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Density and Distribution of Passerines in a Managed Coniferous Forest: the Influence of Landscape Structure.

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This thesis is presented in candidature for the degree of
Doctor of Philosophy

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Abstract

This study utilises breeding bird data collected by Patterson *et al.* 1995 (1991 and 1992) and C.A.McSorley (1998 and 1999), in Kielder Forest, collected using the point count survey methodology. Survey sites in 1998 and 1999 were selected utilising a stratified random technique.

Repeated counts of birds generate seasonally and annually correlated bird densities, however there are some significant differences in density from early to late spring. Thus, it is justifiable to use the maximum density over early and late spring for further analyses. Annual correlations are discussed in terms of resource availability. Small-scale density patterns are affected by the interactions between patch tree age, edge comparison and the distance from the patch boundary. Patch boundary avoidance or preference is observed for many species. Low densities are generally found in hard edges. These results are discussed in the context of the trade-off between higher food availability and higher predation risk at patch edges.

The occurrence and density of passerines in 1999 are modelled using patch variables generated using a geographical information system (GIS) and a spatial quantification program, FRAGSTATS. The power of associations are mediocre to good (r^2 values are generally approx. 0.2). The performances of the models using 1998 data for validation are mixed. However, some of these models could be used as tools for predicting the effects of forest restructuring on the passerines of Kielder. The factors determining why some species are widespread and locally common, and vice versa are investigated. The results show that resource availability affects the interspecific abundance-distribution relationship. Willow warblers aggregate more readily than residents do, perhaps as a result of utilisation of heterospecific and conspecific cues to quantify habitat 'quality'. The results from all chapters are put into a national ornithological context and discussed in terms of forest management. Further work is also proposed in the final chapter.

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No part of this thesis has previously been submitted for a degree in this or any other university. The work described is my own except where duly acknowledged.

Claire McSorley

Claire Alice McSorley 2001

This thesis is dedicated to the memory of

Prof. Peter R. Evans

(1937-2001).

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1 General introduction

1.1 Landscape ecology

The UK has very few unaltered wildernesses left with the majority of its area being characterised by landuse practices such as intensive agriculture and commercial forestry. This has resulted in a national landscape that is fragmented and compartmentalised into clearly delineated patches with abrupt edges. It is becoming increasing obvious that in order to manage the mosaic landscape of Britain in a biologically realistic way it is imperative to investigate the interactive parts of the mosaic. This would include consideration of adjacent habitats to the area under investigation.

There are four mechanisms creating landscape mosaics: 1. substrate heterogeneity (e.g. soil types), 2. natural disturbance (e.g. fire, wind), 3. topography (e.g. altitude) and 4. human activity (e.g. planting of exotic forestry, road building, creation of fields). The UK is characterised by all of these but particularly the latter. The UK landscape is not homogeneous, but is composed of different areas which can range from sharply delineated patches (e.g. fields in an agricultural landscape, clearfells in a forested landscape, patches of burnt heather on a moorland) to gradual transitions from one habitat type to another (e.g. scrubland to moorland) (Forman 1995). The observed heterogeneity of a landscape depends on the scale at which it is measured. The pattern of landscape elements of the UK landscape (10,000 km^2) is different to the pattern observed at a smaller area (10 km^2): viewed from the air, the landscape of the UK is perceived as a mosaic of fields, forests, urban areas and moorland. Closer to the ground a finer scale mosaic of patches can be seen such as patches of burnt heather and birch scrub in moorland. Thus heterogeneity occurs at all spatial scales.

Landscape Ecology emerged in the 1960's as an amalgamation of human geography and landscape management (Wiens *et al.* 1993). It is an integrative discipline including interactions between landscape structure and wildlife movements, abundances and distributions. Its application has built on the paradigms of Island Biogeography Theory, and the SLOSS ('single large' or 'several small') reserve design debate (Simberloff

1988; Angelstam 1992). Landscape Ecology has received international attention since the early 1980's (Wiens *et al.* 1993), and has benefited from the increase in computational quantification of landscape mosaics made possible by the development of geographical information systems (GIS) and spatial statistics.

Landscape Ecology can be investigated at many spatial scales from small grain distribution of a species in a patch (tens of metres) (Hansson 1983, Wiens *et al.* 1997), to the large grain distributions of species on a national scale (hundreds of kilometres) (Osborne & Tigar 1992, Brown *et al.* 1995, Collingham *et al.* 2000, Gregory & Gaston 2000). Landscape Ecology deals with three main themes; landscape physiognomy, composition and connectivity (Taylor *et al.* 1993). The former two give an indication of the physical characteristics of the resource patches and the latter an indication of how the landscape affects wildlife movements amongst patches. This study will investigate the relationships between avian abundance and distribution on several spatial scales and will determine the influence of landscape variables on these relationships. It will concentrate on the breeding passerine community of a highly managed British coniferous forest, Kielder Forest, which is managed using a rotational clearcutting regime that generates a highly patchy landscape. In the present study forest patches refer to all wooded areas and clearfell areas of the forest but do not include the small proportion of agricultural and unplanted land. The present study concentrates on the effect of commercial forest management on songbird densities and distributions, and so bird surveys were not performed in the latter areas because they are not involved in commercial forestry. In addition, inclusion of these rare areas of the forest would have resulted in higher variable to case ratios in multivariate analyses, which, in studies with limited sample sizes, should be avoided.

1.2 Afforestation

The percentage forested area of Britain is 11% (Mason & Quine 1995); of this area, 90% is managed for timber production (Donald *et al.* 1998). Coniferous plantations make up about 70% of this managed area (Donald *et al.* 1998). Many of these plantations occur in agriculturally unproductive uplands (Mason & Quine 1995). Previously deforested areas were reforested by mixed coniferous forest in the early part of the 20th century in the initial afforestation initiatives (Mason & Quine 1995). Considering the ever-changing nature of the British landscape it is difficult to set a base line for what is the 'best' scenario for landuse in Britain, and what percentage 'should' be forested (Petty *et al.* 1995).

The detrimental effects of afforestation by commercial coniferous forestry on moorland wildlife species have been well-documented (Lavers & Haines-Young 1997; Avery & Leslie 1990). However, these types of forest have been beneficial for maintaining populations of threatened species such as red squirrel *Sciurus vulgaris* (Lürz *et al.* 1995), common crossbill, *Loxia curvirostra*, siskin, *Carduelis spinus,* redpoll, *Carduelis flammea* (Petty *et al.* 1995), and goshawk, *Accipiter gentilis* (Newton 1986).

The degradation of continuous natural forests into a fragmented landscape and creation of highly patchy commercial forests has resulted in a mosaic landscape dominated by edges. This has generated a series of biotic and abiotic phenomena termed 'edge effects'. These include both positive edge effects, such as higher wildlife species diversity (Angelstam 1992, Andrén 1995) due to greater vegetational complexity at the edge, and also negative edge effects, such as the loss of interior specialists and of species with large home ranges (Angelstam 1992). The increase in edge habitat has also led to a corresponding increase in predation rates, particularly nest predation at hard edges (edges formed between two dissimilar habitats, e.g. forest and farmland) (Andrén 1995; Angelstam 1992). The reasons for this may be complex, but almost certainly include: 1. higher prey densities at the edges (due to high vegetational complexity); 2. use of edges for predator movement ('travelling lines'); and 3. in a less preferred habitat, the activity of a predator will be concentrated at the edge (Andrén 1995).

1.3 Why study birds?

Birds have often been used as bioindicators of climate change (e.g. decline of the capercaillie, *Tetrao urogallus* Moss *et al.* 2001), landuse change (e.g. declines of agricultural passerines, Donald *et al.* 2001) and habitat fragmentation (e.g. forest fragmentation, Miller & Cale 2000). Their usefulness as bioindicators is attributable to a number of factors, including their high species diversity, broad range of niche requirements, extensive volunteer network (Tucker *et al.* 1997), high visibility (Tucker *et al.* 1997) and resident/migrant status. They have been used as gauges of a landscape's 'ecological worth' (Tucker *et al.* 1997). Indeed the Government has included bird species as 'quality of life indicators' in its recent white paper (DETR 1998)

1.4 Bird distributions

Ideal distribution theory (Ideal Free and Ideal Despotic Distribution termed IFD and IDD respectively) has helped us to understand the distribution of individuals/species in a landscape consisting of patches of varying quality (Fretwell & Lucas 1970, Tyler & Hargrove 1997). Bird habitat preferences can lead to distribution patterns across a qualitatively heterogeneous landscape (Milinski 1979, Sutherland 1996). These theories deal with the premise that an individual chooses the habitat that maximises its fitness (i.e. the 'best' quality habitat); this is the 'ideal' part of the theory (Weber 1998). The 'free' or 'despotic' part determines the costs associated with moving into that habitat, with 'free' implying no costs and 'despotic' implying a cost according to the individual's position in the dominance hierarchy.

Weber (1998) wrote a critique on the application of ideal distribution theories and proposed that caution should be exerted in assuming that the highest quality habitat will contain greater numbers of competitors. Hobbs & Hanley (1990) state that density does not necessarily correlate with habitat quality. As with Van Horne (1983), Hobbs & Hanley (1990) indicate that caution should be exerted in assuming that 'valuable habitats' will have the highest number of competitors in them, as interactions such as disputes between individuals with differing dominance status may exclude some individuals. However, Van Horne (1983) admits that in years with low densities, then density can be correlated with habitat quality, particularly in passerines. Thus, for species conforming to the ideal despotic distribution and occupying territories within habitats where the carrying capacity is not reached, competitive exclusion will not occur. This allows the highest numbers of birds to be contained within the best quality habitats. This hypothesis is discussed in the present study in the context of using bird densities as a proxy for habitat quality.

Patches containing large amounts of resources will become depleted more quickly and the individuals may have to move on to lower quality habitats. This is not so much of an issue for territorial breeding birds, which remain faithful to those territories during the breeding season and space themselves according to the quality of the habitat. Thus territories are generally smaller in higher quality habitats due to the trade-off between costs (defensibility) and benefits (maximum amount of resources) and hence densities are greater in high quality habitats (Krebs & Davies 1993). However, for nomadic colonial species such as crossbill, redpoll and siskin, the quality of the habitat would not remain static because of resource depletion, and thus, the distribution of these species may be temporally variable.

In landscapes exhibiting patchiness on a small spatial grain (tens of metres) it is expected that patch juxtaposition (adjacency) will affect how an individual bird perceives an area's quality, with an area ranging from one to many adjacent patches. Therefore a bird's territory may encompass several forest patches. Thus individual decisions on patch quality will affect small and large grain distributions and abundances over the whole landscape.

1.5 Thesis layout

The first data chapter (Chapter 3) will investigate the point count method. This is one of three internationally recognised ways of surveying bird populations (Bibby *et al.* 1992). This chapter will explore whether methodological and temporal differences affect the results obtained from this monitoring method. Chapter 3 will include an investigation into how well the data from the previous season or year correlates with the data from the current season or year. The effect of resource availability on the densities of birds observed will be discussed. Chapter 3 will set the basis for the following chapters, as it will demonstrate the usefulness and validity of repeat point count data.

The patches of forests managed by rotational clearcutting are internally relatively homogenous (trees are of the same age and species) with clearly delineated boundaries. Small-scale (tens of metres) factors affecting bird distribution across an edge will be identified in Chapter 4. Edges are often associated with higher resource availability, however edges formed between two dissimilar patches have been associated with higher predation. The relative importance of edge type, patch composition and distance from the boundary to different bird species will be highlighted. The results in Chapter 4 will be discussed in terms of the trade-off between predation risk and resource availability.

The link between a species abundance or occurrence and landscape composition and pattern has been studied extensively using GIS technology (Roseberry & Sudkamp 1998; Dettmers & Bart 1999; Edenius & Elmberg 1996). However, there have been very few studies to date determining the role of British forests' spatial structure and composition on songbird communities (McCollin 1993). In Chapter 5 multivariate statistics (logistic regression and Poisson errors generalised linear modelling techniques) will be utilised to generate management strategies incorporating GIS technology. These models will be based on field data collected in 1999, and validated with data from 1998. The effect of patch shape, area, edge contrast and tree age on songbird occurrences and densities will be discussed. Management priorities will be proposed, particularly in terms of avian conservation and the maintenance of avian populations.

Some species are common and widespread across a landscape and some are scarce and rare. This is generally termed the inter-specific abundance-distribution relationship. This commonplace phenomenon is the subject of Chapter 6. The structure of the relationship and the role of resource availability and heterospecific aggregation will be discussed.

The final chapter (Chapter 7) will provide a synopsis of the main findings of this study. It will set the results in a wider context and discuss management applications for this type of study. Suggestions for further work will also be presented.

1.6 Objectives and hypotheses

This thesis has four main objectives:

A. To investigate the relationship between seasonally and annually repeated counts and assess the validity of the repeated point count method.

B. To examine whether interactions between patch tree age, edge comparison and the distance from the patch boundary affect the small-scale (tens of metres) distribution of a species within a patch.

C. To model the occurrence and density of bird species in the patches of Kielder Forest using landscape and patch variables, and to determine the performance of, and thus validity of generating, predictive models.

D. To investigate the factors determining why some species are widespread and locally common, whereas other species are rare and locally scarce.

Within these objectives the following hypotheses will be tested:

1. The use of the repeat point count method is necessitated by seasonal differences in bird density.
2. Habitat types in Kielder are sufficiently dissimilar to minimise stochastic variations in density and thus, produce significant annual correlations of densities.
3. The highest densities of birds are found in their preferred habitats as specified by published literature.
4. Species preferring habitats with low amounts of cover will prefer to displace their nests away from the boundary of a patch.
5. Those edges formed between two highly dissimilar patches will be avoided by species with the highest predation risk.
6. Birds found primarily at the centre of patches will avoid high contrast edges, formed by the adjacency of dissimilar patches.
7. Habitat generalists will be found in heterogeneous landscapes, and habitat specialists will prefer more homogeneous landscapes.
8. Species preferring the edge will prefer those patches with the maximum amount of edge habitats such as small or highly complex patches and vice versa.
9. Widespread birds are common in all patches.
10. The interspecific relationship between distribution and density of species will be affected by resource availability and life history strategy.

2 Methodology

2.1 Study site

Kielder Forest covers an area of nearly 600 km^2 (60, 000 ha) spanning an upland region in Northumberland and Cumbria, U.K., (55°15'N, 2°35'W) making it the largest state owned forest in Britain, Figure 2.1 (Wallace & Good 1995, McIntosh 1995). The forest varies in elevation from approximately 200 - 400 metres above sea level and is characterised by surface water gley and peat gley soils (McIntosh 1995). In 1998 the annual temperature varied from a mean maximum of 11.8 °C and a mean minimum of 4.4 °C, with mean monthly precipitation of 123 mm (data taken from British Atmospheric Data Centre [BADC] records at Kielder Castle meteorological station in 1998).

Plantation of coniferous trees in the Kielder area started in 1926; initially the objective was to provide a 'strategic reserve' for future wars and also to create a source of employment for the region (McIntosh 1995). However, in later years the objectives were broadened to include 1. timber production, 2. enhancement of biodiversity and 3. outdoor sports and tourism, especially with the creation of Kielder Water in 1981-82, a reservoir covering 1000 ha in the centre of the forest (Cosgrove 1995, Mason & Quine 1995, McIntosh 1995).

The fast-growing, high yield, non-native species, Sitka spruce *Picea sitchensis*, covers 72% of the forest's area making it the predominant species, with the rest of the forest consisting of mainly Norway spruce *Picea abies*, Lodgepole pine *Pinus contorta*, Scots pine *Pinus sylvestris*, Japanese larch *Larix kaempferi*, Douglas fir *Pseudotsuga menziesii*, western hemlock *Tsuga heterophylla* and various broadleaved species (McIntosh 1995). For botanical names, Flora Europaea (Tutin *et al.* 1964) will be followed. Planting and clearcutting (felling by complete removal of all mature trees leaving only brash [the discarded small branches], Figure 2.2) has produced a mosaic of sub-compartments (termed patches here). These patches are internally generally uniform in age and species (Figure 2.3), although there are a limited number of mixed patches.

2.2 Kielder Forest Geographical Information System

A Geographical Information System (GIS) is an automated system including software and hardware that integrates spatial and attribute data in a digital form. Such a system has the capacity for complex spatial analyses, and also enables the investigator to manipulate and display the data. C.J.Thomas (Petty *et al.* 2000) created the Kielder Forest GIS utilising Forestry Commission digital stock maps (1:10,000 scale). All patch boundaries were inputted to an ArcInfo (version 7.0) vector based GIS. The process took 2 years and was completed in October 1997. C.A.McSorley added tree planting year and species composition of each patch using data from the Forestry Commission database. Programs written in arc macro language (AML) were used to manipulate the attribute data in the GIS; with over 10,000 polygons, automation of commands made use and manipulation of the GIS data more efficient.

10,669 patches were digitised into the GIS; of these only 7,771 contained planted trees, the remainder being areas of unplanted land (such as car parks and unsuitable land) or agricultural land. Of these 7,771 patches, 5,428 were Sitka spruce or clearfell, with broad-leaved trees, riparian areas, Scots pine, Lodge-pole pine, Japanese larch, Douglas fir, western hemlock, and Norway spruce making up the remaining patches.

Spatial quantification of the forest using software within the GIS (such as FRAGSTATS – section 2.4), makes it possible to generate habitat variables that can be used in statistical modelling of bird field data. Ultimately, these bird/habitat models can be represented visually, using the GIS to create maps of predicted densities and distributions.

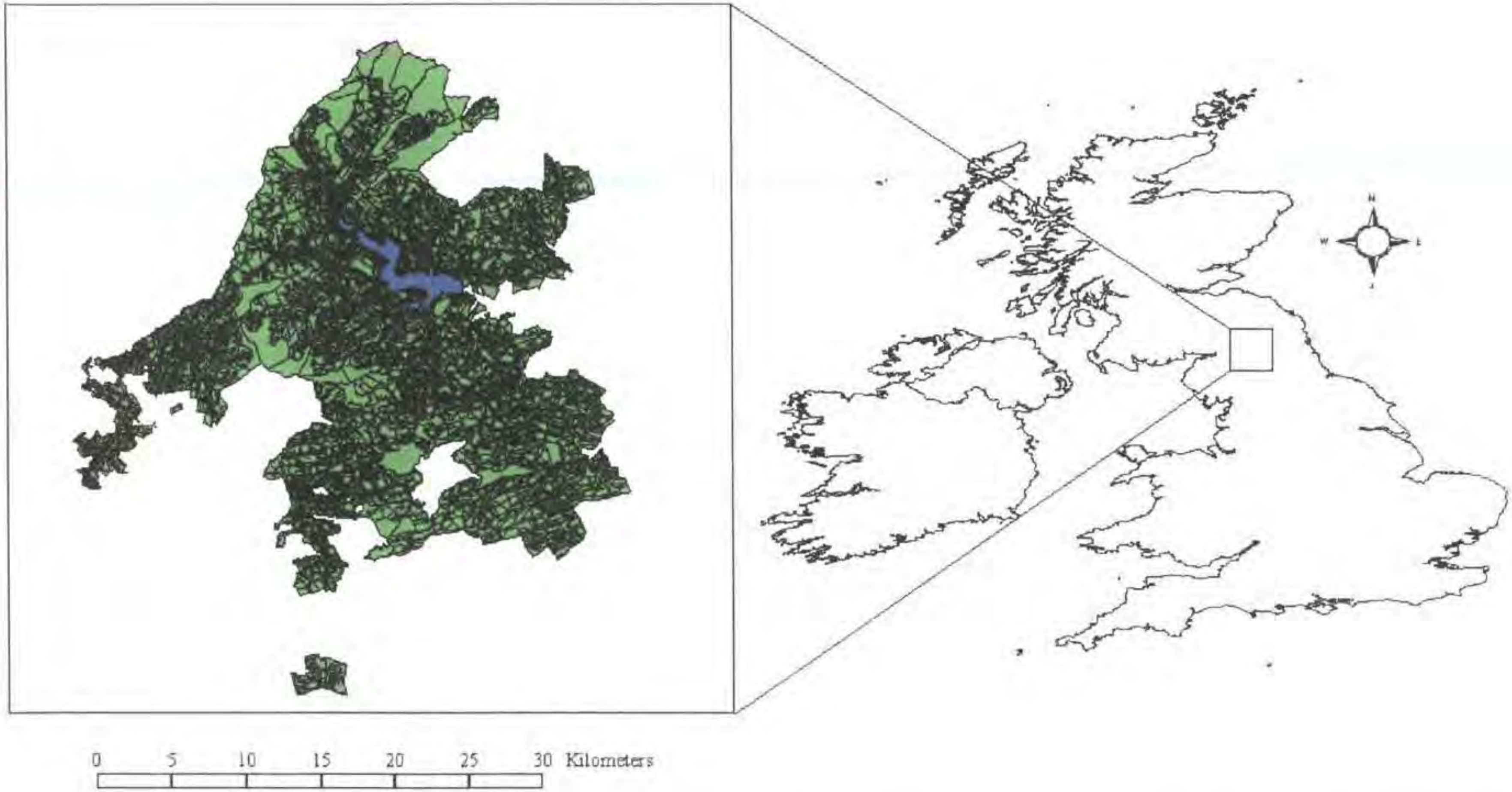


Figure 2.1: Map of Great Britain showing location of Kielder Forest (right map) with smaller scale map (left map) of Kielder Forest sub-compartments (patches). Kielder Water is shown in blue.

Figure 2.2: A recent clearfell showing brash and uniform lines of planting.

Figure 2.3: Aerial view of a section of Kielder Forest showing mosaic structure of different aged patches.

2.3 Bird surveys

Bird surveys were restricted to patches containing Sitka spruce (*Picea sitchensis*). Sitka is the most economically viable species in the forest and is by far the most prevalent species of tree planted. Time did not permit a study investigating all the permutations of possible interactions among patches containing differing tree species. Patches were chosen according to a stratified random design utilising the Kielder GIS. All successional Sitka habitats were surveyed ranging from clearfell to mature forest patches. Patches were divided into three tree age classes; young (clearfell to 5 years old), pre-thicket (6-15 years old), and mature trees (>15 years old) (Figure 2.4). These are termed age categories throughout this thesis. Nomenclature is according to agreed terms by the Forestry Commission and University of Durham. The edge and centre of the patch were surveyed separately because bird abundance is generally higher at the edge of managed coniferous blocks than at the centre (Angelstam 1992; Hansson 1994, Patterson *et al.* 1995).

Of the three most commonly used methods of bird surveying, territory mapping, transect and point counts, the latter was the most apt for this type of study (Bibby *et al.* 1992). Although not as accurate as the territory mapping method, the point count method allows a larger number of patches to be surveyed. The transect method, where the observer walks along a predetermined line at a constant speed, is similar to the point count method in that it also allows a large quantity of data to be collected. However, in dense vegetation or rough terrain, it is difficult, and indeed occasionally impossible, to maintain a constant walking speed, and so transects were not appropriate for forest surveying.

All edge counts were performed adjacent to a Sitka patch of a different age category to the patch under investigation. If a patch was adjacent to two Sitka patches, each of different age categories to the patch in question, the different types of edges were surveyed separately. In Chapter 4 it is assumed that these differing edge counts from the same patch were independent. On a small scale, the structure of different types of edges within the same patch was apparent. However, I was aware of the possibility of spatial

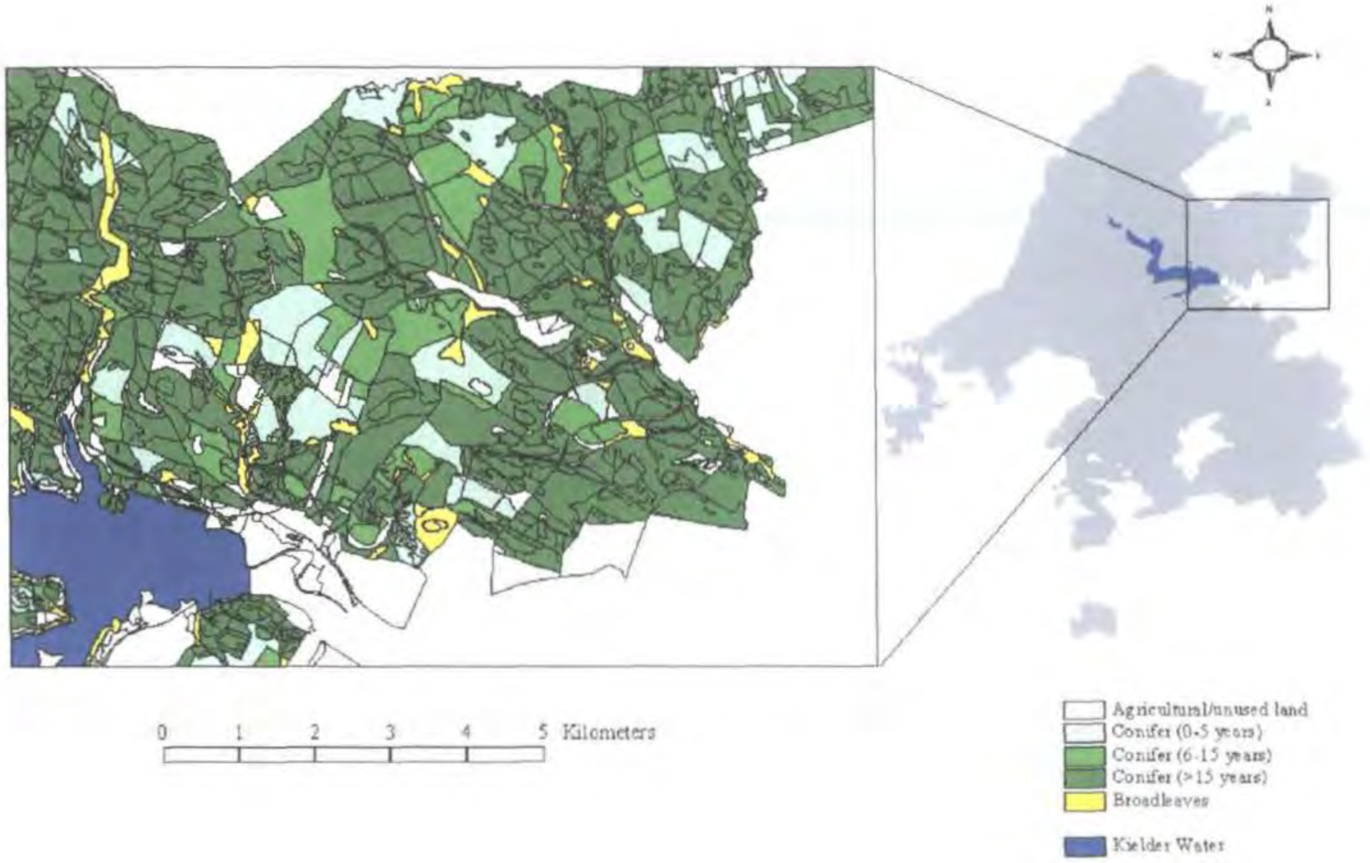


Figure 2.4 : Section of Kielder Forest showing age and species structure at medium resolution (approx 1 cm to the kilometre). Kielder Forest is shown as an inset in grey, with Kielder Water shown in blue.

autocorrelation as a result of adjacency of edges. Despite this, the different edges of a patch were observed to be suitably dissimilar so as to warrant separate analyses. These data were used in Chapter 3 to investigate seasonal and annual differences and in Chapter 4 to investigate how patch adjacency, patch age, and distance from the boundary affect bird densities. However, in the subsequent chapters, as the spatial quantification occurs at the patch level, only one set of data were used for analysis. For these latter chapters the edges surveyed using the highest number of point counts were used for analyses (termed unique sample sites). Therefore the sample sizes for Chapter 3 and 4, and Chapters 5 and 6 differed (Table 2.1).

The fixed radius (60 metres), point count method was used to count bird species. The first five minutes of the count were spent allowing the birds to settle down after disturbance caused by the observer (Bibby *et al.* 1992). The next five minutes were spent counting birds within 30 metres and 60 metres using song and call only. Singing birds were counted as two birds (a male and a female in a territory), and a calling bird as only one. A begging female was also counted as two birds, although this type of call was rarely heard. This methodology is consistent with the methodology used by Patterson *et al.* (1995). Training in song/call identification and distance estimation of all the species was carried out in March 1998. Thus, it was possible to determine the position of and distance to a vocalising bird. Detectability of species using sight observations would have been higher in open sites than in closed canopy sites (Bibby *et al.* 1992). The point count method used here was not standard (as outlined by Bibby *et al.* 1992), with birds detected by sound only. Bibby *et al.* (1992) state that in forested areas more birds are detected using aural cues than visual cues.

Detectability of birds, particularly in forested habitats when using visual cues, decreases with distance from the observer (Buckland *et al.* 1993). In their analogous study on passerines of Kielder Forest, Patterson *et al.* (1995) showed that the estimated density of birds calculated using the detectability functions in DISTANCE software (Buckland *et al.* 1993), was highly correlated with the number of birds per hectare. Therefore, detectability functions were not employed in Patterson *et al.'s* (1995) study. Despite using two distance bands within each point count, detectability functions also were not employed in the present study. Using a tape measure I trained myself in estimating distance to a singing/calling bird in 1997 and 1998. This was performed for many bird species including crossbill, chaffinch, coal tit, dunnock, goldcrest, meadow pipit, robin, redpoll, siskin, wren and willow warbler (for Latin names see Table 2.2). This minimised the need for utilisation of detectability functions.

Surveying was not carried out on days with high winds, heavy rain or fog due to problems of accurate detection and lower activity of the birds (Bibby *et al.* 1992, Cosgrove 1995). Consistent with two previous studies on passerines of Kielder Forest (Patterson *et al.* 1995, Cosgrove 1995) counts were carried out throughout the whole day, although avoiding the dawn chorus, evening chorus and decrease in singing activity during the middle of the day (cf. Patterson *et al.* 1995, Cosgrove 1995). Limiting surveying to dawn and dusk, when singing activity is highest, means that surveying cannot take place during the day when activity is much lower. Although detectability is lower during the day, the time available for surveying is much longer, thereby increasing the number of potential surveyed areas.

Point counts were placed in a grid pattern in the patch, with half point counts aligned across the patch boundary and centre counts 150 metres into the patch, also aligned parallel to the boundary (Figure 2.5). Half point counts cover half of the area of a full point count. This introduces a certain amount of bias, with detection of a species in half point counts being lower because of the smaller area (Paterson *et al.* 1995). This is analogous to the differences between a large sample size (whole point counts) and a small sample size (half point counts). The smaller sample will be biased by chance occurrence of a few birds, introducing a larger potential for chance variability. Despite this, the half point count method was used by the previous two studies (Patterson *et al.* 1995, Cosgrove 1995), and thus, was repeated here.

A compass and 1:10,000 Forestry Commission stock maps were used to determine my position in the forest and distances were measured using a standard pace, which was measured prior to fieldwork. Between one and six full and half point counts were completed per patch. Not only were the point counts divided into two circles (30 metres and 60 metres), they were also divided into sectors of 30 metres parallel to the boundary (Figure 2.5). This was to enable analysis of the change in density of a bird species from the edge to the centre of a patch.

Year	Survey dates	Position of point counts	All survey sites		Unique survey sites	
			Number of patches	Number of point counts	Number of patches	Number of point counts
1998	13th April - 11th May	Centre	53	124	43	109
		Edge	100	272	77	226
	12th May - 15th June	Centre	53	124	43	109
		Edge	100	272	77	226
	TOTAL	**CENTRE**	**106**	**248**	**86**	**218**
		EDGE	**200**	**544**	**154**	**452**
1999	11th April -13th May	Centre	77	146	71	137
		Edge	160	382	133	332
	14th May - 14th June	Centre	77	146	71	137
		Edge	160	382	133	332
	TOTAL	**CENTRE**	**154**	**292**	**142**	**274**
		EDGE	**320**	**764**	**266**	**664**

Table 2.1: Itinerary of fieldwork undertaken in 1998 and 1999.

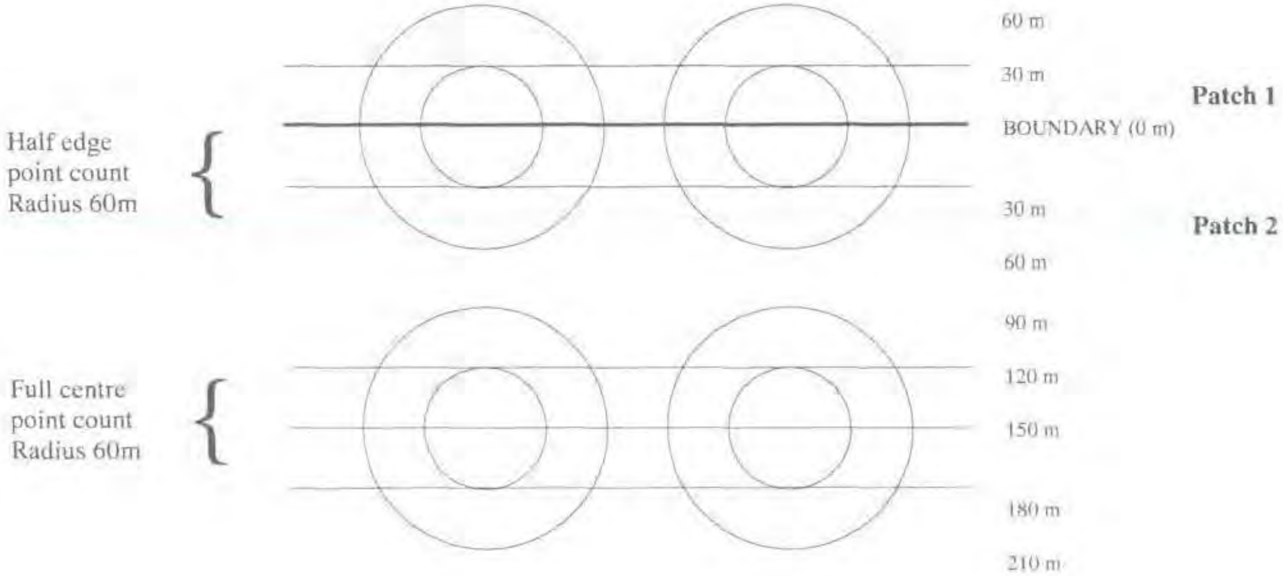


Figure 2.5: Diagram of edge (near the boundary) and centre (90-210 metres into the patch) point counts, showing the zonation pattern and distance from the boundary in question.

Occasionally the patch was not large enough to encompass a centre count, being less than 300 m at the widest part (a centre count, which has a diameter of 120 m, must be placed at least 150 m away from any edge). Under these circumstances, only edge counts were performed. Birds flying *en route* to other areas were not counted; however, species that fly and sing simultaneously such as swallows and meadow pipits were included. Table 2.2 shows a full species list of birds (with Latin names) detected in 1999.

As forest workers may disturb birds, surveying did not occur along major tracks or roads, contrary to Edenius and Elmberg (1996). Table 2.1 gives an itinerary of the sites surveyed with sites being surveyed twice in a year (early and late spring). Most sites surveyed in 1998 were resurveyed in 1999, with addition sites added in 1999. Occasionally in 1999 it was impossible to resurvey 1998 patches as a result of forest operations such as clearcutting.

Maximum density (individuals per hectare) of a species detected (per point count) over the two time periods in a patch was used for statistical analysis in Chapters 4-6, following Bibby *et al.* (1985) and Elmberg and Edenius (1999), and not mean density as used by Norton *et al.* (2000). Poor weather conditions, disturbance, predator threat, and timing of peak of territoriality can affect the density of birds detected, thus the highest value was thought to be the best representation of the actual density in a patch.

ID-Code	*Common name*	*Latin name*
BB	blackbird	*Turdus merula*
BT	blue tit	*Parus caeruleus*
BZ	buzzard	*Buteo buteo*
CB	crossbill	*Loxia curvirostra*
CF	chaffinch	*Fringilla coelebs*
CR	crow	*Corvus corone*
CT	coal tit	*Parus ater*
DN	dunnock	*Prunella modularis*
GC	goldcrest	*Regulus regulus*
GS	greater spotted woodpecker	*Dendrocopus major*
GW	grasshopper warbler	*Locustella naevia*
LN	linnet	*Carduelis cannabina*
MA	magpie	*Pica pica*
MP	meadow pipit	*Anthus pratensis*
MT	mistle thrush	*Turdus viscivorus*
PW	pied wagtail	*Motacilla alba*
RO	robin	*Erithacus rubecula*
RP	redpoll	*Carduelis flammea*
SK	siskin	*Carduelis spinus*
SL	skylark	*Alauda arvensis*
ST	song thrush	*Turdus philomelos*
SW	swallow	*Hirundo rustica*
TP	tree pipit	*Anthus trivialis*
WC	whinchat	*Saxicola rubetra*
WP	woodpigeon	*Columba palumbus*
WR	wren	*Troglodytes troglodytes*
WW	willow warbler	*Phylloscopus trochilus*

Table 2.2: Species list of birds detected in 1999 showing identifying code, common and Latin names.

2.4 Spatial quantification: FRAGSTATS

FRAGSTATS is an arc macro language (AML) based, spatial pattern analysis software package that quantifies patch and landscape variables. Initially FRAGSTATS Version 2.0 (McGarigal & Marks 1995) was used, although latterly an evaluation copy of FRAGSTATS*ARC Version 3.0.1 (1998) became available for two months from June 2000 (http://www.innovativegis.com/products/fragstatsarc/index.html). This version had the advantage over the former version in that it was fully integrated into ArcInfo (version 7.0). Run-time was a matter of hours, whereas the previous version had taken weeks to complete the same task, even using high capacity Unix workstations and servers.

The use of FRAGSTATS has increased recently particularly in wildlife management studies (Roseberry & Sudkamp 1998, Penhollow & Stauffer 2000). Its wide range of metrics and facilities allows the user to alter inputs, which means that it is possible to output variables that are tailored to the study. FRAGSTATS*ARC outputs many different patch, class (a set of patches with the same user defined characteristics) and overall landscape metrics. In this study, only patch characteristics were considered, because the forest is managed at the patch level and therefore, models at this spatial scale are most likely to have management implications.

2.4.1 Metrics generated by FRAGSTATS*ARC

FRAGSTATS*ARC generates several patch and landscape metrics including:

1. patch area (m^2), measured in metres squared;
2. patch fractal dimension (Equation 2.1), which quantifies the shape of a patch;
3. edge comparison (Equation 2.2), which quantifies the type of edge surrounding the patch under investigation, by estimating the theoretical effect of adjacent patches.

2.4.2 Calculation of metrics

Fractal dimension was a function of perimeter length and patch area. It was calculated using Equation 2.1, and the values ranged between the theoretical limit values of 1 (simple patch shapes) and 2 (very complex patch shapes).

$$FD = \frac{2\ln p_x}{\ln a_x}$$

Equation 2.1: Fractal Dimension (FD) equals 1 with simple Euclidean geometric shapes and increases in value up to 2 with increasing patch complexity. p_x = perimeter length of patch x in metres, and a_x = area of patch x in m^2. Taken from Anonymous 1998a.

To calculate edge comparison (E_n), the forest patches were categorised so that they could be grouped and weighted according to their adjacency to other types of patches. Each patch was assigned to one of five categories according to their species and age content (Table 2.3).

Category$_{(AC)}$[1]		*Description*
1		External polygon of the forest, agricultural and unplanted land.
2	Conifer patches	Clear fell and young trees (0-5 years old)
3		Pre-thicket trees (6-15 years old)
4		Mature trees (>15 years old)
5		Mixed and pure riparian and broadleaf patches

Table 2.3: Categories of patch separated by their tree species and age. ([1]AC indicates Age Code).

There is evidence that the type of coniferous tree species is not as important a determinant of songbird communities as landscape structure (Ratcliffe & Petty 1986), thus, individual coniferous tree species were not assigned separate categories$_{(AC)}$. Non-spruce species make up 16% of the forest's total area (McIntosh 1995), which is negligible compared to the 72% of the forest's area covered by Sitka spruce. Separation of all tree species for analysis would have led to extremely high variable to case ratios that would have contravened the assumptions of many statistical techniques.

Edge comparison (E_n) quantifies the effect of the surrounding patches on the type of edges forming the patch in question. Each patch is adjacent to several other patches; therefore the total edge of a patch is divided into segments, according to what is adjacent to it. A weight is applied to each segment of edge created by the juxtaposition of one category$_{(ACx)}$ patch with a neighbouring category$_{(ACy)}$ patch (x and y pertain to different categories$_{(AC)}$). The weights can be determined by investigating the possible reaction of the bird species to different types of edge using either field data or known habitat preferences or both as in this study. E_n is calculated by summing the contribution of each segments' weight along the total edge length, according to how many patches surround the patch under investigation and the length of each segment (Equation 2.2).

$$E_n = \frac{\sum^{m}(p_{x(y)} * d_{x(y)})}{p_x} \times 100$$

Equation 2.2: Edge comparison (E_n) equals the sum of the patch perimeter segment lengths (a segment length is the length of perimeter between the patch under investigation and one of the different adjacent patches) multiplied by their corresponding comparison weights (ranging from 0 to 1), divided by total patch perimeter, and multiplied by 100 to convert it to a percentage. $p_{x(y)}$ = length of perimeter segment of patch x adjacent to patch y, $d_{x(y)}$ = edge contrast weight or dissimilarity between patch x and y, p_x = total perimeter length of patch x, m = number of patch types (categories). Adapted from Anonymous 1998a.

For example if a category$_{(2)}$ patch (young or clearfell conifer) were totally surrounded by category$_{(4)}$ trees (mature), and if the edge weight of young/mature trees was 0.7, then the edge comparison would be 70. Similarly if pre-thicket trees surrounded the young patch, and the edge weight for this comparison was 0.5, then the edge comparison would be 50. However, if three-quarters of the length of the total edge length were comprised of young/mature (Y/M = 0.7) and one quarter of pre-thicket (Y/PT = 0.5), then the total edge comparison for the young patch would be 65 (see Worked example 2.1).

Y/M edge weight = 0.7
Y/PT edge weight = 0.5

Length of Y/M perimeter segment = 75 m
Length of Y/PT perimeter segment = 25 m
Total length of perimeter = 100 m

$$E_n = \frac{(75 * 0.7) + (25 * 0.5)}{100} \times 100 = 65$$

Worked example 2.1: Calculation of edge comparison using sample data.

Six edge comparison weight files were generated for input into FRAGSTATS*ARC, to calculate six slightly differing edge comparisons. Chapter 5 outlines in more detail how these weights were generated. More than one edge comparison was needed as it was expected that different species would react dissimilarly to a particular type of edge. For example, a specialist open habitat species such as the meadow pipit might be expected to have a different reaction to a pre-thicket/young edge than a chaffinch, a generalist.

Because these indices were highly correlated with each other and inclusion of all of them in modelling would generate high variable to case ratios, only two edge comparisons were included in each species model. These two edge comparisons were chosen for each species according to that species known habitat preferences (taken from Chapter 4 and Cramp (1988-1994).

2.5 Multivariate statistics

The following section gives an overview of generalised linear modelling (GLM) techniques, because many of the analyses included this study belong to this suite of statistics. Two types of GLM are used in this study; Poisson GLM and logistic regression. There are two problems associated with count data: a) a high frequency of zero counts skews the distribution of the dependent variable away from normality; and b) all predicted values must be positive (a negative count would be nonsensical). A common method of overcoming these problems is use of logistic regression, where count data are converted to 1 or 0 according to presence or absence (Equation 2.3) (Tabachnick & Fidell 1996, Bosakowski 1997, Villard *et al.* 1999); this is used in Chapter 5 of this thesis utilising SPSS 9.0.0 (1998). However, the details of the density of birds are lost in this type of analysis, except in multinomial logistic regression (Zar 1999).

$$\hat{Y}_i = \frac{e^{(A+\beta_1 x_1+\beta_2 x_2 \ldots\ldots+\beta_n x_n)}}{1+e^{(A+\beta_1 x_1+\beta_2 x_2 \ldots\ldots+\beta_n x_n)}}$$

Equation 2.3: Logistic regression equation showing the probability ($\hat{Y}_i$) of presence of a bird species in the *i*th sample. A is a constant, *x* is a main effect/interaction term, and *β* is a parameter estimate, with *n* being the number of significant variables added to the model. Taken from Tabachnick and Fidell (1996).

The statistical package GLIM 4.09 (Crawley 1993) can overcome these two problems of a high frequency of zero counts and limitation to only positive values, and yet retains the density information. The method by which these two problems are surmounted is utilisation of multiple generalised linear models (GLM) with Poisson errors (non-normal errors) and its associated log link (Equation 2.4) (Crawley 1993; Elmberg & Edenius 1999). Count data such as those in the present study generally include many zero counts and thus do not conform to a normal distribution, being skewed or kurtotic, as well as being unable to have negative values (Crawley 1993). Specification of

Poisson errors in GLIM 4.09 means that the error structure cannot have negative values. The Poisson error structure allows the variance to be equal to the mean (however, overdispersion of data can cause problems, as discussed later). The value for each point count is a Poisson observation. Because there are variable numbers of point counts per patch, inserting this number as a weight variable allows several observations to be entered simultaneously (P. Craig, *pers comm.*; Crawley 1993).

$$\mu_i = \exp(N_i + \beta_1 x_1 + \beta_2 x_2 \ldots\ldots + \beta_n x_n)$$

Equation 2.4: Generalised linear model (GLM) equation with Poisson errors. The subscript *i* denotes the sample in question. The explanatory variable N_i has a coefficient of 1 and is the offset for the model. μ_i is the predicted mean density in the *i*th sample, *x* is a main effect/interaction term, and β is a parameter estimate. The subsripts *1, 2* and *n* denote the main effects/interaction terms included in the model. Taken from Crawley (1993).

GLM has many advantages over other modelling techniques such as multiple regression, because 'the assumption of a linear relationship between the predicted....value (μ) and the systematic part of linear regression models can be relaxed while retaining the linear form of the systematic component of the model' (Norton & Possingham c1993).

In order to fully understand this statement it is important to go back to first principles. In linear regression the straight line is given by Equation 2.5 a), and the fit and slope of the line is determined by the scatter of the data points. However, what occurs when the scatter of data points does not generate a straight line but a curved line where the equation is not according to Equation 2.5 a) but, for example looks more like Equation 2.5 b)? This is still a linear model, as x^2 can be replaced by *z* (Crawley 1993). However, there are some models that are intrinsically non-linear such as Equation 2.5 c).

a. $y = a + bx$

b. $y = a + bx + cx^2$

c. $y = a + \dfrac{b}{c + x}$

Equation 2.5 a-c: Examples of a) a quadratic regression model, b) a linear regression model including a polynomial term, and c) a non-linear regression model including a hyperbolic function. Taken from Crawley (1993).

After the error structure is defined the 'linear predictor' η, must be considered. η is the linear sum of the values generated by the explanatory variables and *x*. As shown above these values need not necessarily be as simple as Equation 2.5 a), and may even be non-linear such as Equation 2.5 c). However, the sum of these is linear and so the right hand side of the equation is called the 'linear structure' (Crawley 1993). When transformed by the 'link function' η generates the mean value of y, which is called μ.

Caution should be exerted when data are overdispersed as the assumption in Poisson error GLM that the variance equals the mean is contravened. Overdispersion can occur if the birds are aggregating in point counts. Overdispersion was checked by fitting the full model and then calculating whether the Pearsons χ^2 value divided by the residual degrees of freedom was equal to one (Crawley 1993). If this value exceeded one then the data were overdispersed. The models were rescaled using this value, called a scale parameter, and modelling resumed.

3 Repeated seasonal and annual point counts of songbirds.

Abstract

This chapter utilises data from two analogous datasets of songbird observations in Kielder Forest in 1991/1992 and 1998/1999 using the point count methodology. Point counts were surveyed twice seasonally and annually.

Studies utilising the point count method to measure the relative densities of birds over large areas (hundreds of km^2), generally involve repeated seasonal counts of sites to improve the probability of detection of individuals (Bibby *et al.* 1985; Edenius & Elmberg 1996; Bosakowski 1997; Cherenkov 1998; Whitaker & Montevecchi 1999; Norton *et al.* 2000). The mean or maximum number of birds detected in a season is then used for further analysis under the assumption that using repeated counts improves the accuracy of density calculations. This study tests the hypothesis that the densities of birds in early and late spring are sufficiently dissimilar to warrant repetition of point counts within a season. The results show that there are some differences in densities of birds detected in early and late spring. This may be a result of inherent biases in the point count methodology, fluctuations in environmental variables, the effect of timing of breeding or changes in activity of birds with progression of the breeding season. The results provide evidence that seasonal repeat counting may improve the accuracy of density calculations.

Annual repeat counts can be used to investigate whether densities in one year are similar to those in the previous year. It is possible to use these data for investigating if birds consistently judge a habitat's quality from one year to the next. The hypothesis that if patches in a landscape are sufficiently dissimilar then annual correlations of density will be high is tested. There was good evidence to support this hypothesis, however there were some significant annual differences in densities, possibly as a result of variations in resource availability and biases in the point count methodology.

3.1 Introduction

The point count bird survey method enables the investigator to collect larger amounts of data than the more labour intensive territory mapping technique (Bibby *et al.* 1992). However, the trade off is that the densities measured using the point count method are generally not as accurate as the densities measured using the latter technique due to problems of detectability (Bibby *et al.* 1992). The relationships between the densities of species detected using repeated counts within a year (early and late spring) and at the same time between years (e.g. early spring in 1998 and 1999) are investigated here. The effect of food availability and temperature fluctuations on the seasonal and annual correlation of songbird density at the centres and edges of forest patches will be particularly concentrated upon. A previous study showed that the songbird communities at the edge and centre of forest patches were dissimilar (Patterson *et al.* 1995) and thus separation of these two areas was necessary.

3.1.1 Stochasticity of bird density

Studies utilising the point count method to measure the relative densities of birds over large areas generally involve repeated counts of sites (at least twice) to improve the probability of detection of individuals (Bibby *et al.* 1985; Edenius & Elmberg 1996; Bosakowski 1997; Cherenkov 1998; Whitaker & Montevecchi 1999; Norton *et al.* 2000). A frequent reason for taking the maximum from two counts is to include the best times of year for the early resident breeders and for the late arriving migrants, so that undercounting is minimised (Dettmers *et al.* 1999; MacNally 1997). The performance of models based on data from single counts in a season is generally poor (MacNally 1997).

This study will test the hypothesis that the repeat counting method is warranted, by investigation of the relationships between densities observed in early and late spring. If the observed densities are not significantly different from early to late spring, and the correlations of density between these two time periods are strong, then this may provide evidence that single point counts may be sufficient for surveying songbirds in this landscape.

Long-term studies over a wide area have shown that bird density within a landscape can vary markedly in time (Hogstad 1993; Balmer & Wernham 1999). Indeed, recent long-term national studies utilising data from the BTO's Common Bird Census have discussed declines of species such as the redpoll in the last 20 years (Balmer & Wernham 1999). However, in the short term (from season to season and year to year), the relative local densities of birds in sites across a landscape may remain quite similar (Hansson 1996), as a result of breeding site fidelity and habitat selection.

Although some small mammals show inter-annual fluctuations in population density, similar sized passerines rarely show marked fluctuation in densities (Hansson 1996). However, fluctuations in food availability, weather and predator threat at a particular site may affect passerine community stability (the temporal consistency of the numbers of individuals found) causing seasonal and annual density variations (Willson & Comet 1996). Thus, suitable habitats may not be occupied or are occupied at a lower density than during more optimal conditions (e.g. at times of great food availability) in prior years or seasons.

Optimality theory includes the Ideal-free and Ideal-despotic distributions (Fretwell 1972 and Milinski 1979 in Krebs & Davies 1993). The Ideal-free distribution hypothesis states that animals will become distributed across a landscape in densities that correspond to the densities of resources in patches across the landscape. The Ideal-despotic distribution includes competitive interactions, with the more dominant individuals gaining disproportionately more resources. Thus, if conditions were relatively static from one time period to the next, it would be expected that the bird populations would be relatively stable. So, a site with high density in one year would hold a relatively similar density in the following year. In recent years these theories have been under fire because of lack of empirical support (Weber 1998); however, they are a useful model for considering the effect of patch 'quality' on the distributions and site fidelity of individuals. This particularly applies to resident species, with migrant species potentially having less predictable densities because of changes in mortality rates in the non-breeding areas, or because prevailing winds may blow them off course away from their regular breeding area.

However, Haila *et al.* (1996) propose that stochastic variations not readily measured by humans will affect birds' decisions and thus the reliability of predictions of the density of birds at sites. In a study of the stochasticity with which individuals choose to place their territory over several years in a boreal coniferous dominated forest, Haila *et al.* (1996) proposed that suitable habitats would be consistently occupied by an individual from year to year (according to the ideal despotic distribution), whereas marginal areas would have a more random occupation. Therefore, if habitat preferences of a particular species are strong for certain patches of the forest, then those habitats would be more likely always to hold that species. This relationship gets weaker the more similar habitats are to one another (Haila *et al.* 1996). Haila's study took place in a natural growth forest with no well-defined edges, thus habitats were continuous. The patches surveyed in my study are relatively distinct and dissimilar. Therefore, using the rule proposed in Haila *et al.* (1996), it would be expected that stochastic variation of the habitat occupancy by a particular species would be low, causing the annual correlation to be high.

3.1.2 Resource availability and temperature

Early breeding passerine individuals generally have the highest number of surviving young (Meijer & Drent 1999; Sokolov 1999), therefore it is better to lay eggs as early as possible. However, several studies have shown that the timing of onset of breeding and laying dates depend on environmental conditions, which, in turn, affect arthropod emergence and abundance (tits - Naef-Daenzer & Keller, 1999; robins - Reuter & Breckling 1999; starlings - Meijer *et al.* 1999). Thus there is a need to match timing of breeding with the maximum food availability (Visser *et al.* 1998) such as caterpillar emergence. If there is a mismatch then there is a decrease in juvenile survival (Naef-Daenzer & Keller 1999). Laying date is constrained by the amount of resources the female has to put into the eggs and where these resources comes from. If the species is a 'capital' breeder then it uses stored reserves for eggs, whereas if the species is an 'income' breeder it uses the food that it gathers daily to provide resources for daily egg production (Meijer & Drent, 1999).

In sustained cold weather 'income' breeders would have to divert much of their available energy to their own survival and away from reproduction (Williams & Cooch, 1996). Hogstad (1993) proposed that temperature fluctuations about 0°C in winter caused an increase in mortality of goldcrest and coal tit because of their high metabolic rates and large surface area to volume ratios. Lower densities than expected may be observed in the breeding season because of this high mortality. In addition to this direct effect, cold temperatures delay arthropod emergence and reduce activity (Balmer & Wernham 1999). Dietary protein, supplied by arthropods, is a limiting factor on egg laying; thus, if arthropod abundance is low then bird breeding output is reduced (Meijer & Drent 1999). Hence, it would be expected that 'income' breeders would be more prone to breeding disruption if arthropods became scarce (due to cold temperatures) than 'capital' breeders, which are buffered against environmental fluctuations. Meijer and Drent (1999) show that of the five passerines in their study (starling, red-billed quelea, pied flycatcher, blue tit and zebra finch) four were 'income' breeders, with the zebra finch being a 'capital' breeder. Because the majority of passerines were ‘income’ breeders, it is assumed in this present study that the passerines are ‘income’ breeders.

Therefore on a succession of cold frosty days when food availability is low, passerines (particularly small species) decrease their breeding activity, and spend most of their time foraging for their own day-to-day survival. Therefore, the impact of weather conditions on the timing of breeding, and thus bird territorial activity, may affect seasonal correlations of bird density.

Common crossbill distribution and breeding activity is highly unpredictable, as their breeding season is affected by the erratic seed availability (Holimon *et al.* 1998). In areas planted with spruce most crossbill breed between February and April (Newton 1972), making crossbills one of the earliest passerine breeders in the forest. Common crossbills are highly mobile in autumn and settle in areas with a high concentration of food, particularly spruce seeds (Newton 1972). The winter of 1990-1991 had a large Sitka and Norway spruce cone crop (termed a mast crop) and thus there were extremely high influxes of common crossbills in early 1991 (Patterson *et al.* 1995).

3.1.3 Aims

The present study uses breeding bird survey data obtained by point count surveys, from 2 studies based in Kielder Forest in the springs of 2 pairs of years (1991 and 1992 - Sample A, and 1998 and 1999 - Sample B). These studies used slightly different methodologies. The consequences of these differences can be explored by comparing the range of results obtained in each study.

Despite fluctuations in environmental conditions and stochastic variation in densities, it would be expected that forest patches would have similar densities and species composition from season to season and year to year, if habitat preferences were strong. However, this relationship may be affected by the birds' resident/migrant status and whether they are early or late breeders. Correlation coefficient values (r) would reflect seasonal and yearly density relationships. My study: a) explores the validity of the seasonal repeat count method; b) examines how weather, breeding strategy, food availability and influxes of birds affect the seasonal and annual density relationships; and c) investigates annual density variations to ascertain the degree of stochasticity (randomness) with which the birds choose their territory from year to year.

3.2 Methods

Point counts of radius 60 metres were placed either at the centre or edge of a forestry patch. Full point counts were used for the centre counts and half point counts for the edge. For a full account of methodology see Chapter 2. Table 3.2.1 shows a synopsis of the differences in Sample A and Sample B methodologies, and Appendices 1 and 2 show example maps of the different study sites (Sample A and B respectively). Point counts were surveyed in early spring and resurveyed in late spring of 1991, 1992, 1998 and 1999 (Table 3.2.1) to allow investigation of seasonal correlation. Point counts were also repeated annually in Sample A (1991 and 1992) and Sample B (1998 and 1999). The mean density of individuals of a species in each site was calculated (number of birds per point count ha^{-1}) (Baker & Lacki 1997). The present study concentrates on the eleven most common small passerine birds; crossbill, chaffinch, coal tit, dunnock, goldcrest, meadow pipit, robin, redpoll, siskin, wren and willow warbler (for Latin names see Appendix 3).

SPSS (1998) was utilised for all analyses. Wilcoxon matched pairs were used to test for differences in median density within and between seasons and years (Zar 1996). This procedure involved calculating the differences between the pairs of values and ranking these differences according their absolute value. The ranks were then summed according to the sign of the difference (positive T+ or negative T-) and rejection of the null hypothesis is justified if either T+ or T- is less than or equal to the critical value (Zar 1996). Non-parametric correlation analyses (Spearman's rank correlations in SPSS 1998) of the repeated counts were carried out for each species to determine if there were any relationships between the values collected in different seasons and also in different years.

Because of the large numbers of tests performed, a Bonferroni type of correction was applied to the significance value to minimise Type I errors, which result in rejection of the null hypothesis when it is actually true (Tabachnick & Fidell 1996). If a p-value of 0.05 is adopted then it is expected that one out of twenty tests would generate a significant result by chance alone. Reducing the p-value to 0.01 decreases this chance to one in one hundred. Therefore a p-value of 0.01 was adopted.

	Sample A (1991 and 1992)	*Sample B (1998 and 1999)*
Survey dates	1991 23/04-14/05 & 22/05-10/06 1992 23/04-16/04 & 20/05-11/06	1998 13/04-11/05 & 12/05-15/06 1999 11/04-13/05 & 14/05-14/06
Centre (WPC) and edge (HPC) point count radius	Fixed radius of 60 m with 30 m internal radius	Fixed radius of 60 m with 30 m internal radius
Tree species in surveyed patches	Pure Sitka spruce and mixed Sitka spruce with broadleaf/Norway spruce/Lodgepole pine/Scots pine	Pure Sitka spruce and clearfell
Placement of 'centre' point counts	No fixed distance from boundary (Appendix 1)	150 m to the boundary in a parallel grid (Appendix 2)
Placement of observation point in HPC	Displaced a few metres away from boundary	On the boundary
Placement of HPC in relation to adjacent patches	Each HPC was placed on a different boundary of the patch in question so that patch adjacency was not kept constant (Appendix 1)	Each HPC was placed on the same boundary of the patch in question therefore the adjacent patch was kept constant (Appendix 2).
Patches adjacent to HPC	Broadleaf/Norway spruce/Lodgepole pine/Scots pine	Only Sitka spruce or clearfell

Table 3.2.1: Methodological comparison between Sample A (1991 and 1992) and Sample B (1998 and 1999). Abbreviations are WPC = Whole Point Count (found in the centre of patches) and HPC = Half Point Count (found at the edge of patches).

3.3 Results

3.3.1 Overall mean density

Overall mean density of each species was calculated across all sites both in early and late spring and at patch edges and centres in all four years (Tables 3.3.1 and 3.3.2). Because the densities were paired, subsequent analyses were performed for each species using the non-parametric method of Wilcoxon-matched pairs. Although overall mean density was not used in these analyses it was instructive to be aware of the total mean densities of birds detected in these types of studies. Generally, the mean density of each species differed between the two pairs of years (comparing 1991 and 1992 with 1998 and 1999), particularly in 1991, when densities of granivorous species were considerably higher than in the other three years. Also, goldcrest were found at much lower densities in 1991 and 1992 (mean density over the four time periods at the centre was 0.146 and at the edge was 0.650) than in 1998 and 1999 (mean density at the centre was 0.408 and at the edge was 0.856).

3.3.2 Seasonal comparisons

Wren were found in consistently higher densities in early spring than late spring, both in 1998 and 1999, and at both the centre and the edge (Table 3.3.4). Indeed in Sample B (1998 and 1999) the majority of seasonal differences for all species were of higher bird densities in early rather than late spring. The opposite was found in 1991 with densities in early spring generally lower than in late spring (Table 3.3.3).

Three species in 1991 (coal tit, wren and willow warbler) and three species in 1992 (chaffinch, redpoll and siskin) showed significant differences in densities (Table 3.3.3). Four species (coal tit, goldcrest, robin and wren) in 1991 and six (crossbill, coal tit, dunnock, goldcrest, robin and wren) in 1992 showed no significant seasonal correlations (Table 3.3.5). Three species in 1998 (coal tit, dunnock and wren) and one in 1999 (wren) showed significant differences in densities observed using paired analyses (Table 3.3.4). Five species in 1998 (crossbill, chaffinch, redpoll, siskin and willow warbler) and three species in 1999 (crossbill, robin and redpoll) had no significant seasonal correlations (Table 3.3.6).

Species	*C/E*	*Mean Density (birds per hectare)*			
		Early spring 1991	*Late spring 1991*	*Early spring 1992*	*Late spring 1992*
crossbill	C	1.263 (0.385)	0.735 (0.269)	0.073 (0.032)	0.0121 (0.089)
	E	2.155 (0.630)	1.381 (0.965)	0.000 (0.000)	0.000 (0.000)
chaffinch	C	1.253 (0.234)	1.294 (0.255)	0.769 (0.209)	1.578 (0.259)
	E	4.200 (0.729)	4.476 (0.829)	0.2431 (0.759)	5.913 (0.930)
coal tit	C	0.483 (0.115)	0.106 (0.0483)	0.378 (0.870)	0.283 (0.086)
	E	1.603 (0.727)	0.442 (0.255)	1.271 (0.685)	0.663 (0.356)
dunnock	C	0.099 (0.046)	0.214 (0.071)	0.165 (0.077)	0.139 (0.051)
	E	0.276 (0.156)	0.884 (0.361)	0.221 (0.221)	0.111 (0.111)
goldcrest	C	0.060 (0.038)	0.048 (0.027)	0.207 (0.088)	0.269 (0.094)
	E	0.608 (0.447)	0.553 (0.386)	0.442 (0.255)	0.995 (0.403)
meadow pipit	C	0.476 (0.163)	0.542 (0.162)	0.404 (0.164)	0.310 (0.100)
	E	0.995 (0.698)	1.216 (0.735)	0.608 (0.447)	0.663 (0.453)
robin	C	0.230 (0.065)	0.129 (0.064)	0.274 (0.084)	0.200 (0.064)
	E	0.608 (0.193)	1.492 (0.527)	0.995 (0.351)	0.774 (0.322)
redpoll	C	0.891 (0.238)	0.153 (0.350)	0.547 (0.295)	1.389 (0.378)
	E	1.824 (0.890)	3.095 (1.346)	0.774 (0.774)	0.995 (0.456)
siskin	C	2.283 (0.370)	2.340 (0.384)	0.367 (0.092)	0.994 (0.204)
	E	3.316 (0.901)	2.763 (0.757)	0.663 (0.285)	0.221 (0.151)
wren	C	0.344 (0.832)	0.143 (0.054)	0.347 (0.096)	0.296 (0.079)
	E	0.608 (0.320)	1.105 (0.481)	1.381 (0.504)	0.000 (0.000)
willow warbler	C	0.459 (0.126)	1.064 (0.250)	1.061 (0.238)	1.213 (0.260)
	E	1.326 (0.491)	3.980 (1.052)	2.210 (0.862)	1.658 (0.614)

Table 3.3.1: Mean density (standard error) of eleven common passerine species across all surveyed patches in 1991 and 1992, in early and late spring, and in both the centre (C) and the edge (E) of patches. Sample sizes of N = 44 for centre and N = 16 for edge.

Species	*C/E*	*Mean Density (birds per hectare)*			
		Early spring 1998	*Late spring 1998*	*Early spring 1999*	*Late spring 1999*
crossbill	C	0.000 (0.000)	0.040 (0.028)	0.020 (0.020)	0.000 (0.000)
	E	0.021 (0.021)	0.096 (0.043)	0.136 (0.046)	0.051 (0.032)
chaffinch	C	0.324 (0.094)	0.562 (0.120)	0.421 (0.082	0.255 (0.080)
	E	0.925 (0.132)	1.015 (0.146)	0.833 (0.117)	0.936 (0.125)
coal tit	C	0.183 (0.074)	0.141 (0.054)	0.170 (0.071)	0.142 (0.052)
	E	0.376 (0.081)	0.100 (0.038)	0.249 (0.066)	0.211 (0.062)
dunnock	C	0.042 (0.031)	0.330 (0.087)	0.177 (0.058)	0.113 (0.052)
	E	0.296 (0.077)	0.431 (0.082)	0.315 (0.077)	0.242 (0.071)
goldcrest	C	0.378 (0.096)	0.265 (0.073)	0.616 (0.135)	0.372 (0.092)
	E	0.702 (0.116)	0.841 (0.120)	1.119 (0.153)	0.763 (0.113)
meadow pipit	C	0.673 (0.143)	0.832 (0.164)	0.791 (0.148)	0.860 (0.155)
	E	0.381 (0.074)	0.422 (0.088)	0.336 (0.074)	0.261 (0.070)
robin	C	0.386 (0.123)	0.303 (0.093)	0.499 (0.103)	0.441 (0.091)
	E	0.747 (0.114)	0.679 (0.107)	0.742 (0.110)	0.716 (0.096)
redpoll	C	0.144 (0.058)	0.337 (0.098)	0.218 (0.063)	0.460 (0.095)
	E	0.144 (0.044)	0.339 (0.090)	0.195 (0.056)	0.377 (0.085)
siskin	C	0.216 (0.082)	0.144 (0.052)	0.134 (0.045)	0.101 (0.042)
	E	0.326 (0.093)	0.298 (0.061)	0.312 (0.055)	0.269 (0.065)
wren	C	0.997 (0.131)	0.476 (0.089)	0.972 (0.114)	0.508 (0.098)
	E	1.814 (0.201)	0.886 (0.124)	1.458 (0.163)	0.913 (0.118)
willow warbler	C	0.819 (0.191)	0.627 (0.141)	0.694 (0.173)	0.728 (0.128)
	E	1.303 (0.221)	1.136 (0.169)	1.192 (0.195)	1.164 (0.137)

Table 3.3.2: Mean density (standard error) of eleven common passerine species across all surveyed patches in 1998 and 1999, in early and late spring, and in both the centre (C) and the edge (E) of patches. Sample sizes of N = 45 for centre and N = 86 for edge.

Species	*1991*		*1992*	
	Significant differences in density	*p-values*	*Significant differences in density*	*p-values*
crossbill		(C: 0.149 E: 0.260)		(C: 0.063 E: 1.000)
chaffinch		(C: 0.684 E: 0.599)	C1 < C2	**C: 0.002** (E: 0.017)
coal tit	C1 < C2	**C: 0.006** (E: 0.127)		(C: 0.295 E: 0.176)
dunnock		(C: 0.028 E: 0.066)		(C: 0.789 E: 0.655)
goldcrest		(C: 0.680 E: 1.000)		(C: 0.208 E: 0.258)
meadow pipit		(C: 0.583 E : 0.180)		(C: 0.755 E: 1.000)
robin		(C: 0.122 E: 0.118)		(C: 0.378 E: 0.631)
redpoll		(C: 0.039 E: 0.279)	C1 < C2	**C: 0.005** (E: 0.492)
siskin		(C: 0.755 E: 0.656)	C1 < C2	**C: 0.002** (E: 0.176)
wren	C1 > C2	**C: 0.008** (E: 0.196)		(C: 0.626 E: 0.017)
willow warbler	C1 > C2	**C: 0.004**		(C: 0.382 E: 0.776)
	E1 < E2	**E: 0.008**		

Table 3.3.3: Seasonal Wilcoxon-Matched Pairs results comparing bird density in early and late spring of Sample A (1991 and 1992). Early spring is denoted by C1 or E1 and late spring by C2 or E2 (centre or edge respectively). N = 44 for centre and N = 16 for edge. P-values shown in bold are significant and those in brackets, not significant.

Species	*1998*		*1999*	
	Significant differences in density	*p-values*	*Significant differences in density*	*p-values*
crossbill		(C: 0.157 E: 0.168)		(C: 0.317 E: 0.156)
chaffinch		(C: 0.058 E: 0.948)		(C: 0.046 E: 0.566)
coal tit	E1 > E2	(C: 0.799) **E: 0.001**		(C: 0.678 E: 0.695)
dunnock	C1 < C2	**C: 0.001** (E: 0.065)		(C: 0.191 E: 0.148)
goldcrest		(C: 0.234 E: 0.247)		(C: 0.048 E: 0.021)
meadow pipit		(C: 0.108 E: 0.604)		(C: 0.473 E: 0.275)
robin		(C: 0.631 E: 0.521)		(C: 0.517 E: 0.909)
redpoll		(C: 0.028 E: 0.089)		(C: 0.024 E: 0.060)
siskin		(C: 0.315 E: 0.844)		(C: 0.371 E: 0.445)
wren	C1 > C2	**C: <0.001**	C1 > C2	**C: <0.001**
	E1 > E2	**E: <0.001**	E1 > E2	**E: 0.003**
willow warbler		(C: 0.329 E: 0.965)		(C: 0.781 E: 0.887)

Table 3.3.4: Seasonal Wilcoxon-Matched Pairs results comparing bird density in early and late spring of Sample B (1998 and 1999). Abbreviations and format as with Table 3.3.3. N = 45 for centre and N = 86 for edge.

In 1998 and 1999 goldcrest and meadow pipit had particularly strong and consistent correlations between the early and late spring densities (Table 3.3.6). Not one species showed seasonal consistency in both 1991 and 1992 (Table 3.3.5).

However, these seasonal results provide evidence that for some species densities in early and late spring are significantly different. Hence, this verifies the need for utilisation of repeat point counts, which may improve the chances of detecting individuals in patches.

3.3.3 Annual comparisons

In the first pair of years considered (1991 and 1992), six of the eight significant differences in the paired data showed that density was significantly higher in 1991 than in 1992, both in early and late spring (Table 3.3.7). In the second pair of years (1998 and 1999) there were only two significant differences (Table 3.3.8). In 1998 there was a sustained cold period (Figure 3.3.1) that may have caused lower activity of goldcrest, a small-bodied species resulting in lower density of goldcrest in 1998 than in 1999.

Significant annual correlations were medium to high with values of r ranging from 0.275-0.858 (Table 3.3.5 and 3.3.6). Ten species showed significant annual correlations in density in early spring of 1991 and 1992, seven in late spring of 1991 and 1992. Seven showed significant annual correlations in density in early spring of 1998 and 1999, and eight in late spring of 1998 and 1999. The densities of meadow pipit and willow warbler demonstrated particularly strong significant annual correlations in all datasets (Tables 3.3.5 and 3.3.6); therefore patches that contained relatively high densities of willow warbler or meadow pipit in one year were highly likely to hold relatively high densities in the following year. The many, strong annual correlations provide evidence that species judge a patches quality consistently from year to year. Therefore, generally, patches containing relatively high densities in one year had relatively high densities in the following year.

		Spearman's Rank Correlation Coefficients (r) for 1991 and 1992			
		Seasonal relationships		*Annual relationships*	
		Early vs. late 91	*Early vs. late 92*	*91 vs. 92 Early*	*91 vs. 92 Late*
crossbill	C	**0.487 (0.001)**	0.237 (0.121)	**0.420 (0.004)**	0.111 (0.472)
	E	0.296 (0.266)	NM	NM	NM
chaffinch	C	**0.772 (0.000)**	**0.387 (0.009)**	**0.551 (0.000)**	**0.665 (0.000)**
	E	0.201 (0.454)	-0.214 (0.426)	0.331 (0.211)	0.493 (0.053)
coal tit	C	0.205 (0.183)	0.355 (0.018)	**0.524 (0.000)**	**0.432 (0.003)**
	E	0.279 (0.295)	0.585 (0.017)	0.119 (0.660)	0.518 (0.040)
dunnock	C	**0.534 (0.000)**	0.190 (0.216)	**0.515 (0.000)**	0.315 (0.037)
	E	**0.712 (0.002)**	-0.067 (0.806)	0.576 (0.020)	-0.171 (0.526)
goldcrest	C	0.301 (0.047)	0.280 (0.066)	**0.473 (0.001)**	**0.406 (0.006)**
	E	0.214 (0.427)	-0.316 (0.234)	0.152 (0.574)	0.031 (0.909)
meadow pipit	C	**0.828 (0.000)**	**0.701 (0.000)**	**0.684 (0.000)**	**0.793 (0.000)**
	E	**0.828 (0.000)**	0.580 (0.019)	0.595 (0.015)	**0.656 (0.006)**
robin	C	0.032 (0.838)	0.255 (0.095)	**0.474 (0.001)**	-0.199 (0.195)
	E	0.316 (0.233)	-0.140 (0.604)	0.506 (0.045)	0.176 (0.514)
redpoll	C	**0.656 (0.000)**	**0.413 (0.005)**	**0.543 (0.000)**	**0.820 (0.000)**
	E	**0.953 (0.000)**	-0.148 (0.585)	0.306 (0.248)	0.518 (0.040)
siskin	C	**0.830 (0.000)**	**0.516 (0.000)**	**0.588 (0.000)**	**0.696 (0.000)**
	E	0.202 (0.454)	0.125 (0.645)	-0.177 (0.512)	0.259 (0.332)
wren	C	0.339 (0.024)	0.097 (0.533)	0.090 (0.561)	-0.055 (0.723)
	E	0.540 (0.031)	NM	0.391 (0.134)	NM
willow warbler	C	**0.795 (0.000)**	**0.679 (0.000)**	**0.699 (0.000)**	**0.748 (0.000)**
	E	**0.786 (0.000)**	0.410 (0.115)	**0.858 (0.000)**	**0.756 (0.001)**

Table 3.3.5: Spearman's Rank Correlation Coefficients (r), with p-values in parentheses, of the relationship between the mean densities of each species found in each patch surveyed in 1991 and 1992, in early and late spring at the centres and edges of patches. Significant correlations are shown in bold. NM denotes no model because of insufficient data points.

		Spearman's Rank Correlation Coefficients (r) for 1998 and 1999			
		Seasonal relationship		*Annual relationship*	
		Early vs. late 98	*Early vs. late 99*	*98 vs. 99 Early*	*98 vs. 99 Late*
crossbill	C	NM	NM	NM	NM
	E	-0.030 (0.786)	0.138 (0.206)	-0.039 (0.720)	-0.052 (0.634)
chaffinch	C	0.247 (0.102)	0.236 (0.119)	0.067 (0.661)	0.057 (0.708)
	E	0.244 (0.023)	**0.306 (0.004)**	0.213 (0.049)	**0.457 (0.000)**
coal tit	C	**0.526 (0.000)**	**0.487 (0.001)**	**0.567 (0.000)**	**0.663 (0.000)**
	E	0.173 (0.111)	-0.055 (0.617)	0.104 (0.340)	0.090 (0.408)
dunnock	C	**0.386 (0.009)**	0.136 (0.372)	0.179 (0.240)	**0.458 (0.002)**
	E	**0.380 (0.000)**	**0.399 (0.000)**	0.149 (0.171)	0.238 (0.027)
goldcrest	C	**0.444 (0.002)**	**0.610 (0.000)**	**0.466 (0.001)**	0.368 (0.013)
	E	**0.557 (0.000)**	**0.457 (0.000)**	**0.622 (0.000)**	**0.519 (0.000)**
meadow pipit	C	**0.729 (0.000)**	**0.848 (0.000)**	**0.774 (0.000)**	**0.834 (0.000)**
	E	**0.621 (0.000)**	**0.652 (0.000)**	**0.656 (0.000)**	**0.532 (0.000)**
robin	C	0.365 (0.014)	0.267 (0.076)	**0.456 (0.002)**	**0.390 (0.008)**
	E	**0.337 (0.002)**	0.256 (0.017)	0.263 (0.015)	0.232 (0.032)
redpoll	C	0.365 (0.014)	0.174 (0.254)	0.259 (0.086)	0.351 (0.018)
	E	0.191 (0.078)	0.119 (0.274)	**0.282 (0.009)**	**0.275 (0.010)**
siskin	C	0.052 (0.737)	**0.470 (0.001)**	0.124 (0.421)	-0.186 (0.228)
	E	0.032 (0.767)	-0.129 (0.239)	0.178 (0.102)	0.010 (0.929)
wren	C	0.377 (0.011)	0.351 (0.018)	0.193 (0.204)	-0.151 (0.321)
	E	**0.302 (0.005)**	**0.399 (0.000)**	**0.366 (0.001)**	0.257 (0.017)
willow warbler	C	0.372 (0.012)	0.305 (0.041)	**0.823 (0.000)**	**0.445 (0.002)**
	E	0.263 (0.015)	**0.561 (0.000)**	**0.715 (0.000)**	**0.616 (0.000)**

Table 3.3.6: Spearman's Rank Correlation Coefficients (r), with p-values in parentheses, of the relationship between the mean densities of each species found in each patch surveyed in 1998 and 1999, in early and late spring at the centres and edges of patches. Significant correlations are shown in bold. NM denotes no model because of insufficient data points.

Species	*Early spring*		*Late spring*	
	Significant differences in density	*p-values*	*Significant differences in density*	*p-values*
crossbill	C191 > C192	**C: 0.000**	C291 > C292	**C: 0.002**
	E191 > E192	**E: 0.005**		(E: 0.180)
chaffinch	C191 > C192	**C: 0.007** (E: 0.084)		(C: 0.116 E: 0.132)
coal tit		(C: 0.276 E: 0.675)		(C: 0.050 E: 0.480)
dunnock		(C: 0.398 E: 0.785)		(C: 0.373 E: 0.068)
goldcrest		(C: 0.084 E: 1.000)	C291 < C292	**C: 0.008** (E: 0.462)
meadow pipit		(C: 0.401 E: 0.285)		(C: 0.028 E: 0.461)
robin		(C: 0.835 E: 0.150)		(C: 0.305 E: 0.170)
redpoll		(C: 0.049 E: 0.279)		(C: 0.592 E: 0.115)
siskin	C191 > C192	**C: 0.000** (E: 0.020)	C291 > C292	**C: 0.000** (E: 0.011)
wren		(C: 0.757 E: 0.079)		(C: 0.137 E:0.024)
willow warbler	C191 < C192	**C: 0.001** (E: 0.168)		(C: 0.400 E: 0.011)

Table 3.3.7: Annual Wilcoxon-Matched Pairs results comparing bird density in 1991 with the same time in 1992 (Sample A). Abbreviations as with Table 3.3.3 followed by the year e.g. C191 is early spring in 1991. N = 44 for centre and N = 16 for edge.

Species	*Early spring*		*Late spring*	
	Significant differences in density	*p-values*	*Significant differences in density*	*p-values*
crossbill		(C: 0.317 E: 0.032)		(C: 0.157 E: 0.366)
chaffinch		(C: 0.302 E: 0.411)		(C: 0.041 E: 0.746)
coal tit		(C: 0.799 E: 0.239)		(C:0.594 E: 0.136)
dunnock		(C: 0.043 E:0.989)	C298 > C299	**C: 0.002** (E: 0.057)
goldcrest	E198 < E199	(C: 0.108) **E:0.004**		(C: 0.330 E: 0.648)
meadow pipit		(C: 0.241 E: 0.398)		(C: 0.955 E: 0.030)
robin		(C: 0.227 E: 0.873)		(C: 0.209 E: 0.546)
redpoll		(C: 0.324 E: 0.640)		(C: 0.114 E: 0.244)
siskin		(C: 0.307 E: 0.801)		(C: 0.361 E: 0.532)
wren		(C: 0.914 E: 0.152)		(C: 0.764 E: 0.742)
willow warbler		(C: 0.285 E: 0.484)		(C: 0.296 E: 0.206)

Table 3.3.8: Annual Wilcoxon-Matched Pairs results comparing bird density in 1998 with the same time in 1999 (Sample B). Abbreviations as with Table 3.3.3 N = 45 for centre and N = 86 for edge.

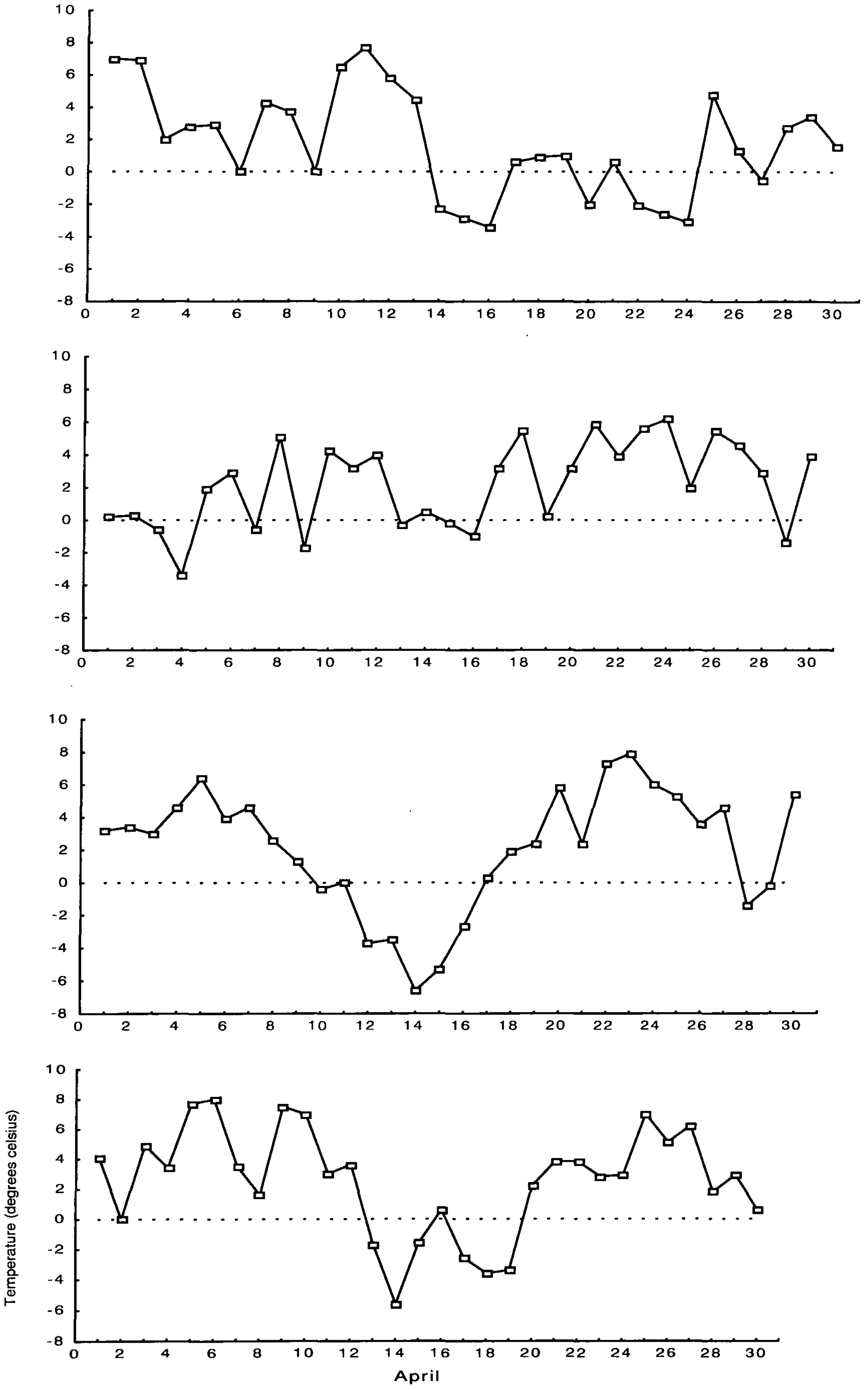


Figure 3.3.1: Daily minimum temperatures for April 1991 (top graph), 1992, 1998 and 1999 (bottom graph) in degrees Celsius (British Atmospheric Data Centre). Temperatures recorded at Kielder Castle.

3.4 Discussion

There are some differences in mean densities measured in both seasons of all four years (Tables 3.3.1 and 3.3.2). The following sections discuss the differences, and similarities, between the datasets used.

3.4.1 Seasonal comparisons

Seasonal effects on the paired densities were not consistent. In 1991 and 1992 early spring density was generally lower than late spring density, whereas in 1998 and 1999 the reverse was true. Singing activity is highest in the initial part of the breeding season (Hegelbach & Spaar 2000). Therefore, it would be expected that resident species would be easier to detect in early spring than late spring, thus making early spring density apparently higher. If there were significant drops in temperature in early spring 1991 and 1992 causing decreases in bird activity, then perhaps the number of birds detected in early spring would be lower than late spring. However, Figure 3.3.1 shows no evidence for this.

Temperature and food availability may play a role in determining the activity and timing of breeding of birds, and thus the relationships between early and late spring densities (Naef-Daenzer & Keller 1999; Reuter & Breckling 1999; Meijer *et al.* 1999). Environmental fluctuations may contribute to daily/seasonal variations in bird activity, and thus detectability, which will introduce a certain amount of variability in densities calculated from both of the counts (early and late spring at the same sites). Disturbance caused by the observer and forest operations will also affect the detected bird density, as will predator activity. Passerines in the vicinity of an avian predator at Kielder became less likely to sing or issued predator threat contact calls, such as the '*pink*' of the chaffinch, thus affecting their detectability. The duration of the effects of disturbance is likely to be species specific. An important contributor to unexplained variation in the data is sampling errors. The point count method has many inherent errors such as double counting when a bird moves, over or undercounting because the singing bird is either facing towards or away from the observer, and insufficient time to detect all the birds in the point count. Small patches may have exacerbated these errors, because in large patches sufficient numbers of point counts could be performed to average out some of the variability in the data. Repetition of counts on the same day may have highlighted some of these errors; however, time of day may also affect the numbers of birds detected.

There were several species for which there were significant differences in paired densities and some with no correlation between early and late spring, with the coal tit being a prime example of this. Therefore, bird density calculated using data from a single count early or late in the season is not a good representation of bird densities in that patch. It is proposed here that the repeat point count methodology will increase the chance of detecting individuals. This validates the use of the maximum or mean density from early and late spring for further analyses (Bibby *et al.* 1985; Venier & Fahrig 1998; Elmberg & Edenius 1999; Norton *et al.* 2000).

3.4.2 Annual comparisons

The paired annual comparisons show how environmental conditions can affect the annual median density in sites across the forest. Mast years (years when the cone crop is unusually high) occur every 2-3 years for Sitka spruce and 6-7 years for Norway spruce (Petty *et al.* 1995). In 1991 large cone crops occurred in both tree species, causing an enormous increase in the amount of seeds available (Petty *et al.* 1995; Patterson *et al.* 1995). Therefore, it is unsurprising that there were accompanying marked increases in the densities of seed-eating finches (Appendix 3) such as crossbill, siskin, and to some extent chaffinch (Table 3.3.7). The large number of crossbill found in Kielder in 1991, associated with the high density of seeds, was probably due to influxes of birds from Europe and Asia (Petty *et al.* 1995). Crossbill move over Europe and stay in areas with large amounts of food (Newton 1972; Holimon *et al.* 1998). The larger numbers of siskin may have been in part caused by influxes of individuals moving north and choosing to stop in Kielder due to favourable conditions. ‘Floating’ non-breeding resident chaffinches may have had the opportunity to breed because of the larger amounts of food, thus causing the increase in breeding pairs detected.

As with 1992, 1998 and 1999 were not mast years, making conditions relatively similar in terms of available seed resources. However, in 1998 there was a sustained cold period covering 7 days in early spring (Figure 3.3.1) that may have caused arthropod emergence to be later than usual and lowered arthropod activity. This coincides with a critical period for timing of breeding for many passerines (Appendix 3). Sustained cold conditions will reduce passerine activity especially in small-bodied insectivores (Hansson 1996). The goldcrest, one of the smallest passerines in Kielder Forest, had significantly lower density in early spring 1998 than 1999 (Table 3.3.8), corresponding with the sustained cold period lasting for 7 days in early spring 1998 (Figure 3.3.1). However, the wren, another small-bodied insectivorous species, was not adversely affected by the cold conditions in April 1998 (Table 3.3.8).

Similar to Brown's (1995) study, annual correlations were medium to high, with significant r-values ranging from 0.275 to 0.858 (Tables 3.3.5 and 3.3.6). If food were the only variable affecting the total densities in the four years, it would be expected that the annual densities of granivorous species would be higher in 1991 than in 1992, 1998 and 1999. On inspection of mean densities this was found to be the case. However, mean densities in 1992 were also quite different to those detected in 1998 and 1999. To take the goldcrest as an example, densities in 1998 and 1999 were found to be 5-6 times greater in some cases than the densities found in 1991 and generally 2-3 times greater than values in 1992. There are no good biological explanations for these anomalies (such as food availability or temperature); however, there may be methodological reasons. It is proposed here that variations in different observers' hearing and detection of contact calls may have generated the difference observed in mean densities. The song of the goldcrest is a very high pitched warbling which can easily be missed at long ranges. High frequency attenuation can begin to occur at young observer ages and thus the goldcrest may have been less detectable to older observers. The difference in the densities of goldcrest detected is possibly a result of this. Differences in the mean densities of other birds detected in 1991/1992 and 1998/1999 may have arisen due to usage of visual as well as aural cues in the former two years, but only aural cues in the latter pair of years. In addition, in 1991 and 1992 the edge type was not kept constant, neither was the distance from the edge for centre counts, which may have had a bearing on the numbers and types of birds detected (Table 3.2.1).

Consistent with the hypothesis that if patches are sufficiently dissimilar the annual correlations of density will be strong, there is evidence from the results presented in the present study, that species' densities in one year were similar to those in the previous year. Therefore, perception of a patch's quality remained unchanged in the small time scale (two years) studied here. Stochastic variations in environmental variables were not enough to nullify these relationships. Therefore, habitat associations were sufficiently strong to maintain relatively similar densities in patches from year to year. These strong relationships show that the point count method is a satisfactory technique for gathering large amounts of bird data.

3.4.3 Conclusions

The results obtained from surveying bird populations are affected by many temporal and spatial factors, such as weather (Veistola *et al.* 1997; Peach *et al.* 1995; Lahti *et al.* 1998), food availability (Petty *et al.* 1995; Summers 1999), influxes of non-native birds (Patterson *et al.* 1995; Petty *et al.* 1995), breeding strategies (Meijer & Drent 1999), and reactions to predators (Götmark & Post 1996). However, these results provide evidence that the point count method is an effective surveying tool for this type of environment. There is some evidence to suggest that repeat counts may improve the accuracy of bird density calculations by increasing the chance of detection. The method of using the maximum or mean density obtained in the two seasonal counts is verified by the results presented here.

The strong annual correlations showed that the habitats surveyed are suitably dissimilar and habitat associations are sufficiently strong to overcome stochastic fluctuations in environmental variables. Stochastic variation of bird densities was low, with species having clear perceptions of habitat quality causing strong annual correlations of density in patches.

4 The effect of edge contrast, tree age and distance from a patch boundary in determining small-scale songbird densities in managed coniferous forest sites.

Abstract

Many studies of European northern forests have shown that the density of birds at the edge of forested patches is generally higher than at the centres; this has been termed a positive edge effect. However, this chapter demonstrates that, despite a predominance of positive edge effects, data from a small-scale study show that in the 30 metres closest to the boundary of the patch (boundary zone) some species display edge avoidance. The density distribution patterns of birds across edges were dependent on the age of the trees. The hypothesis that birds with a high risk of predation, such as those preferring habitats with low amounts of cover will avoid edges was tested. This was found to be the case, with a generalised displacement of the peak of bird density away from the boundary zone in pre-thicket and young trees. However, in mature trees, the peak of density was in the boundary zone, suggesting that increased cover allows birds to exploit the more productive edges. There is also evidence to suggest that many species avoid those edges formed between two dissimilar patches. I propose that higher predation at young or high contrast edges causes birds to avoid these areas; however, detailed field studies will be required to test this hypothesis.

4.1 Introduction

Afforestation in Britain during the 20th century was extensive with forest cover increasing from 4% in 1918 to 11% in 1998, of which 61% comprises fast growing coniferous species such as Sitka spruce (*Picea sitchensis*) (Anonymous 1998b). Many upland forests are dominated by rotational clear-cutting regimes (Atlegrim & Sjoberg 1995) that create a mosaic landscape (Berg 1997) ranging from mature plantation to recent clearcuts and characterised by abrupt and extensive boundaries. Changes in land use are a contributing factor to variations in distribution and density of many farmland (Siriwardena *et al.* 1998; Gregory & Baillie 1998) and forest bird species (Peach *et al.* 1998; Avery & Leslie 1990). Because such changes are rapid, a re-evaluation of landscape management techniques is required for successful conservation of existing bird species and communities (Tittler *et al.* 2001; Mason 2001).

Edge effects are often seen as a positive phenomenon in terms of bird density and species richness (Patterson *et al.* 1995, Hansson 1994, Forman 1995). Thus, landscape managers have tried to enhance the proportion of edge habitat, especially in managed forests, by reducing the size of clearcuts, and creation of border edge cuts (Fleming & Giuliano 1998).

Edges have been associated with high resource availability (Patterson *et al.* 1995; Cody 1985; Chen *et al.* 1992) and predation risk (Wilcove 1985; Angelstam 1992; Andrén 1995; Suarez *et al.* 1997; King *et al.* 1998; Soderstrom *et al.* 1998; DeGraaf *et al.* 1999), they also play a role in regulation of animal movements (Forman 1995, Fagan *et al.*1999). However, the perception of these edge effects must be dependent on the species observing them and the location of individuals in a patch; for example, the distance away from the edge. Despite studies on the width of edge effects (Gates & Mosher 1981; Hansson 1994; King *et al.* 1997), habitat preferences (McCollin 1998) and edge type (Hawrot & Niemi 1996), there has been little attempt to integrate these factors in understanding small-scale songbird distribution. I studied the interaction of tree age, edge type and distance from the boundary to determine how plantation patches affected the density of songbirds on a small (tens of metres) scale.

The definition of 'edge' varies and is sometimes misleading. Traditionally, an edge was characterised as the abrupt boundary between two habitat types (Odum 1971; Hawrot & Niemi 1996). More recently 'edge' has been used to describe the transition zone from the boundary of a habitat to a distance at which conditions (such as wind speed, or amount of light) show no further change with additional movement of the observer away from the boundary. An area where conditions remain unaltered with distance to the boundary is termed the 'centre' of the patch (Hawrot & Niemi 1996). It is the latter definition of edge and centre that will be used in this study.

4.1.1 Microclimate edge effects

Edge effects are a collection of phenomena that include abiotic and biotic gradients from the boundary to the centre of a patch (McCollin 1998). Abiotic conditions at the edge differ from those at the centre in both forested and clearfell patches (Forman 1995). At the edge of forested patches there are increased wind speeds (Forman 1995), sunshine (Matlack 1993) and temperature fluctuations (Matlack 1993), which cause a microclimatic gradient from the edge to the centre, most pronounced at the boundary (McCollin 1998). Trees along the boundary have higher windthrow risk and so potential for creating gaps in the canopy. However, the edges of clearfell and younger patches are sheltered from wind and sun when alongside older patches (Forman 1995). Environmental conditions at the edge of plantation patches thus differ from those at the centre, but not in consistent ways.

4.1.2 Resource availability at the edge

Birds may move along patch boundaries or use them to create a natural border to their territory (Desrochers & Fortin 2000). However, resource availability in the edge zone may also affect the density of birds found. Near to the boundary of a forested patch, higher solar radiation causes increases in cone density (Philipson 1987), generating a proliferation of resources for granivorous birds (Patterson *et al.* 1995). Cones are found in particularly high numbers in mast years, when there are unusually large cone crops in Norway and Sitka spruce (Petty *et al.* 1995). Higher densities of arthropods are found at the edge than the centre due to the higher solar input, biological influxes due to the wind (Helle & Muona 1985), and structural diversity and productivity (Patterson *et al.* 1995; Cody 1985; Chen *et al.* 1992) in the edge zone of forested patches. The trees at the edge of mature forested patches produce many, large side-branches (Patterson *et al.* 1995; Forman 1995), providing more insect niches and thus resources for insectivorous birds (Hansson 1983; Helle & Muona 1985). Young patches do not have as much structural diversity at their edges as mature patches, and clearfells have no differences in structural diversity at all. With such variations in microclimate and resource availability between edges and centres of patches it would be expected that there would be an effect of tree age on the distribution of birds across an edge. However, bird distribution is not controlled solely by resource availability and may also be affected by predation risk and habitat preferences.

4.1.3 Predation risk and edge contrast

Despite a large body of evidence suggesting that bird density and species richness are highest at forest edges (Gates & Gysel 1978; Hansson 1994; Patterson *et al.* 1995), edges are also associated with higher predation pressure, particularly forest/farmland edges (Wilcove 1985; Angelstam 1992; Andrén 1995; Suarez *et al.* 1997; King *et al.* 1998; Soderstrom *et al.* 1998; DeGraaf *et al.* 1999). Gates & Gysel (1978) termed this phenomenon of high resource availability combined with high predation risk an 'ecological trap'. At patch edges the high structural diversity provides dense cover and a larger number of suitable, protected foraging and nesting sites, making edges attractive to birds (Suhonen 1993). Despite this, high quality birds prefer to nest away from edges (Huhta *et al.* 1999), possibly as a predator avoidance strategy.

Predation can affect both adult birds and their nests. Thus, in areas dominated by edges, such as small patches of woodland there is greater nest predation (Wilcove 1985). However, in a study on nest predation in woodland strips, using plasticine and quails eggs in artificial, ground and arboreal nests, Darveau *et al.* (1997) found that the narrowest strips (20 m) had lower predation rates than did wider (60 m) strips, with nest predation decreasing again in yet wider strips. This may have been a product of scale perception with the predators unable to perceive the very smallest strips of habitat as large enough to consider foraging in. Jokimäki and Huhta (1996) found that crows were associated with fragmented areas with a high amount of edge habitat. This species is a generalist predator that is found extensively in Kielder Forest, and may contribute to higher predation pressure at the edge of patches.

Many predators preferentially hunt along edges between highly dissimilar habitats (termed 'hard' edges e.g. mature vs. clearfell or agricultural land) (for a review, see Andrén 1995). Hard edges, particularly those between forest and agricultural land, thus often have higher nest (Suarez *et al.* 1997; Heske *et al.* 1999) and adult (DeGraaf 1992; Gotmark & Post 1996; Krams 1996; Solonen 1997) predation rates than softer, more gradual edges. DeGraaf (1992) found that birds avoid hard edges more than soft edges. Hawrot & Neimi's (1996) study on conifer-hardwood forests showed that birds which displayed a positive edge effect were positively correlated with subtle and intermediate (mature/scrub) edges rather than with hard edges. It is expected therefore that bird density will be lowest in patches with a high edge contrast (Hawrot & Niemi 1996; Sargent *et al.* 1998).

Mammalian predators, including red squirrel, *Sciurus vulgaris* (Darveau *et al.* 1997), weasel, *Mustela nivalis,* stoat, *Mustela erminea* (King 1989) and red fox, *Vulpes vulpes* (Avery & Leslie 1990), all predate nests (eggs and nestlings) and often catch adult birds. Avian predators, including merlin, *Falco columbarius* (Little *et al.* 1995), sparrowhawk, *Accipter nisus* (Petty *et al.*, 1995), goshawk, *Accipter gentilus* (Newton, 1979; Toyne, 1998), kestrel, *Falco tinnunculus* (Village 1990), tawny owl, *Strix aluco* (Petty 1992), and crow, *Corvus corone* (Avery & Leslie 1990), prey on the nestling, fledgling and adult birds. Sparrowhawk is the most important predator of forest passerines (Newton 1986). This species has increased in numbers since major afforestation in the 20th century (Selas & Rafoss 1999) and feeds diurnally (Krams 1996). As mentioned above, the spatial distribution of predators may be affected by edge contrast. The spatial distribution of birds and nests may be affected by perceived predation risk, particularly predation by sparrowhawks (Solonen 1997). Therefore, in the present study, it is assumed that there is a link between edge contrast and perceived predation risk. In Gotmark and Post's (1996) study, relative predation risk by sparrowhawks was calculated for many birds of Swedish forests and farmland. This value gave an indication of the relative proportion of prey in a predator's diet using nest recoveries of prey remains.

4.1.4 Edges as barriers to movement

It has been shown that habitat type affects how birds move in the landscape; riparian strips are used as movement corridors by many passerine species (Machtans *et al.*

1996). Movement and dispersal may be limited by the surrounding habitats, with abrupt edges or highly unsuitable habitats acting as barriers to movement (Stamps *et al.* 1987; Wiens 1992; Forman 1995; Fagan *et al.* 1999). Several studies to date have incorporated edge 'hardness' to determine how an edge's structure will affect movement/distribution patterns of species (Stamps *et al.* 1987; Hawrot & Niemi 1996; see Ims 1995 for review). The simulation study of Stamps *et al.* (1987) showed that the higher the edge permeability (permeability gives an index of 'ease' of crossing a particular edge), the greater the chance of an individual moving into another patch. Small scale movements of foraging birds have been used to investigate edge-mediated movements with many species avoiding movement across edges (Poulsen 1994), perhaps perceiving high contrast edges as barriers to movement (Desroshers & Fortin 2000). The role of landscape structures as barriers to bird movements such as migration is well known (Meyer *et al.* 2000, Grattarola *et al.* 1999, Akesson 1999). It is possible that, on a local scale, hard edges will form a barrier to movement when finding a suitable territory or on a foraging trip.

4.1.5 Hypotheses and aims

I will explore how edge contrast, tree age, and distance from the boundary affect songbird densities. In particular, I will investigate the distribution of bird density from the boundary to the centre in the context of predation risk and resource availability. I will ascertain if hard edges around suitable patches act as barriers to movement and thus cause higher densities of birds in suitable patch types. The following hypotheses will be investigated: a. high densities of birds are found in their preferred habitat according to published preferences; b. species preferring habitats with low amounts of cover will place their nests away from the boundary; and, c. species with the highest predation risk will avoided hard edges.

4.2 Methodology

4.2.1 Bird counts and statistics

Breeding birds were surveyed in Sitka spruce patches in 1998 and 1999, using fixed radius (60 metre) point counts at the edge (on the boundary) and centre (150 m into the patch) according to the methodology outlined in Chapter 2. Data from the eleven most common species were used; these included crossbill, chaffinch, coal tit, dunnock, goldcrest, meadow pipit, robin, redpoll, siskin, wren and willow warbler (scientific names given in Table 4.3.1). Density at the edge and the centre of patches were calculated for each species as the number of birds detected per hectare (ha), to investigate if edge effects occurred at low resolution. Each centre point count covered 1.131 ha and each edge point count covered 0.566 ha. This calculation was performed for early and late spring in 1999 only, and the maximum density achieved over these two time periods was used for further analysis. The maximum density ensures that all breeding birds have been counted in a patch (Chapter 3). Generalised linear modelling in GLIM 4.09 was performed using Poisson errors and a weight file; overdispersion of the data was checked for as outlined in Chapter 2. The significance level was set at the conventional value of 0.05. The edge or centre was coded as 1 or 2 and used as a factor in the analysis.

To investigate edge effects at a finer resolution, point counts were divided into equal distance sectors (zones) using lines parallel to the boundary at 30-metre intervals (Figure 2.5). I was thus able to calculate the density (birds ha^{-1}) of a species from the boundary to the centre at 30 m intervals. Maximum density over early and late spring, in 1998 and 1999, was calculated. All distance bands for each point count (two distance bands for half point counts and four for whole point counts) were collected simultaneously. Therefore, there was interdependence of data in distance bands from the same point count. Because a bird cannot be in the same place at the same time within a point count, there may have been inflated occurrences of false absences (P. Osborne *pers comm.*). If an individual's territory covers an area that spans two distance bands, and it is counted in one distance band, then a false zero occurrence value is automatically assigned to the adjacent distance band. Therefore, the latter distance band is classed as unsuitable habitat. However, the large numbers of point counts and patches surveyed may average out these types of errors.

Although useful for the present study as it utilises data ideal for bird/habitat modelling, this adapted point count methodology is not the ideal method for investigating patch use on a small scale by passerines. A radio-tracking study of the eleven common species would enable analyses of the proportion of time spent in various areas of the patch. However, a previous radio-telemetry study of Kielder Forest passerines in 1992-1993 showed that eight of the nine tagged birds were predated within the first 36 hours, and radio-tracking was consequently abandoned (Cosgrove 1995). The recent reduction in weight and volume of radio-telemetry devices may now enable successful radio-tracking of small passerines.

Tree age was divided into three age classes termed mature (>15 years old), pre-thicket (6-15 years) and young (clearfell-5 years). A stratified random sample of sites was generated using a GIS (Geographical Information System) of Kielder Forest, which showed the age of the Sitka patch, and the age of the adjacent Sitka patch. Three edge contrasts were used; soft edges (mature vs. pre-thicket), intermediate (young vs. pre-thicket) and hard edges (mature vs. young). Soft edges were formed between two similar patches (e.g. forested patches composed of such as mature and pre-thicket trees), hard between two dissimilar patches (e.g. mature and young trees). The young vs. pre-thicket edge contrasts were termed intermediate as they were not well established edges (i.e. they were formed less than 5 years before this study took place), however they were not as dissimilar as the mature vs. young edge contrast. Thus tree age, edge contrast, and distance to boundary were all included in analysis of bird density.

Modelling was carried out for the 1998 and the 1999 data using Poisson errors generalised linear modelling techniques (see Chapter 2 for details of modelling procedure). The hypothesis that there was no significant difference in songbird density among edge types, tree ages, distance from the boundary or any interactions between these variables was tested. The significance level was set at the conventional p-value of 0.05. All three variables were added as factors to the models, with tree age coded as three age codes, edge contrast as three categories and distance to boundary as six categories. The most parsimonious model, with the least number of variables included, was returned for each species. The parameter values were obtained from the model for each variable that significantly contributed to the equation. In Poisson error analysis the parameter values are natural-log values of the true density of birds. These were plotted with the standard errors associated with them. Conversion back to the original units, using the exponential, was not used, as the standard errors would not have been correct for these values. The standard errors give an indication of the precision of the estimation of the sample mean (Zar 1999). If the standard error bars of two samples do not overlap then there is a higher likelihood that they are different to each other (Zar 1999), however this cannot be taken as a test for significant differences (Zar 1999).

4.2.2 Cone counts

Cone counts were measured using eight transects through trees aged between 35-44 years old in September 1999 by Peter Lürz and Claire McSorley. Transects were placed at right angles to the boundary and the numbers of fallen cones were counted every square metre from the boundary to 40 m into the patch, by which point the density of cones had remained relatively unchanged for 20 metres. Kruskall-Wallis non-parametric ANOVA was used in SPSS (1998) to determine whether there was a significant difference in the density of cones from the edge to the centre.

4.2.3 Relative predation risk

Relative predation risk (RPR) was calculated using data from a study in Kielder Forest in 1992 (Petty *et al.* 1995), a non-mast year, utilising a similar method to Götmark & Post (1996). The maximum densities (birds per hectare) between early and late spring were calculated for the eleven most abundant bird species (data taken from Petty *et al.* 1995). The numbers of prey items were counted at sparrowhawk 'plucking posts' near to their nest sites unlike Gotmark and Post (1996) who used prey remains from sparrowhawk nests. The numbers of the eleven passerine species counted at plucking posts were ranked according to their relative abundance in the whole sample, with the species comprising most of the whole sample being assigned the top rank of 1. The RPR was calculated by subtracting the rank value of a species in the sparrowhawk diet from the rank value of the species in the population (Götmark & Post 1996). Unfortunately, only small numbers of prey samples could be taken from plucking posts and so the sample sizes for the numbers of different prey species in the sparrowhawk diet were sometimes very low (Table 4.3.1), rendering the reliability of the RPR calculation questionable. Despite this, it was the best available data at time of writing and so was used in this thesis.

4.3 Results

4.3.1 Cone crop and relative predation risk

Figure 4.3.1 shows the spatial distribution of cones from the boundary to 40 m into the patch. Beyond 40m there were very few or no fallen cones (Lürz *pers obs*). Cone density was highest in the first 15m, with a bimodal peak of density at 4m and 10m (Kruskall-Wallis non-parametric ANOVA; $Chi^2 = 109.634$, df = 39, p-value = <0.001). It is unknown why there should be this bimodal pattern. The distance between the tree trunks was 2 to 3 metres but rarely more (*pers obs.*), and therefore this could not account for the bimodality. Cone density was low to negligible beyond 15m from the boundary. Table 4.3.1 shows the results for the RPR calculations, with robin being predated most by sparrowhawk and goldcrest least, relative to their densities in the population.

4.3.2 Models

Seven of the eleven species showed significant low resolution positive edge effects ($p < 0.05$), with edge half point counts containing significantly more individuals of a species per hectare than the centre full point counts (Table 4.3.2). Only one species, the meadow pipit, showed edge avoidance (Table 4.3.2). However, the higher resolution models explaining bird density variation from the boundary to the centre of a patch, in relation to tree age and edge type showed that edge effects were more complex than the above simple attraction or repulsion models imply.

The higher resolution models of bird density at varying distances from the boundary, tree ages and edge types were quite complex including main effects and interaction terms. Only the chaffinch model included a three-way interaction between distance from the boundary, tree age and edge contrast (Table 4.3.3). In mature trees that were next to young patches, chaffinch were found at lower densities in the 120-150 metre (m) zone than in the same zone in mature trees that were next to pre-thicket areas (Figure. 4.3.2 b_3.). There was some evidence for gradual decreases in density from the boundary to the centre in mature trees (Figure. 4.3.2 b_3.). In pre-thicket patches adjacent to young patches from 90-210 metres the density fell to very low levels (Figure 4.3.2 b_2).

However, in young patches (Figure 4.3.2 b_1) there were no appreciable differences in density from the boundary to 210 metres into the patch, except for boundary avoidance in the young/pre-thicket contrast.

Coal tit (Figure 4.3.2 d.) and goldcrest (Figure 4.3.2 f.) were found at higher densities in mature trees than in pre-thicket or young, with lowest densities in the latter. Coal tit preferred mature trees with softer edges (between mature and pre-thicket trees), to those with hard edges between mature and young trees. They did not occur in young habitat adjacent to pre-thicket habitats. Edge contrast had no effect on the density of coal tit in pre-thicket trees (Figure 4.3.2 c). The boundary seemed to have no effect on the density of coal tit in the mature/pre-thicket edge contrast, consistent with the lack of evidence for a positive edge effect shown in Table 4.3.2. There is evidence of edge avoidance in coal tit in the patches of mature/young edge contrasts (Figure 4.3.2 d.). Goldcrest showed a positive edge effect, with higher density in the boundary zone (0-30m) than in any other zone (Figure 4.3.2 g.).

As with goldcrest, crossbill were found at their highest (but variable) densities in mature trees (Figure 4.3.2 a.), at the edge. This probably accounts for the positive large-scale edge effect found in Table 4.3.2. In pre-thicket trees the density was more uniform across the edge, with negligible density in young trees.

Dunnock (Figure 4.3.2 e.), redpoll (Figure 4.3.2 m.), wren (Figure 4.3.2 q.) and willow warbler (Figure 4.3.2 t.) were all found at higher densities in pre-thicket trees than in any other tree age. Dunnock (Figure 4.3.2 e.), redpoll (Figure 4.3.2 m.) and willow warbler (Figure 4.3.2 t.) all avoided the boundary zone (0-30m) in pre-thicket trees, showing a bimodal distribution of density with peaks in the 30-120m zone and in the 180-210m zone. Wren also had a bimodal pattern of distribution, although they occurred across all tree ages (Figure 4.3.2 s.).

In mature trees, redpoll were found at high densities in the 0-30m zone, although no significant edge effects occurred in young trees (Figure 4.3.2 m.). Redpoll significantly preferred the habitats forming pre-thicket/young edge contrasts, with intermediate density in pre-thicket/mature edge contrast patches and finally significantly lowest density in the hard edges formed between the contrast of mature and young trees (Figure 4.3.2 n.).

Paradoxically, although wren density was higher in pre-thicket trees than in either young or mature trees, density was higher in the mature and young edge contrast (hard edges), with pre-thicket and young (intermediate) having lower density, and pre-thicket and mature (soft edges) having the lowest density. However, willow warbler, which also prefer the pre-thicket patches, had their highest densities in patches that formed pre-thicket and mature edge contrasts (soft edges), then pre-thicket and young (intermediate edges), and lastly lowest densities in mature and young edge contrasts (hard edges). This is consistent with willow warbler density being highest in pre-thicket, then mature and finally young patches.

Consistent with Table 4.3.2, siskin showed a positive edge effect with density gradually decreasing from the boundary to the centre of the patch (Figure 4.3.2 p.). High siskin densities were found in pre-thicket and mature trees (Figure 4.3.2 o.). However, the mature trees adjacent to young trees (forming a hard edge) were avoided, as were young habitats adjacent to both pre-thicket and mature patches.

Meadow pipit displayed a negative, low resolution, edge effect (Table 4.3.2) which is upheld by Figure 4.3.2 i). Meadow pipit were found in their highest densities in young habitats, then pre-thicket but only in negligible numbers in mature trees (Figure 4.3.2 i). In mature habitats the highest density (which is much lower than any values observed in the former two patches) is at the boundary zone (0-30m). The pattern of density distribution in pre-thicket and young tree shows a remarkable similarity. Consistent with this is the overall higher density in trees forming the pre-thicket and young edge contrast and lowest density in the pre-thicket and mature edge contrast (Figure 4.3.2 h).

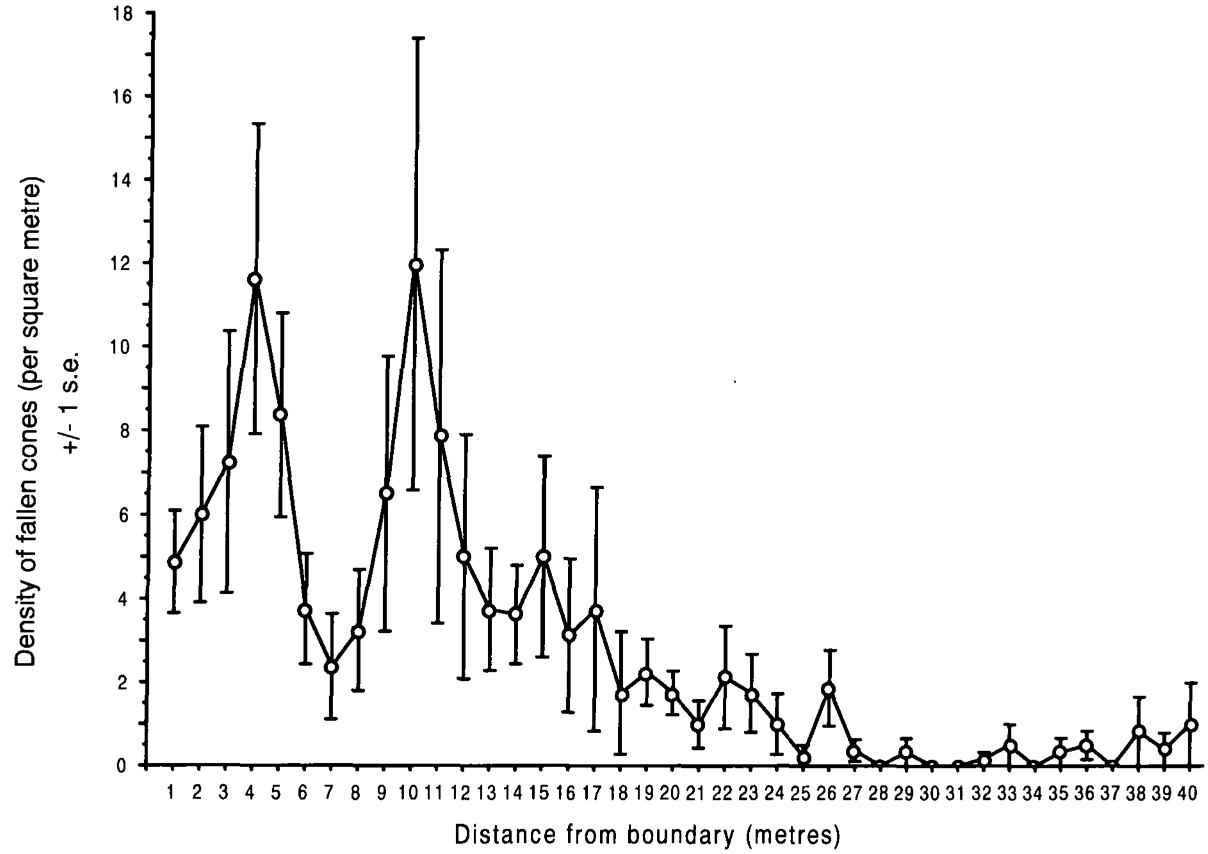


Figure 4.3.1: Transect results of cones counted per square metre from the boundary to the centre of Sitka spruce patches. 8 transects were surveyed. Standard errors of the mean (s.e.) are displayed.

Species	*Latin name*	*prey*	*rank*	*density*	*rank*	*RPR*
robin	*Erithacus rubecula*	16	2	0.51	7	5
meadow pipit	*Anthus pratensis*	9	4	0.46	8	4
wren	*Troglodytes troglodytes*	4	5	0.45	9	4
dunnock	*Prunella modularis*	2	7	0.13	10	3
chaffinch	*Fringilla coelebs*	55	1	8.80	2	1
crossbill	*Loxia curvirostra*	0	11	0	11	0
coal tit	*Parus ater*	3	6	1.28	6	0
siskin	*Carduelis spinus*	9	4	3.04	3	-1
redpoll	*Carduelis flammea*	1	9	1.67	5	-4
willow warbler	*Phylloscopus trochilus*	1	9	2.50	4	-5
goldcrest	*Regulus regulus*	0	11	9.08	1	-10

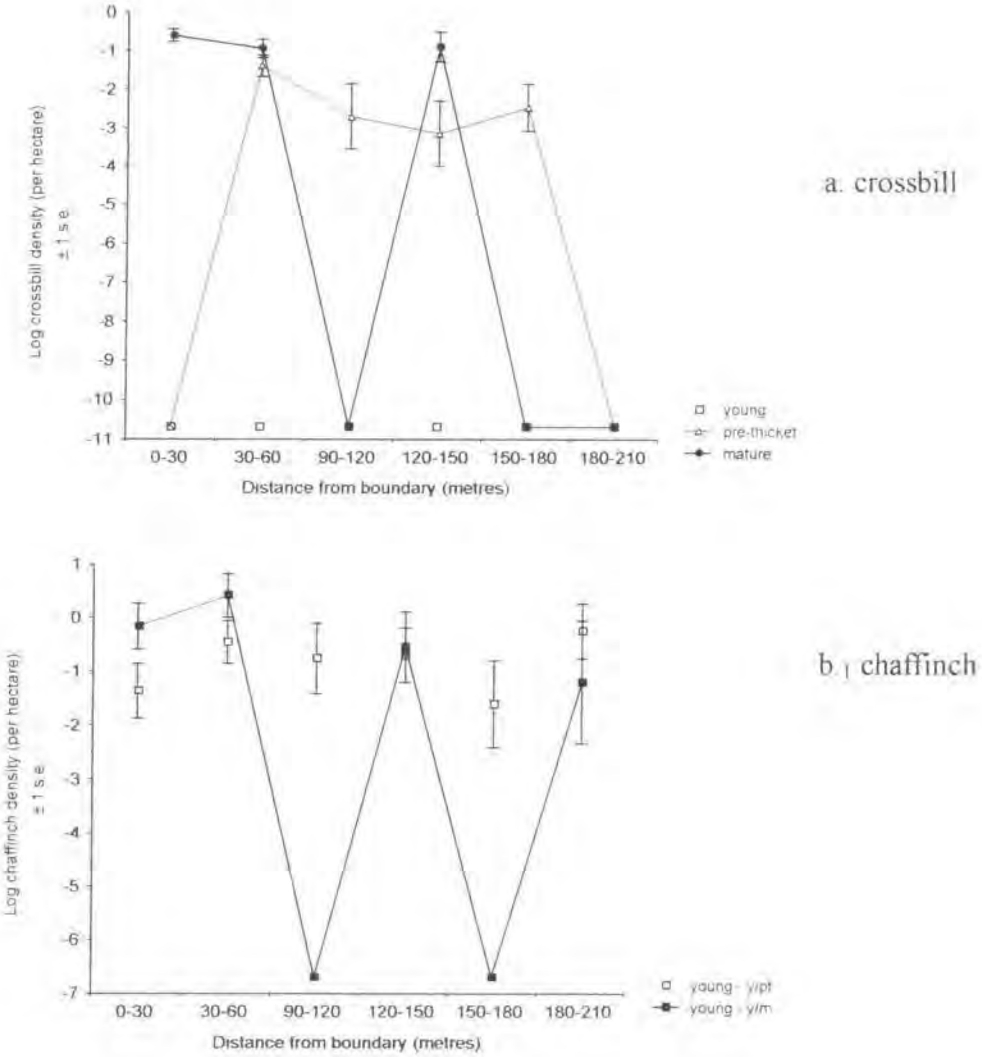
Table 4.3.1: Table of relative predation risk, according to Götmark & Post (1996), in Kielder Forest in 1992, using the prey = number of individuals found in sparrowhawk nests, and density = passerine density in whole forest. Predator and prey data taken from Petty *et al.* (1995).

Species	*Generalised Linear Model*			
	χ^2	*df*	*p-value*	*Direction*
crossbill	6.93	1	<0.01	+
chaffinch	39.57	1	<0.001	+
coal tit	2.60	1	ns	
dunnock	2.22	1	ns	
goldcrest	19.13	1	<0.001	+
meadow pipit	12.90	1	<0.001	-
robin	13.68	1	<0.001	+
redpoll	1.60	1	ns	
siskin	20.50	1	<0.001	+
wren	23.83	1	<0.001	+
willow warbler	5.01	1	<0.05	+

Table 4.3.2: Bird density in 1999 at the edge compared to the centre of patches using GLM and displaying the direction of the edge effect (+ = positive edge effect with more birds found at the edge; - = negative edge effect).

Species	*Generalised Linear Model*				
	Variables included in GLM		χ^2	*df*	*p-value*
crossbill	1.	AC.P	34.50	10	<0.001
chaffinch	1.	AC.C.P	17.99	5	<0.005
coal tit	1.	AC.C	4.11	1	<0.05
	2.	C.P	22.48	10	<0.025
dunnock	1.	AC.P	34.67	10	<0.001
goldcrest	1.	AC	273.80	2	<0.001
	2.	P	16.59	5	<0.01
meadow pipit	1.	AC.C	5.60	1	<0.025
	2.	AC.P	20.33	10	<0.05
	3.	C.P	27.28	10	<0.005
robin	1.	AC.P	23.24	10	<0.01
	2.	C	7.78	2	<0.025
redpoll	1.	AC.P *	35.09	10	<0.001
	2.	C	18.60	2	<0.001
siskin	1.	AC.C	7.75	1	<0.01
	2.	P	30.28	5	<0.001
wren	1.	AC	52.54	2	<0.001
	2.	C	14.31	2	<0.001
	3.	P	47.38	5	<0.001
willow warbler	1.	AC.P	43.63	10	<0.001
	2.	C	13.97	2	<0.001

Table 4.3.3: Generalised linear models of bird density in 1999 using Poisson errors with P = distance from boundary, AC = age code of trees, and C = edge contrast. Chi-squared values (χ^2) are the χ^2 change when a factor is removed from the model. Models that were exactly the same in 1999 as in 1998 are asterisked.



a: crossbill

b.1 chaffinch

Figure 4.3.2 a-b$_1$: Graphical representation of 1999 GLM models (Table 4.3.3) for crossbill and chaffinch showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts. The chaffinch three-way model has been split into b.1-3 for ease of interpretation.

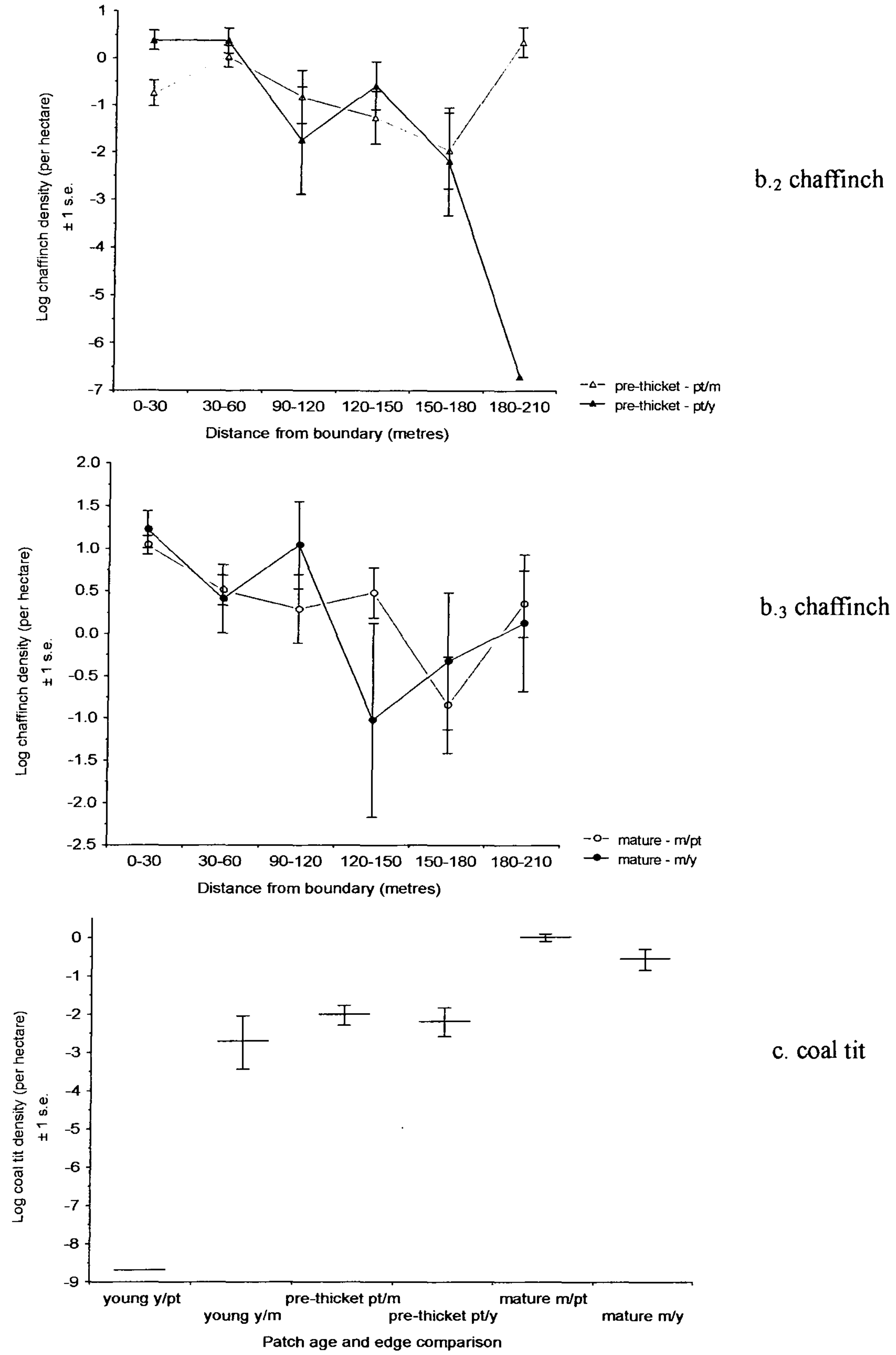


Figure 4.3.2 b$_2$-c: Graphical representation of 1999 GLM models (Table 4.3.3) for chaffinch and coal tit showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.

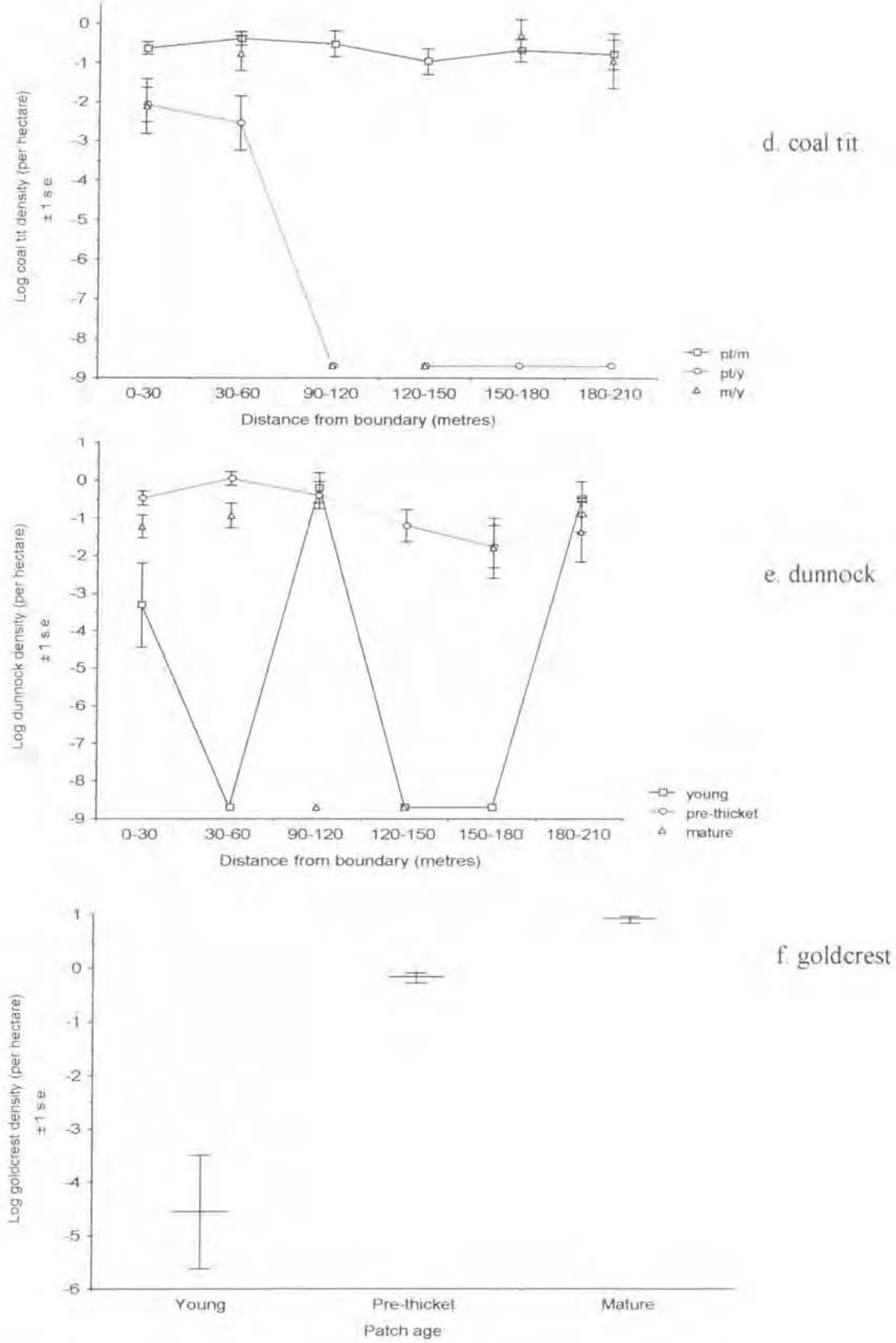


Figure 4.3.2 d-f: Graphical representation of 1999 GLM models (Table 4.3.3) for coal tit, dunnock and goldcrest showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.

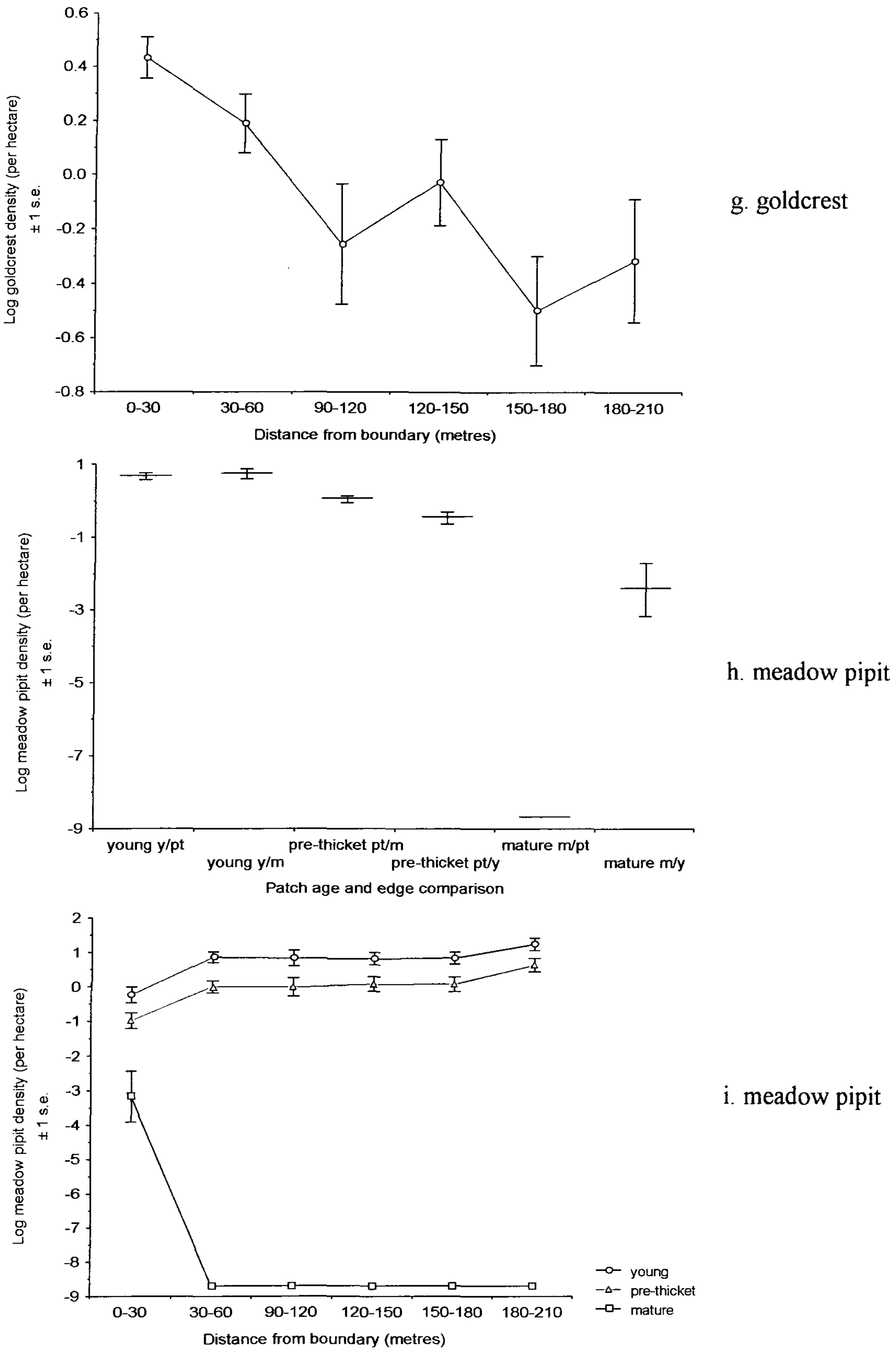


Figure 4.3.2 g-i: Graphical representation of 1999 GLM models (Table 4.3.3) for goldcrest and meadow pipit showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.

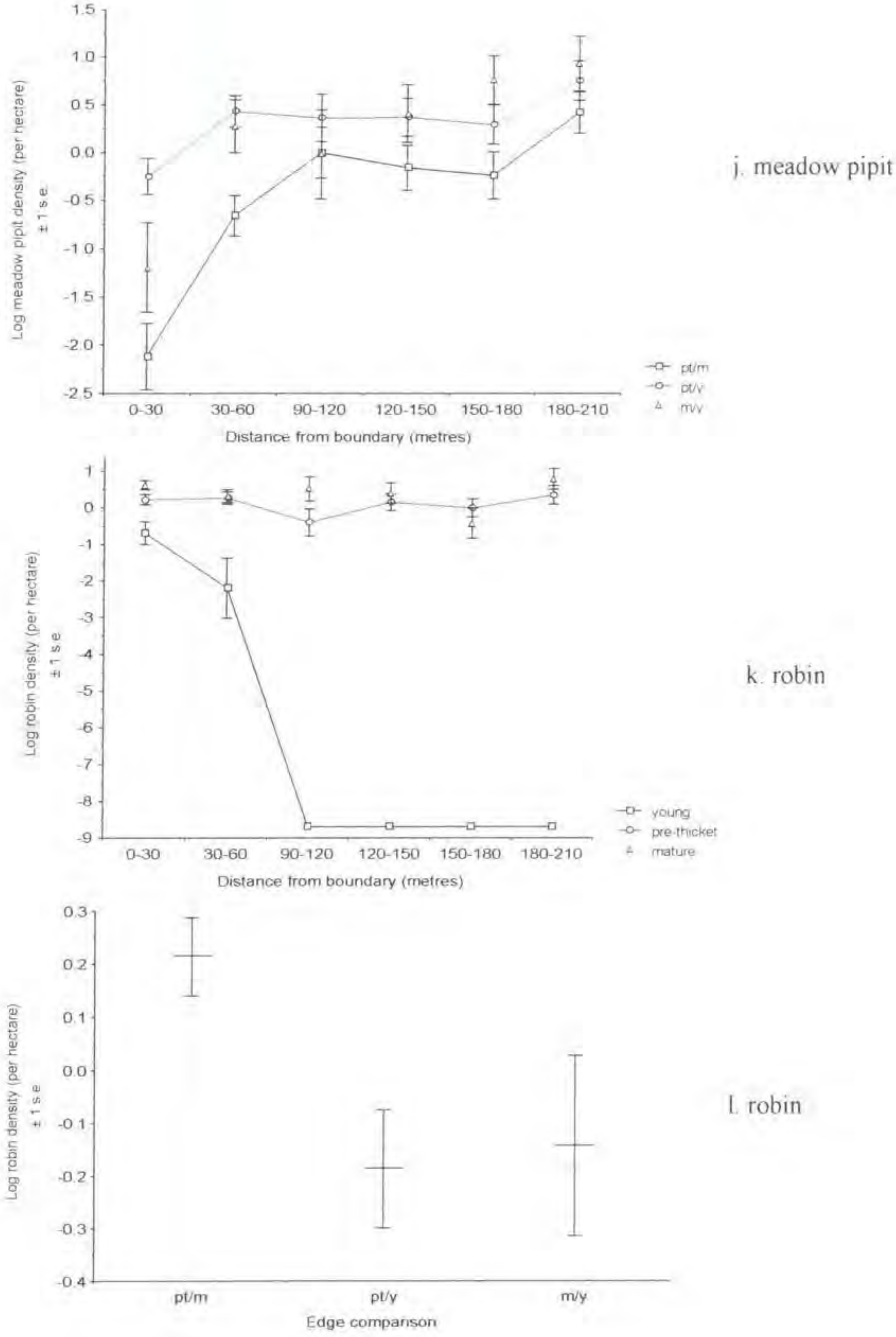


Figure 4.3.2 j-l: Graphical representation of 1999 GLM models (Table 4.3.3) for meadow pipit and robin showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.

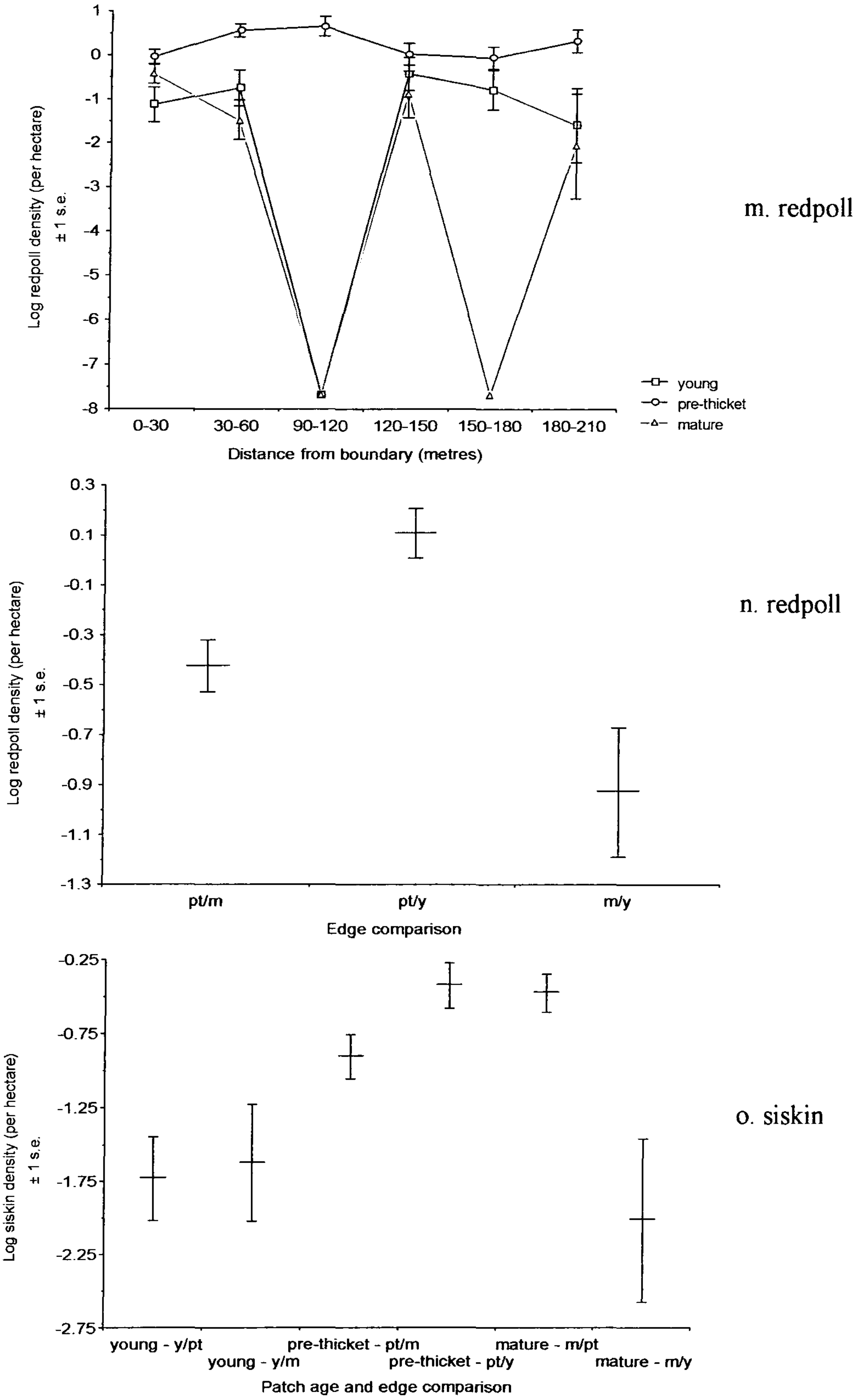


Figure 4.3.2 m-o: Graphical representation of 1999 GLM models (Table 4.3.3) for redpoll and siskin showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.

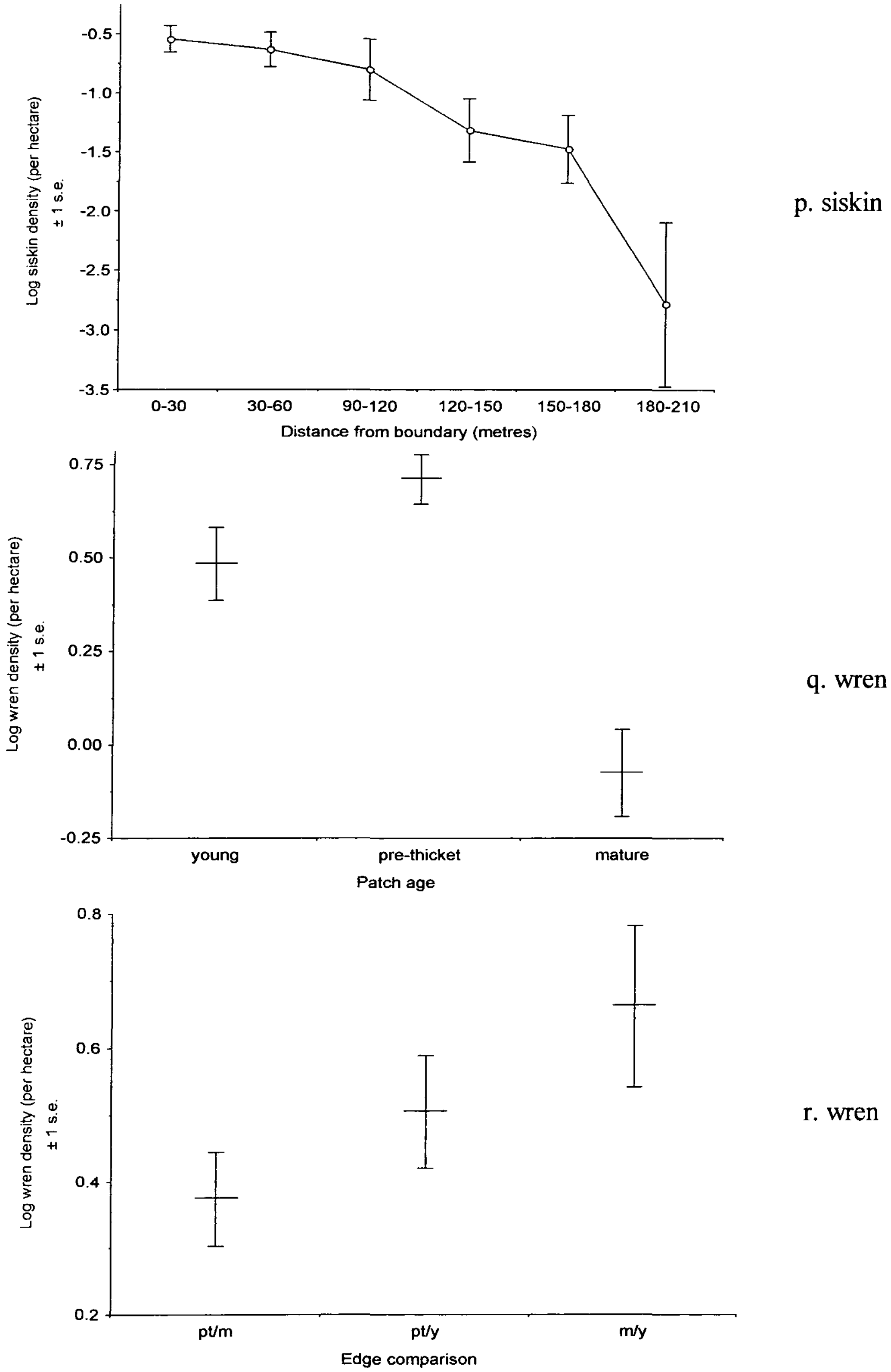
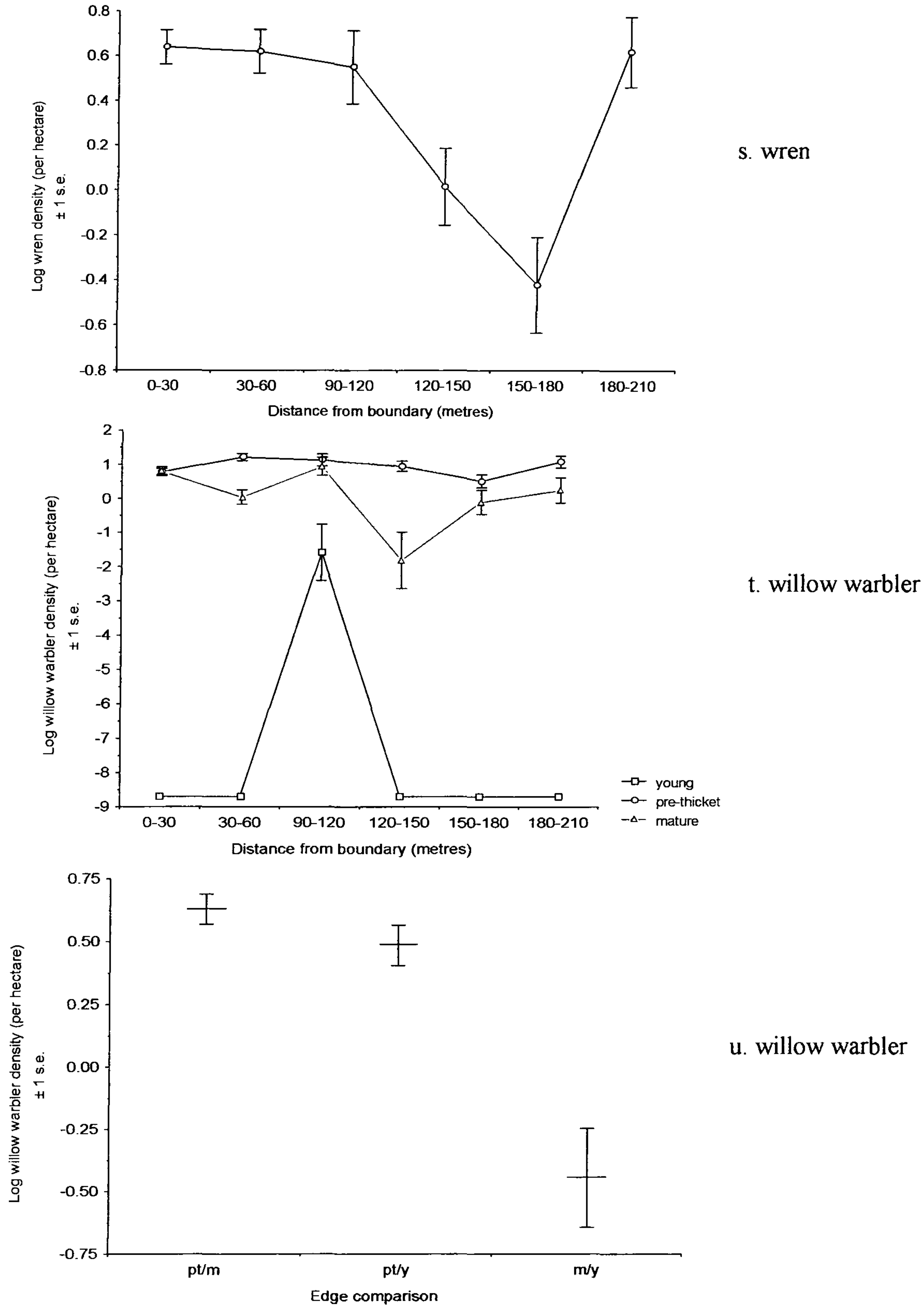


Figure 4.3.2 p-r: Graphical representation of 1999 GLM models (Table 4.3.3) for siskin and wren showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.



s. wren

t. willow warbler

u. willow warbler

Figure 4.3.2 s-u: Graphical representation of 1999 GLM models (Table 4.3.3) for wren and willow warbler showing significant effects of patch age, edge contrast and distance from the boundary on bird density with standard error bars. Abbreviations y, pt and m refer to patch ages of young (0-5 years), pre-thicket (6-15 years) and mature (>15 years), and pt/m, pt/y and m/y refer to edge contrasts using the former patch age contrasts.

4.4 Discussion

4.4.1 Age effects

As was expected from known habitat preferences, crossbill, coal tit and goldcrest were all found at highest densities in mature trees; the highest densities of willow warbler, siskin, wren, dunnock and redpoll were found in pre-thicket trees, and of meadow pipit in young trees or clearfell (Newton 1972; Cramp 1988 - 1994).

4.4.2 Functional edge width

On the larger scale (low resolution) positive edge effects were more prevalent than negative edge effects (Table 4.3.2) with crossbill, chaffinch, goldcrest, robin, siskin, wren and willow warbler all found at higher densities (birds.ha^{-1}) in the edge point counts than in the centre point counts. This positive edge effect may not just be a product of the differences in vegetation and cones at the edge, the trees at the edge may also be used as more obvious territorial song-posts than trees in the centre of patches (Hansson 1994). The positive edge effects for chaffinch, goldcrest, robin, siskin and willow warbler agreed well with Hansson's (1994) study on Swedish forest birds. However, when viewed as a transition zone rather than a linear feature, the results (Figures 4.3.2 a-u.) indicated that edge effects were far from simple. The results presented next challenge the commonly held belief that 'edges' of managed forestry patches generally contain higher densities of birds than the 'interior' of patches (Patterson *et al.* 1995; Hansson 1994).

4.4.2.1 Boundary zone avoidance

Five species had peaks of density displaced away from the boundary zone (0-30 m). These included chaffinch, dunnock, meadow pipit, redpoll and willow warbler. Species with the highest vulnerability to avian predation, for example robin and wren (Table 4.3.1), did not necessarily show peaks of density displaced away from the boundary zone, except for meadow pipit, which had the second highest vulnerability score and showed edge avoidance (Table 4.3.2). Four of these species were found at highest densities in the more open habitats such as young (meadow pipit) or pre-thicket (dunnock, redpoll and willow warbler) trees. As discussed in section 4.1 Introduction, although in European forests edge effects are generally a positive phenomenon, there are also negative edge effects, with birds avoiding patch edges because of higher predation pressure. At large and small scales, there is certainly evidence of edge ambivalence (dunnock and redpoll), and strong evidence of edge avoidance (meadow pipit). Therefore, in terms of management, the habitat adjacent to the boundary does not have a positive effect on these three species mentioned, particularly in young or pre-thicket habitats.

Despite avoidance of the distance band immediately adjacent to the boundary of pre-thicket trees, the densities of willow warbler are greater in each of the three distance bands covering the first 0-120 metres, than in the subsequent three distance bands further into the patch. The management implications are that patch edges remain an important habitat for willow warbler, despite relative avoidance of the boundary zone compared to the distance band immediately adjacent. This is also true for the chaffinch, which also shows an overall positive edge effect, despite boundary avoidance in pre-thicket trees (Table 4.3.2).

It is likely that resource availability, such as food and sufficient cover, at the edges of the younger patches would not be sufficient for the birds to overcome the risk of foraging at the boundary, unlike in the mature trees. When found in young and pre-thicket patches the chaffinch also displayed a peak of density displaced from the boundary. However, in mature trees, in accordance with the higher food availability and cover, there was a density peak at the boundary zone (0-30m).

In pre-thicket trees willow warbler avoided the boundary zone (0-30m) (Figure 4.3.2 t.) however, this is unlikely to be due to predation pressure as its RPR was second lowest overall (Table 4.3.1). This may be a response to this type of habitat structure, and not an actual predator avoidance strategy *per se*. In migrant species it is difficult to tease apart direct responses to the British environment from those in its wintering grounds.

4.4.2.2 Boundary zone attraction

It was predicted that granivorous birds such as crossbill, chaffinch, redpoll, and siskin would be attracted to the boundary zone (0-30 metres) in mature trees, due to the higher cone crop in this area (Figure 4.3.1). This was found to be the case for chaffinch, redpoll and crossbill (Figures 4.3.2 b. m. & a. respectively). There was no interaction between distance from the edge and tree age in the siskin model (Table 4.3.3) and so it was difficult to reach any conclusions about whether boundary attraction was most pronounced in mature trees. However, siskin certainly had higher densities at the edge across all tree ages (Figure 4.3.2 p.). It can be concluded that chaffinch, redpoll and crossbill foraged more readily where food was more abundant and structural diversity was high, such as the boundary zone (0-30m) in mature trees, despite the higher predation pressure at the edge. McCollin (1993) suggested that colonial nesters, such as redpoll and crossbill, were more likely to be edge species. This was probably due to 'safety in numbers', allowing these species to forage in loose flocks at the edge (*pers obs*). In pre-thicket trees, where the difference in food abundance and structural diversity between centre and edge was not as extreme, the advantage to foraging at the boundary zone (0-30m) was less, resulting in boundary zone avoidance.

Goldcrest was found at highest density in the mature trees (Figure 4.3.2 f.). In addition goldcrest had a higher density at the boundary of patches than the centre (Figure 4.3.2 g.). The higher predation pressure at the edge was outweighed by the greater amount of resources at the edges (particularly in the most suitable habitat, the mature patches) because of goldcrest's low RPR. Species with an RPR (Table 4.3.1) close to 0 (wren, siskin, and coal tit) did not have a higher density at the boundary zone; in fact siskin and wren density remained relatively constant from 0-120 metres, and then decreased towards the patch centre (see Figure 4.3.2 p for siskin and Figure 4.3.2 s for wren).

Despite the RPR indices for each species being calculated using data from Kielder Forest in a non-mast year (1992), which was similar to 1998 and 1999, the RPR did not seem to bear strong relationships to the patterns of bird distribution. There are inherent problems of sampling and identifying dead prey species, which may bias the results. In addition to using dead prey data, calculation of the RPR also utilises data from a previous breeding bird survey in 1992 (see Chapter 3 for a comparison of these two studies). Differences in methodology and observers may have caused biases in the two data sets, generating a disparity in the density of birds detected.

4.4.2.3 Bimodal Pattern

Chaffinch, dunnock, goldcrest, robin, redpoll, wren and willow warbler showed some degree of bimodality of density with distance from the boundary. These species showed peaks of density at or near to the boundary, then a significant trough, followed by another peak in density towards the interior of the patch (Figures 4.3.2 b_2, e, g, k, m, s, & t. respectively). This may reflect a trade-off whereby there is segregation of singing/foraging areas and nesting areas because of variations in the habitat quality and predation pressure.

Huhta *et al.* (1999) found that the mass of nestlings in nests closer to the forest edge was lower than those at the centre were. When the nest is placed close to the boundary, it is possible that nest defence has to occur at a higher intensity, because of high predation risk causing inefficient foraging. Resource defence takes place where the benefits outweigh the costs (Krebs & Davies 1993); therefore, at the highly productive edges there will be more intense displays of territoriality, and thus higher numbers of birds detected. The nest is placed in the relatively 'safe' yet resource poor area away from the boundary (McCollin 1998) and foraging activity occurs where resources, yet predation risk, are high at the boundary zone (0-30m). I suggest that nest and resource defence could have caused these peaks in activity in these areas.

4.4.3 Edge contrast

Overall density was generally lower in hard edges (those between two highly dissimilar patches), similar to the results of DeGraaf (1992) who found that lowest density was found at the edges formed between those patches that were most dissimilar i.e. hard edges. However, tree age clearly played a role in determining the perception of edge contrast by a species.

Wren, willow warbler, robin, and redpoll had edge contrast as a main explanatory variable in their models (Table 4.3.3). The wren had a peculiar distribution of density; wren density was highest in pre-thicket trees. However, when edge contrast was considered, the highest density was found in the trees forming the mature and young edge contrast. Why should wren density be highest in the edge contrast formed between the young and mature trees (marginal and unsuitable habitats respectively)? It is highly probable that wren used several patches of different age; their diet is catholic, although most food is taken from the ground or up to only about 2 metres above ground (Cramp 1988 - 1994). The highly diverse habitat of the mature/young edge contrast may have provided plenty of scrub habitat, brash (the twigs and branches left after clear-felling) and fallen trees (Cramp 1988 - 1994).

The densities of robin, willow warbler and redpoll were highest in the edge contrast formed by the two most suitable tree ages, with the lowest densities being found in the unsuitable and intermediate edge contrast. However, when the interaction between tree age and edge contrast is considered the relationship becomes more complex.

There was no evidence of an 'overspill effect' from a suitable patch to adjacent marginal patches, with the exception of siskin where density in mature/pre-thicket edge contrasts was significantly higher than in mature/young edge contrasts. Meadow pipit and coal tit were not affected by edge contrast in this manner. Meadow pipit avoided all edges, and thus it can be inferred that the influence of the adjacent habitat is unlikely to exert much effect on the patch in question. However, meadow pipit was found in higher densities in marginal patches (pre-thicket) that were next to unsuitable patches (mature) than in marginal patches next to suitable patches (young). It is possible that with their high structural diversity, and thus protection from predatory attack, mature/pre-thicket edges were more attractive to meadow pipit than the harder edge formed between pre-thicket trees and young.

High densities of coal tit were also found in the mature/pre-thicket edge contrasts, particularly in the mature component of this edge contrast. Again this was probably attributable to the greater amount of cover in mature/pre-thicket edges than in other types, rather than anything to do with edge permeability. However, coal tit density in the marginal patches (pre-thicket) was not appreciably different when the pre-thicket trees were adjacent to mature trees (suitable) or young trees (unsuitable). This is in contrast to the meadow pipit whose highest densities in marginal patches were found when the marginal patches were adjacent to unsuitable patches. Although coal tit did not have a high RPR, density was not highest at the edge of patches. This lack of edge effect may have generated the coal tit apparent ambivalence to edge contrast in marginal patches. The higher density of coal tit in the young part of the young/mature edge contrast than in the young/pre-thicket may be accounted for by the use of young trees for occasional foraging trips from the mature trees (its preferred habitat).

As with Hansson's (1994) study, the species occurring at the highest density was the chaffinch with maximum density in mature trees at the edge reaching almost 3.5 birds ha^{-1} (exponential of 1.25) (Figure 4.3.2 b_3). The chaffinch model included a three-way interaction between tree age, distance from boundary and edge contrast. In mature trees chaffinch density was not lowest in hard edges (mature/young). In fact when considering pre-thicket trees, those adjacent to young trees (intermediate edges) had higher chaffinch density in the 0-30 m zone than those pre-thicket trees adjacent to mature trees (soft edges) (Figure 4.3.2 b_2). Higher chaffinch density was found at the boundary zone (0-30 m) of young trees that formed a hard edge (adjacent to mature trees) than in young trees that formed an intermediate edge (adjacent to pre-thicket trees). No clear conclusions can be made about chaffinch density in the other zones as a result of high variability in the data. Overall hard and intermediate edges were not correlated with low chaffinch density.

4.4.4 Conclusions

Edge effects were prevalent in this study. However, it was clear that many species' territories included the edge and the centre of forested and clearfell patches. Although the scale of Hansson's study (1994) was similar to my present study, it is possible that both investigations did not encompass the true 'centre' of patches. My study has implications for the core area concept, providing empirical evidence that core area (the area within a patch that is no longer affected by the edge) is not the same for all habitats and all species, agreeing with the simulation study of Öhman & Eriksson (1998).

In terms of management implications, it is clear that if patches are made too small then they may not contain a 'centre' area, which is important for many of the species studied here, particularly those found in pre-thicket or young trees. However, if the patches are made too large, then the edge: centre ratio may become so small, as to reduce any positive edge effects. This may result in a decrease in the densities of those species found particularly in mature edges, such as goldcrest. Therefore, all patches should be larger than 420 metres (two times 210 metres) at their narrowest part, as some species (chaffinch, coal tit, dunnock, meadow pipit, redpoll, wren and willow warbler) show peaks of density at 180-210 m from the patch boundary.

Edge contrast was a major factor in determining bird density. All edge types had their validity for the bird community; however, overall, the mature/young edge comparison was correlated more often with lower bird density than any other edge comparison. It is proposed that softer edges would benefit the bird community overall if migrants, such as the willow warbler, are to be attracted to the forest. Redpoll suffered declines in the 1990's (Balmer & Wernham 1999), possibly because of dramatic declines in their winter food supplies. Thus an increase in the amount of pre-thicket patches may help in the recovery of redpoll, especially in Kielder.

The rotational clearcutting regime generates a heterogeneous landscape pattern that creates enough different types of edge habitat to sustain a varied avian community. If selective felling is implemented, as proposed by the UK Forestry Commission, then this heterogeneity will be lost because of a decrease in the amount of edge habitat. As shown in this present study, many of the passerine species are clearly utilising the edge of patches; therefore, reduction of the amount of edge habitat may contribute to a decline of the existing songbird population. However, border edge cuts (Fleming & Giuliano 1998), where a 'fringe' of mature trees is left standing at the edge of clearcuts, may soften hard edges and therefore, benefit the avian community.

5 Modelling of the density and probability of occurrence of songbirds: a GIS approach.

Abstract

Predictive spatial modelling of animal populations using GIS can give landscape managers practical tools for modifying landuse patterns according to conservation priorities. In this chapter I show how landscape structure and composition affects songbird densities and probabilities of occurrence. Significant models of low to high explanatory power were generated using data collected in 1999, for the eleven songbird species studied here (r^2 ranged between 0.034-0.636 for generalised linear models and r^2 ranged between 0.055-0.582 for logistic regressions). Model validations using the previous year's data (1998) were generally not robust, indicating that model performance was not temporally predictable. However, this study did provide a guide for forest restructuring to enhance the songbird community. I suggest that a forest management strategy with a spatially and temporally hierarchical organisation would be a simple prescription to increasing the density and probability of occurrence of many songbird species in Kielder Forest.

5.1 Introduction

Many of northern Europe's landscapes consist of highly fragmented areas, created by agriculture and commercial forestry. These types of landscape are dominated by abrupt edges between adjacent patches. It is imperative that we gauge how landuse practice affects the avian community, with birds traditionally being used as bioindicators of a landscape's 'ecological worth' (Tucker *et al.* 1997). Predictive GIS (geographical information system) models can be applied to the conservation of threatened avian species (Özesmi & Mitsch 1997, Li *et al.* 1997, Roseberry & Sudkamp 1998) but can also be used to improve the ecological management of reserves or man-made areas, particularly forested landscapes (Edenius & Elmberg 1996, Dettmers & Bart 1999). Utilisation of GIS for spatial modelling is important in landscape management because it makes possible landscape quantification (Roseberry & Sudkamp 1998, Clark *et al.* 1999), spatial autocorrelation analysis (Li *et al.* 1997) and simulation of management strategies (Baskent 1999, Wadsworth *et al.* 2000).

5.1.1 Landscape structure

Large-scale forestry clear-cutting, a method of commercial forest management used particularly in northern Europe's Boreal forests, creates a shifting mosaic landscape (Tang *et al.* 1997) that has a significant effect on the composition and distribution of animal species (Edenius & Elmberg 1996, Baker & Lacki 1997, Berg 1997). The natural pattern of such forests is also a shifting mosaic, caused by natural disturbance (for example fire and windthrow), however, change occurs at a much slower rate than managed commercial forests. Since the early 1990's, with the greater accessibility of GIS and spatial quantification programs, there has been a dramatic increase in the number of studies that quantify various aspects of landscape configuration (Edenius & Elmberg 1996, Jokimäki & Huhta 1996, Tucker *et al.* 1997, Villard *et al.* 1999, Roseberry & Sudkamp 1998).

Landscape structure affects the persistence of communities in fragmented areas (Villard *et al.* 1999, Harrison & Fahrig 1995, Taylor *et al.* 1993), and so patch context (for example *where* a patch is in the landscape, what is *adjacent* to it, how *isolated* or *connected* it is) can affect bird dispersal and thus densities or occurrence (Bellamy *et al.*

1998, Baillie *et al.* 2000). Although useful as a concept, Island Biogeography Theory (MacArthur & Wilson 1967) can not practically be applied to patches embedded in a matrix that is not totally inhospitable, which has led to a mosaic approach to landscape management (Wiens 1994, Estades & Temple 1999).

An investigation of patch age and tree species composition in the Forest of Dean, a low intensity commercial mixed forest, showed that all successional areas and highly dispersed broad-leaved trees were important for bird species (Donald *et al.* 1998). However, intensive commercial coniferous forests in the U.K., such as Kielder Forest studied here, are composed almost exclusively of even-aged stands of high yield Sitka spruce (termed patches) managed by rotational clearfelling. Only 1% of the total area of Kielder Forest is composed of broad-leaved trees (McIntosh 1995). Thus the spatial arrangement of spruce patches determined by clear-felling and re-stocking is likely to dominate the response of wildlife populations to landscape structure in this area.

In recent years U.K. public sector forest managers have been gradually implementing restructuring plans for commercial coniferous forests so that these landscapes have higher spatial and structural diversity (Ratcliffe & Petty 1986). Indeed there have been recent proposals for an increase in broadleaf content, open spaces and restructuring of patch shapes so that they are more irregular and are contoured to the landform (McIntosh 1995). However, quantification of these efforts is necessary in order to determine how forest patterns affect songbird communities, and hence re-assess management decisions on forest design.

5.1.2 Scale and individual habitat choice

In the present study, McGarigal & Marks' (1995) definitions of scale, extent and grain are adopted. Spatial scale includes extent (the overall region that is under investigation, in this case Kielder Forest) and grain (the resolution of the map units used, with fine grain meaning small areas and coarse grain large areas). A limitation to use of patch level variables is perception of the appropriate grain by the observer in creation of predictive models of bird density (Wiens *et al.* 1993, Berg 1997). According to Willson and Comet (1996), factors determining avian distributions are on two interacting levels; the higher level includes 'regional biogeography, landscape configuration and metapopulation structure' and the lower level includes factors such as feeding and nesting resources, and predation risk. Patchily distributed food and predation pressures create conditions whereby animals may have to utilise a range of patches (Baker 1996, Taylor *et al.* 1993). Therefore individual habitat choice influences distributions and densities across a landscape (Wiens *et al.* 1993, Sutherland 1996). Thus the grain at which habitat and landscape variables are measured may affect the results of studies on determinants of songbird species density and distribution.

It is expected that bird populations do not change much from year to year, with perception of a patch's quality remaining temporally relatively static especially if habitat associations are strong (Haila *et al.* 1996). However, Hogstad's (1993) findings show that, in the long term (12 years), bird densities do fluctuate. Using the results in Chapter 3, I will assume that breeding bird populations are relatively static over the time scale of the present study (1998-1999). Another assumption implicit in this type of predictive study is that suitable habitat is occupied and unsuitable habitat is unoccupied. It is possible that the landscape is not saturated, with some suitable habitats remaining unoccupied due to insufficient numbers of birds to fill all habitats. Inclusion of these false negatives affects model performance, but 'unusual' observations are detected by the analysis (P. Osborne *pers comm.*). However, it is important to keep this in mind when interpreting habitat-songbird association models.

5.1.3 Edge effects and landscape configuration

Patch shape, area, age and edge type affect how an organism moves in an environment, and thus determine the distribution of species in a landscape (Baker 1996, Ims 1995, Forman & Godron 1986). Patch shape can be related to: a) the edge to centre ratio, with more complex shaped patches having relatively more edge than a simple shaped patch; and b) the permeability of that patch to organisms, with more complex shaped patches allowing greater exchanges of biota (Forman & Godron 1986, Stamps *et al.* 1987). The age of the trees in a patch will also affect the avian species composition, with many birds having clear preferences according to their ecological requirements (Patterson *et al.* 1995), as shown in Chapter 4.

Edges between patches are not uniform and their physical characteristics depend on the neighbouring patches creating that edge (Chapter 4). The degree of dissimilarity between neighbouring patches gives an index of edge contrast. Villard *et al.* (1999)

remark that late-seral (over 40 years old) stands separated by conifer plantations may be more permeable (permeability is defined as the ease with which an individual can cross a boundary) to bird movements than stands separated by agricultural land. Thus, hard edges formed between two highly dissimilar patches may be more difficult to cross than softer edges formed between two more similar patches (Ims 1995, Stamps *et al.* 1987, Hawrot & Niemi 1996). However, this does not take in to account a bird's perception of that edge and their habitat preferences. Many bird species use a wide range of habitats (Norton *et al.* 2000), and may prefer areas containing a range of habitats. These harder edges may then be perceived as favourable because they encompass areas that will offer the bird two entirely different resource supplies. Indeed, Penhollow and Stauffer (2000) state that, in order to increase the avian diversity in a managed forest, the overall amount of high edge contrast should be increased.

The present study will provide empirical evidence that landscape pattern and patch characteristics affect songbird communities. In particular, it will test the hypotheses that: a) patch shape, area and age affect distributions and densities of songbirds according to species-specific habitat preferences; b) species preferring the centre avoid high contrast edges whereas edge species are attracted to them (Penhollow & Stauffer 2000); c) habitat specialists prefer homogeneous landscapes whereas generalists prefer heterogeneous landscapes (Penhollow & Stauffer 2000); d) edge species prefer patches with the maximal amount of edge habitat, e.g. small patches or complex shaped patches, whereas centre species prefer the contrary; and e) breeding bird density and distribution data, collected using the point count methodology, can be used to generate robust predictive models. Thus it is hoped that this study will provide a framework enabling landscape managers to structure commercial coniferous forests according to species-specific and landscape patterning priorities.

5.2 Methods

5.2.1 Habitat and avian variables

Chapter 2 discusses the creation of the Kielder Forest GIS. It also discusses the metrics generated by a spatial pattern analysis program, FRAGSTATS, used in my study. FRAGSTATS (version 2.0 and version 3.01 after June 2000) was used within the ArcInfo (version 7.0) Kielder Forest GIS. FRAGSTATS has become an increasingly utilised tool in wildlife management studies (Roseberry & Sudkamp 1998, Penhollow & Stauffer 2000). Its wide range of metrics and facilities allow the user to alter inputs, which means that it is possible to output particular variables tailored to particular studies.

As outlined in Chapter 2, the metrics used in modelling included tree age, patch area, fractal dimension and two edge contrast indices (see descriptions later in Section 5.2.2 Statistical analysis). Table 5.2.1 outlines the edge comparison weights utilised by FRAGSTATS to calculate edge comparison. Examination of the ecology and effect of small-scale edge comparison on the birds (Chapter 4) determined the edge comparisons utilised for each species' models in the present study. These are shown in column one of Table 5.2.2.

Mean density (birds ha^{-1}) was calculated for each patch in early and late spring, and at the centre and edge. The maximum density measured over early and late spring in both 1998 and 1999, of each bird species detected in every surveyed patch, was utilised in statistical analyses following Bibby *et al.* (1985) and also Elmberg and Edenius (1999), although, Norton *et al.* (2000) modelled mean densities. The maximum density maximises the chance of detection of an individual (Chapter 3). Only the 11 most common species were chosen for analyses: crossbill *Loxia curvirostra,* chaffinch *Fringilla coelebs,* coal tit *Parus ater,* dunnock *Prunella modularis,* goldcrest *Regulus regulus,* meadow pipit *Anthus pratensis,* robin *Erithacus rubecula,* redpoll *Carduelis flammea,* siskin *Carduelis spinus,* wren *Troglodytes troglodytes* and willow warbler *Phylloscopus trochilus.*

5.2.2 Statistical analysis

Positive spatial autocorrelation occurs when the values (be they physical, such as soil type, or biological, such as vegetation cover) of neighbouring sample sites have a greater probability of being similar than sites further apart (Legendre 1993, Goodchild 1987). This is an important phenomenon to consider because it can produce biased models due to non-independence of data (Tabachnick & Fidell 1996). Moran's *I* Coefficient was applied to assess spatial autocorrelation (Li *et al.* 1997) using ROOKCASE, a macro that works within Microsoft Excel (Sawada 1999). ROOKCASE calculates Moran's *I* (Equation 5.2.1) using an irregular lattice of data points (sites are irregularly placed across the landscape i.e. not in a regular grid pattern) (Sawada 1999). The standardised normal deviate (*Z*) was calculated to test the significance of the Moran's *I* value. These *Z* values were compared with the critical values of *Z* (1.96 at $\alpha = 0.05$, two-tailed test). If the observed *Z* values exceeded this value (i.e. were > +1.96 or < -1.96) then the null hypothesis of a random spatial distribution of values was rejected and the alternative hypothesis of values being spatially autocorrelated was more likely. Moran's *I* was calculated using the mean nearest neighbour distance (mnn) between all sampling sites. Spatial autocorrelation (s.a.) was investigated using the mnn value as the lag increment with s.a. examined at 5 cumulative intervals starting at the smallest grain of [0 to $\text{mnn}_{(x1)}$], then at increasing grain (i.e. larger distances) of [0 to $\text{mmn}_{(x2)}$], up to [0 to $\text{mnn}_{(x5)}$].

$$I = \frac{n\sum_{(c)}(x_i - \bar{x})(x_j - \bar{x})}{J\sum(x - \bar{x})^2}$$

Equation 5.2.1: The equation for Moran's Coefficient (*I*) where n is the number of sample sites, J is the number of joins (the number of edges formed between adjacent patches), x is the value under investigation for a site, $\bar{x}$ is the mean x-values, x_i and x_j are the values for adjacent sites. The small $_{(c)}$ denotes that calculation of the double bracketed expression should occur for each pair of adjacent sites with summation of all of these values.

Using the 1999 data, multiple backwards stepwise generalised linear models were generated with bird presence or absence (logistic regression using SPSS 9.0, 1998) and density (generalised linear models [GLM] with Poisson errors using GLIM 4.09) as the dependent variables, and landscape and patch characteristics as the independent variables (see Chapter 2). The significance level at which the variables were entered into the model was set at 0.1 (Estades & Temple 1999), a value that minimises Type II errors (Norton *et al.* 2000). A Type II error occurs when the null hypothesis is not rejected when, in actual fact, it is false (Zar 1999). Models were built for each species at the edge and the centre of patches.

In SPSS logistic regression it is possible to specify the 'cut-off' classification value according to the frequency of occurrence or prevalence of the species (Tabachnick & Fidell 1996). This value separates the probabilities into predicted presence (greater than the critical value) or absence (less than the critical value). The default critical value is 0.5; however, if on examination of the predicted probabilities against the observed frequencies of occurrence, many of the observed data values are predicted incorrectly, it can be altered. This is particularly important for species that were very rarely or commonly found. For example, the coal tit was found very rarely and thus it would not be found in 50% of the patches surveyed. Thus, the effect of prevalence on the outcome of logistic regression analysis would be to decrease the predictive power of the model, because of false predictions (Manel *et al.* 2001). In my analyses I adjusted the cut-off values to maximise the proportion of correctly classified values.

The maximum likelihood technique is used in Poisson Errors GLM which calculates those parameter estimates that would give the model the best fit (i.e. those that make the observed data most likely). As with the methodology outlined in Chapter 2 and the methods utilised in Chapter 4 the number of point counts was used as a weight file in the GLMs, and overdispersion was corrected for.

When using multivariate statistics it is important to be aware of correlation between independent variables causing multicollinearity (Tabachnick & Fidell 1996). As with most analyses this should be avoided as far as possible. In my analyses, the edge comparison variables were highly correlated (Appendices 4 and 5). Because they were calculated by small changes to the inputs, high correlations were expected. To minimise multicollinearity, only 2 of the 6 edge comparison variables (calculated using the weights in Table 5.2.1) were included in the models for each species, as shown in Table 5.2.2 and according to known habitat preferences. A hard edge contrast and a soft edge contrast were included in these two edge comparisons and weighted according to expected importance to a species (Table 5.2.2).

As the two edge comparisons included in each model (hard and soft) were highly correlated, preliminary logistic regression and generalised linear models were performed for each species including the main effects of patch shape, area, planting year and the two edge comparisons (Table 5.2.2). This used to determine whether the chosen bird species was responding to hard (edges composed of highly dissimilar trees) or soft (edges composed of more similar trees) edges. The edge comparison that contributed most significantly to the "main effects model" was retained in subsequent modelling, eliminating the other edge comparison that did not have as significant an effect on the main effects model. A full model was fitted with main effects and first-order interactions using patch area, shape, tree age and one edge comparison index as explanatory variables. Polynomials were not included in modelling because the variable to case ratio would have been too small, and interpretation of results, in terms of management implications, too complex. However, if these caveats were not in place, it would be interesting to introduce polynomials into the modelling as they may provide a more realistic model of the observed densities.

For generalised linear modelling in GLIM 4.09 the parameter estimates and standard errors were scrutinised and the least significant term at the highest level of interaction (in this case first order interactions) was removed. If the change in deviance was significant (i.e. the p-value for the chi-squared analysis was less than 0.1) then the term was re-entered and retained. However, if it was not significant, then it was rejected. This procedure was continued, moving from interaction levels to main effects, until the most parsimonious model was achieved. This procedure was performed automatically in backward, stepwise SPSS logistic regression.

5.2.3 Model validation

Maps were generated in ArcView version 3.0 using the GIS and utilising the output from the predictive logistic and generalised linear models. The observed data from 1998 were used to validate these models. Classification accuracy was calculated to determine how well the models performed utilising the 1998 data as verification.

Digital land cover classification using remote sensing such as satellite imagery involves a method called 'classification accuracy assessment' (Lillesand & Kiefer 1994), which quantifies the accuracy of land cover classification. An error matrix of the predicted values of a model (for example presence or absence) and the observed values (for example using the data from 1998 to test the predicted values of the 1999 model) is generated, such as Matrix 5.2.1 based on sample data.

		Predicted		$Total_{(p)}$
		Absent	*Present*	
Observed	*Absent*	15[1]	7[3]	22
	Present	4[2]	17[1]	21
$Total_{(o)}$		19	24	*Diagonal sum*
				32

Matrix 5.2.1: An example of an error matrix. This calculates concordance[1] between predicted presence/absence and observed presence/absence, omission[2] and commission[3]. The sum of the diagonal (32) is the number of patches, which were correctly classified out of the total number of patches surveyed (N=43) giving a percentage correctly classified (PCC) as 74.42%.

A test statistic, Kappa can be utilised to express the classification accuracy of a model (Lillesand & Kiefer 1994) (Equation 5.2.2), using the error matrix above (Matrix 5.2.1). The percentage correctly classified (PCC) can also be calculated alongside Kappa by dividing the sum of the diagonal by the total sample size. The Kappa statistic ($\hat{k}$) can be used in conjunction with the percentage correctly classified (PCC) as it provides information not just on how good the model is at correctly classifying patches, as with the PCC, but also on how poorly it performed. A high value of $\hat{k}$ (approaching 1) indicates a model that performs better than chance, and low value (close to 0) indicates a model that does not perform better than chance (Lillesand & Kiefer 1994, Karl *et al.* 2000). A negative value of kappa indicates a model that is subject to a high degree of chance variation and is therefore an inadequate predictive tool (Lillesand & Kiefer 1994).

The author is aware of an alternative method of determining logistic model success using receiver operating characteristics (ROC) using sensitivity (y-axis) plotted against 1-specificity (x-axis) (Osborne *et al.* 2001), and calculating the area under the resulting curve to give the overall fit of the model. The AUC (area under the curve) from ROC plots is well correlated with Kappa (Manel *et al.* 2001). Because of this and time constraints, ROC was not calculated in this study.

$$\hat{k} = \frac{N\sum_{i=1}^{r} x_{ii} - \sum_{i=1}^{r}(x_{i+} \times x_{+i})}{N^2 - \sum_{i=1}^{r}(x_{i+} \times x_{+i})}$$

Equation 5.2.2: Calculation of Kappa statistic (Taken from Lillesand & Kiefer 1994), where r = number of rows in error matrix, x_{ii} = number of observations in row i and column i (diagonal sum), x_{i+} = total of observations in row i, x_{+i} = total of observations in column i, N = total number of sample sites.

In logistic regression, a common mistake is to assume that chance alone could account for 50% of the correctly classified results (PCC = 50). This has been discussed in terms of the cut-off values during modelling; however, it also affects *post-hoc* tests. Recent work has shown that the frequency of occurrence or prevalence affects the percentage correctly classified in logistic regression (Manel *et al.* 2001). If a species occupied only 10% of surveyed patches, a model predicting absence in all patches would be 80% correct. Manel *et al.* (2001) state that use of PCC is misleading and Kappa is a more accurate method of determining model performance.

Kappa and PCC were calculated for all of the models chosen for further interpretation using the 1999 data to build the models and the 1998 data to validate the models. The Kappa statistic for the generalised linear models was more complex to calculate than for the logistic regression models, and involved splitting the predicted and observed values into an arbitrary number of categories, with five being used in this study (see Maps 5.2.1-11 for category values in Maps section). The error matrix was generated using these five categories.

Maps were generated using the outputs from the 1999 models (utilising the values calculated using the output equations from the logistic and generalised linear models) and the 1998 survey data were used to validate the models. Although predicted values were calculated for the whole forest using the 1999 models, only those patches surveyed in 1998 were outputted to the maps for ease of comparison with the 1998 validation data. In addition to Kappa and PCC, a linear regression analysis (SPSS 1998) was used for the GLMs to determine how well the predicted values (1999 models) corresponded with the observed (1998 data).

Edge Comparison	*Category$_{(AC)}$ A*	*Category$_{(AC)}$ B*	*Weight*	*Edge Comparison*	*Category$_{(AC)}$ A*	*Category$_{(AC)}$ B*	*Weight*
E_1				E_4			
	1	2	0.1		1	2	0.1
	1	3	0.15		1	3	0.15
	1	4	0.2		1	4	0.2
	1	5	0.2		1	5	0.2
	2	3	0.5		2	3	0.3
	2	4	0.7		2	4	0.5
	2	5	0.8		2	5	0.8
	3	4	0.3		3	4	0.7
	3	5	0.8		3	5	0.8
	4	5	0.8		4	5	0.8
E_2				E_5			
	1	2	0.1		1	2	0.1
	1	3	0.15		1	3	0.15
	1	4	0.2		1	4	0.2
	1	5	0.2		1	5	0.2
	2	3	0.7		2	3	0.3
	2	4	0.5		2	4	0.7
	2	5	0.8		2	5	0.8
	3	4	0.3		3	4	0.5
	3	5	0.8		3	5	0.8
	4	5	0.8		4	5	0.8
E_3				E_6			
	1	2	0.1		1	2	0.1
	1	3	0.15		1	3	0.15
	1	4	0.2		1	4	0.2
	1	5	0.2		1	5	0.2
	2	3	0.5		2	3	0.7
	2	4	0.3		2	4	0.3
	2	5	0.8		2	5	0.8
	3	4	0.7		3	4	0.5
	3	5	0.8		3	5	0.8
	4	5	0.8		4	5	0.8

Table 5.2.1: Table of edge comparison weights for input in to FRAGSTATS*ARC. Categories $_{(AC)}$ are according to tree age with 1 = Agricultural and unplanted land, 2 = Clearfell and young Sitka, 3 = Pre-thicket Sitka, 4 = Mature Sitka, and 5 = Pure broadleaf and conifer/broadleaf mixes.

	Tree age preference	*Soft Edge Comparison*	E_n	*Hard Edge Comparison*	E_n
crossbill	Mature	1. Mature:Pre-thicket	E_4	1. Mature:Young	E_5
		2. Mature:Young		2. Mature:Pre-thicket	
chaffinch	Mature	1. Mature:Pre-thicket	E_4	1. Mature:Young	E_5
		2. Mature:Young		2. Mature:Pre-thicket	
coal tit	Mature	1. Mature:Pre-thicket	E_4	1. Mature:Young	E_5
		2. Mature:Young		2. Mature:Pre-thicket	
dunnock	Young	1. Young:Pre-thicket	E_2	1. Young:Mature	E_1
		2. Young:Mature		2. Young:Pre-thicket	
goldcrest	Mature	1. Mature:Pre-thicket	E_4	1. Mature:Young	E_5
		2. Mature:Young		2. Mature:Pre-thicket	
meadow pipit	Young	1. Young:Pre-thicket	E_2	1. Young:Mature	E_1
		2. Young:Mature		2. Young:Pre-thicket	
robin	Mature	1. Mature:Pre-thicket	E_4	1. Mature:Young	E_5
		2. Mature:Young		2. Mature:Pre-thicket	
redpoll	Pre-thicket	1. Pre-thicket:Mature	E_3	1. Pre-thicket:Young	E_6
		2. Pre-thicket:Young		2. Pre-thicket:Mature	
siskin	Pre-thicket	1. Pre-thicket:Mature	E_3	1. Pre-thicket:Young	E_6
		2. Pre-thicket:Young		2. Pre-thicket:Mature	
wren	Young	1. Young:Pre-thicket	E_2	1. Young:Mature	E_1
		2. Young:Mature		2. Young:Pre-thicket	
willow warbler	Pre-thicket	1. Pre-thicket:Mature	E_3	1. Pre-thicket:Young	E_6
		2. Pre-thicket:Young		2. Pre-thicket:Mature	

Table 5.2.2: Preferred tree age of the common species (Taken from Chapter 4), and edge comparisons included in the models. To determine which type of edge had the strongest impact on the model of each species two different types of edge contrast were included, soft and hard. In this table the numbers 1. and 2. correspond to the order of importance (measured by the value of the weight [see Table 5.2.1] with higher weight values denoting greater importance) in the total edge comparison (soft or hard) of each type of edge comparison. For example in the soft edge comparison of willow warbler, the pre-thicket-mature edge comparison has a higher weighting than the pre-thicket-young edge comparison (see Table 5.2.1), thus creating a higher value for that edge comparison. In this study a high value of edge comparison does not imply a high value for edge contrast but rather is used as an index for expected preference. E_n = edge comparison ($_n$ = 1-6).

5.3 Results

5.3.1 Correlation and spatial autocorrelation

Correlation analysis of independent habitat variables showed that the edge comparison (E_n) indices were highly correlated (Appendices 4 and 5) because calculation of these indices is based on small changes in the inputs (Table 5.2.1) with the higher correlation co-efficient values ranging between 0.66-0.96.

Spatial autocorrelation was investigated at 5 spatial grains in 1999 data using the mean nearest neighbour (mnn) distance (metres) as the lag increment (mnn_{centre} = 565.8 metres, mnn_{edge} = 331.8 metres). The reason for the smaller mean distance between edge neighbouring sites was due to the higher sample size of the edge samples, and thus they were in closer proximity to one another (see Maps 5.1.1-11 and Maps 5.2.1-11). There was no evidence of spatial autocorrelation at these grains amongst the independent habitat variables, or the bird occurrence or density data (all Moran's Z ranged between ±1.96), except for dunnock density and occurrence, and siskin density, all at the centre of patches. Spatial autocorrelation was only observed at one spatial scale for these two species; at three times the mean nearest neighbour distance for dunnock and at five times the mean nearest neighbour distance for siskin. These spatial autocorrelation Z values were only just significant (Z = - 2.498, - 2.08 and - 2.126 respectively). Spatial autocorrelation was tested for up to ten times the mnn distance for these two species and no other significant spatial autocorrelation was observed. The low significance values and lack of any other spatial autocorrelation in these species occurrence and density implies that perhaps these significant values are anomalies. Given the high number of tests performed, it would be expected, by chance alone, that some of these tests would be significant. Lowering the significance value to 0.01 renders these significant results, insignificant.

5.3.2 Predictive models

Table 5.3.1 shows that positive edge effects predominate, with seven out of the eleven common species preferring the edge. Only the meadow pipit prefers the centre of patches. Appendices 6-9 display the results of logistic regression models and GLM at the centre and edge for the eleven common species. The following results section applies to Tables 5.3.2-5.3.7 showing the best fit logistic regression models and GLMs for the eleven most common species. In this chapter r^2 values are quoted for both the logistic and generalised linear regression models, with logistic regression values written as $r^2_{(lr)}$ and GLM regression values written as $r^2_{(glm)}$. The strength of the associations of the models were highly variable with $r^2_{(lr)}$ ranging between 0.055 and 0.582 and $r^2_{(glm)}$ between 0.034 and 0.636.

5.3.2.1 Logistic regression models (LRM)

In this section a negative association is assumed to imply absence or avoidance and a positive association implies presence or preference. Tables 5.3.2 and 5.3.3 show that crossbill, chaffinch, coal tit, and robin avoided young trees, whereas meadow pipit and wren preferred them. Complex patches were not preferred by any species, with dunnock, robin and siskin avoiding them. However, dunnock and robin preferred young patches that were of a complex shape. Willow warbler avoided young complex patches. Soft edges were preferred over harder edges by goldcrest and willow warbler. Redpoll and wren preferred large patches with soft edges. The young component of hard edges was avoided by chaffinch and of soft edges by goldcrest. Most logistic regressions were weak with $r^2_{(lr)}$ values rarely achieving values greater than 0.25. Section 5.4.1 discusses why this is the case.

5.3.2.2 Generalised linear models (GLM)

In this section a negative association is assumed to imply zero to low density or avoidance and a positive association implies medium to high density or preference. As with the logistic regression analyses, tree age had a strong effect on many of the species' density models. Tables 5.3.5 and 5.3.6 show that crossbill, coal tit, goldcrest, robin and redpoll avoided young trees, whilst meadow pipit preferred them. Complex shaped patches were generally avoided (coal tit, goldcrest, robin, redpoll, siskin and willow warbler), although meadow pipit preferred them. However, when the interaction between patch age and patch shape was considered coal tit, goldcrest, redpoll, and wren preferred complex shaped young patches, and meadow pipit avoided them. Low redpoll and wren densities were found in large complex shaped patches, whereas goldcrest and coal tit were found at high densities in these types of patches. Dunnock, redpoll and willow warbler preferred the soft edges to the harder ones, whereas, chaffinch and wren preferred hard edges to soft. Low goldcrest and meadow pipit densities were found in large patches with hard edges. Wren avoided complex shaped patches with hard edges and redpoll avoided the young patches with soft edges.

5.3.3 Model validation

Maps of the 1999 predictive logistic regression and generalised linear models, and the validation of these models with the 1998 data, show that some of the models perform well (Maps 5.1.1-11 and Maps 5.2.1-11). The 1999 logistic regression models were classified according to the tabulated cut-off points using the 1998 data to validate them (Table 5.3.2).

The logistic regression models for crossbill, dunnock, siskin and wren had very low PCC values (Table 5.3.4). However, the models for chaffinch, coal tit, goldcrest, meadow pipit, robin, redpoll and willow warbler occupancies had high PCC values. Although, the PCC values must be treated with caution because they do not include any information on the incorrectly classified results, those species with low PCC generally had low Kappa values (crossbill, dunnock, siskin and wren). This implies that these models were particularly poor at predicting the occurrence of the relevant species. Kappa values for coal tit and meadow pipit were high (>0.85) making the performance of these models especially robust.

Validations of the GLMs included a regression analysis of predicted and observed bird density. The regression analysis of predicted (1999 model) and observed (1998) values generated medium to low r^2 values (Table 5.3.7), with only four species' analyses resulting in r^2 values higher than 0.15 (crossbill, meadow pipit, wren and willow warbler). The validations of the GLMs were slightly different to the logistic regression models; the observed and predicted data were categorised into 5 groups (according to the values in Maps 5.2.1-11) to create the best fit models. The PCC and $\hat{k}$ values were not as high as the logistic regression values because a binary response (0 or 1), is more limited in its scope for misclassification than a multinomial response (1–5). Despite this, the GLM PCCs were quite high with only four species having values below 30%: dunnock, robin, redpoll and willow warbler (Table 5.3.7). These were also the species with the lowest $\hat{k}$ values. However, the siskin model had a relatively high PCC (41.9%) but a very low Kappa value (0.010), implying that the incorrectly classified data points were inaccurate by several categories (Table 5.3.7).

Species	χ^2	*df*	*p-value*	*Direction*
crossbill	6.93	1	<0.01	+
chaffinch	39.57	1	<0.001	+
coal tit	2.60	1	ns	
dunnock	2.22	1	ns	
goldcrest	19.13	1	<0.001	+
meadow pipit	12.90	1	<0.001	-
robin	13.68	1	<0.001	+
redpoll	1.60	1	ns	
siskin	20.50	1	<0.001	+
wren	23.83	1	<0.001	+
willow warbler	5.01	1	<0.05	+

Table 5.3.1: Taken from Chapter 4. Bird density at the edge compared to the centre of patches using Poisson error GLM and displaying the direction of the edge effect (+ = positive edge effect with more birds found at the edge, - = negative edge effect).

Bird Species	*Centre or Edge*	*Model*					
		Cox & Snell $r^2_{(lr)}$	*Chi*^{2}	*df*	*p-value*	*Cut-off*	$(B_0 + B_1X_1 + B_2X_2 + ... B_nXn)$
crossbill	E	0.055	7.47	2	<0.05	0.12	65.8377 + 0.0277*A.FD – 0.0345*Y
chaffinch	C	0.210	16.77	2	<0.001	0.53	194.881 – 0.000018*E5.Y – 0.0973Y
coal tit	C	0.183	14.32	1	<0.001	0.26	169.5981 – 0.0860*Y
dunnock	C	0.104	7.76	2	<0.05	0.26	-21.8004 + 0.0494*FD.Y – 82.1286*FD
goldcrest	E	0.493	90.25	2	<0.001	0.50	-1.208 – 0.0095*E4.Y + 19.0221*E4
meadow pipit	C	0.541	55.34	1	<0.001	0.42	-996.574 + 0.5007*Y
robin	C	0.582	61.96	3	<0.001	0.50	27139.39 + 10.1797*FD.Y – 13.6180*Y – 20288.3*FD
redpoll	E	0.071	9.78	1	<0.002	0.40	-1.0322 + 0.0013*A.E3
siskin	C	0.148	11.38	2	<0.005	0.27	35.5608 + 0.0000233*A.Y – 29.2981*FD
wren	E	0.244	37.27	2	<0.001	0.71	-108.252 + 0.0018*A.E2 + 0.0547*Y
willow warbler	C	0.204	16.23	2	<0.001	0.55	30.2181 – 0.0123*FD.Y + 0.0421*E3

Table 5.3.2: Logistic regression models of common songbird distribution according to the best fit model (Appendices 6 and 7) i.e. the model based on data from the centre or the edge of patches depending on which performed the best (see first column 'Centre or edge'). Variables included in analysis are patch area (A), edge comparison (E_n), fractal dimension (FD), and planting year (Y)

Species	*Main Effects*		*2^{nd} Order Interaction*	
	Positive Association	*Negative Association*	*Positive Association*	*Negative Association*
crossbill		Young trees	Large complex shapes	
chaffinch		Young trees		Young hard edges (m/y > m/pt)
coal tit		Young trees		
dunnock		Complex shapes	Young complex shapes	
goldcrest	Soft edges (m/pt > m/y)			Young soft edges (m/pt > m/y)
meadow pipit	Young trees			
robin		Young trees Complex shapes	Young complex shapes	
redpoll			Large soft edges (pt/m > pt/y)	
siskin		Complex shapes	Young complex shapes	
wren	Young trees		Large soft edges (y/pt > y/m)	
willow warbler	Soft edges (pt/m > pt/y)			Young complex shapes

Table 5.3.3: Synopses of logistic regression model results (taken from Table 5.3.2) showing main effects and first order interactions with associations for each species.

	Model used	*PCC*	$\hat{k}$
crossbill	E	53.2	0.014
chaffinch	C	72.1	0.408
coal tit	C	90.7	0.795
dunnock	C	39.5	-0.430
goldcrest	E	68.8	0.284
meadow pipit	C	86.1	0.718
robin	C	81.4	0.625
redpoll	E	66.2	0.213
siskin	C	48.8	-0.035
wren	E	58.4	0.154
willow warbler	C	74.4	0.490

Table 5.3.4: Validation of models built using the 1999 dataset for eleven common breeding songbird species in Kielder Forest showing the percentage correctly classified (PCC) and Kappa statistic ($\hat{k}$) for the logistic regression best-fit models.

Bird Species	*Centre or Edge*	*Model*					
		$r^2_{(glm)}$	Chi^2	*df*	*p-value*	*Scale value*	$(B_0 + B_1X_1 + B_2X_2 +\ldots B_nXn)$
crossbill	C	0.182	6.27	2	<0.05	1.64	118.2 – 0.07298*A – 0.06024*Y
chaffinch	E	0.278	55.97	2	<0.001	1.22	0.21 + 1.693*E5 – 0.00086*E5.Y
coal tit	C	0.379	31.63	5	<0.001	1.46	3963 – 3.343*A – 2944*FD – 1.965*Y + 2.57*A.FD + 1.458*FD.Y
dunnock	E	0.034	3.68	1	<0.1	1.71	-2.208 + 0.01625*E3
goldcrest	C	0.457	49.82	7	<0.001	1.67	2295 – 5.5*A – 1611*FD – 1.132*Y – 0.00096*A.E5 + 1.262*A.FD + 0.001978*A.Y + 0.7921*FD.Y
meadow pipit	C	0.636	107.00	6	<0.001	1.39	-5779 – 13.87*A + 4385*FD + 2.901*Y – 0.00127*A.E1+ 0.006988*A.Y – 2.201*FD.Y
robin	C	0.214	16.93	2	<0.001	1.78	86.27 – 10.52*FD – 0.03684*Y
redpoll	E	0.173	21.10	7	<0.005	2.22	1481 + 0.997*A + 3.197*E3 – 1234*FD – 0.7512*Y – 0.7701*A.FD – 0.0016*E3.Y + 0.625*FD.Y
siskin	C	0.088	4.95	1	<0.05	1.59	21.84 – 18.3*FD
wren	C	0.280	31.17	5	<0.001	1.06	-33.9 + 1.046*A + 0.6184*E1 – 0.8317*A.FD – 0.4864*E1.FD + 0.0136*FD.Y
willow warbler	C	0.069	4.78	1	<0.05	3.93	8.726 + 0.01598*E3 – 7.049*FD

Table 5.3.5: Generalised linear models of common songbird density according to the best fit model (Appendices 8 and 9) i.e. the model based on data from the centre or the edge of patches depending on which performed the best (see first column 'Centre or edge'). Variables included in analysis are patch area (A), edge comparison (E_n), fractal dimension (FD), and planting year (Y).

	Main Effects		*2nd Order Interaction*	
	Positive Association	Negative Association	*Positive Association*	*Negative Association*
crossbill		Large area Young trees		
chaffinch	Hard edges (m/y > m/pt)			Young hard edges (m/y > m/pt)
coal tit		Large area Young trees Complex shapes	Large complex shapes Young complex shapes	
dunnock	Soft edges (pt/m > pt/y)			
goldcrest		Large area Young trees Complex shapes	Large complex shapes Large young Young complex shapes	Large hard edges (m/y > m/pt)
meadow pipit	Complex shapes Young trees	Large Area	Large young	Large hard edges (y/m > y/pt) Young complex shapes
robin		Young trees Complex shapes		
redpoll	Large area Soft edges (pt/m > pt/y)	Young trees Complex shapes	Young complex shapes	Large complex shapes Young soft edges (pt/m > pt/y)
siskin		Complex shapes		
wren	Large Area Hard edges (y/m > y/pt)		Young complex shapes	Large complex shapes Complex hard edges (y/m > y/pt)
willow warbler	Soft edges (pt/m > pt/y)	Complex shapes		

Table 5.3.6: Synopses of generalised linear model results (taken from Table 5.3.5) showing main effects and first order interactions with associations for each species.

	Models used	*Linear Regression*		*PCC*	$\hat{k}$
		r^2	p		
crossbill	C	0.242	0.001	86.0	0.201
chaffinch	E	0.121	0.002	33.8	0.140
coal tit	C	0.030	0.267	63.4	0.168
dunnock	E	0.032	0.120	28.6	-0.121
goldcrest	C	0.028	0.281	46.5	0.270
meadow pipit	C	0.550	0.000	48.8	0.309
robin	C	0.059	0.116	23.3	0.058
redpoll	E	0.002	0.703	22.1	-0.010
siskin	C	0.033	0.246	41.9	0.010
wren	C	0.200	0.003	34.9	0.183
willow warbler	C	0.175	0.005	20.9	0.073

Table 5.3.7: Validation of models built using the 1999 dataset for eleven common breeding songbird species in Kielder Forest showing the percentage correctly classified (PCC) and Kappa statistic ($\hat{k}$) for the best fitting generalised linear models.

5.4 Discussion

5.4.1 Explanatory power

There are intrinsic problems in trying to predict the distribution or density of highly mobile organisms (Tucker *et al.* 1997). However, the common breeding bird species of Kielder Forest were affected to varying degrees by patch and landscape characteristics with $r^2_{(glm)}$ values ranging between 0.034 and 0.636, and $r^2_{(lr)}$ between 0.055 and 0.582. This is an important finding as it shows that it is not possible always to predict with a high degree of certainty the presence/absence or density of some songbird species in this type of landscape, as with Penhollow and Stauffer (2000). This also agrees well with Edenius and Elmberg's (1996) study on the role of landscape level effects on the density of songbirds in Swedish Boreal forests, which generated species models that had r^2 values ranging between 0.067 and 0.357.

Logistic regression models were generally weak. Inclusion of polynomials may have created more robust models. This could be further explored in subsequent studies. In addition, the large amount of unexplained variation in most of the models presented here implies that there may be other factors affecting the songbird community. Fluctuations in food supply, weather or disturbance may have affected the observers' ability to detect the birds sufficiently well. Chapter 3 showed that count densities in 1999 were correlated with 1998. However, results here indicate that these correlations are not tightly coupled with landscape metrics used in these models. Factors outside of the scale of the study may have affected the density of birds. Fine-grain habitat variabilities, such as fallen trees and amount of scrub, may have affected the density detected in counts. In addition factors such as soil type, orientation of the patch, dispersal ability, distance to farmland and distance to nearest suitable patch may have affected the bird community.

The generalised linear and logistic models for dunnock, redpoll, siskin and crossbill tended to perform quite poorly, with $r^2_{(lr)}$ and $r^2_{(glm)}$ values being very low (Tables 5.3.2 and 5.3.5 respectively). Crossbill, redpoll, and siskin are granivorous species feeding on the spatially and temporally variable spruce seed crops, preferring to forage and breed in groups (Newton 1972, Holimon *et al.* 1998). They tend to forage widely over an area in loose flocks and focus on areas of high seed concentration, moving on when the supply is diminished (Newton 1972, Summers 1999). Thus their distributions and densities are highly erratic (Patterson *et al.* 1995). The secretive behaviour and muted contact calls of the dunnock (Cramp 1988 - 1994) make it a species likely to be under-counted.

However, some species' models had quite high predictive power, particularly logistic and generalised linear models for both goldcrest and meadow pipit ($r^2_{(lr)} = 0.493$, $r^2_{(glm)} = 0.457$ and $r^2_{(lr)} = 0.541$, $r^2_{(glm)} = 0.636$, respectively). The generalised linear models for both of these species were complex, unlike their logistic models. Avian habitat selection occurs at the highest level of geographical scale determining occurrence, and then at higher resolution to the small-scale patch, or even smaller scale, determining the density of birds in those occupied patches (Özesmi & Mitsch 1997). It is possible that the logistic regression models are measuring habitat selection at a lower resolution than the generalised linear models, with presence/absence being an 'easier' decision to make, requiring fewer cues, than relative quality of patches (determining density distributions).

The species-specific reactions to forest variables, and differences in explanatory power of the models in this study, highlight the need to treat separate species as the functional unit (Jokimäki & Huhta 1996) and not to aggregate them into functional groups, as Donald *et al.* (1998) attempted to do.

It may be possible to use other species densities or occurrences as predictors in the models. This would highlight those species whose perceptions of a habitat's quality were similar, and thus generate models that were applicable to many species. This may be particularly pertinent to migrants such as willow warbler. Migrant species use heterospecific and conspecific cues to quickly assess habitat quality on reaching the breeding grounds, and thus migrant density is correlated with residents densities (Mönkkönen *et al.* 1997). This concept is discussed further in Chapter 6. Chapter 6 also discusses the phenomenon increases in food availability resulting in increases in density and distribution of those species most reliant on that food source e.g. an increase in seeds resulted in increases of density and distribution of granivorous species. These granivorous species are colonial birds, and thus may not be good predictors of a more territorial species' density or occurrence not reliant on that food source.

5.4.2 Spatial autocorrelation

A problem with stratified random sampling on a limited spatial extent is that of spatial autocorrelation in the environmental or the response variables. However, there was no significant spatial autocorrelation in the environmental variables, the residuals, or the bird occurrence and density data, with the exception of dunnock density and occurrence, and siskin density, all at the centre of patches. However, it is assumed here that these barely significant spatial autocorrelations are a product of small sampling sizes, and may not actually be significant because of the large numbers of tests performed. When using multiple tests, adoption of the 0.05 significance level may allow too many Type I errors, whereby the null hypothesis is rejected when it is, in fact, true (Tabachnick & Fidell, 1996). Therefore, it can be deduced that my sampling regime was successful in randomly selecting areas that were far enough away from each other to make them independent sampling units. In addition Kielder Forest has a management regime that generates a highly heterogeneous mosaic landscape that is unlikely to be spatially autocorrelated.

5.4.3 Perceptual grain

As already discussed, choice of spatial scale can raise concerns. The low to medium $r^2_{(glm)}$ and $r^2_{(lr)}$ values in this study and others (Hawrot & Niemi 1996, Donald *et al.* 1998, Penhollow & Stauffer 2000) may be due, in part, to sampling errors, detectability and weather differences, but may also be attributable to landscape variables not measured or outside the extent of the study. It is impossible in a study of this type to measure every aspect of a landscape's structure, from the micro- to macro-habitat range, and relate these to bird data, because of problems of landscape quantification and high variable to case ratios, which contravene many statistical techniques' assumptions (Tabachnick & Fidell 1996). Jokimäki and Huhta (1996) show that bird-habitat relationships are sensitive to the grain at which they are measured, and so do not act as fractals where the same patterns are seen at all spatial grains. It may be interesting in later studies of this sort to try to quantify the spatial grain at which a bird species is operating so that other meaningful variables can be incorporated into the predictive models. Burkhardt *et al.*'s (1998) work showed that nuthatch *Sitta europaea* habitat choice differed on two scales in deciduous trees, showing that small and large-scale variables are important for habitat selection. In logistic or Poisson GLM modelling, utilisation of environmental variables measured at different scales, such as small-scale variables immediately adjacent to the nesting and feeding sites and larger-scale variables (e.g. landscape connectivity), may provide an insight into how a species perceives the proximal and distal landscape (Pribil & Picman 1997; Burkhardt *et al.* 1998).

5.4.4 Predictive models of bird density

If a variable is included in a model it can be inferred that the quality of the patch or area as perceived by that bird species is affected. However, there can be no firm conclusions as to whether the quality of that habitat can be measured by species' density, as demographic data such as survival or nesting success are unknown (Penhollow & Stauffer 2000). Despite this, these habitat associations are used as a rough proxy for habitat preferences.

5.4.4.1 Fractal dimension, planting year and patch area

The variables in this study have contributed to models that have captured some of the variance of bird density or occurrence despite concerns over spatial grain. Fractal dimension (FD), which gives an indication of a patch's complexity, is clearly very important in determining many of these species' densities or occurrences. Complex patch shapes generate higher edge:centre ratios than more simple shaped patches. However, despite the predominance of positive edge effects in bird species (Table 5.3.1), it was found that many species formed negative associations with fractal dimension. Indeed the hypotheses that edge species prefer complex patches and centre species prefer simple patches are not upheld for any species (Table 5.3.3 and 5.3.6). The American study by Hawrot & Niemi (1996) showed that an edge-loving forest species (American robin) had a negative association with fractal dimension, and an open habitat species had a positive association, again in contradiction to my hypothesis. However, in this American study, fractal dimension was highly correlated with habitat type (Hawrot & Niemi 1996), and so their results concerning this variable should be treated with caution.

Complex shapes are generally associated with greater boundary crossing frequency, because of greater permeability to dispersal and movement (Forman & Godron 1986, Stamps *et al.* 1987). So, with low FD (simple shapes) a patch would be expected to contain higher densities of birds due to limitations to dispersal causing aggregation. In addition, if a complex patch is more permeable to songbirds, it also may be more permeable to predator species. Another explanation for the general negative association with FD is that avian predators may be able to see a larger length of boundary if the boundary is curvilinear rather than straight, with predation pressure being higher at the edge than the centre of forested patches (Angelstam 1992, Andrén 1995, Suarez *et al.* 1997, Soderstrom *et al.* 1998). These two factors may increase predation pressure in complex shaped patches.

Tree planting year was an important predictor of songbird density (Bibby *et al.* 1985, Donald *et al.* 1998). There was a clear separation of forest birds and open habitat birds with only wren and meadow pipit falling into the second category. Meadow pipit had the highest $r^2_{(glm)}$ value ($r^2_{(glm)} = 0.636$); high densities of meadow pipit were found in almost every clear-fell/young patch surveyed (Table 5.3.5 and 5.3.6). Most of the species expected to have a negative association with planting year (therefore associating with older trees) such as goldcrest, coal tit, crossbill and chaffinch (Haila *et al.* 1996, Bibby *et al.* 1985, Newton 1972) fulfilled this expectation (Tables 5.3.3 and 5.3.6).

There was a strong link between fractal dimension and planting year. Many species that avoided young trees and complex patches were found to have a positive association with patches that were both young and complex (logistic regression: robin [Table 5.3.3]; GLM: coal tit, goldcrest, redpoll [Table 5.3.6]). Conversely high meadow pipit density (GLM) was found in young and complex patches but low densities in patches that were both young and complex (Table 5.3.6). This contradiction between these two groups may arise from the interpretation of these results. It is possible that the former group, instead of being attracted to young complex patches (which is contrary to the ecology of these species, especially the coal tit which forages almost entirely in mature trees), may avoid old simple shaped patches. If this is the case then the management implications are that clearcut edges should be linear to attract young habitat specialists such as meadow pipit, but that more mature, forested patches should be made more complex to attract the mature tree specialists such as the coal tit.

These results show that consideration of the main effects and interaction terms together is important in order to make a realistic interpretation. To my knowledge this is the first proposal for a staged approach to patch management with treatment in different successional patches. It may provide a method of satisfying the habitat preference criteria of a wider range of species than the current static management regime.

The results become more complicated to interpret when area is also included in these models. Goldcrest avoid patches with a large area or that are young, yet appear to be found at high densities in large young patches (Table 5.3.6). Again interpretation is difficult and consideration of the main effects is important for further explanation of the interactions. Using the converse explanation, it is more likely that goldcrest are found at low densities in patches that are mature but small. This is contrary to the hypothesis that edge species, such as the goldcrest (Table 5.3.1), will be attracted to smaller patches.

A patch with a large area will have a lower edge to centre ratio than a smaller patch. Meadow pipit (GLM) preferred large young patches and avoided young complex shaped patches (Table 5.3.6). This result reinforces the evidence that meadow pipit avoids edges (Table 5.3.1), with individuals preferring patches that are less likely to be affected by edges. Thus, meadow pipit is attracted to simple shaped or large young patches that minimise its risk of predation.

Wren is found at low densities in large patches with complex shapes. Wren also prefers young patches; however, they display edge attraction (Table 5.3.1). Evidence for wren's edge attraction is reinforced by the result that wren prefers small patches. Wren also prefers complex young patches, where the convoluted edge creates more edge habitat than for a simple patch of the same area. Although wren and meadow pipit prefer young patches it is clear that they respond differently to other variables measured here. What causes these differences in perception of habitat quality?

Whereas wren tends to sing from a song post, meadow pipit proclaims its territory with a song and an aerial display that covers a large area. This difference in their behaviours may allow wren to exploit areas that meadow pipit does not perceive as being attractive, for example, small patches. This lack of competition in small patches may have led to wren preferring them due to competitive exclusion by meadow pipit in the larger patches (Hanski 1995). Small patches also have a larger edge:centre ratio, which may attract the wren to them. It is highly probable that small young patches are used less by predators than large patches because of a lower patch encounter rate (a small patch is more likely to be missed by a wide ranging predator than a large obvious one), and limitations of the amount of available suitable habitat for foraging predators.

5.4.4.2 Landscape structure

Optimal foraging theory involves the dispersion of resources (Ims 1995). Those species choosing territories that are positively affected by total edge comparison will be optimising their foraging efficiency by including many different tree ages within a territory so that their resource needs are satisfied. Thus, when species such as redpoll or goldcrest choose a territory with several different tree ages within it, they are making a decision about how resources are dispersed.

Edge comparison gave an index of the age of all of the trees next to the patch in question and so was an indicator of landscape structure. Care had to be taken in building the models, as there were high correlations between these indices (Appendices 4 and 5). A positive association with any of the edge comparisons showed that the birds were reacting to habitat heterogeneity or the type of edge formed between the patches. Edge comparison as a main effect contributed to the logistic regression models for goldcrest and willow warbler (both preferring soft edges over hard), and to the GLM's for chaffinch, wren, meadow pipit, dunnock, redpoll and willow warbler (the latter three preferring soft edges, chaffinch and wren preferring hard edges, and meadow pipit avoiding hard edges). The results for chaffinch and wren satisfy the hypothesis that species with positive edge effects prefer hard edges to softer ones. In addition, landscape heterogeneity can be quantified as increasing with more highly dissimilar patches creating it. Thus the hypothesis that generalists, such as the chaffinch, prefer heterogeneous landscapes is also upheld.

However, goldcrest (LRM), willow warbler (LRM), dunnock (GLM) and redpoll (GLM) do prefer patches with softer edges. Like chaffinch, goldcrest is a generalist, but is not so catholic in its tastes. Chaffinch is often found in all successional stages, whereas goldcrest avoids areas with grass (Haila *et al.* 1996, Bibby *et al.* 1985). Therefore, although the goldcrest is an edge species and prefers edges between dissimilar patches, it does not prefer those patches that are within a highly heterogeneous landscape including young patches. Avoidance of the younger part of a soft edge is seen in goldcrest and redpoll despite a positive association with the soft edges as a main effect. Redpoll shows no positive edge effects but clearly benefits from a heterogeneous landscape despite avoidance of the younger elements.

Meadow pipit was found at low densities in large patches with hard edges (mature/young edges) which is consistent with the hypothesis that centre specialists avoid hard edges. The meadow pipit's aerial display and ground nest make it particularly vulnerable to predatory attack from the air and the ground. With predators mainly foraging along the edge, this strategy minimises meadow pipit predation risk. By avoidance of complex patch shapes, small patches, and hard edges (in large patches) meadow pipit maximises its edge avoidance strategy.

The willow warbler is the most common migrant in the forest. High densities were found in patches surrounded by the soft edges of pre-thicket and mature comparisons. There was no tree age-related interaction. This species also had a positive edge effect. Its preference for patches with mainly pre-thicket/mature edges indicates that it prefers areas including patches of these two different types.

Perception of the landscape by willow warbler may occur at a different spatial grain to the resident bird species. Returning migrants need to make quick decisions about where to form a territory, as early arriving males tend to form territories in the 'best' quality habitat (Alatalo 1984). It has been found in Finland that migrants such as willow warbler and chaffinch (a migratory species in Finland) respond to aggregations of tits. They may thus judge the quality of a habitat, not only by its characteristics, but also by the density or distribution of other species in the habitat according to the 'heterospecific attraction' hypothesis (Mönkkönen *et al.* 1990). Forsman *et al.* (1998) found that willow warbler density was highest in areas where manipulated tit density was also higher. Changing forest management plans to increase the amount of pre-thicket/mature edges may indirectly benefit willow warbler by attracting other species. Thus, willow warbler density or distribution may be an indication of a habitat's 'ecological worth' (Tucker *et al.* 1997).

5.4.5 Model validation

Despite high annual correlations between the 1998 and 1999 data because the same sites were resurveyed (see Chapter 3), the 1998 data were the only suitable option for validation. The 1992 dataset would have been ideal for validation of the models had the survey methodology been the same (see Chapter 3). The 1991 dataset could not be used, also for this reason. Additionally the mast crop affected the density of birds surveyed in 1991 that year (Chapter 3). Jack-knifing or split sample tests were not carried out as the models were not very robust and required the large sample sizes used for the full models. In addition, the amount of computing effort with this large number of models would have been prohibitively costly in terms of time.

The present study assumed that the bird community in Kielder was in equilibrium, with annual changes in density or occurrence being negligible as found by Bibby *et al.* (1985). However, Willson and Comet (1996) state that non-equilibrium conditions can occur due to extreme weather conditions, disease, changes in predation pressure or competitors, or, as in the case of newly felled areas, insufficient time for the bird population to establish an equilibrium. Despite these factors, this study showed that models built on a dataset in one year (1999) could occasionally predict the species distribution and density values from the dataset of the previous year (1998). Validation of the GLMs using regression analysis produced relatively good positive relationships ($r^2 > 0.15$) for four species (crossbill, meadow pipit, wren and willow warbler). The linear regression analysis for the GLMs did not take into account actual densities found but rather looks at the relationship between the predicted densities in 1999 and observed in 1998. So, a good positive relationship may exist between the predicted values of 1999 and the observed values of 1998, but the paired values may be *consistently* different.

It can be inferred that for those high performing models, with high $\hat{k}$ (coal tit, goldcrest, meadow pipit, robin, willow warbler [LRM] and goldcrest, meadow pipit [GLM]), species' perceptions of patch quality were static and did not change appreciably from year to year in this type of landscape. However, periodically the spruce trees of Kielder Forest produce large cone crops (mast years) resulting in large influxes of siskin and crossbill to the region (Patterson *et al.* 1995). Neither 1998 nor 1999 were mast years.

Venier *et al.* (1999) also used logistic regression to investigate the effects of macroclimate on breeding-bird distributions and used a split sample technique of model validation using 50% of the data collected. Concordance values were of 70% to 86% showing good classification accuracy. The present study used data from the previous year to validate the logistic models and generated seven models with concordance values (PCC) of between 66.2% to 90.7% (Table 5.3.4). Therefore, inclusion of interyear variation still generated high performance logistic regression models for these species.

On investigation of the maps (Maps 5.1.1-11 and Maps 5.2.1-11), the models generally tended to under-predict, with omission scores (prediction of either absence or lower density when the species is either actually present or at high density) generally being higher than commission. In terms of sensitive forest management, it is obviously better to use models that err on the side of omission so that there is more scope for increasing the population of certain species rather than creating conditions that may limit bird populations.

5.4.6 Management implications and conclusions

In terms of providing a landscape with a variety of successional habitat types for birds, rotational clearfelling is a good method of coniferous timber harvesting. My study has highlighted the need for managed forests to be viewed as spatially and temporally changing successional mosaics that can be restructured not only in space but also in time. It is proposed here that management regimes be tailored to different successional areas particularly in consideration of patch shape. Patches could be felled to create large, simple shaped clearfells that could be restocked to create smaller more complex patches.

Chapter 4 presents evidence to show that edge effects extend deep in to the patch for some species. The present chapter (Chapter 5) reinforces this evidence with edge mediated variables, such as edge comparison and fractal dimension, affecting birds at the ‘centre’ of patches. This indicates that the concept of core area in this study is probably not encompassed, and shows that this concept is highly species and even habitat specific. Of the hypotheses discussed here, there were equivocal results for all (Table 5.4.1), except for the general pattern of generalists preferring heterogeneous landscapes. Indeed if only main effects are considered, the hypothesis that edge species will prefer either small patches or complex shaped patches is wholly rejected. However, if interaction terms are interpreted it can be seen that complex mature patches hold more individuals of some species.

If migrants, such as willow warbler, are to be attracted to the forest, clearfelling should not occur directly opposite mature trees but perhaps buffer zones of pre-thicket spruce could be planted or retaining some residual mature trees (Tittler *et al.* 2001) so that hard edges are not formed. The only species that preferred these harder edges were chaffinch and wren. Chaffinch is a generalist species found so ubiquitously throughout the forest that perhaps it should not be seen as a management priority. This study is not in accordance with Penhollow and Stauffer's (2000) finding that increasing the amount of hard edges enhances overall avian diversity; however, it agrees well with Hawrot and Niemi (1996) where many species showed a preference for intermediate or soft edges. Suarez *et al.* (1997) study on predation risk of Indigo buntings (*Passerina cyanea*) at different types of edge, showed that individuals at hard edges, such as those between clearfells and mature trees, had a higher risk of being predated than at more gradual edges. But, as with much terminology, these findings are dependent on the perception of 'hardness' of an edge by both the observer and the bird species.

A logical progression from this study would be to use these models within the GIS to simulate maps of the effects of different landuse practices over space and time, and to quantify how these practices would most likely affect the different bird species of the forest. In this manner landuse could be planned according to species-specific priorities.

As many predictive modelling studies have shown, the predictive power of these avian-habitat association models is not high (Hawrot & Niemi 1996, Edenius & Elmberg 1996, Penhollow & Stauffer 2000). However, the wildlife management implications are considerable. Their value as a management tool thus is enhanced by their potential impact on landscape restructuring. This study shows that the benefits of economic gain in terms of an easily managed highly productive crop such as Sitka spruce need not be at the cost to the existing wildlife. It is possible to manage these highly utilitarian forests with economic and ecological priorities in mind by simple measures such as increasing the amount of 'soft' edges and using a temporally and spatially hierarchical approach to felling and restocking.

	Hypothesis	*Logistic Regression Models*		*Generalised Linear Models*	
		+	-	+	-
a)	patch shape, area, edge comparison and age can affect distributions/densities of songbirds according to bird species specific differences	All species		All species	
b)	centre preferring species will avoid high contrast edges and edge species will be attracted to them Centre $_{(C)}$ Edge $_{(E)}$		Meadow pipit $_{(C)}$ Goldcrest $_{(E)}$ Willow warbler $_{(E)}$	Meadow pipit $_{(C)}$ Chaffinch $_{(E)}$ Wren $_{(E)}$	Willow warbler $_{(E)}$
c)	habitat specialists prefer homogeneous landscapes and generalists prefer heterogeneous landscapes Generalist $_{(G)}$ Specialist $_{(S)}$	Goldcrest $_{(G)}$ Willow warbler $_{(G)}$		Chaffinch $_{(G)}$ Wren $_{(G)}$ Willow warbler $_{(G)}$	Redpoll $_{(G)}$
d)	edge species will prefer patches with the maximal amount of edge habitat, e.g. small patches or complex shaped patches and centre species would prefer the contrary Centre $_{(C)}$ Edge $_{(E)}$		Robin $_{(E)}$ Siskin $_{(E)}$		Meadow pipit $_{(C)}$ Goldcrest $_{(E)}$ Robin $_{(E)}$ Siskin $_{(E)}$ Willow warbler $_{(E)}$
e)	breeding bird data can be used to create temporally robust predictive models that include main effects and interactions between variables, Logistic regression PCC > 0.65 GLM PCC> 0.25	Chaffinch Coal tit Goldcrest Meadow pipit Robin Redpoll Willow warbler	Crossbill Dunnock Siskin Wren	Crossbill Chaffinch Coal tit Dunnock Goldcrest Meadow pipit Siskin Wren	Robin Redpoll Willow warbler
	Kappa > 0.15	Chaffinch Coal tit Goldcrest Meadow pipit Robin Redpoll Willow warbler	Crossbill Dunnock Siskin Wren	Crossbill Coal tit Goldcrest Meadow pipit Wren	Chaffinch Dunnock Robin Redpoll Siskin Willow warbler

Table 5.4.1: How models of species occurrence (logistic regression) and density (GLM) correspond to the proposed hypotheses. + = species conforms to the hypothesis and - = species contradicts the hypothesis.

6 Inter-specific abundance-distribution relationships: the effect of resource availability and aggregation.

Abstract

Some species are locally common and widespread across a landscape (patch occupancy is high), and some species are locally scarce and rare (patch occupancy is low). This is termed the inter-specific abundance-distribution relationship, and can be investigated using linear regression analysis. It was found in this chapter that food availability and aggregations affected the abundance-distribution relationships of the bird species in Kielder. The abundance and distribution of granivorous species such as crossbill, redpoll and siskin (and to a lesser extent chaffinch) were much higher in mast years than in non-mast years. It is hypothesised that the aggregations of willow warbler was also the result of attraction of willow warbler to patches with high concentrations of singing conspecifics, as found by Mönkkönen *et al.* (1997).

6.1 Introduction

The inter-specific abundance-distribution relationship has been well documented over recent years using field data (Brown 1984; Gaston *et al.* 1998 a & b; Blackburn *et al.* 1997; Blackburn *et al.* 1999) and simulation models (Venier & Fahrig 1996). Generally, the former studies have been on large-scale abundance-geographical range size relationships (Newton 1997; Blackburn *et al.* 1997; Gaston *et al.* 1998 a & b; Blackburn *et al.* 1999). Animals with a greater geographical range (1000's km^2) display higher local abundance than animals with a limited range. There are only a few studies based on data from a small regional scale (100's km^2) (Venier & Fahrig 1998; see Hanski 1982 for a review of invertebrate examples). The mechanisms behind abundance-distribution relationships have been discussed at length (Gregory & Gaston 2000; see Gaston *et al.* 1997 for a review) and include "sampling artefacts, phylogenetic non-independence, range position, resource breadth, resource availability, abundance-dependent habitat selection, metapopulation dynamics, and vital rates" (Gaston *et al.* 1998b). The present chapter reports results of a study conducted in a forested landscape covering 600 km^2, to investigate whether coniferous forest passerines display similar abundance-distribution relationships when data are analysed on a small regional spatial scale (fine resolution), as opposed to on a larger geographical range-size scale (coarse grain). I also consider some factors affecting abundance-distribution relationships.

One of the suggested mechanisms behind the abundance-distribution relationship is that generalist species have more access to resources, and thus are less selective in their foraging and nesting areas (Brown, 1984). Resources limit specialists to restricted foraging areas. Thus it would be expected that generalist species would be widely dispersed and locally abundant, and specialist species would have both a lower abundance and more restricted distribution. This has been termed the resource breadth (sometimes termed the resource use) hypothesis. Gregory & Gaston (2000) separated the resource breadth (Brown 1984) and resource availability (Venier & Fahrig 1996) arguments and found that the latter hypothesis is more likely to explain the abundance-distribution relationship. This agrees with Venier & Fahrig's (1996) proposal that it is resource availability that determines the abundance-distribution relationship. Species (including specialists) that utilise widespread and common resources are also widespread and common.

Another suggestion by Venier and Fahrig (1996) is similar, yet subtly different and involves dispersal after breeding. If a species utilises a high proportion of a landscape then dispersal would be more successful, resulting in higher abundance and distribution (see also Lawton 1996). In a highly fragmented habitat, when habitat preferences are strong (due to available resources), it should be expected that dispersal and metapopulation dynamics will be important in maintaining the songbird population (Lawton 1996).

Ideal distribution theory (Fretwell 1972) has been used by many authors in explaining the distribution of individuals or species in a 'patchy' or heterogeneous environment (Fryxell 1991; Møller 1991; Wahlstrom & Kjellander 1995; Mönkkönen *et al.* 1996; Mönkkönen *et al.* 1997; Tyler & Hargrove 1997). According to the Ideal Free Distribution (IFD), patches of varying 'quality' across the landscape will be occupied sequentially, with the most suitable habitats being filled up first. Thus the most attractive patches will contain the highest densities (Fryxall 1991; Tyler & Hargrove 1997). The Ideal Despotic Distribution (IDD) includes competitive interactions, with the most dominant individuals settling in the 'best' patch until it is full, then the next most dominant in the second best patch (Fretwell 1972, Møller 1991). Møller (1991) states that territorial passerines are most likely to follow the IDD due to territorial interactions, and colonial passerines to follow the IFD.

A simplistic way to judge patch quality is to assess the amount of resources in that patch. Food and nesting resources are important in determining where passerine species choose to form territories and breed (Burke & Nol 1998). This is particularly true of nomadic species (Holimon *et al.* 1998), which tend to search for areas with high densities of food resources. Northern European coniferous forests have years when the cone crop is poor (non-mast years) when only mature trees produce cones. However, periodically they have years when the cones are plentiful (mast years), when not only mature trees but pre-thicket trees bear large numbers of cones (Petty *et al.* 1995). Thus, in mast years the cones are at higher density and more widespread in distribution than in non-mast years. Influxes of large numbers of nomadic siskin and crossbill occur in areas with a high proportion of spruce that has a mast crop (Newton 1972), such as Kielder Forest in 1991 (Patterson *et al.* 1995). If resources decrease in distribution and abundance then it would be expected that the distribution and abundance of those species most reliant on those resources would decrease accordingly. There is no conclusive, consistent evidence to suggest that when a species' abundance declines its range also declines (Gaston & Curnutt 1998); however the expansion of the northern fulmar, *Fulmaris glacialis*, in numbers as well as range does provide evidence for the reverse phenomenon (Newton 1997). I hypothesise that granivorous species will have lower abundance and more restricted distribution in non-mast years than in mast years as a result of a restriction in the range and decrease in abundance of resources. Competitive interactions in territorial species following the IDD would force individuals into marginal habitats. This is less likely if the species follow the IFD, such as non-territorial colonial species, as more individuals can forage in the same patch. Using Møller's (1991) predictions, colonial species (like the crossbill) would be expected to have a higher abundance:distribution ratio than the more highly competitive territorial passerines, due to flock foraging and reduced competitive interaction.

Resources may not be the only cues by which birds select or avoid sites in which to establish territories. Intra-specific (Doligez *et al.* 1999) and inter-specific (Forsman *et al.* 1998) attraction, competition for food, predation and parasitism may also play a role (Mönkkönen *et al.* 1997). Mönkkönen *et al.* 's (1990) experiment to investigate the effect of heterospecific competitive interactions on northern European passerine communities showed that artificially increased densities of resident tits did not competitively exclude migrants. Indeed there was some evidence for heterospecific attraction, with higher densities of migrants in areas of high tit density. This conclusion was further explored and reinforced by a similar study in Boreal North America by Mönkkönen *et al.* (1997).

Mönkkönen *et al.* (1997) state that northern Boreal regions are characterised by highly variable conditions (i.e. the weather conditions are highly variable throughout the breeding season), a short breeding season and high predation pressure. Although not a northern Boreal region, Kielder Forest is also characterised by these features. Newly arriving migrants thus need to make a quick decision based on habitat cues or more probably, if the species is a generalist (Mönkkönen *et al.* 1997), on the existing resident population. Thus, migrants use residents as a cue to assess: a) the amount of resources or 'quality' of a patch (Gaston *et al.* 1997); and perhaps also b) the predation risk which would take a relatively long time to assess not using heterospecific cues. Alatalo *et al.* (1984) found that male pied flycatchers that arrived early in the breeding season tended to occupy better territories, in terms of nesting resources, than those individuals that arrived later. The only common migrant of my study is a generalist, the willow warbler, *Phylloscopus trochilus* (Cramp 1988 - 1994). Later arriving males might use conspecifics to assess the quality of the habitat. However, the mechanism by which habitat quality is judged by the early arrivals may indeed be by heterospecific attraction. One of the more established theories is that aggregations occur in order to attract more females by increasing the volume of song (see examples in Krebs & Davies 1993). Therefore it would be expected that willow warbler abundance would be higher than expected as a result of its distribution due to conspecific and heterospecific attraction generating aggregations of these warblers.

I investigated the form of the inter-specific abundance-distribution relationship (hereafter referred to as the relationship) of a small-scale (100's km^2) study area, so that I could compare this with larger scale (1000's km^2) abundance-range relationships. The hypothesis that abundance and distribution are affected by resource availability was investigated, and the effect of aggregation was discussed.

6.2 Methods

Previous large scale (UK-wide) studies, such as the Common Bird Census organised by the British Trust for Ornithology, have relied on a large body of volunteers to attain the bird data by the labour intensive, yet accurate, survey method of territory mapping (Bibby *et al.* 1992). However, the present relatively small-scale study utilised the point count methodology using only one observer with two visits (early and late spring) to each site, as with Venier and Fahrig (1998).

Data from two studies were used: point count survey data from 1991 (Patterson data), and from 1998 and 1999 (McSorley data) (see Chapter 3 for a review of the differences between the two studies). 1991 was a mast year for Norway and Sitka spruce, whereas 1998 and 1999 were non-mast years for both species (Appendix 10). Crossbill and siskin irruptions occurred in the winter and spring of 1990/1991 (Patterson *et al.* 1995).

An occupied patch was one in which one individual from a species was detected at least once. If a site was unoccupied by the species in question it was not used to calculate abundance as inclusion of zero values can lead to artifactual abundance-distribution relationships (Wright 1991; Venier & Fahrig 1998; Blackburn *et al.* 1999). The data from species that occurred in more than two patches surveyed were used for analysis. I calculated the abundance (number of individuals per hectare) of a species in each occupied patch at the centre and edge in early and late spring. For each species the maximum, mean and minimum abundance over all of these patches was calculated for the early and late spring datasets, at both the edge and the centre. Chapter 4 shows that the abundance of birds is different at the centre and edge of patches. Over these two time periods, the highest value of the maximum, the mean and the minimum abundance per species was determined, as with Venier & Fahrig (1998). Distribution was calculated as the number of occupied patches divided by the total number of patches surveyed, giving proportional occupancy in early and late spring, for both the centre and the edge. Again, the highest value achieved by each species between early and late spring was used for analysis.

All abundance and distribution values were ln (natural log) transformed. All kurtosis values were not significantly different from that of a normal distribution (SPSS 1998), and thus the assumptions for linear regression analysis were not contravened. Abundance-distribution relationships were calculated using the ln proportion of occupied surveyed patches by a species (distribution) as the independent variable and the maximum, mean or minimum local ln abundance the species attained (abundance) as the dependent variable in ordinary least squares regression analysis (SPSS 1998). Regression analyses were performed for each sample (i.e. for maximum, mean and minimum abundance, at both the centre and edge in 1991, 1998 and 1999). Abundance was used as the dependent variable to conform to many recent studies on the abundance-distribution relationship (Gaston *et al.* 1998a; Gaston *et al.* 1998b; Blackburn *et al.* 1999). This assignation does not attempt to imply that distribution is causative (i.e. widespread distribution generates high abundances) (Zar 1999). The relationship was not significant if the p-value exceeded 0.05.

Outliers were removed if they exceeded ±3 standard deviations (s.d.), although Tabachnick & Fidell (1996) quote ±3.29 s.d. as the critical value. Differences between regression slopes and elevations for centre and edge (1999) were determined using SPSS (1998) ANCOVA. All graphs were produced using STATISTICA (1995).

6.3 Results

Between 13 and 19 bird species were used for analysis (Table 6.3.1). None of the data points was a significant outlier (exceeding ±3 s.d.) and so all species were retained for further analysis.

Table 6.3.1 presents the linear relationships between ln-abundance and ln-distribution. Maximum abundance generated relationships that were positive (positive β-values), highly significant (p-values ranged between 0.025 and < 0.001) and strong (all but one r^2 value ranged between 0.661 and 0.723). Figures 6.3.1 and 6.3.2 display the relationships graphically for 1991 and 1999 for centre sites. Using maximum abundance, it can be seen that widely distributed species tended to be locally abundant, and rare species were scarce. The relationships resulting from the 1998 dataset are not shown graphically as they were very similar to the 1999 relationships. Utilisation of mean, and particularly *minimum* abundance generated abundance-distribution relationships that were not strong and, in the case of minimum abundance, were generally insignificant, weak and negative (Table 6.3.1). In 1998 at edge sites there was a significant negative relationship between distribution and minimum abundance.

If the maximum, mean and minimum abundance data points for each species are viewed together (Figures 6.3.1 and 6.3.2) then it can be seen that the spread of data points creates a triangular (polygonal) relationship as found by Gaston *et al.* (1998). Thus, rare species generally had consistently low abundances, and widespread species were found at high abundances in some patches and low abundances in others.

There were no significant differences between the abundance-distribution slopes of the edge and centre in all three years (Table 6.3.2). Figure 6.3.3 presents this graphically (1999 data). Edge and centre relationships were quite similar, although the edge abundance-distribution slopes generally had significantly higher elevations (Table 6.3.2) than the centre. This is evidence that the density at the patch edge was significantly and consistently higher than in the patch centre.

In non-mast years (e.g. 1999) crossbill and siskin were relatively scarce birds with restricted distributions (Figure 6.3.2). However, in 1991 they were found at much higher abundances and had wider distributions than in 1999 (Figure 6.3.1). In relation to the maximum abundance regression line of 1991, crossbill abundance was higher than expected by its distribution (Figure 6.3.1). Figure 6.3.4 presents the differences within granivorous species (crossbill, chaffinch, redpoll and siskin) from 1991 to 1999, with some insectivorous species (robin, willow warbler, song thrush, pied wagtail, dunnock and meadow pipit) for comparison. The granivorous species, particularly the irruptive (Newton 1972) crossbill, show much greater variations in both their abundances and their distributions than the insectivorous species. For chaffinch, crossbill and siskin, abundance and distribution were several times greater in 1991 than in 1999. Crossbill was found in over ten times as many census sites with more than six times the abundance in 1991 compared to 1999 (Figure 6.3.4). Redpoll density was much higher in 1991 than 1999, even though its distribution was relatively similar over the two years.

Although the 1999 willow warbler data point was not a significant outlier, willow warbler abundance was higher than was predicted by their distribution (Figure 6.3.2). This was not as obvious in 1991, perhaps because the granivorous species may have biased the regression line. If this is taken into consideration, then willow warbler abundance in 1991 was further above the regression line than any other species in its insectivorous guild (Figure 6.3.1). In 1999, song thrush was also found at high abundance with limited distribution. It is possible that their loud song may have caused the observer to over count this species. In 1991 another migrant, the tree pipit, also had higher abundance than was predicted using its distribution.

				Maximum Abundance			*Mean Abundance*			*Minimum Abundance*		
Year	*Site*	N_1	N_2	r^2	β	p	r^2	β	p	r^2	β	p
1991	C	45	15	0.661	0.813	<0.001	0.513	0.717	0.003	0.006	-0.077	0.784
	E	17	13	0.432	0.658	0.015	0.092	0.304	0.313	0.058	-0.241	0.427
1998	C	43	16	0.709	0.842	<0.001	0.485	0.696	0.003	0.019	-0.137	0.612
	E	77	19	0.723	0.850	<0.001	0.503	0.709	<0.001	0.312	-0.558	0.013
1999	C	71	13	0.656	0.810	0.001	0.358	0.599	0.031	0.135	-0.367	0.217
	E	133	18	0.664	0.815	<0.001	0.368	0.607	0.008	0.057	-0.239	0.339

Table 6.3.1: Least squares regression analysis of ln local abundance (maximum, mean and minimum birds per hectare) against ln proportion of census sites occupied (distribution) showing the ß value (standardised coefficient), r^2 and significance value (p) for each sample (year and centre [C] or edge = [E]). N_1 = the total number of patches surveyed and N_2 = the number of species used for analysis.

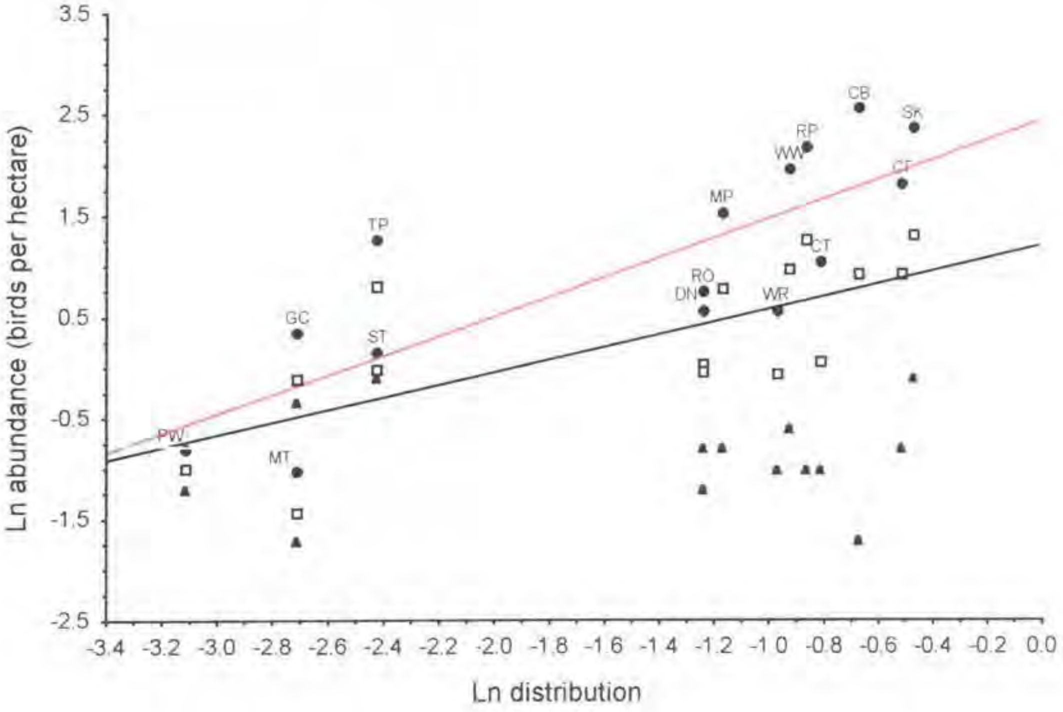


Figure 6.3.1: The 1991 abundance-distribution relationships, utilising ln local abundance (maximum – red line, filled circles; mean – black line, open squares; minimum – grey line, filled triangles) in relation to proportion of census sites occupied (distribution). Species names are shown for maximum abundance only; CB = crossbill, CF = chaffinch, CT = coal tit, DN = dunnock, GC = goldcrest, MP = meadow pipit, MT = mistle thrush, PW = pied wagtail, RO = robin, RP = redpoll, SK = siskin, ST = song thrush, TP = tree pipit, WR = wren and WW = willow warbler.

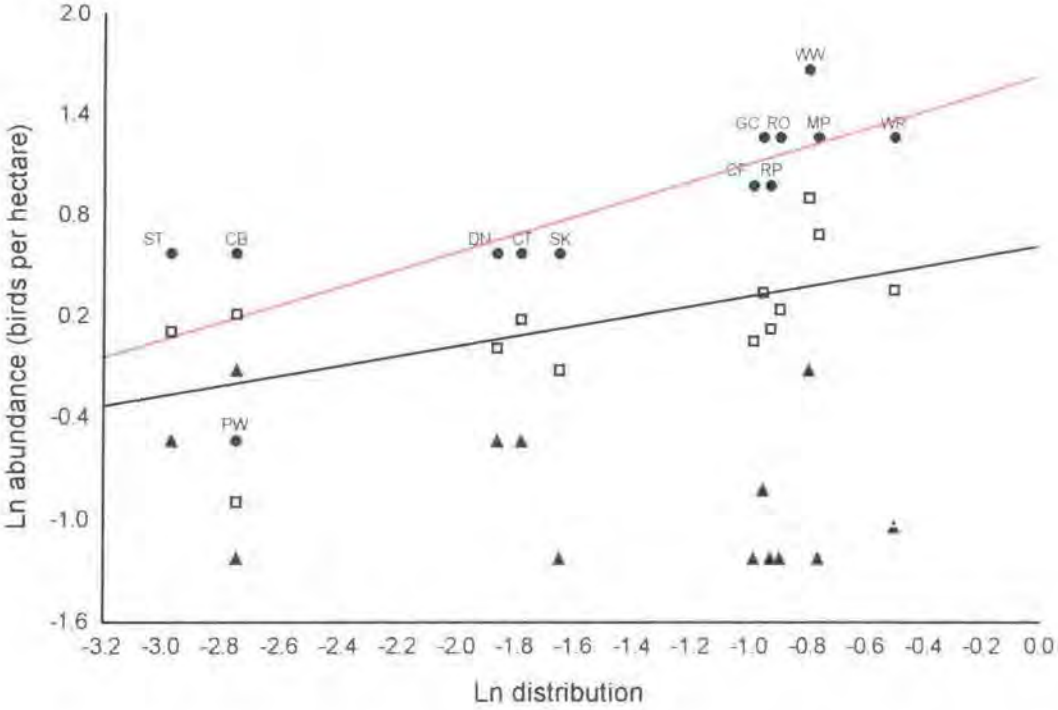


Figure 6.3.2: The 1999 abundance-distribution relationships, utilising ln local abundance (maximum - red line, filled circles; mean - black line, open squares; minimum - grey line, filled triangles) in relation to ln proportion of census sites occupied (distribution). Species names are shown for maximum abundance only CB = crossbill, CF = chaffinch, CT = coal tit, DN = dunnock, GC = goldcrest, MP = meadow pipit, PW = pied wagtail, RO = robin, RP = redpoll, SK = siskin, ST = song thrush, WR = wren and WW = willow warbler.

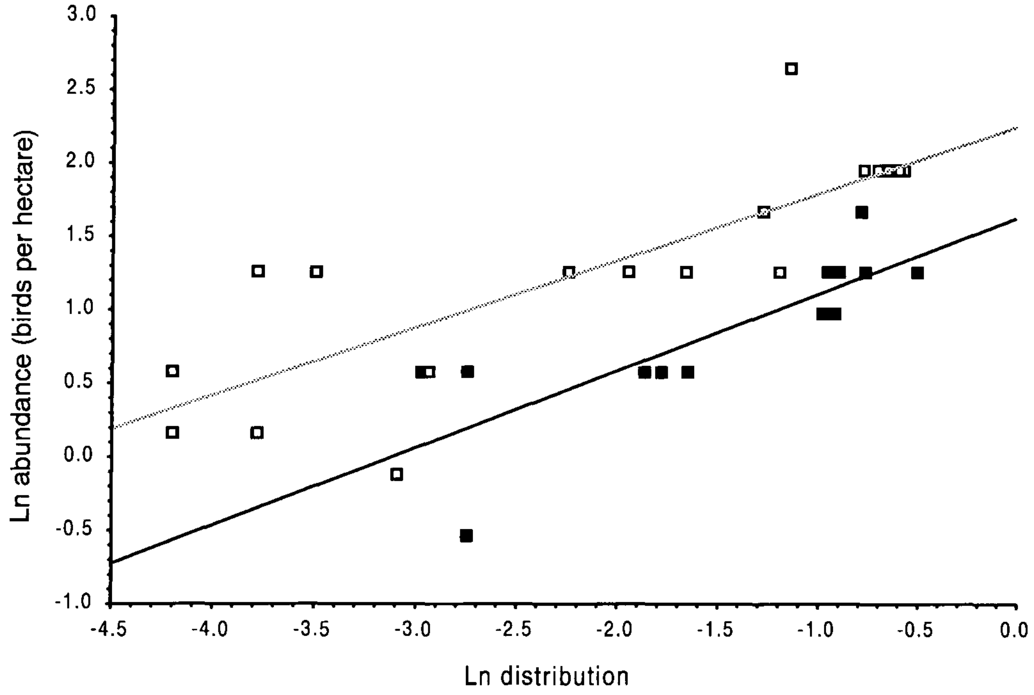


Figure 6.3.3: Ln maximum abundance-distribution relationships for species in centre and edge sites in 1999. Black line with filled squares denotes centre data and grey line with open squares denotes edge data.

		Ancova		
Year		*SS*	*F*	*p*
1991	Slope	0.73	2.44	0.132
	Elevation	4.02	12.74	0.001
1998	Slope	0.37	2.77	0.106
	Elevation	3.10	22.28	<0.001
1999	Slope	0.03	0.18	0.678
	Elevation	3.56	21.01	<0.001

Table 6.3.2: Comparisons between the slope and elevation of centre and edge abundance-distribution relationships utilising ln maximum densities and ln proportions of occupied census sites in three years. The analysis used was ANCOVA (SPSS 1998) and the table shows the sum of squares (SS), F-statistic and significance value (p).

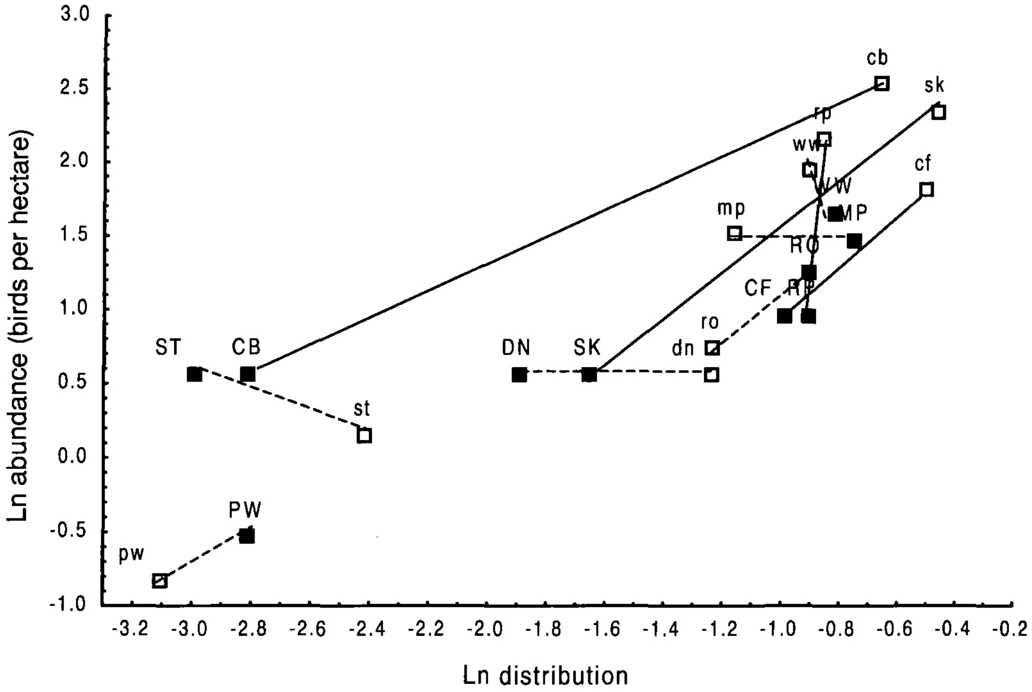


Figure 6.3.4: Differences between two years in ln abundance and ln distribution of granivorous passerines (solid lines) and a selection of insectivore passerines (dotted lines) in 1991 (open squares) and 1999 (solid squares). Lower case labels are for 1991 and capitals for 1999.

6.4 Discussion

6.4.1 Form of inter-specific abundance-distribution relationship

Previous studies of this relationship have concentrated on geographical range size (proportional occupancy of 10x10 km squares) (Newton 1997; Blackburn *et al.* 1997; Gaston *et al.* 1998 a & b; Blackburn *et al.* 1999), whereas the present study investigated distribution as the proportion of occupied patches on a small scale (as with Venier & Fahrig 1998). The importance of my study is that it shows that the abundance-distribution relationship found at a geographical-range scale is also found at a local, landscape scale.

The results from this abundance-distribution study show that maximum abundance (rather than mean or minimum) generates the strongest and most significant positive inter-specific abundance-distribution relationships. Thus, more widespread species had higher local maximum abundance.

Mean abundance also generated relatively strong relationships, whereas those between minimum abundance and distribution were weak and generally insignificant. These results were consistent across two sampling areas (centre and edge) in all three years (Table 6.3.1). However, contrary to the consistently positive relationships for maximum and mean abundance, minimum abundance generated negative relationships with distribution (negative beta values). However, only one relationship was significant (1998 at the edge). Thus, the scarcer species were found at greater minimum abundance than the more common species resulting in a negative abundance-distribution relationship. It is proposed here that the abundance of rare species was generally overestimated.

The polygonal relationships observed by plotting maximum, mean and minimum abundance against distribution (Figures 6.3.1 and 6.3.2) were also observed by Gaston *et al.* (1998b). Thus rare species were scarce in every occupied site whereas widespread species were common in some sites and scarce in others. Or more simply put, '...all species are rare somewhere, but restricted species are rare everywhere' (Gaston *et al.*

1998b). In another study not included in this thesis (McSorley *in prep*), I discuss why a particular species is less abundant at some sites than others, giving rise to the intra-specific abundance-distribution relationship.

6.4.2 Resources

There were significant differences in the elevations between edge and centre regression lines in 1998 and 1999, with the edge line having higher elevations (Table 6.3.2). Thus higher densities of individuals were found at the edge in both scarce and widespread species. This is associated with the higher structural diversity and greater amounts of available resources at the edge (Angelstam, 1992; Chapter 4). Thus, despite higher predation pressure at patch boundaries (Angelstam 1992; Andrén 1995; Suarez *et al.* 1997; Soderstrom *et al.* 1998), edge sites were perceived as being more suitable; more individuals were able to forage and form territories at the edge than the centre. Maurer's (1990) results based on a simulation and field-data study showed that sites with high productivity had steeper abundance-distribution slopes than those sites with low productivity due to higher resource availability and thus higher bird abundance. This proposal is partially substantiated by my results presented here, with the highly productive edge sites having significantly higher elevations of abundance-distribution slopes in 1998 and 1999 than centre sites. However, the slopes were not significantly steeper; resource availability was consistently higher at the edge for rare and common species keeping the lines' slope similar to the centre lines. So, the proportion of patches occupied by a bird species (be it scarce or common) is generally higher in the sample of patches surveyed at the edge than those surveyed at the centre. In addition, the local bird density was also generally higher. Thus, if density and distribution of resources are higher, as found at the edge, then the abundance and distribution of species in the patch are affected, reinforcing the hypothesis that resource availability is an important factor affecting the interspecific relationship.

Another body of evidence reinforcing the resource use hypothesis is that reductions in the abundance and distribution of available resources reduce granivorous species' abundance and distribution (Figures 6.3.1, 6.3.2 and 6.3.3). It was hypothesised that the lower seed abundance and proportion of coning trees (mature only) in 1999 compared to 1991 (when both mature and pre-thicket trees had exceptionally large crops of cones), would cause a decline in the abundance and distribution of crossbill, siskin, redpoll and chaffinch (Appendix 10). Figure 6.3.4 presents evidence for this. The insectivorous species (for example willow warbler, meadow pipit, robin, song thrush and dunnock) did not show such dramatic differences between 1991 and 1999 in abundance and distribution. Annual variations in food availability affected the granivorous species, which had lower abundances and distributions in non-mast years than in mast years. The hypothesis that resource availability (Gregory & Gaston 2000) affects the species most reliant on that resource, with abundance and distribution decreasing as the resource declines, is upheld. Therefore, using these two bodies of evidence, I propose that one of the mechanisms behind the inter-specific abundance-distribution relationship must be related to resource availability.

6.4.3 Aggregations

The present study also considered the effect of aggregation on the abundance-distribution relationship, by investigating whether species predicted to form aggregations (migrants and colonial species) had higher abundances predicted by their distribution than the resident, territorial species. Cardueline finches (including crossbill, redpoll and siskin) are colonial nesters and forage in flocks (Newton 1972); thus where they occur, they do so at high densities. This is not true of more territorial birds (such as the insectivores and including the fringilline finches e.g. the chaffinch) (Newton 1972) that provided the majority of the data points contributing to the abundance-distribution relationships I established. Thus, I found that the cardueline finches were more likely to form conspecific aggregations, causing higher abundance:distribution ratios, than more territorial species (Figure 6.3.1). The disparity between the abundance and distribution of territorial species and colonial species, with the colonial species having relatively higher densities for their distributions than the territorial species, conforms well with Møller's hypothesis that territorial species conform to the IDD. If territorial interactions and dominance affect an individual's decision to form a territory in a patch, then the overall density will be lower in suitable patches than for colonial, non-territorial species, which are affected primarily by resource availability.

It was expected that those species required to make a quick decision on where to form a territory (i.e. migrants) would not be able accurately to assess the quality of the habitat using environmental cues only. Thus migrants would use conspecific or heterospecific cues to assess habitat quality (Alatalo *et al.* 1984; Mönkkönen *et al.* 1990; Mönkkönen *et al.* 1997). It has previously been shown that migrants in Boreal regions (Mönkkönen *et al.* 1997) use heterospecific cues to assess habitat quality. In addition, female house wrens are attracted to areas where male house wrens sing (Johnson & Searcy 1996), so aggregations of singing males of breeding migrants in Kielder Forest would presumably cause increased chance of attracting females when they arrive (c.f. 'stimulus pooling' by lekking grouse, see Krebs & Davies 1993; Mönkkönen *et al.* 1997). This difference in the ecology of migrants and territorial residents (territorial residents would generally have time to follow the IDD in distributing themselves across a landscape) (Møller 1991) would therefore affect migrants' abundance and distribution. Aggregation would cause a higher abundance of migrants than that predicted by their distribution using the inter-specific abundance-distribution relationship.

In 1991 (Figure 6.3.1) the only species above the regression line (and thus with higher abundance:distribution ratios than those on or below the line) were the colonial granivorous species, as already discussed, and migrants (tree pipit and willow warbler). In addition, willow warbler abundance was higher than expected using the abundance-distribution regression line in 1999 (Fig 6.3.2). Blackburn *et al.* (1999) found that, over its British range, willow warbler was located at higher abundances in 10 km^2 squares adjacent to other squares occupied by willow warbler. However, paradoxically in the same study high willow warbler abundances were also associated with unoccupied 10 km^2 squares. It was unknown why this result occurred. Despite this apparently contradictory result from Blackburn *et al.* (1999), the hypothesis that aggregation will affect the position of a species on the abundance-distribution graph is upheld in my study, with migrants forming aggregated distributions, perhaps as a result of heterospecific and conspecific attraction.

6.4.4 Summary

This interspecific study, on a smaller spatial scale than geographical range, resulted in robust, predictable abundance-distribution relationships, which had a similar form to those found in the larger scale abundance-geographical range size studies. The present study has shown that resource availability and aggregation have roles to play in the abundance-distribution relationship. More work needs to be done to try to tease apart the mechanisms of the abundance-distribution relationship. Although large-scale experimental manipulations of resources are extremely costly, naturally occurring variations in food availability, such as variabilities in cone crop, provide ideal opportunities for studying the form and mechanisms of abundance-distribution relationships.

7 Final discussion

The main objectives of my study were to survey the breeding birds of Sitka spruce patches in Kielder Forest using the point count survey technique, assess the usefulness of this methodology and relate bird densities and distributions on several scales to landscape and patch variables. This chapter presents the main conclusions of the investigations carried out, puts them into a wider biological context and sets priorities for further work.

7.1 Integration of results and proposals for further work

The primary aim of this thesis was to investigate if the repeated point count method utilised in this type of landscape was a useful tool for studying the relative abundances of passerines. It was found in Chapter 3 that stochastic variations were minimised due to the high degree of heterogeneity in the landscape, which provided a range of patch 'qualities' as perceived by each bird species. Birds were clearly consistently judging patches by their inherent characteristics, shown by the range of density values observed, and also by the annual and seasonal correlations. Thus, if local density was relatively low in one year or season then the density would be relatively low in the next year or season. This was a very important finding because it was then possible to justify the use of the maximum seasonal value for further analysis in Chapters 4, 5 and 6. To verify the results of Chapter 3 it would be interesting to carry out territory mapping investigations in parallel to the point counts. This would determine whether the bird densities generated from the point count study were analogous to the actual densities (territory mapping).

Despite medium to high annual correlations (Chapter 3), the small-scale density models built using the 1998 dataset in Chapter 4 did not agree well with those generated using the 1999 data. In addition, validations of the 1999 landscape density and occurrence models in Chapter 5 using the 1998 datasets were not generally good. It is proposed here that, despite these medium to high annual correlations, for some species there were some annual fluctuations (paired comparisons in Chapter 3) which may have affected the models' performances. A problem with multivariate analyses is that of low case to variable ratios. Even with a modest number of variables, once the number of factors in those variables and interactions between variables are taken into consideration, the sample size has been divided up considerably. Sensitivity to minor variations or fluctuations of density is heightened in models with low case to variable ratios, and thus the resultant models may change from year to year. The only good way to avoid this problem is to increase the sample size; however, time limitations prevented this in the present study.

Once the methodological investigations were carried out, the subsequent objectives were to investigate the effect of landscape structure and composition on the density and distribution of breeding passerines in Kielder. The structure and composition of the landscape had a direct effect on the density and distribution of the birds studied here. On the small scale, i.e. within a patch, birds were not found uniformly distributed within a relatively homogeneous patch, with some species preferring and others avoiding the boundary zone (Chapter 4). The age of trees and adjacent patches also had an effect on the numbers observed. On the whole hard edges were avoided and softer edges preferred. This result was reinforced by the results of the larger scale study in Chapter 5; patches with predominantly soft edges were preferred by more species than those patches surrounded by hard edges. The avoidance of the boundary and of hard edges implies that sharply delineated hard edges, particularly those formed between clearfell and mature trees, were not favourable to the bird community overall, possibly due to higher predation rates. It is proposed here that by making the proportion of soft edges higher in Kielder Forest, boundary avoidance will be lessened and the more highly productive, and thus more attractive, edges can be utilised by more individuals.

It would be interesting to find out if birds spent a disproportionate amount of time at the edge, and if the type of edge affected this. Vigilance behaviour and predation pressure would also need to be quantified to determine if predation risk affects the behaviour of passerines. Thus, further fieldwork needs to be carried out to determine why these results occur. This would involve radio-telemetry of passerine and predator movements, coupled with behavioural observations of both predators and prey. Quantification of the invertebrate community in Kielder Forest would be crucial in determining the resource availability at the edges and centre of patches. These data could be used in conjunction with the cone distribution data already collected. The results from these further investigations would give us an insight as to why passerines are distributed across patches (Chapter 4) and the landscape (Chapter 5 and 6) in the patterns observed here.

More fieldwork would clearly enhance this study in terms of understanding the mechanisms behind the observed patterns. However, these observed patterns can also be used within simulation models to give forest managers the tools to effectively plan forest restructuring.

Simulation studies utilise statistical models and can create predicted scenarios by the inputs to the model being altered. These scenarios can then be displayed graphically or cartographically using GIS. They have large implications for investigations into the effects of climate change (Simas *et al.* 2001, Kienast *et al.* 1998) and landuse (Baskent 1999), as they can provide the best estimate of what will happen under certain conditions. Chapter 5 describes a proposal to adopt a hierarchical approach to forest structuring, with clear fells being large and regular shaped and more mature patches being smaller with more complicated shapes. Simulation studies could display the changes in the forest over time needed to achieve this management proposal.

Despite evidence suggesting that resource and habitat type affect the density and distribution of birds found in Kielder (Chapters 4, 5 and 6), it is probable that birds are using the presence and perhaps quality of other individuals to assess habitat quality. In Chapter 6, I showed that increases in resources, such as seeds, resulted in a corresponding increase in density and distribution of those species most reliant on those food items (e.g. crossbill, siskin). However, I also found that willow warbler aggregates more readily than do residents, probably because they have less time to assess a territory's quality and thus utilise con- and/or heterospecific cues to assess an area's suitability. Experimental manipulation of conspecifics and perhaps heterospecifics in Kielder Forest, following the experiments of Mönkönnen *et al.* (1990), could provide insights into whether willow warbler does aggregate using cues from other willow warbler individuals or other species. However, this type of experiment is difficult to carry out effectively in a non-island situation because of influxes of birds from the surrounding habitats.

It would be interesting to use the logistic models of species occurrence (Chapter 5) to calculate what percentage of the landscape is suitable for each species and to explore whether this bore any relationship to the distribution observed (Chapter 6). Quantification of all coniferous patches into suitable or not-suitable, according to the probabilities of occurrences generated by the models, could be used to calculate the proportion of the landscape that is potentially 'suitable' for each species. It is possible that those species that used a high percentage of the landscape are more widespread than are those that use a small percentage of the landscape. However, some sort of weighting of the observed distribution should be considered which takes into account the proportions of the types of patches surveyed in this study. For example, the number of mature, pre-thicket and young patches surveyed is approximately a third each of the total sample size. Figure 2.4 shows cartographically that the proportions of the landscape made up of these three patch ages are certainly not equal. This is only one of the variables; fractal dimension, area and edge contrast also affect bird populations and should be taken into consideration when comparing the observed distribution and the proportion of the habitat that is 'suitable' generated by the logistic regression models

The results of Chapter 3 show that willow warbler densities are annually correlated, with density being relatively similar in 1998 and 1999. However, it cannot be assumed that the data from 1998 would generate high percentage correctly classified and Kappa values in Chapter 5. The low PCC and Kappa values, but good correlations between the observed and the expected values in the models of Chapter 5, show that although density was not the same in the patches surveyed in 1998 and 1999, the values were relatively similar. If this species is mainly utilising cues from other birds to form the density and distribution patterns observed, then it is unsurprising that the models in Chapter 5 did not have high r^2 values (particularly the GLM with a value of 0.069).

7.2 Can bird density and distribution be used as a proxy for habitat quality?

I have shown that bird density is higher in some patches than in others. However, can songbird density be used as a proxy for habitat quality? Chapters 4, 5, and 6 show that resources are important in influencing the density and distribution of bird species on a small and large scale, as predicted by the ideal free and ideal despotic distribution (Fretwell & Lucas 1970). However, the habitats with high density may not necessarily be of the highest quality (Hobbs & Hanley 1990). Despite this, when overall densities are low (as found in Chapter 3) and there is minimal competition for good quality habitats, then it would be expected that competitive exclusion may not occur (Van Horne 1983). In this instance density may indeed be highest in the good quality patches. Bird densities in Kielder Forest were low making Van Horne's (1983) proviso applicable to this landscape. Therefore Van Horne's (1983) hypothesis, that the good quality habitats do indeed contain the highest numbers of individuals in areas of low overall densities, may be correct.

Can occurrence be said to be a better indicator of patch quality? It would be logical to assume that those patches that are occupied are of higher quality than those unoccupied by a species (logistic regression Chapter 5). However, this is under the assumption that all suitable patches are occupied. It is highly probable that Kielder operates under non-equilibrium conditions, where fluctuations in environmental conditions, predator/competitor concentrations, disease or insufficient time for equilibrium to be reached, causes the density of birds not to be as high as optimal conditions would allow (Willson & Comet 1996). If this were the case, then some suitable habitats may remain unoccupied. The fact that the 1998 data were not good at validating the 1999 models provides some evidence for this, because it is possible that patches previously occupied may not be occupied in the next year.

Consistency of occupation may be a better measure of habitat quality. If Van Horne's (1983) hypothesis is correct, then it does not necessarily follow that the consistently occupied habitats have the highest densities of birds in them. Indeed in years when bird density across a landscape is high and the good habitats are saturated, dominant individuals may push subordinate individuals into marginal patches. It is here that perhaps the highest densities may be found. In all conditions it would be expected that patches that consistently contain a species are of the highest quality. Poor consistency of occupation will occur in those marginal patches that may contain subordinate individuals in years of overall high densities, and may not contain a individuals of that species in a low-density year. Unfortunately, bird densities were only measured over a two-year period, which is not long enough to establish consistency of occupation.

7.3 The rôle of managed coniferous forests in bird conservation.

This statement may seem like an oxymoron. However, despite the negative effects of afforestation on upland waders (Avery & Leslie 1990), afforestation can also have positive effects. Nightjar *Caprimulgus europaeus* and woodlark *Lullula arborea* have been shown to benefit from afforestation by coniferous plantation woodland (Anonymous 1999). Nightjar have been heard singing in Kielder Forest (*pers obs*), which is near the limit of its northern range in Britain (Gibbons *et al.* 1993). Species found regularly in Kielder and used for analysis in my study include willow warbler, dunnock, and redpoll. These three species have suffered from declines of 23%, 21% and a staggering 92% respectively since 1970, with no significant signs of recovery or even of the declines abating (Anonymous 1999). Encouragingly, the results from my study show that these three species are common and widespread in Kielder Forest (Chapter 6) with willow warbler being found in 45% of patches surveyed at the centre, 39% for redpoll and 15% for dunnock. Indeed, Chapter 6 showed that willow warbler is one of the most locally common and widely distributed species in Kielder. Redpoll is also locally common and widespread. Kielder Forest offers these species an area where pesticides and herbicides are rarely used, where vegetation complexity and landscape heterogeneity are high, and where dead wood is allowed to lie. Thus, despite healthy populations of predators, the forest creates suitable habitat for many declining species.

7.4 Management Recommendations

In light of the results found in this thesis, several recommendations for forest management have emerged.

- Positive edge effects were found with the area 60 m from the boundary into a patch being generally associated with higher densities of birds than the area covering 90 – 210 m into the patch. Therefore the current management strategy of rotational clear-cutting creates a mosaic landscape that is beneficial to many of the species observed here.
- There is some evidence for peaks of density in the 180 – 210 m zone particularly in pre-thicket trees. Thus, patches should be no smaller than 420 m at their narrowest part to include these areas for breeding birds.
- Clearfells should be made as large and as linear (with no complex shaped edges) as possible to decrease the edge to centre ratio, because meadow pipits (the only very common species found in this type of habitat) avoid edges.

- Mature patches should be kept as small (keeping in mind the 420 m limit) and as complex shaped as possible to increase the edge to centre ration, which would be beneficial to birds such as goldcrest, coal tit, redpoll and robin.
- Clearfelling adjacent to mature trees should be avoided to minimise the amount of hard edge. Leaving some mature trees and early successional trees at the edge of clearfells may soften these types of edges (Tittler *et al.* 2001).
- The soft edges between mature and pre-thicket patches should be increased. This would be beneficial to the only common migrant, the willow warbler.
- The likely effects of forest restructuring on Kielder Forest passerines may be monitored, by investigation of logistic and GLM multivariate models outputs, after inputting the effects of time (succession) and changes in forest composition (replanting) into the GIS.
- Patch occurrence can be used as a proxy for densities as a simple gauge of the 'health' of the bird community in Kielder, and to monitor threatened birds such as redpoll.

The paradigm of landscape ecology, with its associated landscape quantification and geographical information system tools, can enable landscape managers in Kielder Forest to generate a comprehensive information base of what determines avian species' abundance and distribution. The decision making process for forest restructuring, steered by conservation and economic priorities, can be made easier by incorporating the methods and results generated here.

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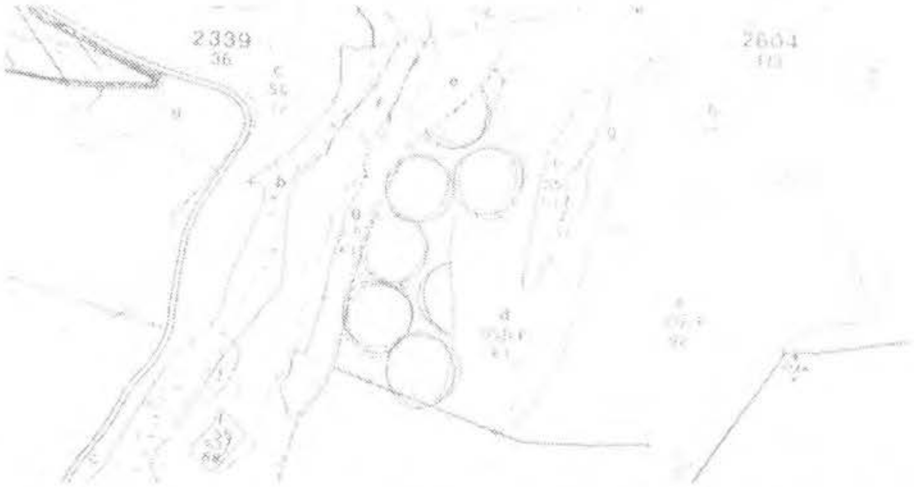
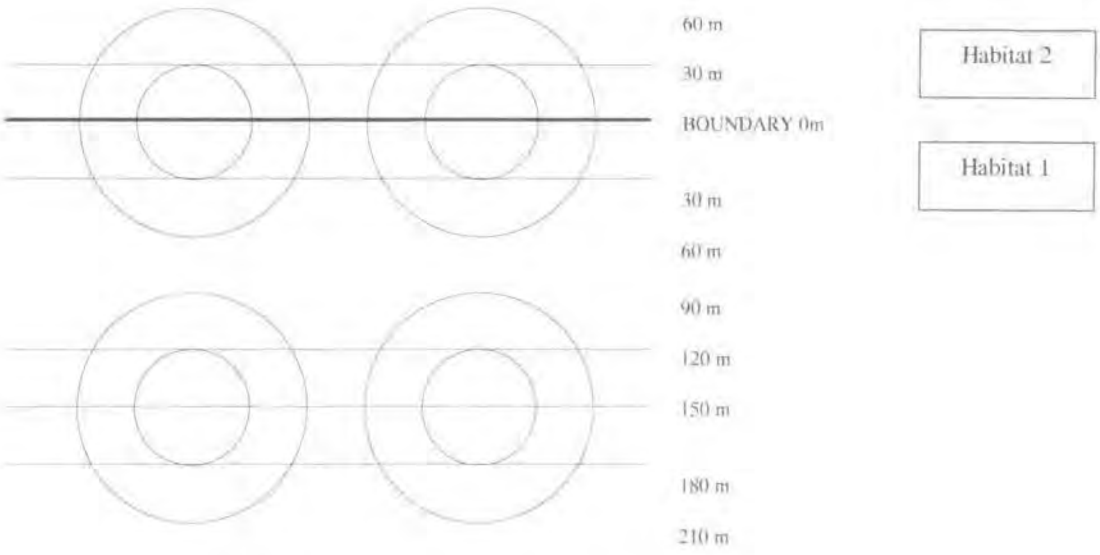
Appendices



Appendix 1: Map of one survey patch from Sample A (1991/1992) showing patch structure and content with centre and edge point counts.



Appendix 2: Two patches (Habitats 1 and 2) from Sample B with centre and edge counts, the boundary between them, and the distances of each point count segment from the boundary (30m intervals). In both studies, the placement of the point counts in the patch was completely replicated in each second year, using detailed maps (see App. 1), so that the replicated samples were analogous.

Name	*Latin name*	*Resident or Migrant*	*Breeding season*	*Broods*	*Food*
crossbill	*Loxia curvirostra*	R/M	August - April	-	Spruce seeds
chaffinch	*Fringilla coelebs*	R	Late April to mid June	1-2	Seeds plus invertebrates in BS
coal tit	*Parus ater*	R	Mid April - July	1-2	Ad and larval insects plus spiders and spruce seeds
dunnock	*Prunella modularis*	R	Late March/early April - June	2-3	Insects
goldcrest	*Regulus regulus*	R	Late April - mid July	2	Insects (esp. Hemiptera, Collembola and larval Lepidoptera)
meadow pipit	*Anthus pratensis*	R	Mid April - late July	2	Ground arthropods and disturbed flying insects
robin	*Erithacus rubecula*	R	Early March - June	2	Invertebrates esp. beetles
redpoll	*Carduelis flammea*	R	Mid-May - early June	2	Small seeds plus invertebrates in BS
siskin	*Carduelis spinus*	R	Mid May - August	2	Coniferous seeds plus some invertebrates in BS
wren	*Troglodytes troglodytes*	R	Early April - May	1	Arthropods esp. beetles and spiders
willow warbler	*Phylloscopus trochilus*	M	Late April - June	1	Insects and spiders

Appendix 3: Feeding and breeding behaviour of the 11 common birds in Kielder Forest from Cramp (1988 - 1994).

		A	E1	E2	E3	E4	E5	E6	F	Y
Correlation Coefficient	A	1								
Sig. (2-tailed)		.								
N		71								
Correlation Coefficient	E_1	0.014236								
Sig. (2-tailed)		0.906202								
N		71	71							
Correlation Coefficient	E_2	0.064239	0.952915							
Sig. (2-tailed)		0.594569	1E-06							
N		71	71	71						
Correlation Coefficient	E_3	0.07145	0.664531	0.728415						
Sig. (2-tailed)		0.55377	1E-06	1E-06						
N		71	71	71	71					
Correlation Coefficient	E_4	0.043237	0.732347	0.706134	0.940547					
Sig. (2-tailed)		0.720329	1E-06	1E-06	1E-06					
N		71	71	71	71	71				
Correlation Coefficient	E_5	0.009214	0.910674	0.826283	0.796004	0.914613				
Sig. (2-tailed)		0.939209	1E-06	1E-06	1E-06	1E-06				
N		71	71	71	71	71	71			
Correlation Coefficient	E_6	0.081032	0.785779	0.884214	0.943582	0.85378	0.790666			
Sig. (2-tailed)		0.501728	1E-06	1E-06	1E-06	1E-06	1E-06			
N		71	71	71	71	71	71	71		
Correlation Coefficient	FD	-0.02994	-0.03241	-0.11872	-0.18231	-0.10517	-0.01634	-0.18846		
Sig. (2-tailed)		0.804239	0.788426	0.324094	0.128084	0.382748	0.892422	0.115509		
N		71	71	71	71	71	71	71	71	
Correlation Coefficient	Y	-0.14863	0.276195	0.298363	-0.06101	-0.05948	0.115863	0.116952	0.062369	
Sig. (2-tailed)		0.216065	0.019727	0.011495	0.613282	0.622179	0.335951	0.331396	0.605361	.
N		71	71	71	71	71	71	71	71	71

Appendix 4: Correlation co-efficients of variables measured for centre surveys. A = Area, E_n = Edge comparison, FD = Fractal dimension, Y = Planting year

		A	E1	E2	E3	E4	E5	E6	F	Y
Correlation Coefficient	A	1								
Sig. (2-tailed)		.								
N		133								
Correlation Coefficient	E_1	0.106142								
Sig. (2-tailed)		0.223995	.							
N		133	133							
Correlation Coefficient	E_2	0.138817	0.967477							
Sig. (2-tailed)		0.11104	1E-06							
N		133	133	133						
Correlation Coefficient	E_3	-0.05132	0.664347	0.735283						
Sig. (2-tailed)		0.557412	1E-06	1E-06						
N		133	133	133	133					
Correlation Coefficient	E_4	-0.06556	0.732305	0.742773	0.961963					
Sig. (2-tailed)		0.453378	1E-06	1E-06	1E-06					
N		133	133	133	133	133				
Correlation Coefficient	E_5	0.011449	0.923453	0.880496	0.81996	0.912452				
Sig. (2-tailed)		0.895934	1E-06	1E-06	1E-06	1E-06				
N		133	133	133	133	133	133			
Correlation Coefficient	E_6	0.031346	0.806517	0.891589	0.948671	0.898339	0.849982			
Sig. (2-tailed)		0.720211	1E-06	1E-06	1E-06	1E-06	1E-06			
N		133	133	133	133	133	133	133		
Correlation Coefficient	FD	-0.25536	-0.19852	-0.25851	-0.24587	-0.19606	-0.17082	-0.28292		
Sig. (2-tailed)		0.003012	0.021982	0.002661	0.004336	0.023717	0.049314	0.000968		
N		133	133	133	133	133	133	133	133	
Correlation Coefficient	Y	0.220414	0.452344	0.481345	0.153429	0.150068	0.317658	0.3175	-0.19687	
Sig. (2-tailed)		0.010792	1E-06	1E-06	0.077869	0.084689	0.000195	0.000196	0.023134	.
N		133	133	133	133	133	133	133	133	133

Appendix 5: Correlation co-efficients of variables measured for edge surveys. A = Area, E_n = Edge comparison, FD = Fractal dimension, Y = Planting year

	Model					
Bird Species	*Cox and Snell* r^2	*Chi*^{2}	*df*	*p-value*	*Cut-off*	$(B_0 + B_1X_1 + B_2X_2 + ... B_nXn)$
crossbill	NM					
chaffinch	0.210	16.769	2	0.0002	0.53	194.881 – 0.000018*E5.Y – 0.0973Y
coal tit	0.183	14.318	1	0.0002	0.26	169.5981 – 0.0860*Y
dunnock	0.104	7.762	2	0.0206	0.26	-21.8004 + 0.0494*FD.Y – 82.1286*FD
goldcrest	0.443	41.510	1	0.0000	0.44	590.3367 – 0.2969*Y
meadow pipit	0.541	55.344	1	0.0000	0.42	-996.574 + 0.5007*Y
robin	0.582	61.955	3	0.0000	0.50	27139.39 + 10.1797*FD.Y – 13.6180*Y – 20288.3*FD
redpoll	0.070	5.165	1	0.0231	0.57	-92.6594 + 0.0467*Y
siskin	0.148	11.380	2	0.0034	0.27	35.5608 + 0.0000233*A.Y – 29.2981*FD
wren	0.145	11.147	1	0.0008	0.77	-142.844 + 0.0725*Y
willow warbler	0.204	16.231	2	0.0003	0.55	30.2181 – 0.0123*FD.Y + 0.0421*E3

Appendix 6: Logistic regression models for songbird distributions at the centre of patches. N = 71.

	Model					
Bird Species	*Cox and Snell r^2*	*Chi^2*	*df*	*p-value*	*Cut-off*	$(B_0 + B_1X_1 + B_2X_2 + ... B_nXn)$
crossbill	0.055	7.466	2	0.0239	0.12	65.8377 + 0.0277*A.FD – 0.0345*Y
chaffinch	0.191	28.144	4	0.0000	0.65	-0.44 – 0.0020*E5.Y – 0.0029*A.E5 + 3.9454*E5 + 0.1569*A
coal tit	0.161	23.376	1	0.0000	0.25	110.3008 – 0.0562*Y
dunnock	NM					
goldcrest	0.493	90.252	2	0.0000	0.50	-1.208 – 0.0095*E4.Y + 19.0221*E4
meadow pipit	0.469	84.079	1	0.0000	0.30	-689.666 + 0.3463*Y
robin	0.079	10.953	2	0.0042	0.58	88.0232 – 0.0385*Y – 8.7857*FD
redpoll	0.071	9.784	1	0.0018	0.40	-1.0322 + 0.0013*A.E3
siskin	NM					
wren	0.244	37.265	2	0.0000	0.71	-108.252 + 0.0018*A.E2 + 0.0547*Y
willow warbler	0.041	5.591	1	0.0181	0.51	-0.5900 + 0.0232*E3

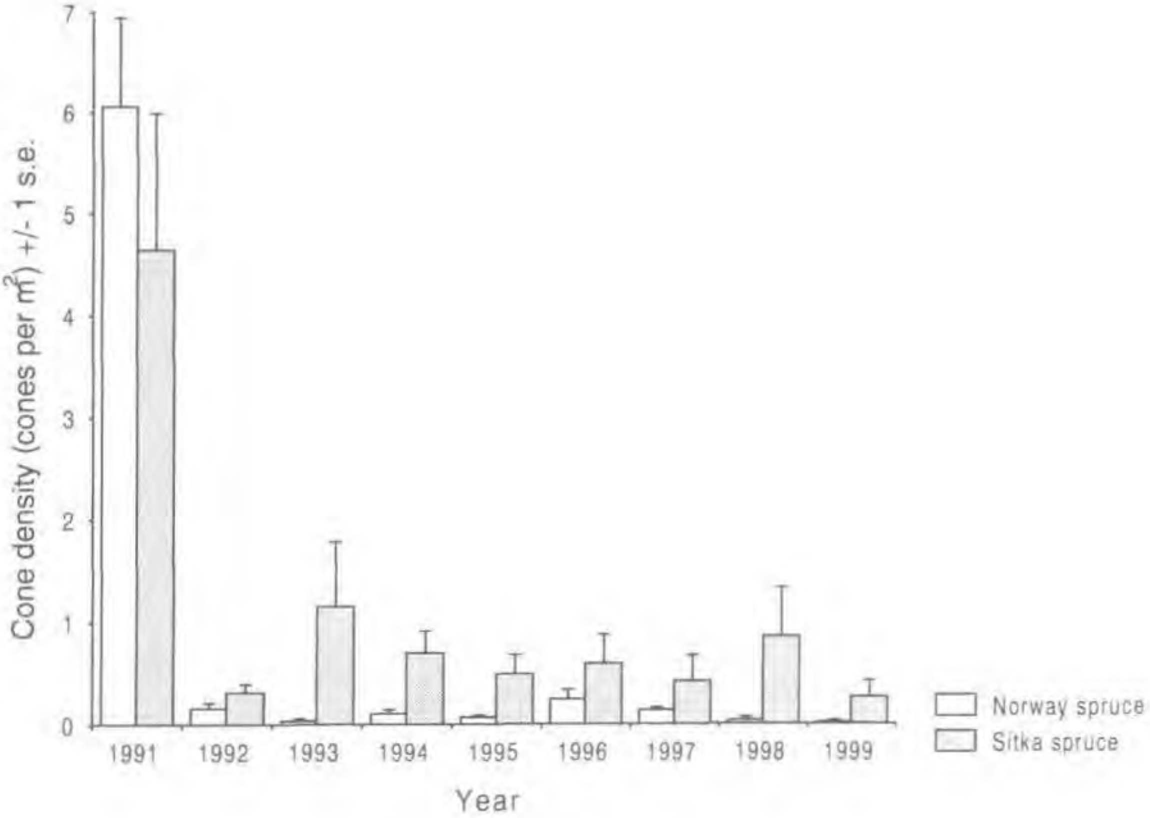
Appendix 7: Logistic regression models for songbird distributions at the edge of patches. N = 133.

Model						
Bird Species	r^2	Chi^2	*df*	*p-value*	*Scale Parameter*	$(B_0 + B_1X_1 + B_2X_2 +\dots B_nXn)$
crossbill	0.182	6.266	2	<0.05	1.64	118.2 – 0.07298*A – 0.06024*Y
chaffinch	0.172	13.17	1	<0.001	1.478	70.93 – 0.036*Y
coal tit	0.379	31.63	5	<0.001	1.459	3963 – 3.343*A – 2944*FD – 1.965*Y + 2.57*A.FD + 1.458*FD.Y
dunnock	0.009	0.04617	1	Ns	2.063	-1.117 – 0.00263*E6.FD
goldcrest	0.457	49.82	7	<0.001	1.672	2295 – 5.5*A – 1611*FD – 1.132*Y – 0.00096*A.E5 + 1.262*A.FD + 0.001978*A.Y + 0.7921*FD.Y
meadow pipit	0.636	107.0	6	<0.001	1.388	-5779 – 13.87*A + 4385*FD + 2.901*Y – 0.00127*A.E1+ 0.006988*A.Y – 2.201*FD.Y
robin	0.214	16.93	2	<0.001	1.778	86.27 – 10.52*FD – 0.03684*Y
redpoll	0.169	13.20	4	<0.01	1.84	-40.2 + 1.564*A + 30.65*FD + 0.0216*E3 – 1.231*A.FD
siskin	0.088	4.954	1	<0.05	1.589	21.84 – 18.3*FD
wren	0.280	31.17	5	<0.001	1.055	-33.9 + 1.046*A + 0.6184*E1 – 0.8317*A.FD – 0.4864*E1.FD + 0.0136*FD.Y
willow warbler	0.069	4.783	1	<0.05	3.927	8.726 + 0.01598*E3 – 7.049*FD

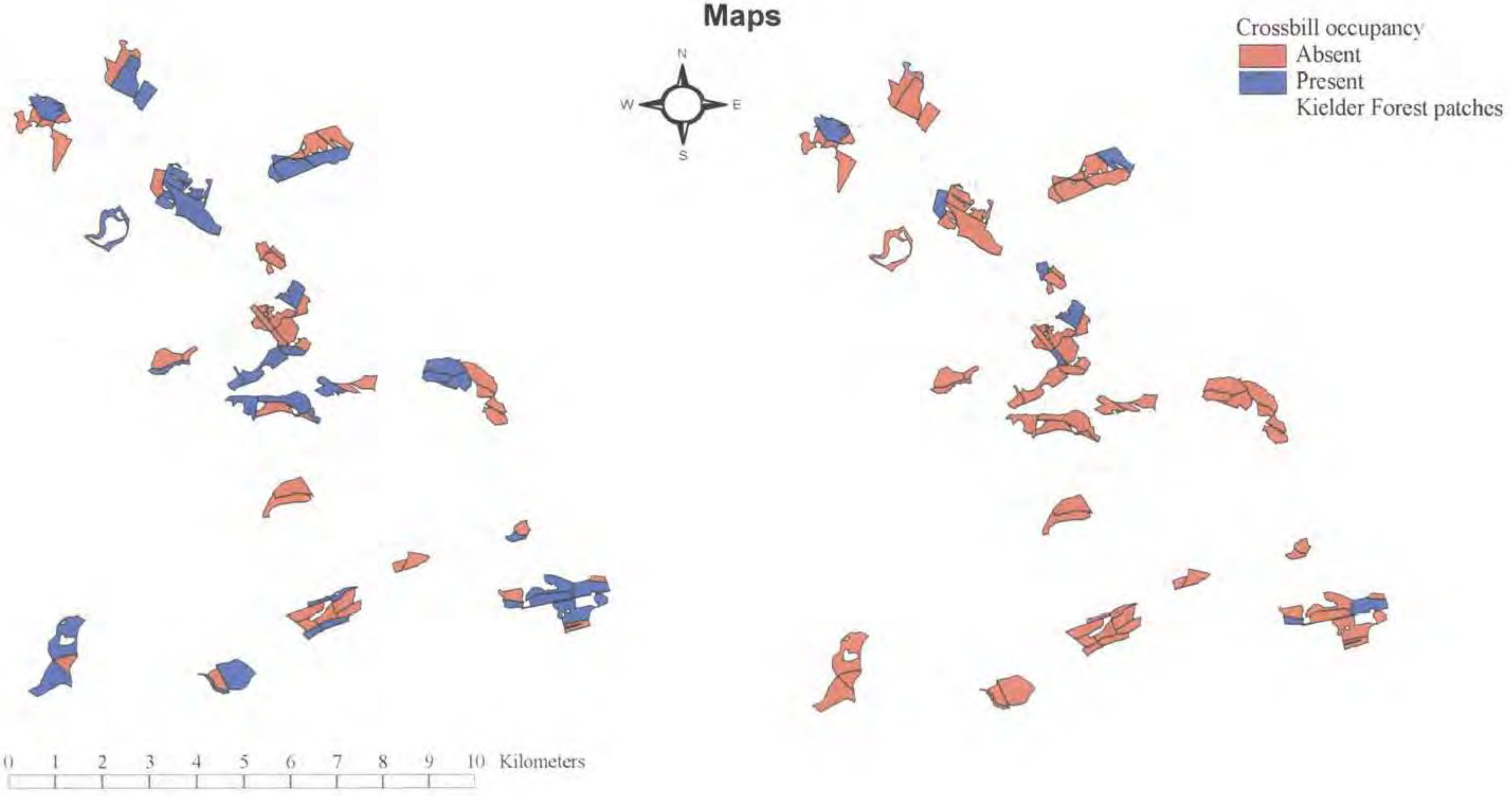
Appendix 8: Generalised linear models of songbird density at the centre of patches. N = 71.

	Model					
Bird Species	r^2	Chi^2	*df*	*p-value*	*Scale Parameter*	$(B_0 + B_1X_1 + B_2X_2 +.... B_nXn)$
crossbill	0.181	15.44	2	<0.001	1.627	77.91 – 0.04088*Y + 0.03678*A
chaffinch	0.278	55.97	2	<0.001	1.222	0.21 + 1.693*E5 – 0.00086*E5.Y
coal tit	0.255	37.31	1	<0.001	1.28	84.48 – 0.0435*Y
dunnock	0.034	3.681	1	<0.1	1.705	-2.208 + 0.01625*E3
goldcrest	0.313	64.22	1	<0.001	1.698	70.81 – 0.03593*Y
meadow pipit	0.515	122.2	1	<0.001	1.134	-337.3 + 0.1688*Y
robin	0.128	20.01	2	<0.001	1.553	54.3 – 5.793*FD – 0.0239*Y
redpoll	0.173	21.10	7	<0.005	2.223	1481 + 0.997*A + 3.197*E3 – 1234*FD – 0.7512*Y – 0.7701*A.FD – 0.0016*E3.Y + 0.625*FD.Y
siskin	0.034	5.046	1	<0.025	1.024	25.54 – 0.01347*Y
wren	0.234	45.83	5	<0.001	1.326	-1206 + 2.922*A + 851.7*FD + 0.6085*Y – 0.00147*A.Y – 0.4299*FD.Y
willow warbler	0.038	5.768	1	<0.025	2.608	-0.4679 + 0.01165*E3

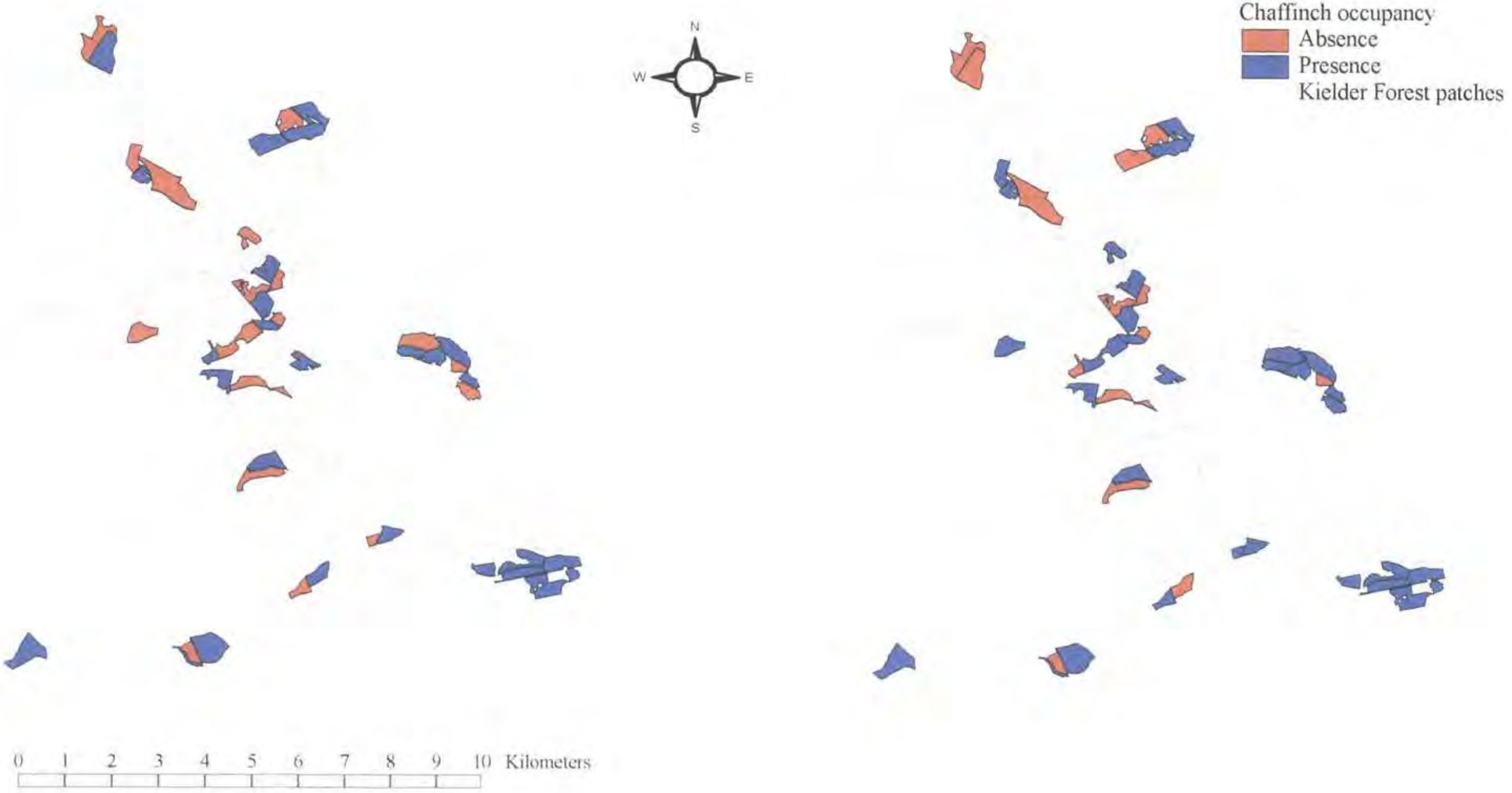
Appendix 9: Generalised linear models of songbird density at the edge of patches. N = 133.



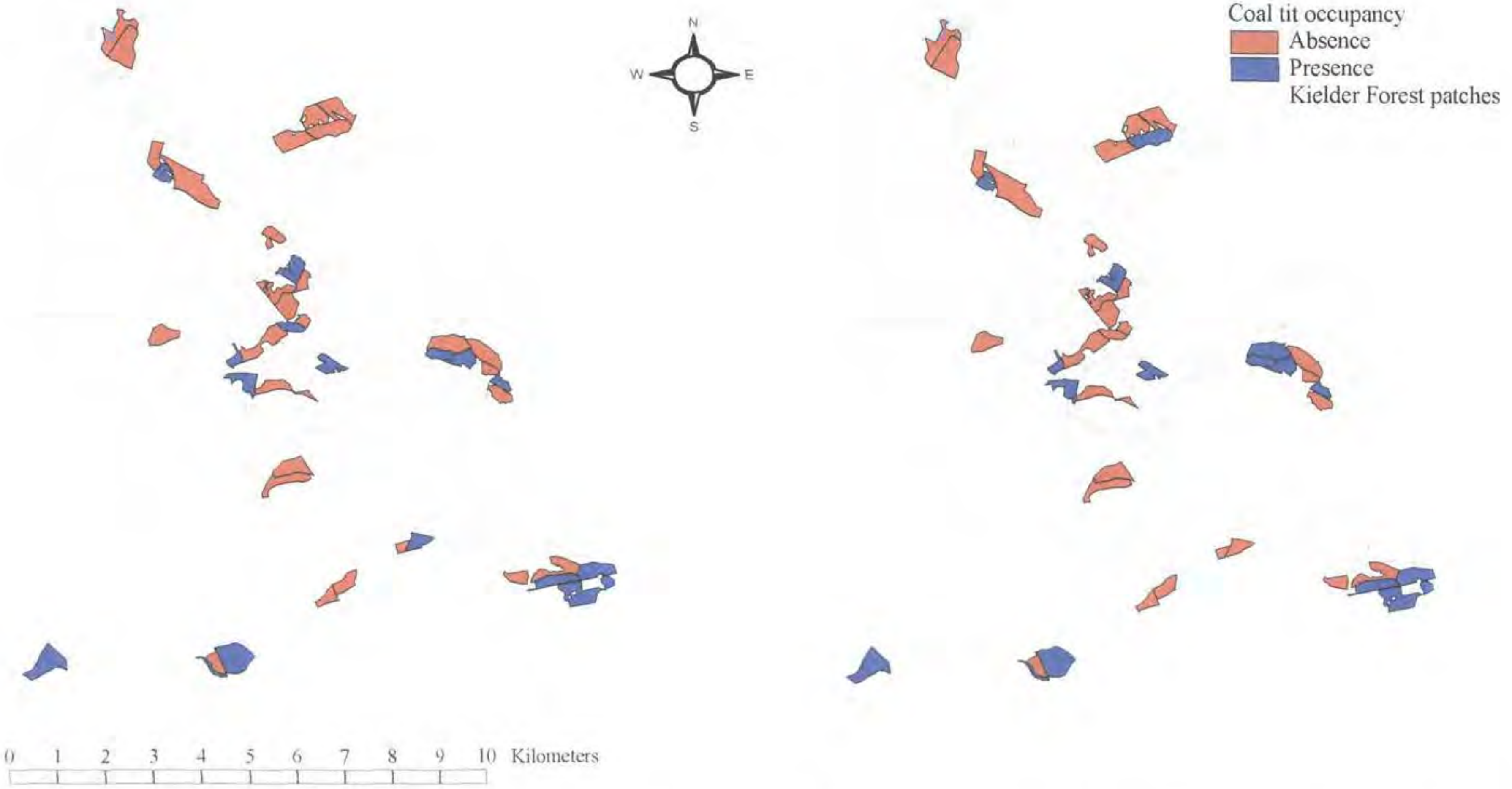
Appendix 10: Norway and Sitka spruce cone crop data from 1991 to 1999 showing standard error bars. Data obtained by Peter Lürz (Newcastle University) from transect studies of mature spruce in Kielder Forest.



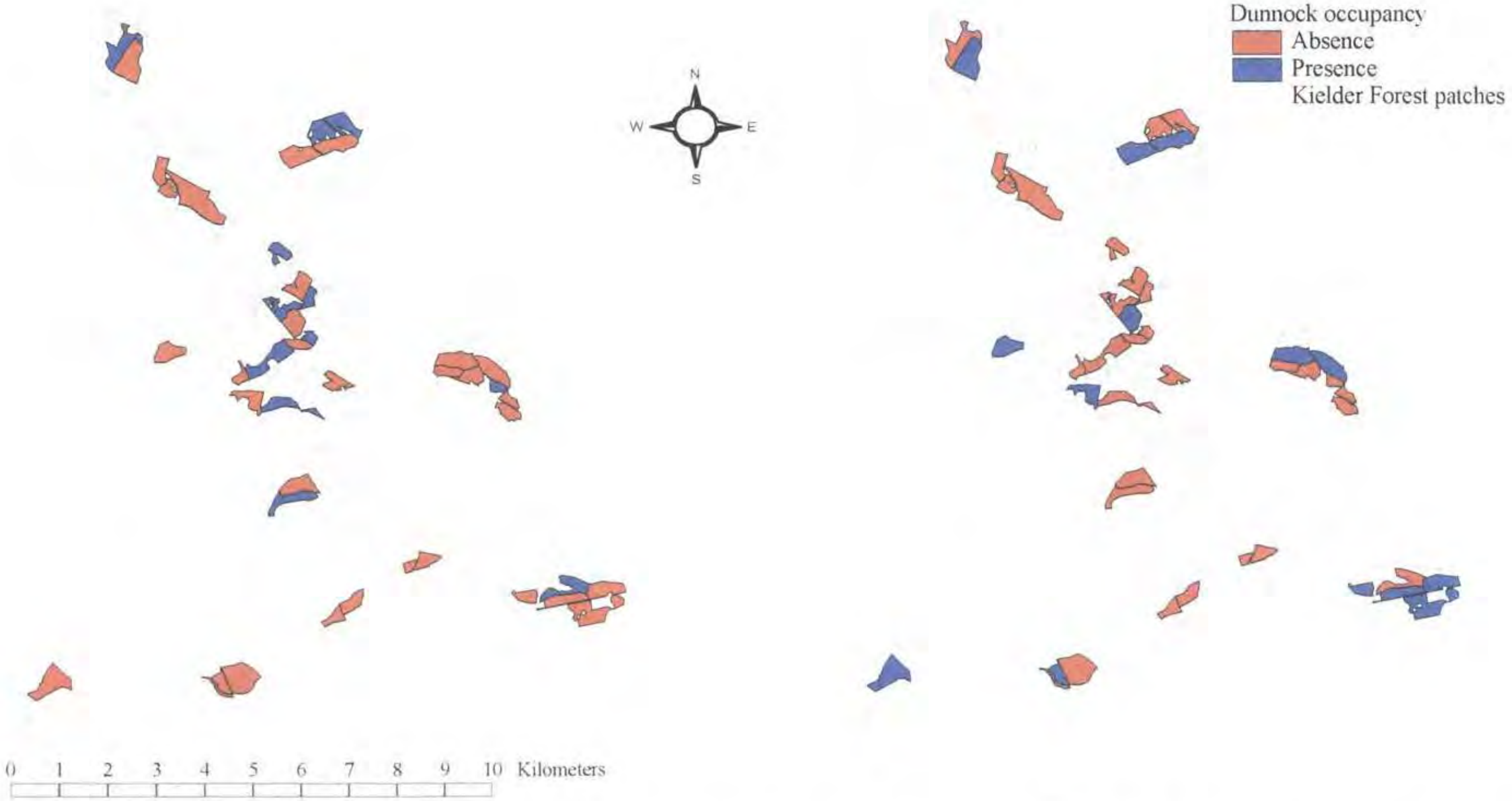
Map 5.1.1: Logistic regression model of predicted crossbill occurrence in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



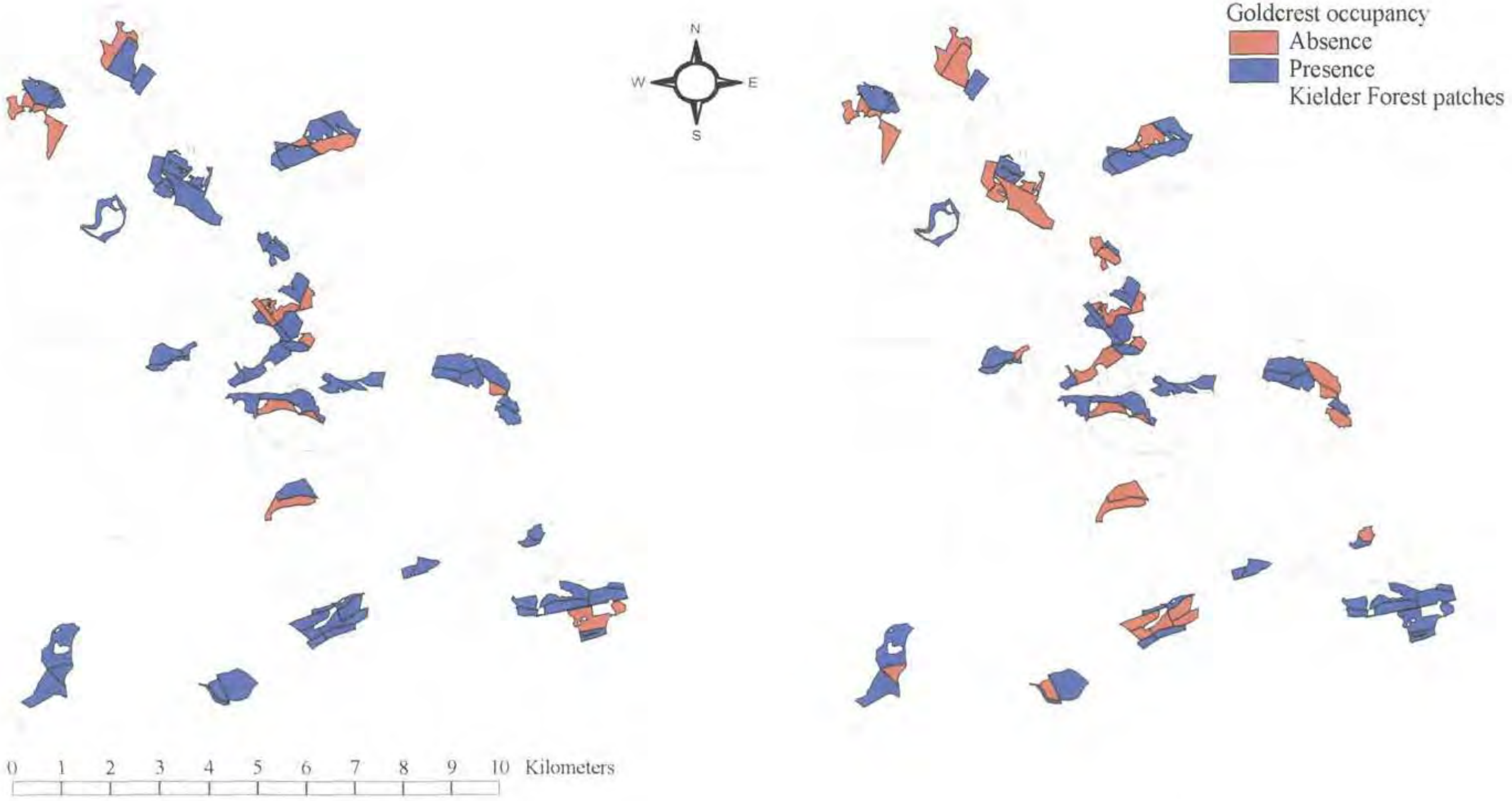
Map 5.1.2: Logistic regression model of predicted chaffinch occurence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



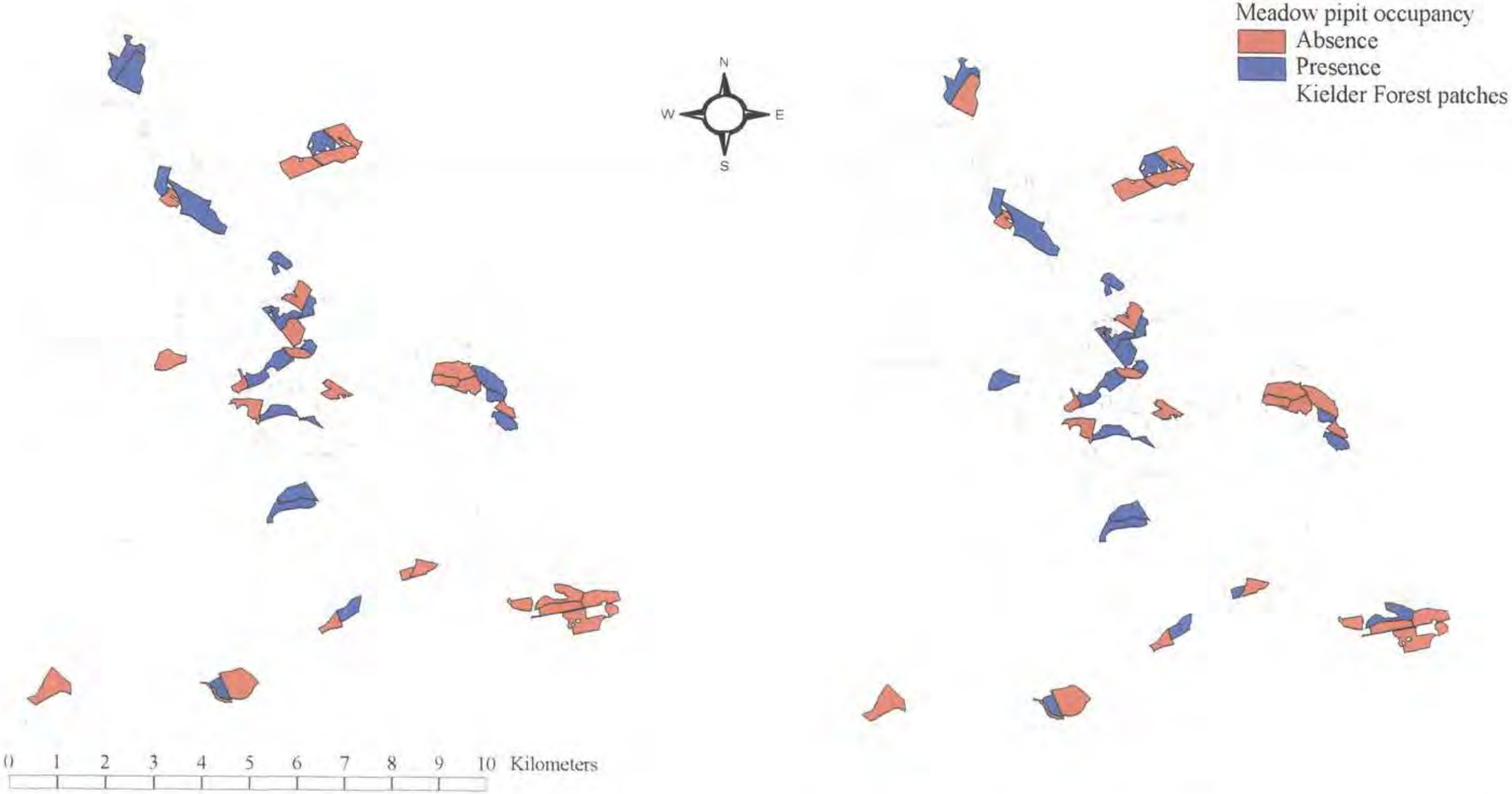
Map 5.1.3: Logistic regression model of predicted coal tit occurrence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



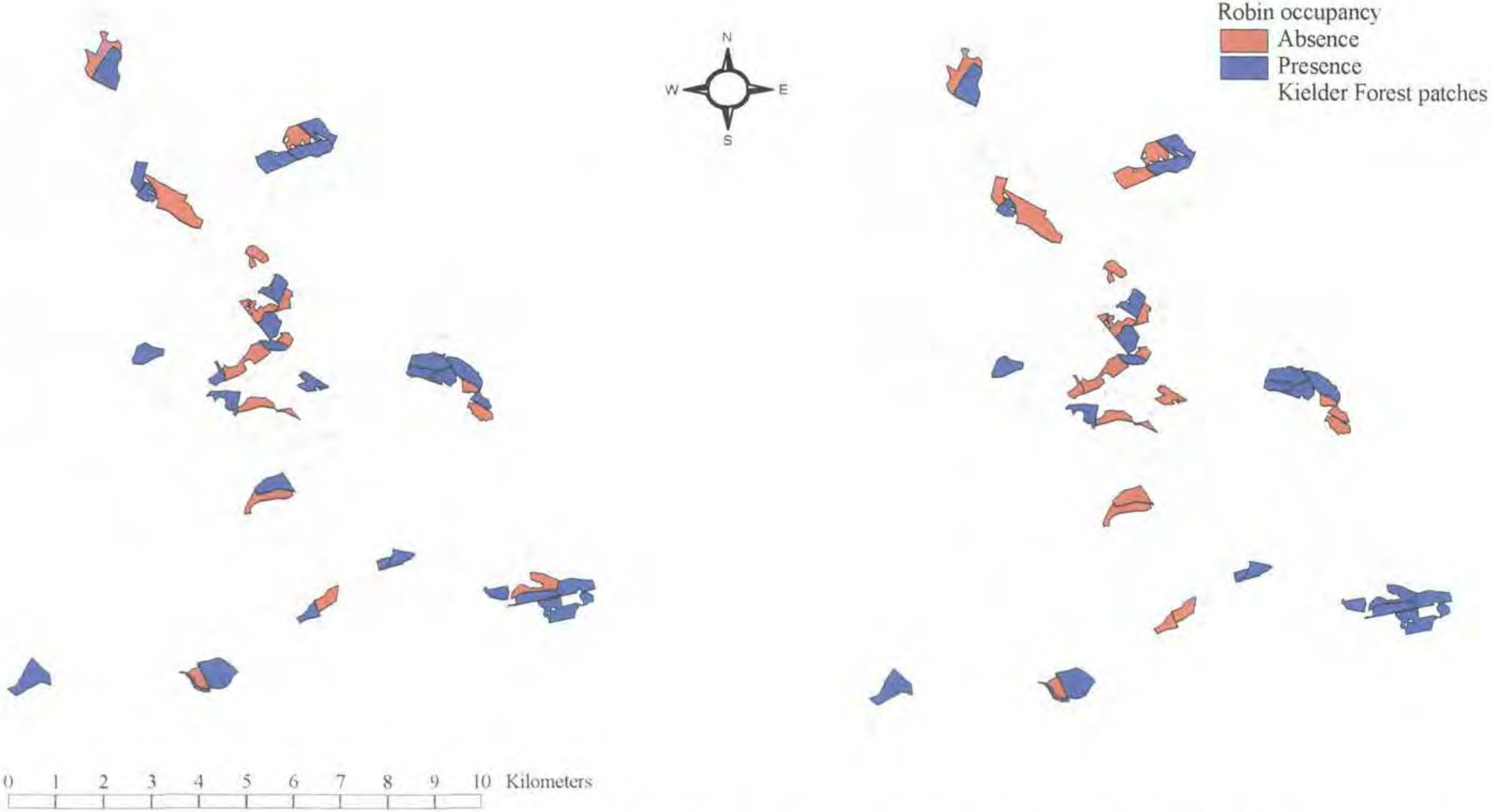
Map 5.1.4: Logistic regression model of predicted dunnock occurrence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



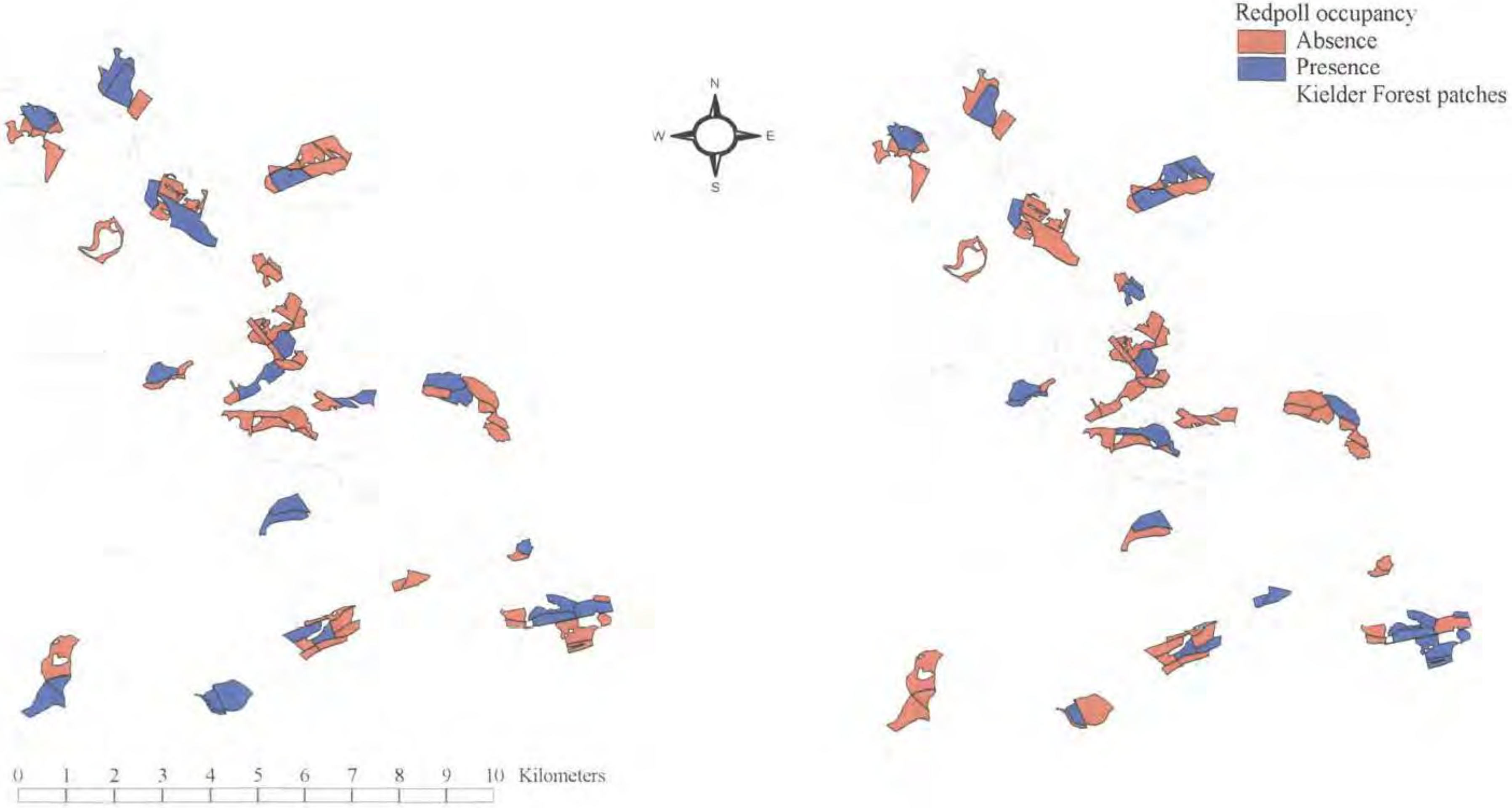
Map 5.1.5: Logistic regression model of predicted goldcrest occurrence in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



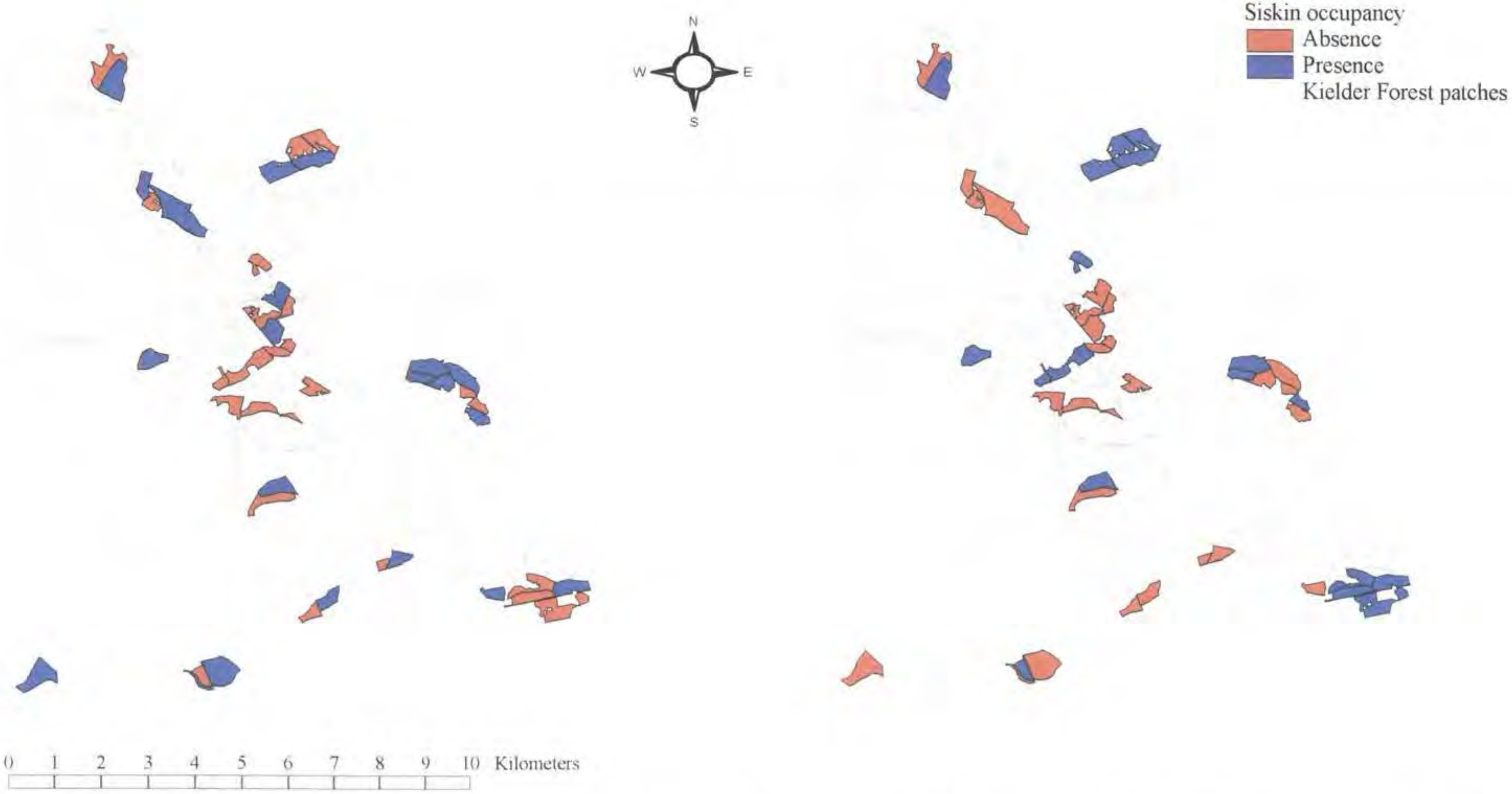
Map 5.1.6: Logistic regression model of predicted meadow pipit occurrence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



Map 5.1.7: Logistic regression model of predicted robin occurrence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.

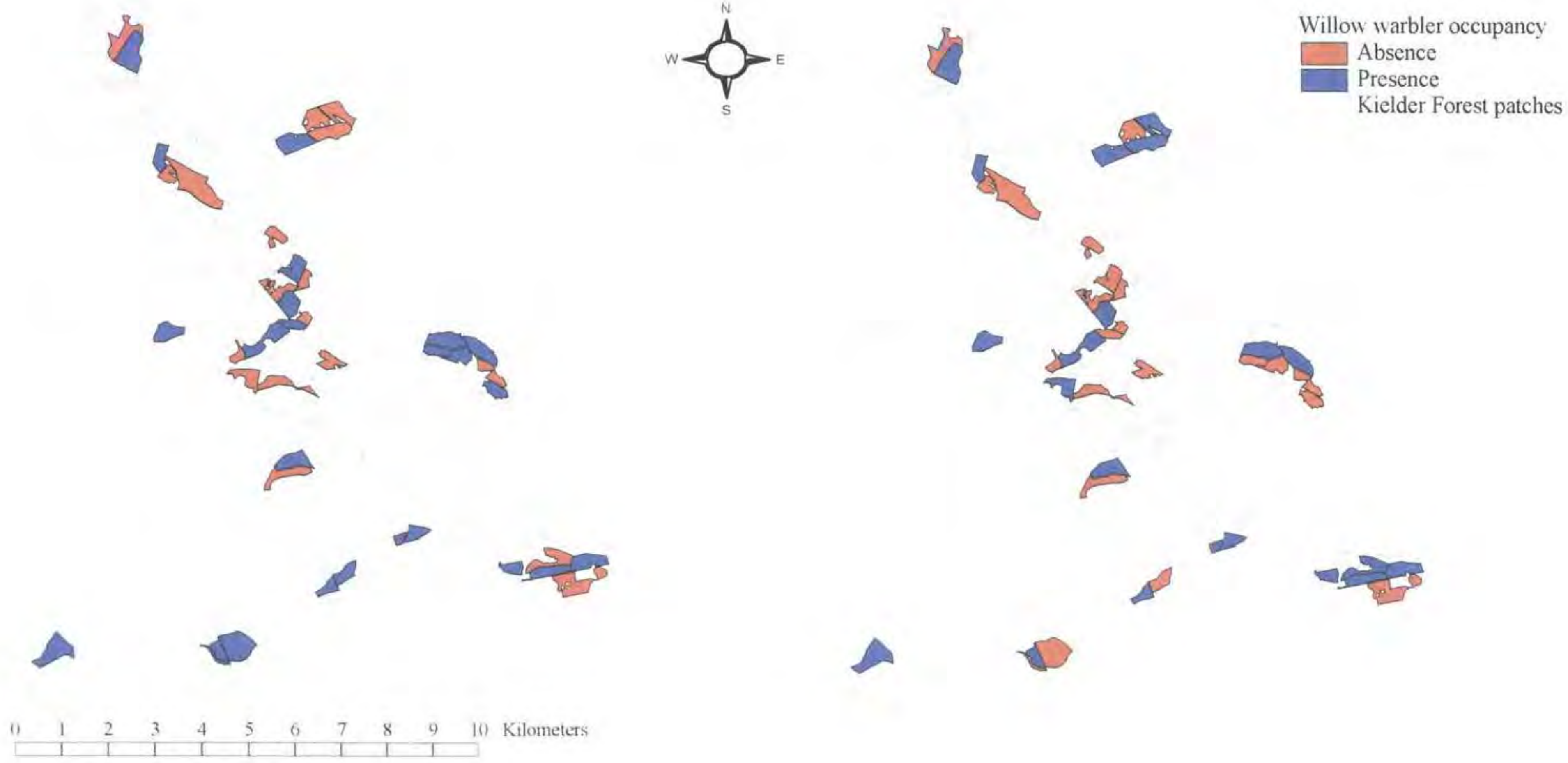


Map 5.1.8: Logistic regression model of predicted redpoll occurrence in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



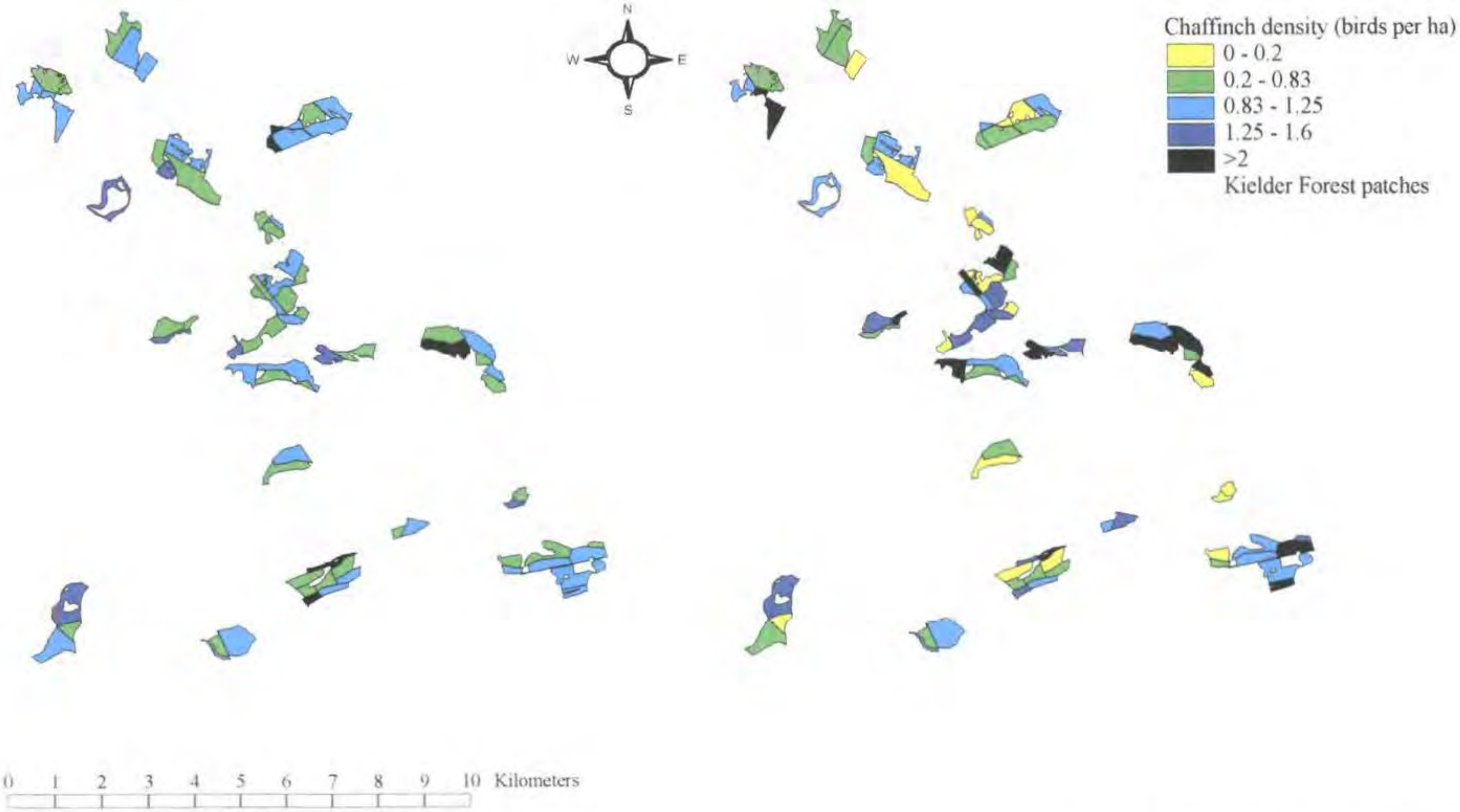
Map 5.1.9: Logistic regression model of predicted siskin occurrence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.

Map 5.1.10: Logistic regression model of predicted wren occurrence in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.

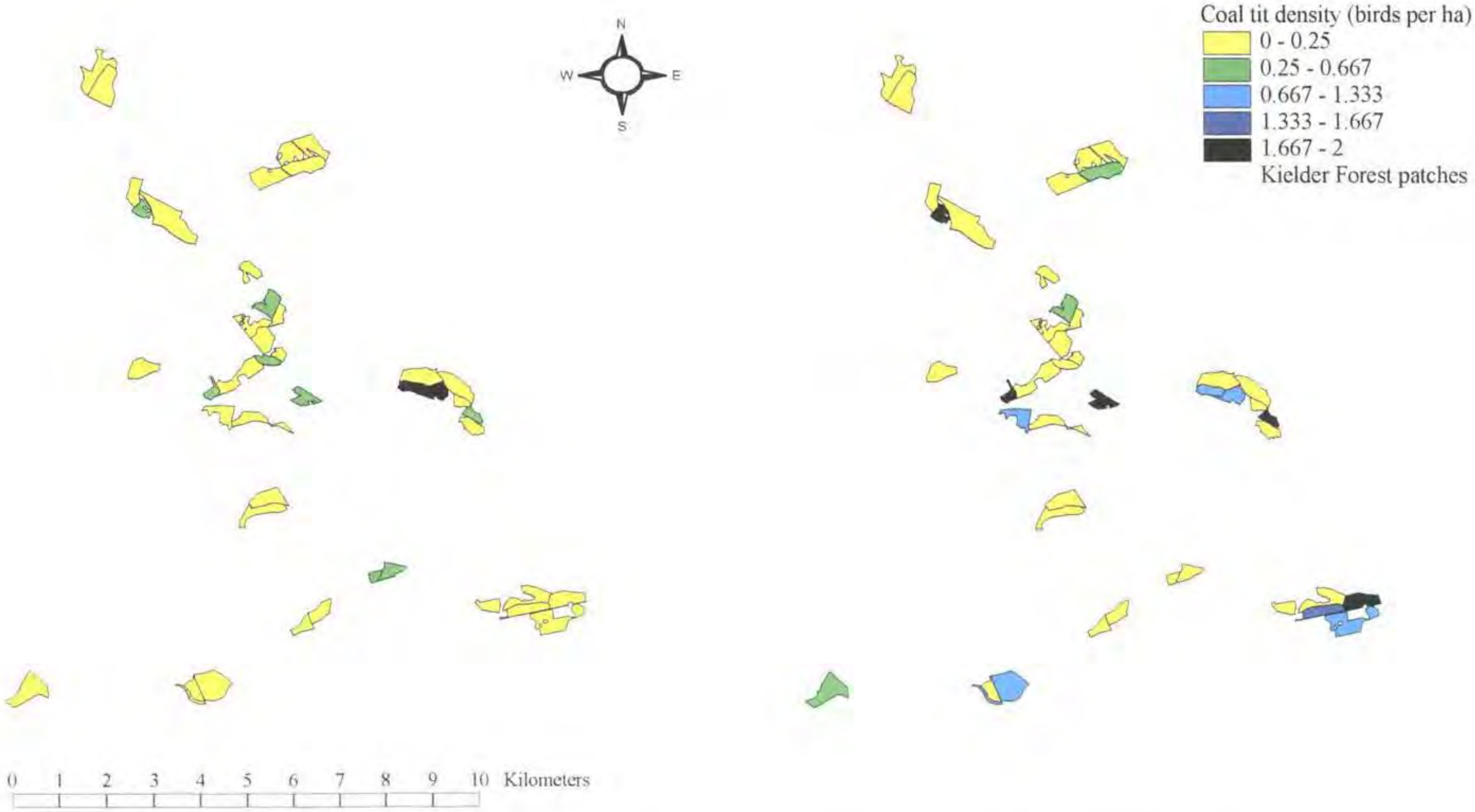


Map 5.1.11: Logistic regression model of predicted willow warbler occurrence in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.

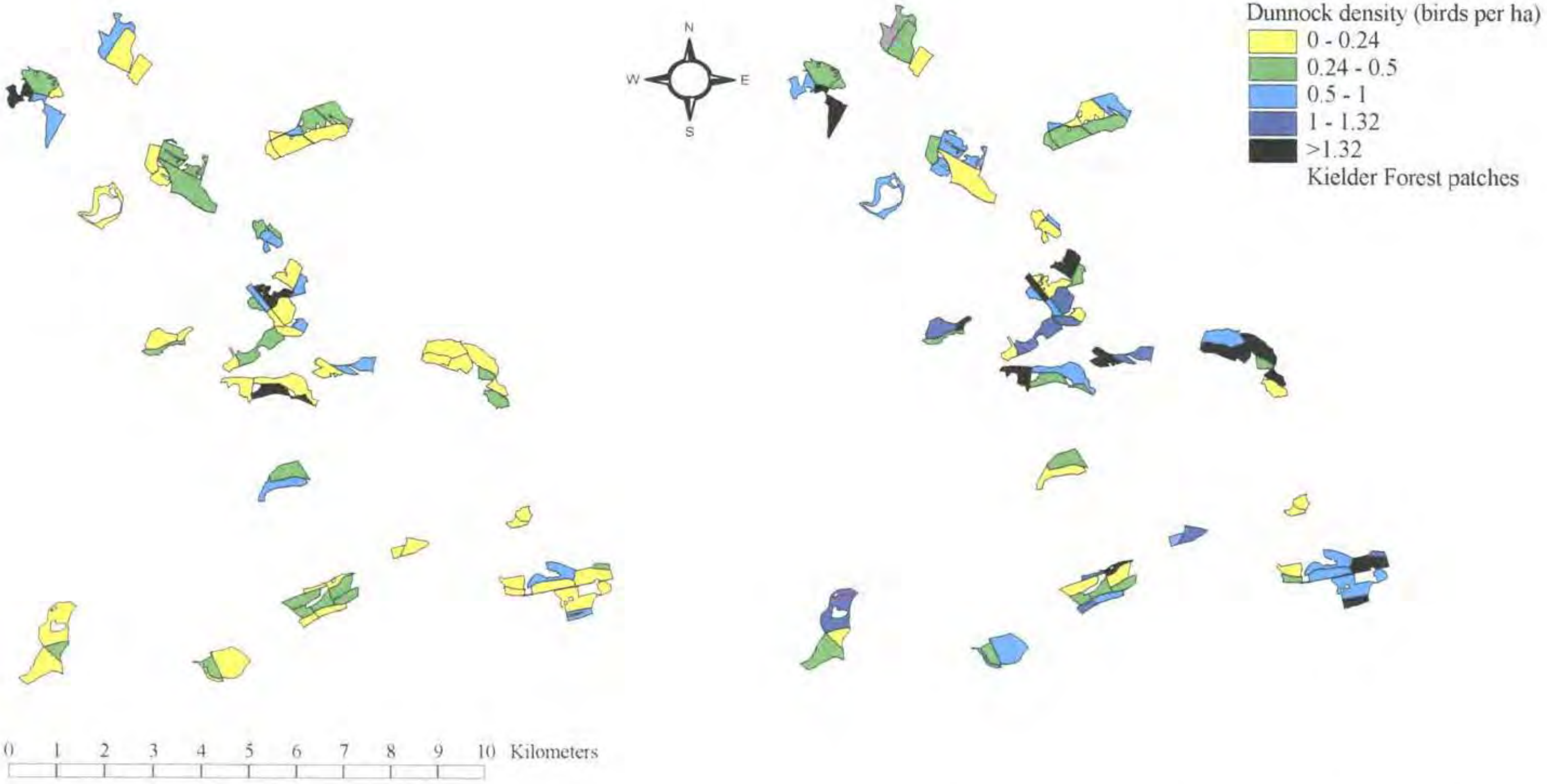
Map 5.2.1: Generalised linear model of predicted crossbill density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



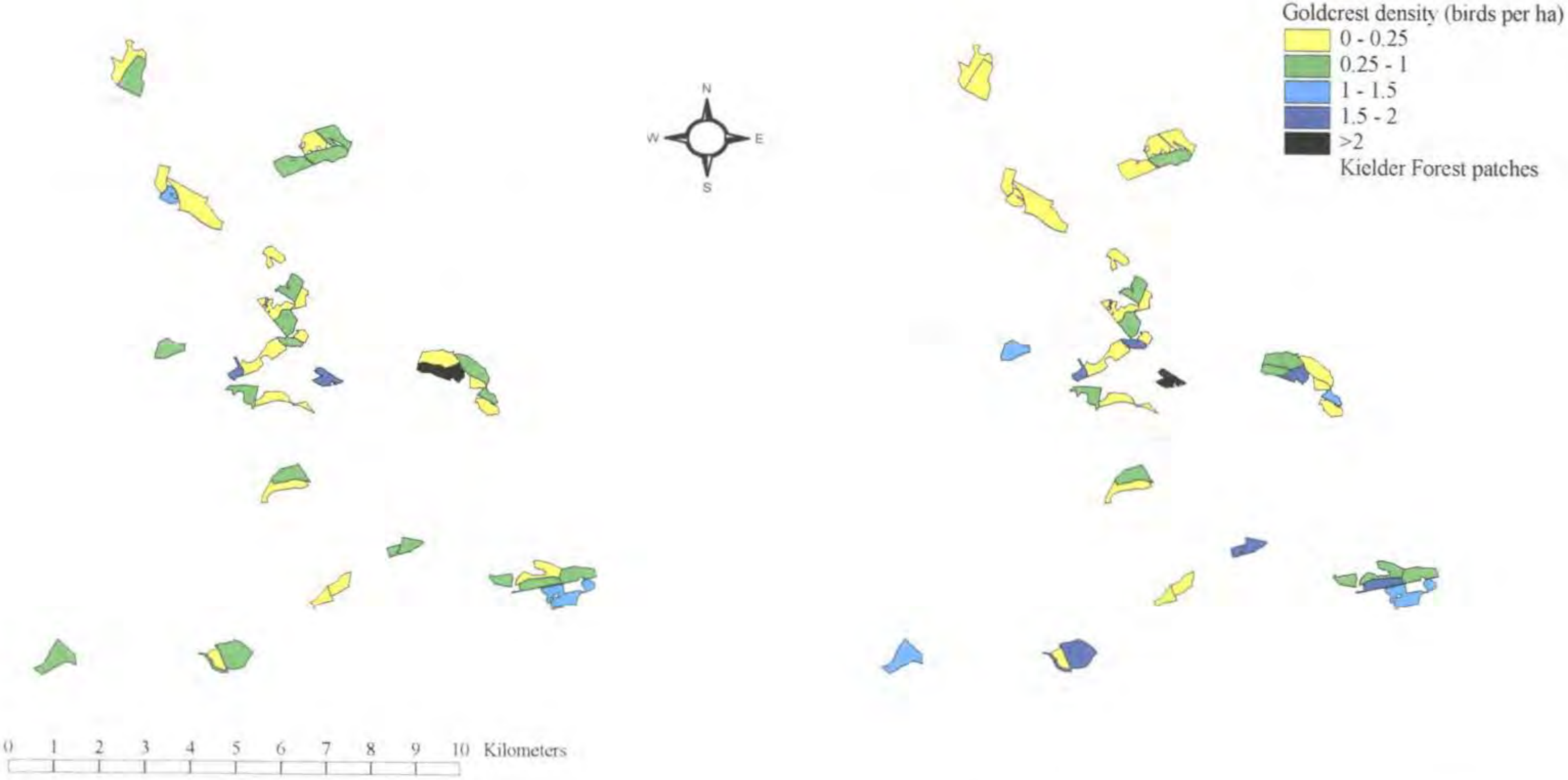
Map 5.2.2: Generalised linear model of predicted chaffinch density in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



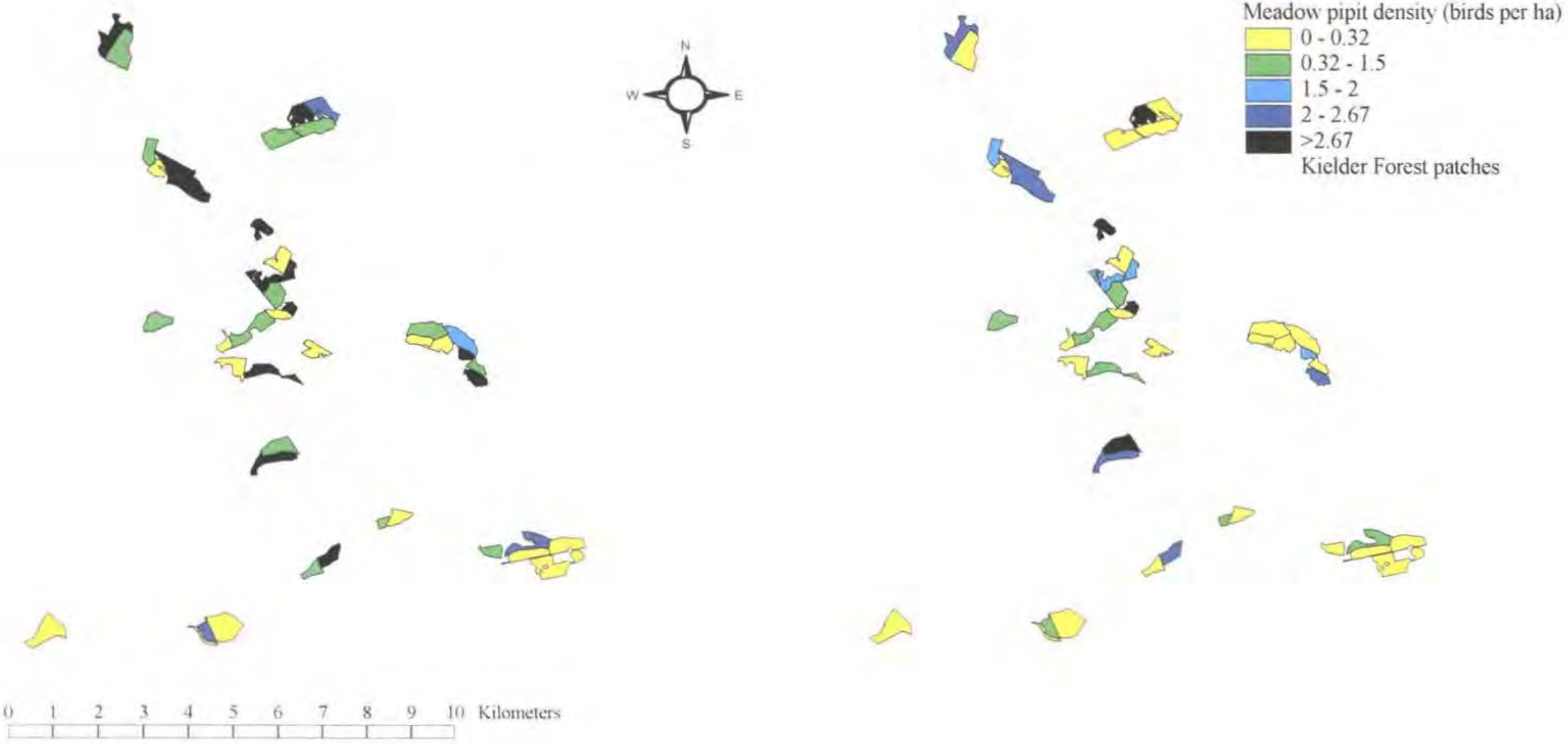
Map 5.2.3: Generalised linear model of predicted coal tit density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



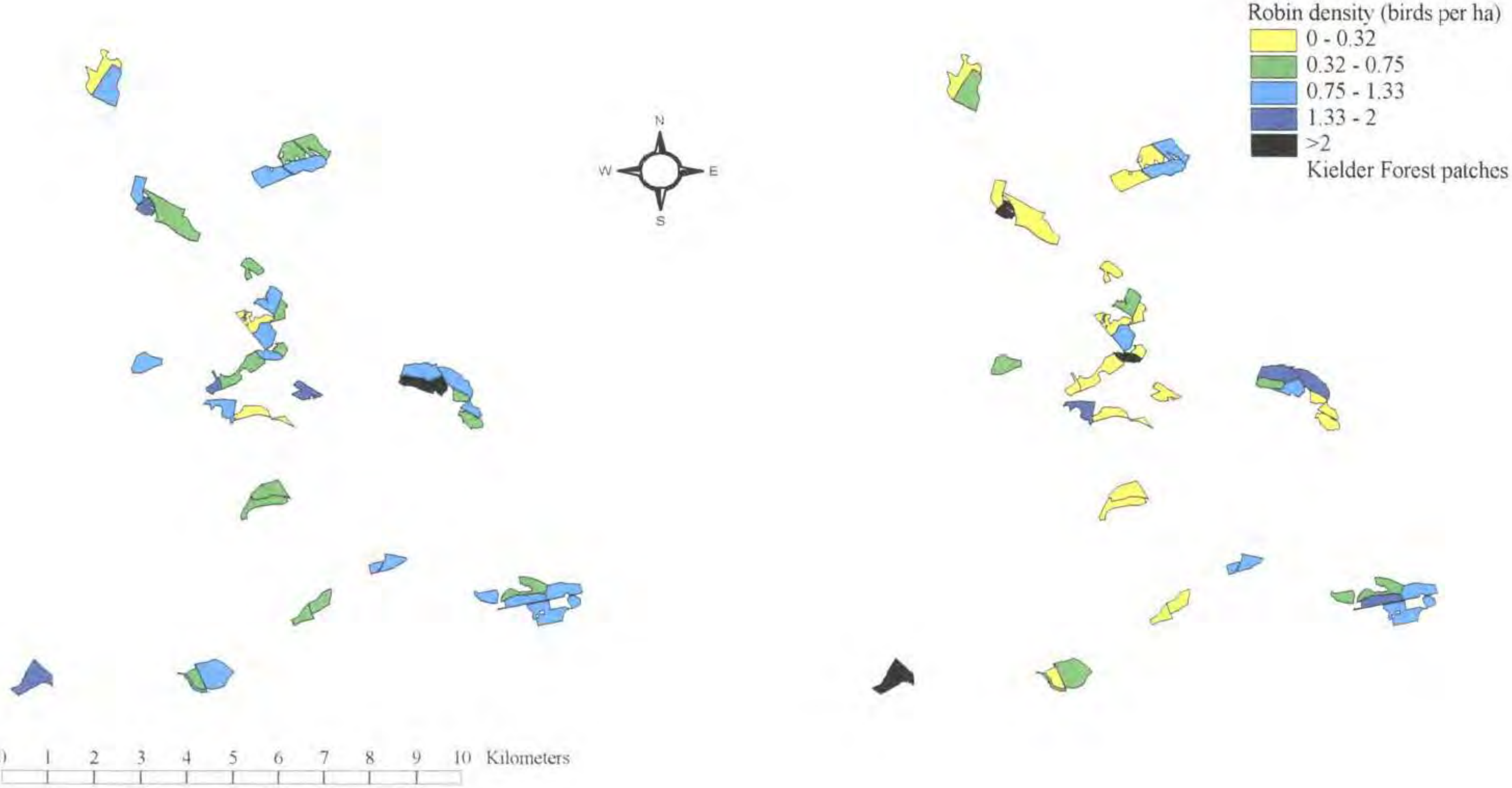
Map 5.2.4: Generalised linear model of predicted dunnock density in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



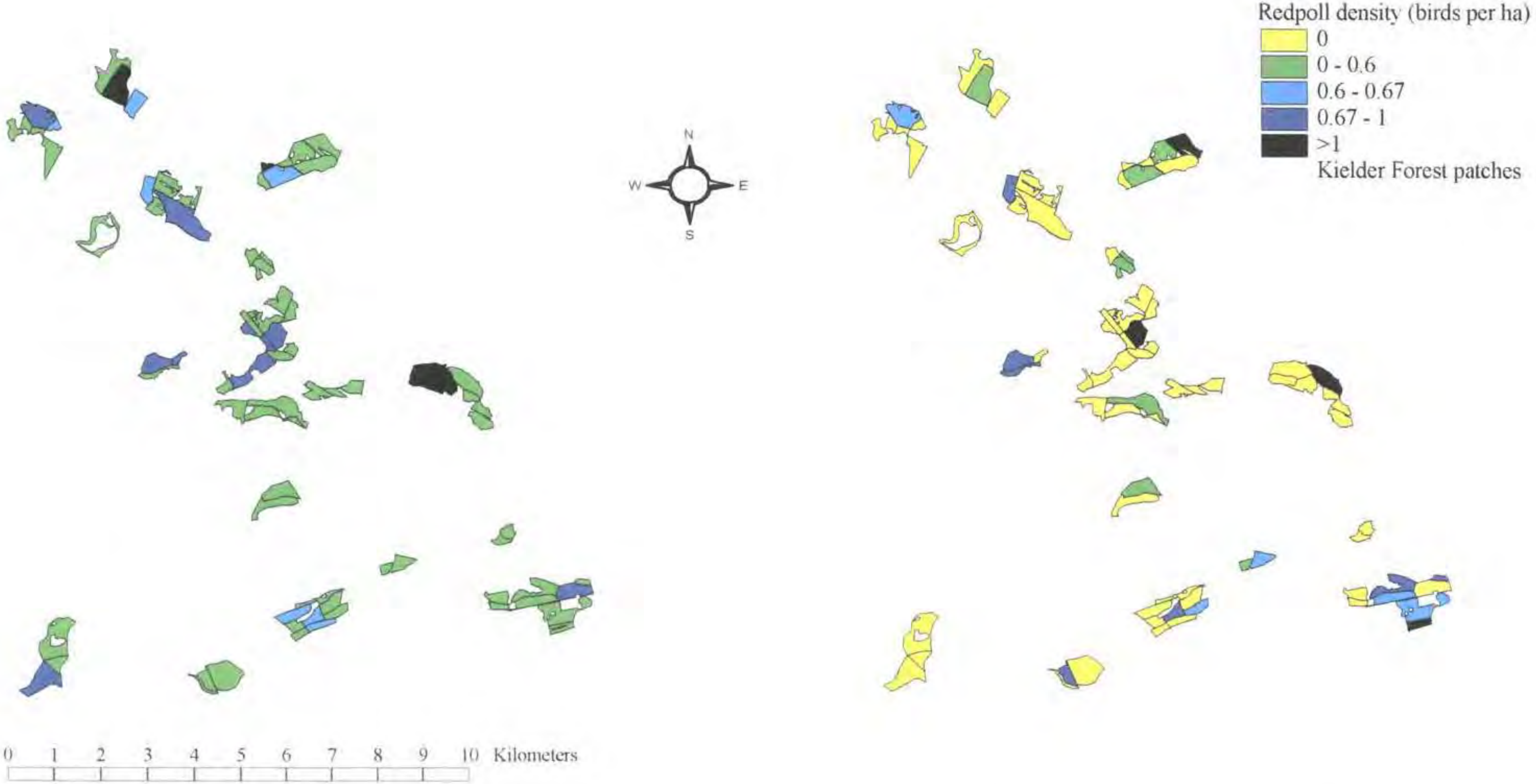
Map 5.2.5: Generalised linear model of predicted goldcrest density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



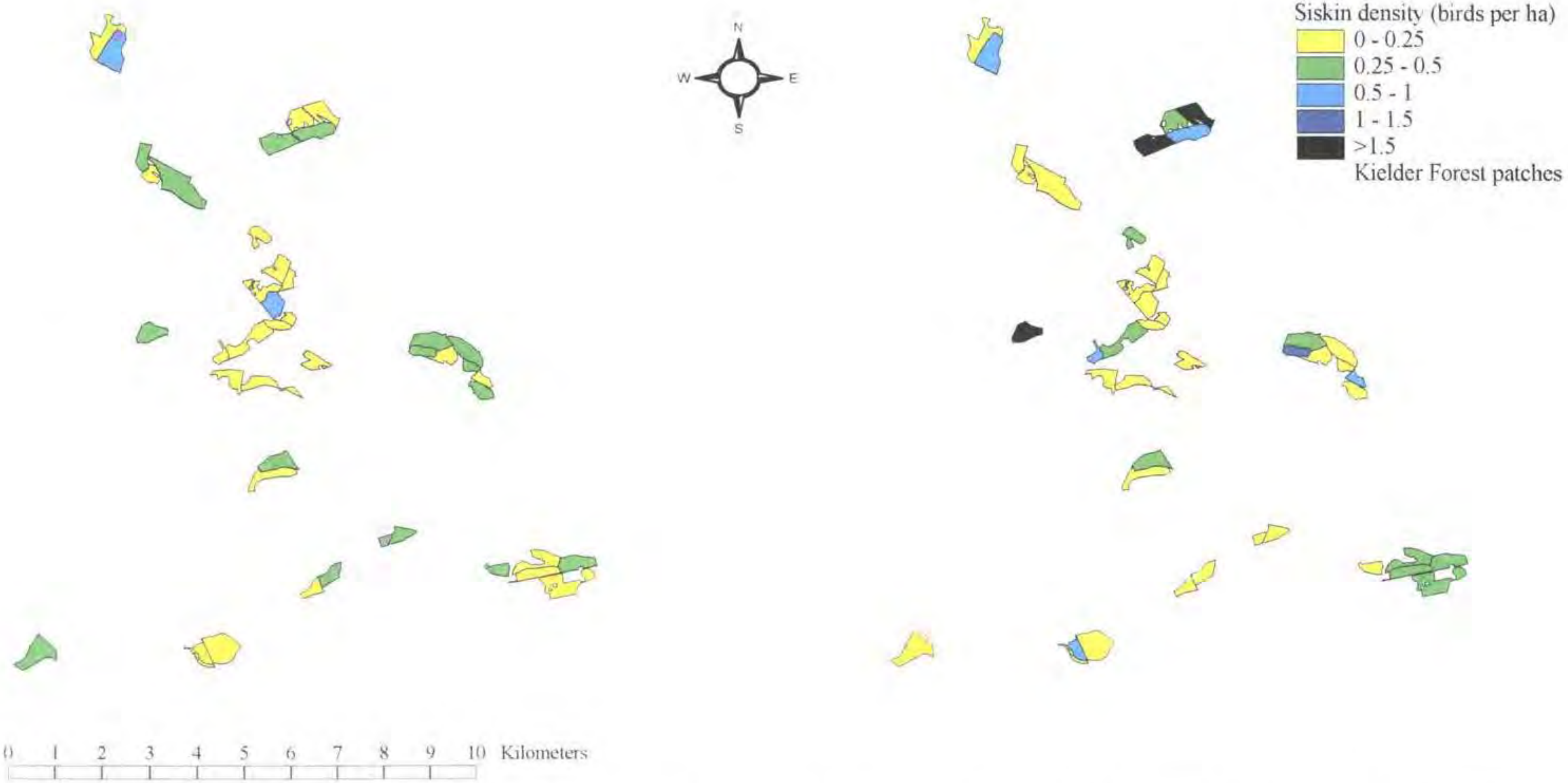
Map 5.2.6: Generalised linear model of predicted meadow pipit density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



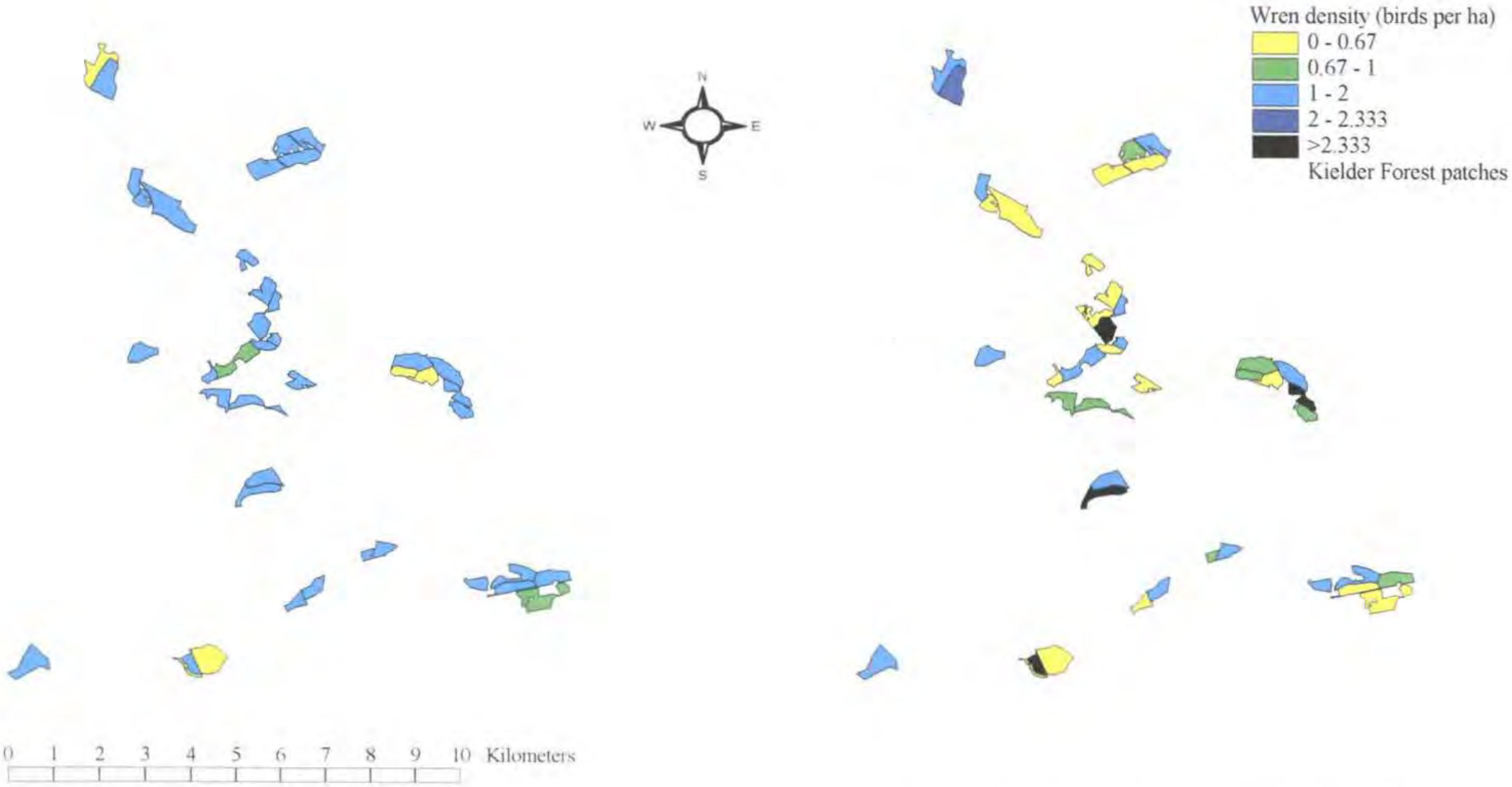
Map 5.2.7: Generalised linear model of predicted robin density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



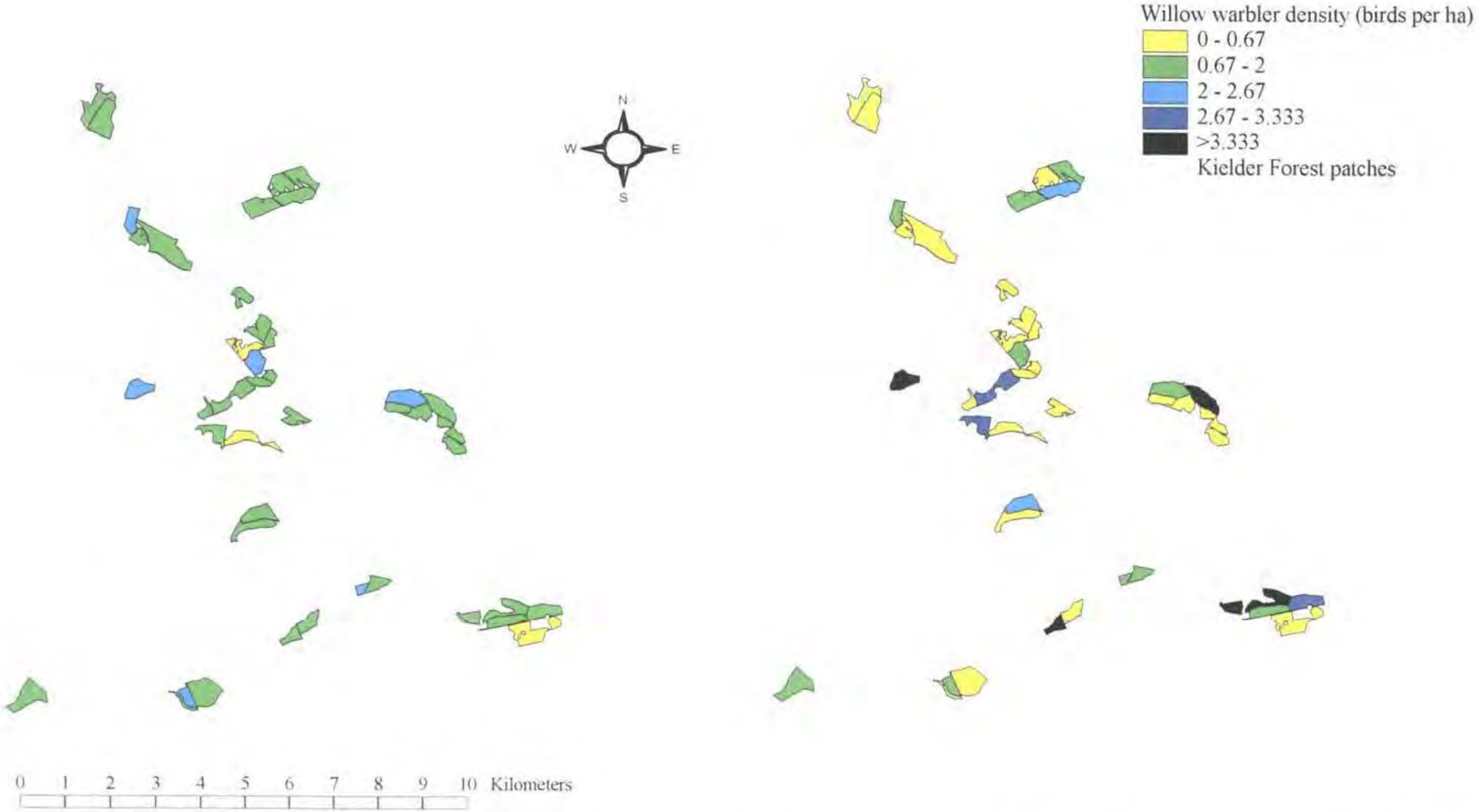
Map 5.2.8: Generalised linear model of predicted redpoll density in patch edges (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



Map 5.2.9: Generalised linear model of predicted siskin density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



Map 5.2.10: Generalised linear model of predicted wren density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.



Map 5.2.11: Generalised linear model of predicted willow warbler density in patch centres (left map) using data collected in 1999 and 1998 validation data (right map). Only those sites surveyed in 1998 are shown on both maps for ease of comparison.