broad-leaved, BLSnag = Broad-leaved snags, HA = Hawthorn, HZ = Hazel, OA = Oak, RO = Rowan, TSR = Tree species richness and Ground = % Ground cover.

## (ii) CSF99

| Variable | AL | AS | BE | BI | BL | BLSnag | EL | EM | GE | HA | HO | HZ | LI | OA | RH | RO | SY | WW | TSR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AS | -0.022 | | | | | | | | | | | | | | | | | | |
| BE | -0.081 | -0.064 | | | | | | | | | | | | | | | | | |
| BI | 0.076 | **-0.339** | -0.097 | | | | | | | | | | | | | | | | |
| BL | 0.147 | 0.028 | -0.001 | **0.510** | | | | | | | | | | | | | | | |
| BLSnag | 0.129 | 0.167 | -0.001 | -0.078 | 0.156 | | | | | | | | | | | | | | |
| EL | 0.016 | -0.043 | -0.009 | -0.101 | 0.023 | 0.010 | | | | | | | | | | | | | |
| EM | 0.052 | 0.287 | 0.115 | -0.181 | 0.086 | 0.192 | 0.125 | | | | | | | | | | | | |
| GE | 0.028 | 0.058 | -0.013 | -0.064 | 0.119 | 0.154 | 0.066 | 0.204 | | | | | | | | | | | |
| HA | 0.157 | 0.233 | -0.075 | -0.068 | 0.191 | 0.128 | 0.111 | 0.244 | 0.084 | | | | | | | | | | |
| HO | -0.032 | -0.042 | 0.107 | -0.054 | 0.071 | -0.001 | 0.036 | 0.104 | -0.045 | 0.037 | | | | | | | | | |
| HZ | -0.045 | 0.205 | -0.031 | -0.045 | 0.050 | 0.121 | -0.068 | -0.014 | 0.148 | 0.077 | -0.037 | | | | | | | | |
| LI | -0.041 | 0.002 | 0.097 | -0.106 | -0.037 | -0.141 | -0.062 | -0.100 | 0.016 | -0.058 | 0.079 | -0.047 | | | | | | | |
| OA | -0.040 | -0.049 | 0.080 | -0.070 | -0.026 | 0.100 | -0.106 | -0.126 | -0.020 | 0.004 | -0.044 | 0.155 | -0.019 | | | | | | |
| RH | -0.024 | -0.020 | -0.022 | 0.014 | -0.007 | 0.010 | -0.037 | -0.060 | -0.034 | 0.009 | -0.020 | -0.028 | 0.130 | -0.089 | | | | | |
| RO | 0.039 | -0.114 | 0.009 | 0.253 | 0.287 | -0.069 | -0.066 | -0.043 | 0.067 | -0.043 | 0.049 | 0.011 | 0.096 | 0.111 | 0.007 | | | | |
| SY | -0.105 | 0.075 | 0.149 | -0.244 | 0.161 | 0.017 | 0.114 | 0.066 | 0.032 | 0.001 | 0.096 | -0.105 | 0.015 | -0.116 | 0.057 | -0.080 | | | |
| WW | -0.066 | 0.051 | -0.083 | 0.131 | 0.231 | 0.089 | 0.036 | -0.101 | -0.049 | 0.051 | -0.055 | -0.019 | -0.069 | -0.086 | -0.041 | 0.017 | -0.119 | | |
| TSR | 0.168 | 0.257 | **0.354** | 0.019 | 0.231 | 0.093 | 0.187 | **0.346** | 0.254 | **0.345** | 0.174 | 0.157 | 0.184 | 0.174 | 0.085 | **0.316** | 0.258 | 0.037 | |
| Ground | 0.067 | 0.112 | -0.212 | -0.017 | 0.020 | 0.171 | -0.092 | 0.071 | 0.127 | 0.113 | -0.112 | 0.082 | -0.182 | 0.001 | -0.131 | 0.016 | -0.189 | 0.046 | -0.159 |

Codes are as for the ELL98 correlation matrix, with additional variables coded as: BE = Beech, EL = Elder, EM = Elm, GE = Gean, HO = Holly, LI = Lime, RH = Rhododendron, SY = Sycamore, WW = Willow

## (C) Correlations of coniferous related habitat variables.

### (i) ELL98

| | CF | CFSnag | LA | PI | SP | Height3 | DeadCF | Canopy | Ground | Litter |
|---|---|---|---|---|---|---|---|---|---|---|
| CFSnag | **0.771** | | | | | | | | | |
| LA | **0.422** | **0.380** | | | | | | | | |
| PI | **0.393** | **0.338** | 0.042 | | | | | | | |
| SP | ***0.868*** | **0.731** | 0.216 | 0.212 | | | | | | |
| Height3 | **0.673** | **0.669** | **0.504** | 0.161 | **0.665** | | | | | |
| DeadCF | **0.362** | **0.443** | 0.277 | 0.253 | 0.257 | 0.282 | | | | |
| Canopy | **0.375** | **0.353** | 0.219 | 0.054 | **0.364** | **0.452** | -0.193 | | | |
| Ground | **-0.613** | **-0.611** | -0.255 | -0.138 | **-0.657** | **-0.573** | **-0.442** | **-0.336** | | |
| Litter | **0.496** | **0.444** | 0.208 | 0.171 | **0.476** | **0.473** | 0.084 | **0.616** | **-0.516** | |
| Brash | 0.014 | 0.024 | 0.225 | -0.029 | -0.106 | -0.005 | **0.581** | -0.288 | -0.237 | -0.076 |

All tree variables are for >7cm dbh. CF = Coniferous trees, CFSnag = Coniferous snags, LA = Larch, PI = Pine, SP = Spruce, Height3 = trees of 4-10 m tall, DeadCF = Dead coniferous wood on the ground, Canopy = % Canopy cover, Ground = % Ground cover, Litter = % Litter cover and Brash = % Brash cover.

### (ii) CSF99

| | CF | CFSnag | LA | PI | SP | Height3 | DeadCF | Canopy | Ground | Litter |
|---|---|---|---|---|---|---|---|---|---|---|
| CFSnag | **0.344** | | | | | | | | | |
| LA | **0.606** | 0.137 | | | | | | | | |
| PI | **0.537** | **0.421** | 0.081 | | | | | | | |
| SP | **0.552** | 0.222 | 0.083 | 0.162 | | | | | | |
| Height3 | 0.190 | 0.198 | 0.156 | 0.169 | 0.029 | | | | | |
| DeadCF | **0.634** | 0.244 | **0.414** | **0.320** | **0.349** | 0.164 | | | | |
| Canopy | 0.163 | 0.023 | 0.203 | -0.068 | 0.030 | 0.209 | -0.051 | | | |
| Ground | -0.280 | -0.022 | -0.168 | 0.039 | -0.223 | -0.139 | -0.164 | **-0.344** | | |
| Litter | 0.239 | 0.060 | 0.107 | 0.036 | 0.215 | 0.066 | 0.128 | 0.237 | **-0.471** | |
| Brash | **0.409** | 0.010 | **0.336** | 0.024 | **0.302** | 0.153 | **0.487** | -0.083 | -0.256 | 0.108 |

Codes are the same as at ELL98

### (D) Correlations between the numbers of broad-leaved trees (BL) and coniferous trees (CF) greater than 7cm dbh and habitat area and edge variables from 50 to 5000m.

| Landscape | ELL98 | | CSF99 | | Landscape | ELL98 | | CSF99 | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | BL | CF | BL | CF | Variable | BL | CF | BL | CF |
| BL50m | **0.567** | **-0.743** | 0.154 | **-0.359** | M50m | 0.136 | 0.166 | -0.035 | 0.195 |
| BL100m | **0.577** | **-0.730** | 0.181 | **-0.345** | M100m | 0.127 | 0.122 | -0.042 | 0.220 |
| BL200m | **0.571** | **-0.713** | 0.214 | **-0.310** | M200m | 0.186 | 0.058 | -0.063 | 0.287 |
| BL500m | **0.481** | **-0.590** | 0.192 | -0.266 | M500m | 0.114 | 0.115 | -0.103 | **0.318** |
| BL1000m | **0.406** | **-0.535** | 0.219 | -0.254 | M1000m | -0.094 | 0.172 | -0.094 | **0.336** |
| BL2500m | **0.377** | **-0.363** | 0.202 | -0.145 | M2500m | -0.144 | 0.085 | -0.018 | 0.236 |
| BL5000m | 0.149 | -0.006 | 0.092 | -0.194 | M5000m | -0.157 | 0.105 | 0.171 | 0.025 |
| BLO50m | 0.257 | **-0.509** | 0.044 | -0.230 | MO50m | -0.062 | 0.067 | 0.002 | 0.106 |
| BLO100m | **0.424** | **-0.663** | 0.045 | -0.280 | MO100m | -0.057 | 0.099 | -0.013 | 0.146 |
| BLO200m | **0.491** | **-0.672** | 0.099 | -0.285 | MO200m | -0.005 | 0.066 | -0.043 | 0.220 |
| BLO500m | **0.365** | **-0.576** | 0.126 | -0.230 | MO500m | -0.071 | 0.126 | -0.089 | 0.261 |
| BLO1000m | **0.307** | **-0.408** | 0.167 | -0.234 | MO1000m | **-0.371** | **0.327** | -0.088 | 0.291 |
| BLO2500m | **0.313** | **-0.309** | 0.212 | -0.232 | MO2500m | **-0.336** | 0.267 | 0.033 | 0.193 |
| BLO5000m | 0.174 | -0.189 | 0.196 | -0.235 | MO5000m | **-0.302** | 0.226 | 0.205 | -0.020 |
| CF50m | **-0.545** | **0.767** | -0.115 | **0.347** | WD50m | -0.033 | 0.244 | 0.025 | 0.064 |
| CF100m | **-0.560** | **0.744** | -0.108 | **0.312** | WD100m | -0.174 | **0.438** | 0.087 | 0.081 |
| CF200m | **-0.595** | **0.728** | -0.099 | **0.311** | WD200m | **-0.357** | **0.589** | 0.089 | 0.110 |
| CF500m | **-0.580** | **0.649** | -0.128 | **0.340** | WD500m | **-0.513** | **0.610** | 0.020 | 0.165 |
| CF1000m | **-0.561** | **0.562** | -0.149 | **0.346** | WD1000m | **-0.558** | **0.504** | 0.047 | 0.184 |
| CF2500m | **-0.386** | 0.225 | -0.040 | 0.174 | WD2500m | -0.294 | 0.119 | 0.137 | 0.119 |
| CF5000m | **-0.450** | **0.360** | 0.157 | -0.211 | WD5000m | **-0.560** | **0.456** | 0.227 | -0.227 |
| CFO50m | -0.074 | 0.156 | -0.036 | 0.231 | WDO50m | 0.125 | -0.290 | -0.017 | -0.039 |
| CFO100m | -0.258 | 0.244 | -0.089 | 0.240 | WDO100m | 0.153 | **-0.334** | -0.090 | -0.066 |
| CFO200m | **-0.379** | **0.387** | -0.085 | 0.258 | WDO200m | 0.144 | **-0.344** | -0.031 | -0.114 |
| CFO500m | **-0.541** | **0.530** | -0.134 | **0.347** | WDO500m | -0.181 | -0.033 | 0.005 | 0.019 |
| CFO1000m | **-0.572** | **0.500** | -0.137 | **0.361** | WDO1000m | **-0.425** | 0.246 | 0.061 | 0.061 |
| CFO2500m | **-0.420** | **0.360** | -0.079 | 0.197 | WDO2500m | -0.257 | 0.218 | 0.191 | -0.071 |
| CFO5000m | **-0.604** | **0.561** | 0.147 | -0.169 | WDO5000m | -0.293 | 0.223 | 0.252 | -0.192 |

## (E) Correlations between area and edge variables from 50m to 5000m scale for broad-leaved, coniferous, mixed and general wooded habitats.

### Broad-leaved area and edge variables

### (i) ELL98

| | BL50m | BL100m | BL200m | BL500m | BL1000m | BL2500m | BL5000m | BLO50m | BLO100m | BLO200m | BLO500m | BLO1000m | BLO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BL100m | ***0.961*** | | | | | | | | | | | | |
| BL200m | ***0.889*** | ***0.943*** | | | | | | | | | | | |
| BL500m | **0.695** | **0.736** | ***0.833*** | | | | | | | | | | |
| BL1000m | **0.559** | **0.611** | **0.711** | ***0.908*** | | | | | | | | | |
| BL2500m | 0.274 | 0.287 | 0.281 | 0.128 | 0.065 | | | | | | | | |
| BL5000m | 0.085 | 0.101 | 0.117 | 0.270 | 0.279 | 0.254 | | | | | | | |
| BLO50m | **0.357** | **0.352** | **0.363** | **0.375** | **0.403** | 0.109 | 0.124 | | | | | | |
| BLO100m | **0.703** | **0.685** | **0.642** | **0.500** | **0.421** | 0.264 | 0.103 | **0.738** | | | | | |
| BLO200m | **0.758** | **0.781** | **0.784** | **0.657** | **0.585** | **0.316** | 0.130 | **0.555** | ***0.832*** | | | | |
| BLO500m | **0.613** | **0.660** | **0.750** | ***0.842*** | **0.797** | 0.146 | 0.203 | **0.485** | **0.615** | **0.750** | | | |
| BLO1000m | **0.413** | **0.462** | **0.557** | **0.761** | ***0.853*** | 0.059 | **0.308** | **0.392** | **0.381** | **0.514** | ***0.828*** | | |
| BLO2500m | 0.242 | 0.288 | 0.297 | 0.117 | 0.059 | **0.778** | 0.146 | 0.128 | 0.234 | **0.305** | 0.231 | 0.204 | |
| BLO5000m | 0.162 | 0.210 | 0.266 | **0.458** | **0.565** | **0.332** | **0.771** | 0.213 | 0.191 | 0.280 | **0.466** | **0.667** | 0.286 |

## (ii) CSF99

| | BL50m | BL100m | BL200m | BL500m | BL1000m | BL2500m | BL5000m | BLO50m | BLO100m | BLO200m | BLO500m | BLO1000m | BLO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BL100m | ***0.964*** | | | | | | | | | | | | |
| BL200m | ***0.909*** | ***0.955*** | | | | | | | | | | | |
| BL500m | **0.789** | ***0.827*** | ***0.890*** | | | | | | | | | | |
| BL1000m | **0.651** | **0.695** | **0.757** | ***0.896*** | | | | | | | | | |
| BL2500m | **0.343** | **0.367** | **0.443** | **0.559** | **0.683** | | | | | | | | |
| BL5000m | 0.111 | 0.154 | 0.212 | 0.297 | **0.387** | **0.530** | | | | | | | |
| BLO50m | **0.340** | **0.313** | **0.305** | 0.296 | 0.203 | 0.180 | 0.263 | | | | | | |
| BLO100m | **0.612** | **0.597** | **0.551** | **0.497** | **0.381** | 0.235 | 0.265 | ***0.826*** | | | | | |
| BLO200m | **0.733** | **0.739** | **0.756** | **0.689** | **0.562** | **0.363** | 0.292 | **0.682** | ***0.869*** | | | | |
| BLO500m | **0.648** | **0.664** | **0.726** | ***0.828*** | **0.741** | **0.536** | **0.399** | **0.503** | **0.650** | ***0.820*** | | | |
| BLO1000m | **0.504** | **0.539** | **0.606** | **0.736** | ***0.820*** | **0.684** | **0.520** | **0.308** | **0.443** | **0.593** | ***0.840*** | | |
| BLO2500m | 0.272 | **0.306** | **0.368** | **0.458** | **0.575** | **0.771** | **0.668** | 0.235 | **0.311** | **0.382** | **0.573** | **0.785** | |
| BLO5000m | 0.192 | 0.226 | 0.268 | **0.334** | **0.428** | **0.478** | ***0.803*** | 0.251 | 0.290 | **0.335** | **0.494** | **0.674** | ***0.802*** |

## Mixed area and edge variables

### (i) ELL98

| | M50m | M100m | M200m | M500m | M1000m | M2500m | M5000m | MO50m | MO100m | MO200m | MO500m | MO1000m | MO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M100m | ***0.859*** | | | | | | | | | | | | |
| M200m | **0.663** | ***0.812*** | | | | | | | | | | | |
| M500m | **0.489** | **0.612** | ***0.817*** | | | | | | | | | | |
| M1000m | **0.364** | **0.447** | **0.591** | **0.786** | | | | | | | | | |
| M2500m | 0.161 | 0.194 | **0.339** | **0.537** | **0.591** | | | | | | | | |
| M5000m | 0.077 | 0.111 | 0.156 | **0.320** | 0.292 | **0.494** | | | | | | | |
| MO50m | **0.407** | **0.332** | 0.259 | 0.199 | 0.217 | 0.097 | -0.052 | | | | | | |
| MO100m | **0.528** | **0.656** | **0.516** | **0.403** | **0.353** | 0.242 | 0.040 | **0.535** | | | | | |
| MO200m | **0.414** | **0.522** | **0.697** | **0.570** | **0.443** | **0.365** | 0.092 | **0.338** | **0.668** | | | | |
| MO500m | 0.216 | **0.310** | **0.513** | **0.686** | **0.528** | **0.567** | **0.400** | 0.145 | **0.395** | **0.656** | | | |
| MO1000m | 0.046 | 0.076 | 0.161 | **0.321** | **0.529** | **0.500** | **0.537** | 0.114 | 0.227 | **0.356** | **0.670** | | |
| MO2500m | -0.003 | -0.026 | -0.025 | 0.161 | 0.278 | **0.582** | ***0.817*** | -0.034 | 0.101 | 0.084 | **0.417** | **0.683** | |
| MO5000m | 0.077 | 0.077 | 0.078 | 0.257 | 0.276 | **0.527** | ***0.936*** | -0.036 | 0.066 | 0.128 | **0.415** | **0.625** | ***0.851*** |

## (ii) CSF99

| | M50m | M100m | M200m | M500m | M1000m | M2500m | M5000m | MO50m | MO100m | MO200m | MO500m | MO1000m | MO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M100m | ***0.981*** | | | | | | | | | | | | |
| M200m | ***0.917*** | ***0.945*** | | | | | | | | | | | |
| M500m | **0.800** | ***0.831*** | ***0.910*** | | | | | | | | | | |
| M1000m | **0.667** | **0.699** | **0.782** | ***0.851*** | | | | | | | | | |
| M2500m | **0.313** | **0.339** | **0.393** | **0.417** | **0.539** | | | | | | | | |
| M5000m | 0.173 | 0.200 | 0.251 | 0.260 | 0.272 | **0.448** | | | | | | | |
| MO50m | **0.447** | **0.426** | **0.401** | **0.369** | **0.323** | 0.073 | 0.012 | | | | | | |
| MO100m | ***0.851*** | ***0.828*** | **0.754** | **0.651** | **0.540** | 0.171 | 0.039 | **0.669** | | | | | |
| MO200m | ***0.892*** | ***0.896*** | ***0.915*** | ***0.812*** | **0.690** | 0.280 | 0.133 | **0.565** | ***0.890*** | | | | |
| MO500m | ***0.810*** | ***0.818*** | ***0.875*** | ***0.947*** | **0.798** | **0.350** | 0.164 | **0.498** | **0.762** | ***0.887*** | | | |
| MO1000m | **0.638** | **0.660** | **0.733** | ***0.803*** | ***0.950*** | **0.529** | 0.248 | **0.382** | **0.570** | **0.702** | ***0.814*** | | |
| MO2500m | **0.331** | **0.348** | **0.406** | **0.433** | **0.548** | ***0.903*** | **0.482** | 0.116 | 0.221 | **0.321** | **0.394** | **0.565** | |
| MO5000m | 0.164 | 0.176 | 0.221 | 0.221 | 0.213 | **0.356** | ***0.855*** | 0.009 | 0.056 | 0.138 | 0.165 | 0.240 | **0.536** |

## Coniferous area and edge variables

### (i) ELL98

| | CF50m | CF100m | CF200m | CF500m | CF1000m | CF2500m | CF5000m | CFO50m | CFO100m | CFO200m | CFO500m | CFO1000m | CFO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CF100m | ***0.956*** | | | | | | | | | | | | |
| CF200m | ***0.908*** | ***0.963*** | | | | | | | | | | | |
| CF500m | **0.792** | ***0.848*** | ***0.920*** | | | | | | | | | | |
| CF1000m | **0.697** | **0.749** | ***0.822*** | ***0.931*** | | | | | | | | | |
| CF2500m | 0.232 | 0.258 | 0.276 | 0.253 | **0.404** | | | | | | | | |
| CF5000m | **0.401** | **0.424** | **0.414** | **0.421** | **0.510** | **0.519** | | | | | | | |
| CFO50m | 0.158 | 0.181 | 0.235 | 0.271 | 0.265 | 0.087 | 0.168 | | | | | | |
| CFO100m | 0.273 | **0.311** | **0.351** | **0.390** | **0.382** | 0.167 | 0.210 | **0.636** | | | | | |
| CFO200m | **0.495** | **0.545** | **0.584** | **0.600** | **0.602** | 0.261 | 0.291 | **0.464** | **0.774** | | | | |
| CFO500m | **0.651** | **0.709** | **0.768** | ***0.807*** | ***0.836*** | **0.390** | **0.433** | **0.326** | **0.534** | **0.797** | | | |
| CFO1000m | **0.611** | **0.668** | **0.743** | ***0.830*** | ***0.914*** | **0.473** | **0.507** | 0.264 | **0.444** | **0.670** | ***0.919*** | | |
| CFO2500m | **0.301** | **0.332** | **0.370** | **0.321** | **0.415** | ***0.896*** | **0.412** | 0.079 | 0.212 | 0.292 | **0.447** | **0.531** | |
| CFO5000m | **0.556** | **0.604** | **0.642** | **0.636** | **0.711** | **0.709** | **0.787** | 0.191 | **0.345** | **0.495** | **0.711** | **0.792** | **0.775** |

## (ii) CSF99

| | CF50m | CF100m | CF200m | CF500m | CF1000m | CF2500m | CF5000m | CFO50m | CFO100m | CFO200m | CFO500m | CFO1000m | CFO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CF100m | ***0.960*** | | | | | | | | | | | | |
| CF200m | ***0.875*** | ***0.920*** | | | | | | | | | | | |
| CF500m | **0.737** | **0.786** | ***0.856*** | | | | | | | | | | |
| CF1000m | **0.673** | **0.714** | **0.760** | ***0.869*** | | | | | | | | | |
| CF2500m | **0.391** | **0.409** | **0.440** | **0.490** | **0.596** | | | | | | | | |
| CF5000m | **-0.311** | **-0.347** | **-0.383** | **-0.374** | **-0.405** | -0.018 | | | | | | | |
| CFO50m | **0.387** | **0.377** | **0.342** | 0.248 | 0.206 | 0.169 | -0.061 | | | | | | |
| CFO100m | **0.728** | **0.738** | **0.666** | **0.552** | **0.505** | **0.343** | -0.187 | **0.594** | | | | | |
| CFO200m | ***0.825*** | ***0.856*** | ***0.928*** | **0.775** | **0.684** | **0.446** | **-0.312** | **0.445** | **0.779** | | | | |
| CFO500m | **0.734** | **0.769** | ***0.834*** | ***0.959*** | ***0.845*** | **0.532** | **-0.317** | **0.321** | **0.614** | ***0.810*** | | | |
| CFO1000m | **0.665** | **0.699** | **0.742** | ***0.847*** | ***0.970*** | **0.644** | **-0.363** | 0.226 | **0.519** | **0.690** | ***0.855*** | | |
| CFO2500m | **0.391** | **0.385** | **0.399** | **0.445** | **0.541** | ***0.821*** | -0.044 | 0.211 | **0.412** | **0.469** | **0.539** | **0.652** | |
| CFO5000m | -0.245 | -0.267 | **-0.301** | -0.284 | -0.279 | 0.077 | ***0.863*** | -0.050 | -0.143 | -0.237 | -0.228 | -0.227 | 0.141 |

## General woodland area and edge variables

### (i) ELL98

| | WD50m | WD100m | WD200m | WD500m | WD1000m | WD2500m | WD5000m | WDO50m | WDO100m | WDO200m | WDO500m | WDO1000m | WDO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| WD100m | **0.614** | | | | | | | | | | | | |
| WD200m | **0.388** | ***0.812*** | | | | | | | | | | | |
| WD500m | 0.175 | **0.481** | **0.721** | | | | | | | | | | |
| WD1000m | 0.007 | 0.228 | **0.439** | ***0.845*** | | | | | | | | | |
| WD2500m | -0.088 | -0.015 | 0.065 | **0.398** | **0.602** | | | | | | | | |
| WD5000m | -0.023 | 0.112 | 0.258 | **0.540** | **0.733** | **0.562** | | | | | | | |
| WDO50m | ***-0.829*** | **-0.726** | **-0.452** | -0.236 | -0.073 | 0.048 | -0.035 | | | | | | |
| WDO100m | **-0.539** | ***-0.816*** | **-0.583** | **-0.359** | -0.153 | 0.048 | -0.148 | **0.692** | | | | | |
| WDO200m | **-0.373** | **-0.600** | **-0.563** | **-0.375** | -0.128 | 0.127 | -0.150 | **0.422** | **0.776** | | | | |
| WDO500m | -0.157 | -0.296 | -0.227 | -0.053 | 0.221 | **0.390** | 0.147 | 0.195 | **0.346** | **0.529** | | | |
| WDO1000m | -0.060 | -0.055 | 0.081 | **0.413** | **0.653** | **0.562** | **0.515** | 0.078 | 0.042 | 0.130 | **0.677** | | |
| WDO2500m | 0.009 | 0.015 | 0.042 | 0.233 | **0.311** | **0.616** | 0.240 | -0.037 | -0.018 | 0.069 | **0.340** | **0.567** | |
| WDO5000m | -0.002 | 0.075 | 0.098 | **0.316** | **0.419** | **0.736** | **0.414** | -0.041 | -0.092 | 0.015 | **0.372** | **0.639** | ***0.852*** |

## (ii) CSF99

| | WD50m | WD100m | WD200m | WD500m | WD1000m | WD2500m | WD5000m | WDO50m | WDO100m | WDO200m | WDO500m | WDO1000m | WDO2500m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| WD100m | ***0.847*** | | | | | | | | | | | | |
| WD200m | **0.727** | ***0.923*** | | | | | | | | | | | |
| WD500m | **0.497** | **0.673** | ***0.812*** | | | | | | | | | | |
| WD1000m | **0.325** | **0.484** | **0.607** | ***0.851*** | | | | | | | | | |
| WD2500m | 0.088 | 0.200 | 0.264 | **0.427** | **0.531** | | | | | | | | |
| WD5000m | -0.146 | -0.126 | -0.078 | 0.023 | 0.123 | **0.475** | | | | | | | |
| WDO50m | ***-0.904*** | ***-0.882*** | **-0.759** | **-0.520** | **-0.355** | -0.088 | 0.167 | | | | | | |
| WDO100m | **-0.678** | ***-0.866*** | ***-0.863*** | **-0.687** | **-0.491** | -0.201 | 0.097 | **0.754** | | | | | |
| WDO200m | **-0.414** | **-0.560** | **-0.563** | **-0.518** | **-0.430** | -0.131 | 0.146 | **0.474** | **0.712** | | | | |
| WDO500m | -0.231 | -0.256 | -0.163 | 0.073 | 0.064 | 0.212 | **0.418** | 0.271 | **0.313** | **0.534** | | | |
| WDO1000m | -0.120 | -0.064 | 0.024 | 0.274 | **0.386** | **0.398** | **0.492** | 0.127 | 0.121 | 0.214 | **0.750** | | |
| WDO2500m | -0.089 | -0.032 | 0.035 | 0.206 | 0.280 | **0.589** | **0.662** | 0.099 | 0.060 | 0.152 | **0.583** | **0.760** | |
| WDO5000m | -0.163 | -0.075 | -0.010 | 0.142 | 0.239 | **0.399** | **0.706** | 0.163 | 0.095 | 0.141 | **0.517** | **0.699** | ***0.820*** |