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Granivorous passerines across an agricultural gradient in winter: from habitat use to community structure

by

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A thesis submitted to the University of Dublin, Trinity College, for the degree of Doctor of Philosophy

Department of Zoology

2008

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Summary

In recent decades, agricultural intensification has had profound adverse effects on farmland biodiversity, especially within the more industrialised regions of Western Europe. Among the most severely affected groups have been granivorous birds, where decreases in over winter survival as a result of the loss of winter foraging resources, are strongly implicated in dramatic population and range declines among many species. Little detailed information exists with which to assess the impacts of agricultural intensification on granivorous birds on Irish farmland, and an intensive sampling exercise of ten granivorous passerine species was conducted in an agricultural area characterised by relatively high levels of intensification, to gauge possible national impacts. Transect censuses were undertaken over the course of two winters and two springs (Winter 2001 – Spring 2003) in the Fingal region of north County Dublin.

Advantage was taken of a west to east agricultural gradient that represented two (at least) component consequences of intensification; an increase in the severity of field boundary management, and a decrease in habitat heterogeneity. A hierarchical nested sampling strategy enabled a detailed description of species year round abundance and distribution in relation to habitat variation associated with the gradient. Species responded differentially within seasons, and consistent patterns in species' ranked abundance and fine scale distribution patterns, between seasons and years suggested a robust community response. Overall, abundance estimates were highest for most species during the winter, and two movement patterns were suggested in this data; winter migration, especially in Chaffinch, Skylark, Linnet and Goldfinch; and short distance regional movements toward rich foraging resources within the area.

Analyses focused on elucidating patterns for the second winter by identifying broader agricultural correlates of community variation, and by modelling fine scale patterns in species habitat use. In particular, the effects of variation in field boundary management of hedges and trees were examined, addressing the notion that seed food resources are the overwhelming factor determining species distribution during the winter. Community variation was rather evenly divided among the three spatial levels of the sampling design, and was considerable over short distances (500m). Species' relative abundances (community structure) differed in a predictable way across the gradient. Individual species varied in their dependence on the area of cereal stubbles on transects, and in their relationships to mean hedgerow height on transects. There was a strong geographic dimension in these relationships.

Fine scale habitat use differed among species and reflected variation in hedge height, the availability of trees, and spatial variation in hedgerow density. The greatest contrast found was between Skylark and Chaffinch, while other species showed intermediate patterns, varying in their dependence on, and aversion to, the measured field boundary attributes. These patterns emerged irrespective of species behaviour type: within potentially seed rich habitat, the foraging imperative did not appear to override preferred habitat/niche considerations.

To examine the consequences of species fine scale distribution patterns for broader community pattern, a measure of transect "weight of use" for each species (WOU), based on fine scale habitat use, was determined using the Brillouin Index of diversity. This measure implicated aspects of abundance *and* spatial distribution: species fine scale abundance was positively correlated with increasing fine scale habitat use, and species transect abundance was positively correlated with the spatial extent of occurrence. WOU showed species-specific positive and negative correlations with simple measures of the spatial extent of habitat attributes on transects. Where these correlates agreed with patterns observed in fine scale habitat use, it was suggested these were important factors determining broader scale variation in community structure.

Species diversity was lowest at either end of the agricultural gradient i.e. in the Pastoral and Market Gardening strata, and highest in the more diverse mosaic of the Mixed stratum. Differing management of field boundaries, often characteristic of these farming types, produced spatial variation in the vertical components of habitat, giving rise to a mosaic of "open" and "closed" areas, enhancing habitat/niche diversity. Winter conservation measures (especially the provisioning of winter foraging resources) aimed at benefitting as many granivores as possible could be implemented at locations straddling such a mosaic. More general management should be directed at maintaining or enhancing "open" and "closed" patchiness at spatial scales from several, to tens of hectares.

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PART 1. INTRODUCTION AND REGIONAL SYNOPSIS

Chapter 1. Agricultural intensification and the threat to farmland biodiversity in Ireland

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1.1 Agricultural intensification and its consequences for farmland biodiversity

In recent decades, the intensification of European agriculture, particularly in northwestern Europe, has transformed the rural environment to the point that it can no longer sustain populations of plants and animals (Potter 1997, Krebs et al. 1999, Donald et al. 2000, Benton et al. 2003). Under the auspices of the Common Agricultural Policy (CAP), and facilitated by mechanical and technological innovations, agricultural intensification became a paradigm of maximum production that has brought fundamental changes to the way agriculture is practiced. Traditional mixed farming practices have been superseded by a range of industrialised and streamlined practices. These broadly concurrent changes were encouraged and facilitated through CAP policies of income guarantee and grant aid, and have resulted in increasingly specialised farming enterprises, focused on few or single products. Economies of scale have been pursued, with the result that farms have increased in size, and agricultural patterns have become more regionalized (Quigley 1994, Potter 1997). The area of land under crops has been maximised through the removal of woodlands and pockets of scrub, ponds, and the draining wetlands. The use of larger and more efficient farm machinery engendered field enlargement and the removal of hedgerows. Huge increases in the use of agro-chemicals have occurred. The use of artificial fertilisers has obviated traditional crop rotation practices for replenishing soil nutrients and fertility. Traditional approaches to pest control have been discontinued, replaced instead by herbicide and pesticide treatment. Leaving land fallow was perceived as inefficient and hardier crop varieties were developed that could be sown in the autumn and winter. Specialisation at the farm and regional level has become more prevalent, following the dictates of climate, topography, soils, and market forces. Generally, landscapes have become increasingly homogeneous across a range of spatial scales, leading to *agricultural polarisation*. While these developments represent the characteristic components of intensification, their occurrence has varied regionally and temporally. Intensive farming developed especially in areas that already had well developed agricultural economies. Thus, landscapes in northwest Europe in particular have seen extensive physical alteration, and whole scale changes in farming practices. In southern and eastern regions of Europe, agricultural change has been slower for various reasons, although these areas have generally not favoured the development of intensive farming systems. Nonetheless, considerable pressures have been placed on habitats and species in these farming landscapes as a result of CAP policies, including the effects of land abandonment, the discontinuation of small-scale traditional farming practices, farm diversification, and the over-exploitation of marginal areas (e.g. Preiss et al. 1997).

Conservationists were quick to express concern regarding the pace and scale of the environmental changes that were occurring, and growing public and political awareness of general environmental deterioration, and mounting evidence of declines in biodiversity (notably in bird populations) inspired the introduction, during the 1980s, of "agri-environment" schemes (AES). These schemes sought to encourage farmers, by way of financial compensation and inducements, to safeguard sensitive habitats, and generally farm in more "environment friendly" ways. At about the same time, broad policy reform was underway to address the general and considerable problem of agricultural over-production that was a consequence of price support policies. In arable farming, various set-aside and extensification schemes were introduced that compensated farmers for taking land out of production. Continued reform has seen the de-coupling of income support from production levels, and the integration into broader policy, of environmental management initiatives for biodiversity (among other cultural interests), as legitimate and attractive alternatives to intensive production. Thus, the 1990s saw a break put on hitherto "runaway" intensification, especially in relation to policy, and it is arguable that the worst excesses of this period (ca. 1970-1990) are past. Nevertheless, agricultural modernisation and rationalisation, involving many aspects of intensification continues, especially within the less developed jurisdictions.

Amongst the various groups of species that have been affected by intensification, a relative wealth of data exists for birds, and it is probably true that this group has acted as the primary indicator of environmental problems within farmland (notably alerting conservation bodies in the 1960s to the disastrous residual effects of organochlorine insecticides, such as DDT, in food chains). It was the long-term population monitoring programmes conducted in various European countries, which provided quantitative evidence of disproportionate levels of decline within farmland species. Plausible causes and mechanisms were suggested (e.g. O'Connor & Shrubb 1986, Lack 1992) implicating many of the changes associated with intensification, however, there was a need for stronger evidence to convince policy makers, and research to inform conservation strategies. Since, strong correlative evidence has emerged linking regional and temporal patterns of declines, with broad changes in farming practice (e.g. Donald et al. 2000, Saris et al. 1994, Fox 2004, Chamberlain et al. 2001). These studies serve to illustrate the massive scale of the problem. More focused studies have demonstrated specific adverse ecological effects of intensive practices across a range of taxa (e.g. in plants, Bodil Hald 1999, Kleijn & Verbeek 2000; in insects, Burel & Baudry 1995, Hutton & Giller 2003; and birds, Green & Stowe 1993, Potts 1997). Indeed, such a range indicates diverse mechanisms of disruption. In this respect, Benton et al. (2002, 2003) have emphasised the importance of the interdependence among these taxa, and warned of broader functional consequences of declines. They argue for more holistic management measures aimed explicitly at restoring and maintaining habitat heterogeneity (generally evoking the former traditional mixed farming, low intensity regimes). Too narrow a focus on selected species (or problems), they warn, may not address problems of broader ecosystem function caused by the patterns of habitat loss and homogenisation associated with intensification.

As mentioned, the level and characteristics of intensification have varied considerably among different regions and countries, and it might be expected that impacts on the environment and on biodiversity would show corresponding patterns. This hypothesis was examined by Donald et al. (2001) for farmland birds. They computed indices of intensification for European states, based on several agricultural statistics from 1993. These included measures of agricultural worker population density, agricultural produce and inputs, and farm machinery to worker ratios. A principal component analysis identified three broad groupings of EU states of similar agricultural intensity. A pronounced regional dimension was apparent, distinguishing eastern European countries (new EU member states), Scandinavian countries, and the other countries of northwestern Europe (this included most of the older EU member states, however Spain, Portugal and Greece were grouped with the eastern European countries). Farmland bird population trends differed significantly among these groupings, and were most negative in the old EU member states. Cereal yield explained the greatest amount of variation in mean population declines and (correlated) range declines, and was interpreted as a broad indicator of a suite of changes in crop- and livestock-husbandry practices that have had adverse ecological effects on farmland birds. Of particular interest with respect to this study is the association shown by Ireland with the UK, France and Germany, in scoring highly for the examined indices of intensification. It showed similar cereal and milk yields, cattle stocking rates, and degree of farm mechanisation. While recent decades have certainly seen considerable changes in Irish farming that bear all the hallmarks of intensification, it is a moot point whether these changes have occurred at a scale sufficient to warrant great alarm. The conventional perception has been that relative to other European countries, Ireland has not seen major or broad scale environmental problems resulting from industrial or agricultural development, and that therefore, all is well. The fact is, however, that little has been achieved in terms of environmental and biodiversity audit (i.e. the establishment of baseline databases and subsequent monitoring schemes), and we are really quite limited in our ability to make reliable assessments of the health of our environment and biodiversity. The study of Donald et al. (2001) places Ireland firmly in the group of the most agriculturally industrialised countries in the world. This fact alone underlines the need for vigilance, and farmland management policy informed, at the very least, by regional understanding of habitat interactions with agriculture. While the relatively small scale of arable agricultural production in Ireland (the intensification of pastoral farming may, however, warrant concern, as it is conducted on a far broader scale) may have lessened various environmental impacts associated with intensive practices, structural changes continue apace in Irish farming, bearing many of the characteristics of intensification (Crowley et al. 2004). The recent reforms to the CAP, which provide for measures and actions aimed explicitly at safeguarding and enhancing farmland biodiversity and habitats (agri-environment schemes) are, therefore, of the utmost importance; the opportunity to practice all round sustainable management for both agriculture, and the environment, must be grasped. Thankfully, national agencies and research bodies are now coordinating efforts to address the general dearth of information on Irish biodiversity to identify areas where conservation actions are needed, and where agri-environment schemes might be of benefit.

1.2 The study: a regional assessment of farmland granivorous passerines and their comparative ecology in winter

Throughout the rest of this work, attention is focused on the granivorous passerines of farmland, a group of birds that has shown particular sensitivity to the environmental changes associated with intensification (Marchant & Gregory 1994, Fuller 1995, Siriwardena et al. 2000b). A study of this group was conducted in a region of farmland in north County Dublin considered one of the most intensively farmed areas in Ireland. As such, results could be considered as a gauge of the possible impacts of intensification at broader regional or national levels. Bird survey, agricultural land use, and other environmental data were collected over the course of two years to describe seasonal abundance and distribution patterns on 1km transects, in relation to variation in agricultural land use and management. The survey results provide baseline data, and an assessment of how granivorous species are faring in this intensively farmed region. Beyond this regional characterisation, investigations concentrate on detecting differences in habitat requirements and patterns of habitat use among the species during the second winter of the study. The data are considered at three spatial levels, with the broad aim of relating variation in community structure i.e. species composition and relative abundances, observed at the different levels, to habitat associations, requirements and use patterns. To place the study in context, I first consider how historical developments in Irish farming might have affected these species, and examine their current conservation status. The potential for the various components of arable intensification to have affected populations is then briefly considered, and an appraisal is made of the relevance and implications of findings from studies conducted in other countries, especially the UK, for the Irish agricultural context.

1.3 The effects of agricultural change on granivorous passerines in Ireland

The geographical pattern of agricultural practices in Ireland is broadly reflective of the climatic influences of Atlantic weather systems; drier and sunnier regimes of southern and eastern regions have favoured arable enterprises, while grass growth is favoured by the wetter and milder conditions of western areas. Only 9% of agricultural land is devoted to the production of crops (~6% of the total land area), while 80% is devoted to pasture, silage or hay. This difference has not always been so extreme, but follows a substantial long-term decline in the area of arable cropping since the 1850s. A dramatic regional dimension is evident in this decline (see Taylor & O'Halloran 1999), with by far the greatest losses occurring from western regions, as it gradually contracted to give the present day concentration in eastern and southern counties. This *polarisation* represents a fundamental habitat change that is likely to have had consequences for populations of granivores (Taylor & O'Halloran 1999). Farmland granivores are generally found at higher densities in areas where more arable farming is practiced, because of the increased availability of seeds of weed species associated with tillage (Telleria et al. 1994, Gregory & Baillie 1998, Atkinson et al. 2002). The reduction in the area of this land use is, therefore, likely to have reduced the carrying capacity of western regions for granivores, although the importance to individual species of arable habitat, and the availability of suitable alternative habitats, will have influenced the likelihood of range contractions. An analogous, but more recent polarisation of agricultural practices in Britain has been linked to population declines, and especially to range contractions, among some farmland granivores (Robinson et al. 2001). Hitherto, lower levels of arable habitat in northern and western Britain had been sufficient to maintain populations of granivores, including those of farmland *specialist* species i.e.

species that rely on fields for nesting and food. But as polarisation progressed, specialists suffered local extinctions, whereas habitat *generalists* did not (Fuller 2000). Polarisation (essentially, habitat loss) may not have been the only pressure acting on these species, as other changes in arable farming practice may have taken a toll (e.g. reductions in seed and insect food resources as a result of increasing use of pesticides and herbicides).

While little data on the distribution and abundance patterns of granivores on Irish farmland exists for the period before intensification, only the most basic information exists for the period of peak intensification (ca. 1970-1990), in the form of two breeding atlas studies. The first (Sharrock 1976) covered the period 1968 – 1972, and the second, some 20 years later (Gibbons et al. 1993), covered the period 1988 – 1991. Comparisons between the two have indeed provided evidence of recent breeding range declines in several granivores, including Greenfinch *Carduelis chloris*, Goldfinch *Carduelis carduelis*, Reed Bunting *Emberiza schoeniclus*, Linnet *Carduelis cannabina*, and Yellowhammer *Emberiza citrinella.* Worryingly (Taylor & O'Halloran 1999), the extent of these contractions has generally been greater than the well documented range contractions of their counterparts in Britain, with the suggestion that more severe populations declines have occurred on Irish farmland. Taylor & O'Halloran's primary aim was to refute the recent probable extinction of the once widespread Corn Bunting *Miliaria calandra* as a breeding species in Ireland, and explore the possible causes of its demise. A series of surveys of former breeding haunts along the west coast (Sharrock 1976, Gibbons et al. 1993) was undertaken, but no Corn Buntings were found. Historical records suggest a long-term decline since at least the 1900s (Hutchinson 1989) that may have been associated with the broad reduction in arable farming, and especially in cereal farming, which occurred during the 20th century. In this respect, it is noteworthy that R.F. Ruttledge and fellow ornithologists speculated, through the pages of the Irish Naturalists Journal (ca. 1938 – 1944), as to whether the Yellowhammer was in decline during the 1930s. Although this species shows an affinity for scrub and woodland edge habitats, the bulk of its population is associated with cereal farming (Kyrkos et al. 1998), and it should be of no surprise that populations should respond to fluctuations in the area of this land use. The authors suggest two broadly distinctive processes operated to leave the two latter-day populations of Corn

Bunting (one along the west coast, the other in the south-east) that persisted up to the time of the second atlas study. For the western population, the continued reduction of arable farming, and the loss of temporary grasslands and meadows associated with it, led eventually to critical levels of habitat loss. This perhaps had its greatest impact on over-winter survival, when stubble fields, especially of oats, would have been important winter foraging habitat. The loss of temporary grasslands is likely to have had an impact during the breeding season (Brickle et al. 2000), as these habitats provide a source of important invertebrates (in the of diet chicks) *and* weed seeds (for adults). The southeastern population, on the other hand, may have been vulnerable to the more industrial and practical changes associated with intensification (especially those leading to the loss of fine scale habitat mosaics as a result of farm specialisation), as there was relatively little loss of arable farming from this region. Donald & Evans (1994) highlighted a period of contrasting population trends in Corn Bunting and Cirl Bunting *Emberiza cirlus* in Britain, perhaps in response to the abandonment of cereal farming during the early decades of the 20th century. They suggested that the Cirl Bunting responded positively to an increase in weedy and scrubby habitat in areas that ceased cereal farming, while the Corn Bunting declined in response to a loss of breeding habitat. This loss occurred principally in the form of ley grass and under sown cereal fallows, which were a likely consequence of reductions in cereal farming. It is worth noting that the event(s) leading to the ultimate demise of Irish Corn Bunting populations may have been unrelated to the primary drivers of the longer-term decline. Declining populations become increasingly vulnerable to the range of environmental adversities that they may normally endure. Given the endangered status of the Corn Bunting before the advent of intensification in Ireland, even low levels of relatively minor changes in farming practices might have been critical.

The suggested dual process appears similar to patterns observed in the British population (Donald & Evans 1994), and to a more general pattern observed there, in granivores (Marchant & Gregory 1994, Fuller et al. 1995, Robinson et al. 2001): range declines and local extinctions occurring in western regions in response to polarisation (the loss of arable habitat), and population declines occurring in eastern regions due to changing practices *within* arable farming. Thus, the potential for agricultural polarisation to have impacted negatively on granivorous passerines in Ireland seems to be intuitive. What is far less clear is the extent to which arable intensification has affected these species.

1.4 The conservation status of farmland granivores in Ireland

A recent report on the conservation status of Irish birds (Newton et al. 1999) expressed concern at the disproportionate representation of farmland birds in red and amber lists (indicating high and moderate conservation concern, respectively). In the absence of quantitative data, this assessment was based on the canvassed opinion of local experts in different counties, as to the nature of the population trends for species in the period 1973-1997. It is not indicated, however, the extent to which the suggested trends represent those observed in the 20 year period between the breeding atlas studies (coinciding broadly with a period of dramatic change in Irish agriculture), or if these continued through the 1990s, when the rate of agricultural change may have slowed, and levels of environmental protection increased. Ireland now operates an annual national breeding bird survey to monitor change in species breeding populations. The scheme, the Countryside Bird Survey (CBS) has been running since 1998, and two reports (Coombes et al. 2002, Coombes et al. 2006) have been published. While the authors stress the need for a longer run of data to determine reliable trends, granivores generally appear to have remained stable or increased in recent times. The notable exception is a continuing and widespread downward trend in breeding Skylarks *Alauda arvensis*. Interestingly, Goldfinch, Bullfinch *Pyrrhula pyrrhula* and Linnet appear to have increased in western regions; however, whether these trends reflect population growth on farmland is not reported. It is possible these trends are associated with the expansion of housing and gardens in towns and villages, and in the wider countryside (especially for Bullfinch and Goldfinch), and with the creation of ruderal habitats more generally, associated with an expanding urban and sub-urban infrastructure.

An apparent stronghold for most farmland granivores remains in the south and east, where the farmland is broadly "mixed" in character i.e. comprising farms that combine livestock and crop production, but also landscapes that are not predominantly one farming type or the other: individual farms may be specialised while the landscape retains a mixed character. Avian landscape ecological studies conducted on farmland in Britain typically define mixed farming landscapes as those where the percentage area of pastoral, or arable farming, does not exceed 60% - 80% of the total agricultural land use within 10km national grid squares (e.g. Robinson et al. 2001, Atkinson et al. 2002). Atkinson et al. (2002) found higher overall bird species diversity in mixed farming landscapes than in predominantly pastoral or arable landscapes, and demonstrated that they were particularly important during the winter. Granivores generally maintained a strong positive year round association with arable farming, however, Corn Bunting, Reed Bunting and Skylark appeared to show shifts away from purely arable habitat during the winter, to more mixed farming landscapes. By definition, mixed farming landscapes provide a greater diversity of habitats, and several studies have illustrated the importance of habitat mosaics in providing complementary and substitutable resources at various times of the year. For example, during the breeding season, Corn Buntings may forage for insects, important in the diet of chicks, in grassy areas, and grain and seeds on arable fields (Brickle & Harper 2000). Sward height is a critical determinant of the suitability of breeding habitat in Skylarks, and the use of a succession of fields with the appropriate vegetation structure, often of different crops, allows multiple broods during the season (Chamberlain & Gregory 1999). Benton et al. (2003) reviewed the general positive effects on biodiversity of habitat diversity within farmland, through ecological interactions among species, and suggested source-sink type dynamics increase biodiversity in the greater area, maintaining, for example, food supplies for birds (insects, weed seeds) even in intensively managed pockets.

The mixed farming landscapes of the east and southeast of Ireland thus represent not only an important regional refuge for Irish farmland granivores, but also, the broader biodiversity benefits of increased habitat diversity. Nevertheless, this region has lost two farmland bird species in recent decades. The plight of the Corn Bunting has already been described, while the Grey Partridge *Perdix perdix* has disappeared from former haunts. While recent years have seen a slowing in intensification generally, the agro-economic environment remains highly competitive, demanding continued rationalisation and economies of scale, resulting in continued trends toward farm specialisation and increasing farm size (Crowley et al. 2004). Both trends will have particularly negative effects on farmland habitats and biodiversity, where farming practices are intensive. It is critical, therefore, to recognise that arable land comprises a very small proportion of agricultural land cover in Ireland (~9%, compared with ~50% in England) and must be managed sensitively for all the species dependent on it. Ominously, national agricultural productivity is highest in these mixed farming regions, broadly favouring the development of intensive operations.

1.5 Multiple effects of intensification

What is striking in Taylor & O'Halloran's (1999) review, and in others concerned with bird population change and farming practices e.g. Fuller (2000) and Newton (2004), is the variety of proposed factors and mechanisms associated with intensification, with adverse effects. The majority of examples given are from studies conducted in the UK, where a wealth of long-term data on the abundance and distribution of farmland birds, on demographic parameters, and on land use and other environmental measures, has allowed ecologists to identify and investigate problems, and develop conservation strategies (Vickery et al. 2004, Grice et al. 2004). While broad effects (e.g. reduced food supplies, Wilson et al 1996; reduced area or quality of nest site habitat, Gillings & Fuller 1998) are likely to have impacted most granivores to a greater or lesser extent, it has become increasingly apparent from autecological studies (e.g. Evans & Smith 1994, Kyrkos et al. 1998, Donald & Forrest 1995, Potts 2000, Whittingham et al. 2001), and from broader demographic studies (Siriwardena et al. 2000b), that despite the dietary similarity of these species, differences in life history and ecological requirements have determined species-specific vulnerabilities to the environmental changes associated with intensification. Although all are small passerines which share a common food source, they differ *inter alia* in nest site selection, vagility and sedentariness, the extent to which insects are required during the breeding season, preferences for areas with small wetland features, requirement of crop mosaics, hedgerows, and trees. Studies of trends in demographic parameters including abundance, survival rates and fledgling production per nesting attempt (Siriwardena et al. 2000b) have detected shared *and* species-specific patterns of change. Distribution patterns measured at the 10km square resolution have indicated species-specific associations with regional cropping/farming characteristics i.e. the type of crop (e.g. cereal or vegetable, brassica or root crops) and the associated management and environmental correlates (e.g. chemical inputs, field sizes, winter cropping, time of harvest, soil type etc.) (Siriwardena et al. 2000a, Atkinson et al. 2002). The results of these different types of study underline the importance of the ecological differences among species, and argue for a heightened awareness of how farmland habitats accommodate species, and how this might be threatened, sustained and enhanced.

The present study pursues the implications of species differences for the ability of farming landscapes to accommodate and sustain species. In this regard, much work has focused on the breeding season, resulting in a broad understanding of species habitat preferences and breeding requirements. In contrast, far less ecological detail is available describing the winter niche, and it has often been assumed that for wintering granivores, the farmed landscape is simply a food/non-food matrix, where environmental variation is of little consequence. The main part of this work tests this assumption by describing community patterns and species habitat use, in relation to broad *and* fine scale, farming and management gradients. Greater understanding of species-habitat relationships and patterns of habitat use during the winter is desirable not only in its own right, but also to better inform conservation actions that may be implemented during the winter, e.g. measures aimed at increasing winter food.

This overview illustrates some of the advances in understanding the processes of change in northwest European agri-ecosystems. The majority of the cited studies, however, were conducted in the UK, and broad questions remain relating to whether, or how, findings might apply in relation to Irish farmland. On one hand, research conducted in the UK may be more relevant to Ireland from a biogeographical and cultural point of view than, say, similar research conducted in France. On the other hand, the scale and nature of the impacts of intensive farming practices are quite different, and studies from less impacted regions may have more relevance, notwithstanding biogeographical or cultural considerations. If the dearth of data from Ireland requires us to turn to studies of processes and trends from the UK or elsewhere, a much fuller understanding of the similarities and differences between jurisdictions would seem necessary. This may include an appreciation of historical and cultural influences on developing farming practices and patterns, of differences in the economic scale of farming, and an appreciation of the biogeographical factors governing regional biota.

1.6 Summary of main points

- Agricultural intensification is a complex, multivariate phenomenon that has occurred recently and rapidly, especially within the agricultures of western developed nations. It has had profound detrimental consequences for farmland biodiversity.

- Contemporary trends in Irish agricultural patterns and practices bear many of the hallmarks of intensification. A dearth of data for farmland biodiversity, however, has hampered attempts to assess possible impacts. The relatively small scale of implementation of intensive practices in Ireland, however, may have lessened impacts, especially during the “peak period”, ca. 1970-1990.

- Agricultural polarisation, frequently associated with intensification, is likely to be a principal cause of historical and recent range contractions in several farmland granivorous passerine species. The importance of more technological and industrial changes in farming practices, for range and population declines observed during the period between the two breeding bird atlas studies is not clear. Such changes may be implicated in the probable extinction of Corn Bunting, and the endangerment of Yellowhammer and Grey Partridge. The more recent assessments of granivore population trends, however, are favourable, showing most species to be stable or increasing. An exception is the Skylark, which shows a continuing population and range decline, consistent with trends observed in other European countries.

- The mixed farming landscapes of the east and southeast of Ireland represent not only an important regional refuge for Irish farmland granivores, but also, the broader biodiversity benefits of increased habitat diversity. Given the small proportion of agricultural land under arable crops in Ireland generally (~9% of all crops), and the predominant location of this farmland in eastern and southeastern regions that are very suitably disposed to an expansion in intensive operations, regional agricultural policy and farm management must be mindful of the conservation implications of such developments. It is imperative that species' interactions with regional agricultural practices are understood, including how year round habitat requirements are met, so that this can be sustained in the face of future change.

Chapter 2. Study area, sampling strategy, thesis outline, and results of surveys

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2.1 The study area

The study was conducted during the winter and breeding seasons of 2001-02 and 2002-03, over an area of approximately 150 square kilometres of intensively farmed land in north Co. Dublin (Fig 2.1), in the Republic of Ireland. The climate is broadly typical of the general Irish climate - mild winters and summers with temperatures rarely dropping below 0° C, or exceeding 30° C. The study area, however, tends to be drier, sunnier and warmer than most parts of Ireland. Physiographically, the area constitutes a rolling lowland, and is drained eastwards by the Broadmeadow, Ballyboghill and Corduff rivers, and numerous small channels. Drainage ditches are a ubiquitous feature of the landscape, bordering almost every field. Fertile grey brown podzolic soils and gley soils underlie and reflect an

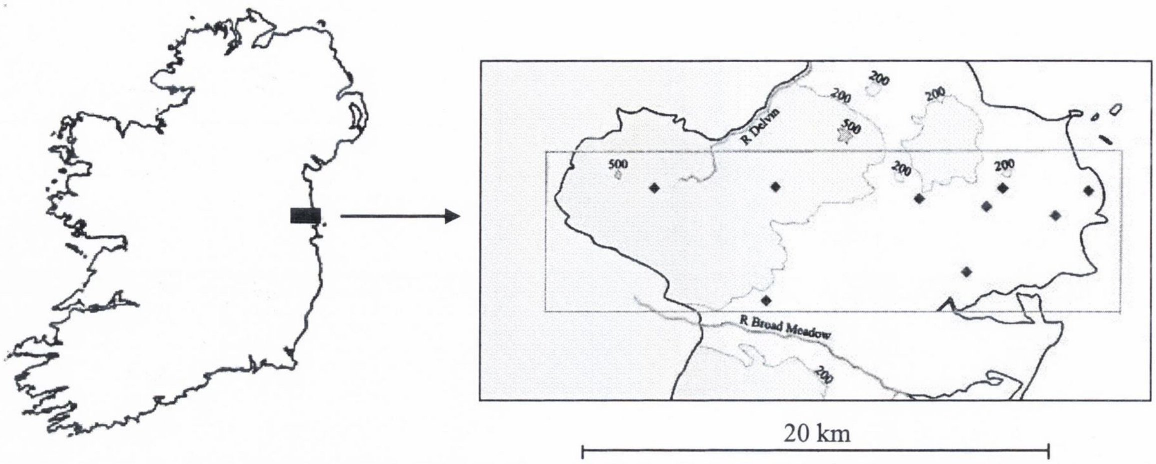

Figure 2.1. Location of study area in County Dublin and distribution of study sites. Sites were located to sample an agricultural land use gradient – a predominance of pastoral farming toward the west of the county grading to mixed-arable and arable regimes centrally and market gardening coastally.

east/west arable/grassland gradient, the former being associated mainly with the predominantly arable east, and the latter with a gentle east-northwest rise in altitude and a predominance of pasture. Such soils are typical of the drier and better-drained regions of the south and east of Ireland (Collins & Cummins 1996), and support good grassland as well as arable production. These factors, and the area's proximity to Dublin City and a steady urban market, have favoured the development of a diverse and flexible regional agriculture. The area comprises an estimated 4.2% woodland, mainly small plantations in demesnes (Hickie 1985), and reflects a broader regional absence of any significant natural woodlands. The study area's southern boundary lies approximately 10km north of suburban Dublin, and the location of a major international airport within this zone, with its associated developmental restrictions, provides a reasonable environmental buffer between the rural and urban landscapes. Within the study area, urban development is restricted toward the coastal fringe around the village of Rush, and inland around the village of Lusk (Fig 2.2). These villages comprise the only considerable urban centres within the study area. The remaining landscape is essentially rural, but contains several small villages. The average size of farm holdings is in the order of 25-30 hectares (Collins & Cummins 1996).

The hedgerow infrastructure is overwhelmingly of recent origin, and planted typically with thorny species such as Hawthorn *Crataegus monogyna* and Blackthorn *Prunus* *spinosa*, or Ash *Fraxinus excelsior*. Most hedges tend to be species poor (Doogue et al. 1998), containing a limited range of other common species e.g. Rose *Rosa* spp., Bramble *Rubus fruticosus* agg., Ivy *Hedera helix* and Elder *Sambucus nigra*. Common trees include Ash, Sycamore *Acer pseudoplatanus*, Pedunculate Oak *Quercus robur*, Holly *Ilex aquifolium*, Beech *Fagus sylvatica* and Horse Chestnut *Aesculus hypocastanum*. For sampling, the study area was stratified three ways on the basis of a perceived zonation of farming practices. A coastal fringe of primarily market gardening enterprises gives way inland to a predominance of cereal cropping and the appearance of small pockets of pasture. To the west, pastoral farming predominates over small pockets of arable. For convenience, strata were identified as “MG” for the market gardening stratum, “Mixed” for the cereal growing stratum, and “Past” for the Pastoral stratum. At broader spatial scales, this spectrum more closely corresponds to an “Arable to Mixed farming” gradient (see Discussion 2.6 and Survey Results – Cropping patterns 2.5.1).

2.2 Methodology

As noted in Chapter 1, the second aim of the study was to investigate if, and how, landscape and habitat characteristics associated with the different farming regimes might influence species distribution, and therefore, community structure i.e. the relative abundance of species. The approach taken was to examine abundance and distribution patterns at different spatial scales. The sampling strategy was, therefore, intended to provide a hierarchical dataset characterising farming type habitat gradients, and species’ responses to these gradients, at several spatial resolutions and levels. This investigation focuses on data from the second winter only, and is the subject matter of the remaining chapters.

2.2.1 *Site selection and survey methods*

The UK Breeding Bird Survey (BBS) census methodology (Gregory et al. 1998), devised to estimate species’ breeding densities in a wide range of habitats, was adapted for the purposes of this study. This methodology has been adopted by the Irish Countryside

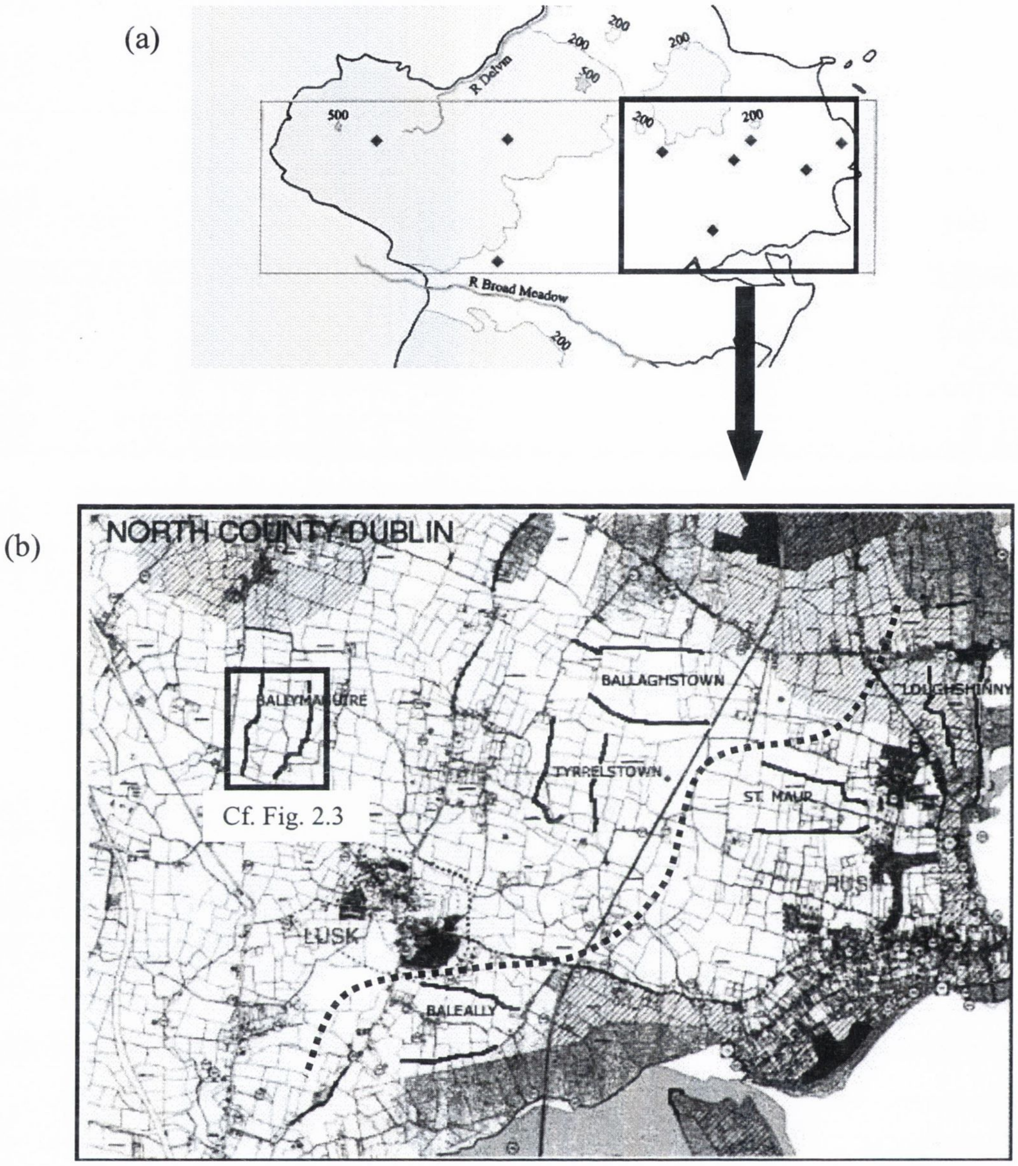

Fig. 2.2. (a) Study area, and (b) landscape character map detailing individual field boundaries and locations of sites and transects in the Market Gardening (coastal) and Mixed farming strata. The dashed line was superimposed on the map to represent a notional boundary between strata. Inset in (b) is the site example used to demonstrate data extraction procedures (see Fig. 2.3).

Bird Survey (CBS) (Coombes et al. 2002), so results from the present study relate to the same spatial scales, permitting broadly reliable comparisons. Briefly, 1km Irish National Grid squares are sampled by conducting censuses on two fixed, parallel 1km transects, separated by approximately 0.5km. For my study, potential study sites (approximating 1km squares, but not necessarily coinciding with the national grid) were identified in each farming type stratum after consulting field boundary maps (e.g. Fig 2.2b) and aerial photographs. Land managers were then contacted to ask permission to access their land.

In choosing sites, consideration was given to transect straightness and separation, however two squares represent compromises of the above standard (transects were of unequal length or were not parallel). Aerial photographs were consulted to ensure that the farmland in sampled squares was broadly typical of its stratum. Straighter transects were considered to minimise disturbance of birds before they were counted, and instances of double counting. Three sites were established in each stratum (Fig 2.2a, Table 2.1). The number of fields sampled per transect ranged from 5 to 17 (median = 10.5), and the number of farms ranged from 2 to 5. Sixteen of the 18 transects sampled between 18 and 24 hectares, ten of these sampled 20 hectares. See Appendix 1 for transect route detail and characteristic landscape and habitat features at each site.

2.2.2 *Survey censuses*

Censuses were carried out during two winters and two springs, however the number of censuses varied between seasons and years (Table 2.1). Most sites received 8 or 9 censuses during each season, but surveying during the first spring was curtailed by personal injury with the result that only 3 or 4 out of a planned 9 were completed. It was decided, therefore to conduct a second spring survey the following year, as the broader intention was to be able make seasonal ecological comparison more reliable through similar survey effort. Census counts were usually made at three sites in a day, the first commencing at least half an hour after sunrise, and the last usually being completed by 13:30. A census *count* was undertaken by walking transects at a moderate pace and using aural and visual cues to locate, identify and count birds. Every effort was made to reduce potential bias in counts caused by missing birds obscured by hedges or tall field vegetation. This included alternating which side of the transect was walked between counts, and taking advantage of gates, and gaps in hedges, to inspect the "other side" of the transect by forward scanning with binoculars. The sampling schedule alternated the order of counts among sites and transects to avoid systematic diurnal biases. Transect pairs at sites were always counted

Table 2.1. Details of hierarchical sampling frame, seasonal survey effort and sample transect characteristics (see also Appendix 1). Winter 1; October 25th 2001 - February 27th 2002. Spring 1; April 9th – May 2nd 2002. Winter 2; October 23rd 2002 – March 3rd 2003. Spring 2; March 31st - June 20th 2003.

Hierarchical sampling frame			No. hectares sampled	No. farms sampled	No. fields sampled	No. of census counts made			
Stratum	Site	Transect				Winter 1	Spring 1	Winter 2	Spring 2
Market Gardening	Loughshinny	"Coast"	18	2	13	6	4	7	9
		"Inland"	11	3	7	6	4	7	9
	St. Maur	"Open"	20	3	14	7	4	9	9
		"Wall"	21	3	17	7	4	8	9
	Baleally	"Dump"	20	3	12	8	4	9	9
		"Boylan"	20	3	10	8	4	9	9
Mixed	Tyrrelstown	"Clinton"	20	2	10	8	4	9	9
		"Hooey"	20	3	11	8	4	9	9
	Ballaghstown	"Railway"	21	4	7	8	4	9	10
		"Baldongan"	22	3	10	8	4	9	10
	Ballymaguire	"Farm"	20	3	11	7	4	9	10
		"Nick"	20	3	14	7	4	9	10
Pastoral	Damastown	"River"	20	3	10	none	4	9	9
		"Farm"	19	4	10		4	9	9
	Rowlestown	"Maguire"	20	3	13		4	9	9
		"Rooney"	20	2	10		4	9	9
	Baldwinstown	"Horses"	12	2	5		3	8	9
		"Reynolds"	24	4	11		3	8	9
			348			88	70	155	166

consecutively, however, and all sites in the pastoral stratum were usually sampled on the same day.

Because species "detectability" often varies among habitat types, and among species within habitats, *distance-sampling* methods (Bibby et al. 1992) are often used to produce more accurate estimates of densities. Bird count data from different distance categories are used to define *detection functions*, which may be specific to particular habitat types and/or specific to species within those habitats. In the BBS, three distance categories are used; 0-25m, 25-100m and >100m and detection functions are defined accordingly for the different habitats sampled by transects, to provide more accurate overall density estimates, and enable more reliable density comparisons among habitats. This approach was not used in the current context because only one habitat type i.e. farmland, was sampled. It was felt also that in view of the open nature of this habitat, and the ecological similarities among species (most occurred in flocks, showed a tendency to forage for seeds on the ground in the open, flushed quickly from fields when approached, and were generally conspicuous when in hedges), detection probabilities were high, and similar. A strip transect approach was, therefore, considered adequate for providing precise estimates of species' relative abundances.

For each count, the location and details of all observations of the study species within 100m either side of the transect line (defining a strip transect, or quadrat of ~1km by 0.2km) were recorded directly onto large-scale maps of the study sites (e.g. Fig. 2.3A). Priority was always given to observing the behaviour of the study species when encountered; however, it was generally possible to make counts of other species. With the exception of hunting raptors, species over-flying transects were not recorded. All foraging observations of the study species were noted, and the distance to cover of the furthest individual was estimated by eye. During the breeding season, the study species were observed for territorial behaviour or other breeding related activities. Adult birds were counted separately from juveniles, although it was not always possible to make this distinction. In such cases, it was assumed that all birds were adult, and it is acknowledged that this could lead to some overestimation of breeding bird densities. For each count, weather and light conditions were noted, as were start and finishing times. Counts were not undertaken in high winds or heavy rain.

2.2.3 *Habitat description*

The crop and management status of each field sampled was monitored over the course of each season. During each census visit, all crop and field events, including the application of pesticides or fertilisers, the harvesting of crops, or cultivation (ploughing and tilling) were noted, as were all non-field management events, such as hedge trimming or cutting of ditch vegetation. Field boundary habitat was described during the summer of 2003. A boundary was defined as the area of land separating crops in adjacent fields. Typically, this comprised two narrow grassy/herbaceous strips raised above the surface of the adjacent fields, on either side of a hedge growing from a hedge bank, and a substantial ditch. Individual field boundaries were described at a minimum of three regularly spaced 20m sub-sections (Fig. 2.3B), the actual number depending on the length and perceived uniformity of the boundary. Boundary width, hedge height, and hedge width at height intervals - 0.5m, 2m, 4m and 6m, were estimated at the beginning of each 20m section with the aid of a 4-metre rod. All trees present in sub-sections were counted and identified. The heights of individual trees were estimated by eye, but only when the hedge was not essentially a tree line (observed usually as tall unmanaged Ash hedges). A “tree” was defined as a woody species whose height exceeded by at least 50%, the local height of the hedge. Trees were usually greater than 5m tall. The three major woody species constituting each hedge sub-section were recorded.

A broad range of hedge types was encountered on transects and these were classified following the scheme of Pollard et al. (1974) (see Appendix 2 or Fig. 5.2). This typology broadly reflects management preferences for degrees of “management intensity” i.e. the frequency and severity of hedge trimming and the management or disturbance of woody or herbaceous peripheral or ditch vegetation. Such management has general effects on the overall quality of field boundaries as a multi-species habitat. Increasing intensity results in reduced structural and/or botanical diversity, which can have important consequences for species (e.g. for birds, Green et al. 1994, Moles & Breen 1995; or insects, Moreby 1994). In addition to classification, each 20m boundary sub-section was scored for two aspects hedgerow structure – management level, and hedge “tightness”, following the criteria of Doogue (1996) (Appendix 2). This information was instrumental in deriving the management index (Index M, Table 5.1) analysed in Chapter 5.

The above comprises a comprehensive qualitative and quantitative description of habitat and management practices sampled by transects, however, not all this data has been incorporated into the thesis. In particular, some of the more detailed boundary structural measures were described for the purposes of analysing species-habitat relationships during the breeding season, when structural and floristic components of habitat are particularly important in territory selection (e.g. MacDonald & Johnson 1995). The recording of individual management type events provides a basis for estimating their typical frequency in the study area, however, neither is this part of the thesis. Instead, specific investigations in Part 2 focus on the effects on species’ distribution and habitat use during the winter, of coarser variation in structural aspects of field boundaries, especially relating to hedge height and management intensity.

2.2.4 *Data collation, treatment and analyses*

This broad data set characterises aspects of landscape structural and compositional variation of 348 hectares of farmland, and species' abundance and distribution patterns observed during 479 transect counts (Table 2.1), down to the level of the field boundary (specifically, to a resolution of 0.02km^2). The sample transects are assumed to be representative of habitat variation within and among the farming landscapes (strata), and species' distribution and abundance patterns on transects are assumed to reflect the availability and quality of habitat resources. The data, however, required considerable further collation for the purposes of presentation and analysis. The hierarchical sampling design was intended to permit investigations at several spatial levels, the results of which could then be examined and compared. Each "level" required an appropriate expression or representation of the data for it to be useful in statistical analyses, and/or ecologically relevant. For example, at the transect scale (cf. Fig. 2.3A), a species' *abundance* may depend on the area available of particular field types or the prevalence in the landscape of particular habitat attributes, in which case, quantitative terms would be appropriate. However, at finer spatial scales (e.g. the section scale, cf. Fig. 2.3C), species *occurrence* may be governed by the presence or absence of such factors, so a presence/absence term would be appropriate. From a statistical viewpoint, this term addresses the problem of the many zero values that could occur in a quantitative summary, which would compromise *normal* parametric procedures. Different response variables were analysed at the different spatial scales. Thus, while transect importance was measured using species mean abundance across census counts, these counts individually provided a measure of *fine scale distribution* and *habitat use* over the survey period. Briefly, transects were divided into 100m sections (e.g. Fig. 2.3C), and using the mapped locations of observations from individual censuses, a cumulative map of species occurrence in sections was generated. Each section could then be given a species "use score" – the fraction of the total number of visits (usually 9) recording a presence. The two response measures are related and this relationship is discussed below and developed further in Chapter 6. Further details of data treatment and rationale are given with analyses.

Fig 2.3. Data collection and extraction. Site example – Ballymaguire cf. Fig 2.2. **A.** Typical count data sheet. Species observations and habitat management recorded on map during each count. For transect scale summaries, species relative abundances were expressed as the mean count across census visits, per hectare. **B.** Field boundary description. Notches indicate location of 20m field boundary sub-section samples described to characterise individual field boundaries. **C.** Fine scale data extraction. Map shows the division of each transect into 100m sections. Bird count and habitat data were extracted for each section.

2.3 Thesis outline

This thesis considers both pure and applied perspectives in relation to the ecology of granivorous farmland birds. Below, the results of the four seasonal surveys are presented and discussed. The validity of the *a priori* stratification of the study area into three farming landscapes is considered by examining observed cropping patterns. Then, species seasonal abundances and fine scale distribution are examined across the study area as a whole, and are compared among the farming strata. This includes a synthesis of the seasonal abundance patterns in relation to current knowledge of seasonal migratory strategies. In the remaining chapters, the resolution of enquiry increases to focus on data from one season, Winter 2002-03, which is analysed at two spatial scales. In Chapter 3, *community patterns* are examined in relation to the three farming strata, by considering data summarised at the transect scale. This investigation is introduced by considering the results of a Principal Component Analysis (PCA). Several analytical techniques are then used to explore the geographical structure in the environmental and species data sets, and to quantify and elucidate the community variation captured at the different spatial scales/levels of the nested sampling design. Chapter 4 provides a descriptive gradient analysis of community variation in relation to several landscape variables describing cropping and field boundary management. Focus then increases in Chapter 5 to consider fine scale patterns of *habitat use* among individual species. Multiple logistic regression analyses were conducted to model species' "use scores" for 100m transect sections. This is the finest spatial scale of the study, and stops short of an assessment of within-field habitat, and seed food resource levels. For the latter, broad assumptions were made that food resources were generally or randomly available across stubble fields and types, and that variation in the level of these resources was spatially random. The relative importance to species of 100m sections (measured by *section use*) was assessed in terms of stubble type, and structural and infrastructural variation in field boundary habitat. The results of analyses at the two spatial scales are then considered in tandem in an exploratory "bridging analysis" in Chapter 6, to identify important landscape structural characteristics affecting community structure. Finally, Chapter 7 presents a general summary and synthesis of findings.

2.4 Seasonal surveys

Objectives

- to characterise the agricultural gradient of the study area
- to establish species baseline seasonal relative abundance estimates for the study area
- to compare species' abundance and distribution between seasons and years
- to assess the influence of broad farming *type* on species abundance and distribution
- to examine these patterns in relation to species' broader habitat affiliations
- to explore the migration implications of variation in species' seasonal abundances

2.4.1 *Data treatment and statistical methods*

Seasonal cropping patterns for each farming type stratum (Fig. 2.4) were described using the mean % cover per transect of the different crop classes (see Section 3.1 for details). Species' overall seasonal abundances and seasonal stratum abundances were described by their respective means calculated from transect abundance estimates. Comparisons among species' abundances, and fine scale distribution across 100m transect sections, among strata and between seasons, were made in *rank* terms. Spearman's rank correlation tests were used to test two abundance-distribution relationships: species overall abundance was tested against overall % fine scale distribution (the % of 100m sections recording a species); and species transect abundance was tested against the number of transect sections recording the species. A simple assessment of species relative specialisation in strata was made by calculating the coefficient of variation V of species' *mean sectional distribution* per stratum. V is a standardized measure of variability among group samples (given by – sample Standard Deviation / sample Mean x 100%) that is useful when there are big differences among group means (Sokal & Rohlf 2003). V (corrected (V^*) for small sample size i.e. n = 3 strata) of species' (groups) mean stratum section scores was calculated for the first and second springs, and the second winter (as only 2 strata were sampled in Winter 1). Species were ranked accordingly, showing which species were more, or less, evenly distributed among the farming landscapes in each season. An overall measure of relative specialisation was derived by calculating species mean ranking across considered surveys.

2.5 Survey results

2.5.1 *Cropping patterns*

The east-west agricultural gradient was stratified on the basis of the perceived extent of four broad categories of cropping – grassland, cereals, root crops and vegetables. The latter comprised brassica crops and smaller areas of leeks, onions, celery, lettuce and herbs. These were classified as Brassica and Market Garden crops (MG crops). Root crops sampled by transects were mainly potatoes, and a very minor cover of turnips, carrots and parsnips. It was decided to classify carrots and parsnips as MG crops, as the broader intention was to group crops on the basis of growth form and management similarity. Cereals comprised spring and winter varieties of wheat and barley; one field of oats was sampled during the first winter of the study. Sampled grasslands overwhelmingly comprised improved pasture and grass grown for silage or hay. The cropping characteristics of strata are presented in Fig. 2.4. The proportion of land under grass in all strata remained relatively constant between seasons and years. Roughly twice as much occurred across the Mixed farming transects, as it did across the MG transects. These strata also differed markedly in the proportion of land devoted to the production of vegetables, especially brassica crops, and land devoted to cereal production. The MG transects had at least twice as much land under MG crops, during all seasons. Conversely, a substantially greater area of land was under cereals in the Mixed stratum. Nevertheless, cereal stubbles were a prominent feature of both strata during both winters, and there was a low level of seasonal carry-over (of stubbles), presumably representing short-term setaside obligations (at time of writing, setaside is no longer a legal requirement). The area of winter cereals sampled differed between years, and cereals were the only substantial crop other than grass sampled by the pastoral transects. A considerably greater area of MG crop stubbles was encountered on MG transects than on Mixed transects, especially during the winter. The area under root crops was broadly similar between the MG and Mixed strata, but occurred

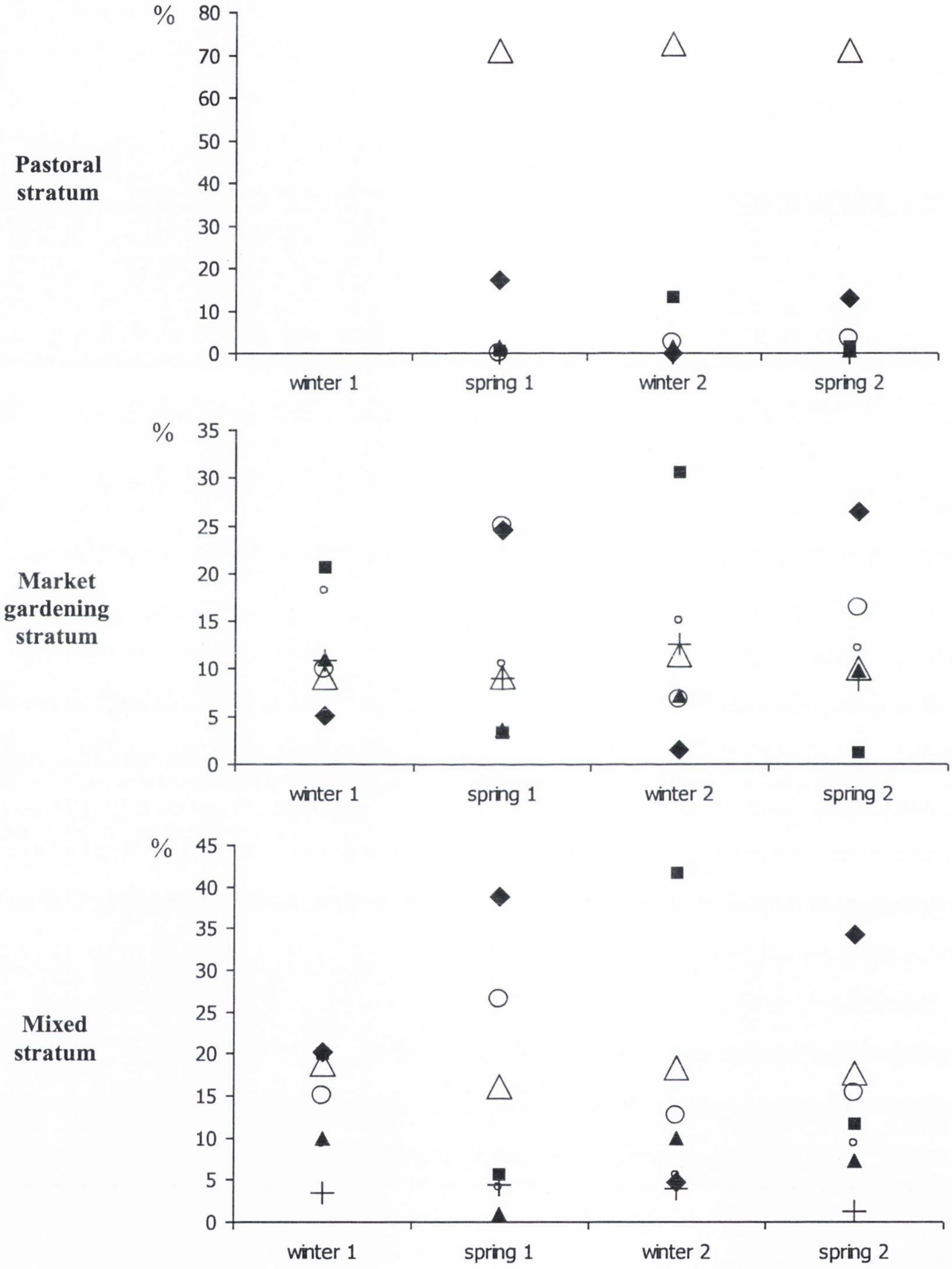

Fig. 2.4. % Composition of main agricultural land cover by stratum and survey season, Oct '01 – July '03. Δ = Grassland; ◆ = Cereals; ■ = Cereal stubbles; ○ = Plough and till; O = Brassicas and Market Garden crops; + = Brassica and Market Garden stubbles; ▲ = Root crops and stubbles (overwhelmingly potato). Points are means, n = 6.

at very low levels across the pastoral transects. Noteworthy patterns in the distribution of non-farmed land included a greater area of scrub and ruderal habitats in the MG stratum, and a similar pattern for miscellaneous urban land uses (football pitch, residential, small gas refinery). Farm properties were not encountered on the MG transects. These land uses comprised a minor proportion of transects generally, although scrubby habitats accounted for approximately 10% of the area sampled in MG stratum.

2.5.2 *Abundance and distribution*

Species' seasonal abundances (overall and stratum) were broadly similar between years (Table 2.2a,b,c,d, Fig. 2.5), particularly for the more, and less, abundant species. Abundance *rankings* remained broadly consistent across surveys; however, seasonal abundance estimates differed considerably in Linnet and Skylark. Both occurred at highest densities during the winter, which then fell considerably during the spring, when Chaffinch and Yellowhammer were more abundant. With the exception of Greenfinch during the second spring, the abundance of all species was highest during the winter. Greenfinch, Bullfinch, Reed Bunting and House Sparrow were the least abundant species during both seasons. Among strata, peak abundance in all species, with the exception of Goldfinch and Linnet, occurred in the Mixed stratum during one or other of the winters (Fig. 2.5). Variation in abundance among transects within strata tended to be greatest in the Mixed stratum in winter, producing the widest 95% confidence intervals around means. Within-season stratum effects on abundance are suggested only for Chaffinch – between the MG and Pastoral strata in both springs, and Goldfinch – between the MG and Pastoral strata in the second winter. Seasonal abundance differed considerably in some species – in the MG stratum for Linnet and Goldfinch, and for Skylark in the Mixed stratum. Yellowhammer abundance was generally similar between seasons within strata. Greenfinch estimates were considerably higher in Spring 2 than in Spring 1, while Chaffinch and Yellowhammer consistently high ranking in particular strata for all surveys, notably Skylark, Linnet and Goldfinch in the MG stratum, and Yellowhammer, Tree Sparrow and Bullfinch in the Mixed stratum. Chaffinch and Greenfinch scored higher in the Mixed stratum during the winter, and higher in the Pastoral stratum during the spring. Rankings were less consistent

Table 2.2 (a,b). Summary of species distribution and abundance on seasonal surveys. (a) October 25th 2001 - February 27th 2002. (b) April 9th – May 2nd 2002. MG = Market Gardening stratum; Mixed = Mixed stratum; Pastoral = Pastoral stratum. Overall abundance estimate is the mean of abundance estimates across individual transects expressed as birds per hectare.

(a)

Winter 2001-02						% of 100m sections on which recorded			
Species	Total Count	% of census' on which recorded n = 88	Number of transects on which recorded n = 12	Overall abundance estimate /ha ± S.E.	Abund. Rank	Overall n=117	MG n=56	Mixed n=61	Pastoral
Chaffinch *Fringilla coelebs*	570	67	11	0.321 ± 0.101	3	47.9	39.3	55.7	no counts
Greenfinch *Carduelis chloris*	93	28	9	0.059 ± 0.020	8	16.2	12.5	19.7	
Bullfinch *Pyrrulha pyrrhula*	28	14	8	0.018 ± 0.007	10	11.1	5.4	16.4	
Reed Bunting *Emberiza schoeniclus*	77	25	8	0.041 ± 0.012	9	12.0	7.1	16.4	
Yellowhammer *Emberiza citrinella*	251	45	12	0.153 ± 0.029	6	32.5	26.8	37.7	
Linnet *Carduelis cannabina*	1635	40	10	0.989 ± 0.322	1	27.3	33.9	21.3	
Goldfinch *Carduelis carduelis*	381	26	11	0.239 ± 0.067	5	21.4	23.2	19.7	
Skylark *Alauda arvensis*	1075	65	12	0.655 ± 0.211	2	38.5	42.9	34.4	
Tree Sparrow *Passer montanus*	521	31	9	0.280 ± 0.116	4	23.1	12.5	32.8	
House Sparrow *Passer domesticus*	80	7	5	0.061 ± 0.038	7	5.1	3.6	6.6	
Total	4631								

(b)

Spring 2002						% of 100m sections on which recorded			
Species	Total Count	% of census' on which recorded n = 70	Number of transects on which recorded n = 18	Overall abundance estimate /ha ± S.E.	Abund. Rank	Overall n=177	MG n=56	Mixed n=61	Pastoral n=60
Chaffinch *Fringilla coelebs*	186	77	15	0.138 ± 0.024	1	49.2	25.0	52.5	68.3
Greenfinch *Carduelis chloris*	24	26	14	0.019 ± 0.005	7	9.6	8.9	8.2	11.7
Bullfinch *Pyrrulha pyrrhula*	12	11	7	0.008 ± 0.003	8.5	5.1	1.8	8.2	5.0
Reed Bunting *Emberiza schoeniclus*	9	7	4	0.006 ± 0.003	10	2.3	1.8	3.3	1.7
Yellowhammer *Emberiza citrinella*	146	67	16	0.108 ± 0.017	2	35.6	23.2	50.8	31.7
Linnet *Carduelis cannabina*	88	30	11	0.062 ± 0.022	4	12.4	16.1	8.2	13.3
Goldfinch *Carduelis carduelis*	36	13	5	0.025 ± 0.011	6	4.5	12.5	1.6	0.0
Skylark *Alauda arvensis*	99	57	13	0.072 ± 0.022	3	28.2	48.2	32.8	5.0
Tree Sparrow *Passer montanus*	62	17	10	0.043 ± 0.018	5	6.2	1.8	16.4	0.0
House Sparrow *Passer domesticus*	8	11	6	0.008 ± 0.004	8.5	3.4	3.6	4.9	1.7
Total	662								

Table 2.2 (c,d). Summary of species distribution and abundance on seasonal surveys. (c) October 23rd 2002 – March 3rd 2003. (d) March 31st - June 20th 2003. MG = Market Gardening stratum; Mixed = Mixed stratum; Pastoral = Pastoral stratum. Overall abundance estimate is the mean of abundance estimates across individual transects expressed as birds per hectare.

(c)

Winter 2002-03						% of 100m sections on which recorded			
Species	Total Count	% of census' on which recorded n = 155	Number of transects on which recorded n = 18	Overall abundance estimate /ha ± S.E.	Abund. Rank	Overall n=177	MG n=56	Mixed n=61	Pastoral n=60
Chaffinch *Fringilla coelebs*	944	69	18	0.297 ± 0.073	2	58.7	37.5	70.5	66.7
Greenfinch *Carduelis chloris*	159	28	15	0.053 ± 0.015	7	19.8	17.9	29.5	11.7
Bullfinch *Pyrrulha pyrrhula*	58	21	14	0.018 ± 0.004	9	22.6	8.9	31.1	26.7
Reed Bunting *Emberiza schoeniclus*	67	17	11	0.023 ± 0.007	8	11.9	16.1	13.1	6.7
Yellowhammer *Emberiza citrinella*	489	45	16	0.159 ± 0.047	4.5	31.2	28.6	54.1	25.0
Linnet *Carduelis cannabina*	1910	39	15	0.686 ± 0.234	1	29.2	46.4	26.2	18.3
Goldfinch *Carduelis carduelis*	443	17	13	0.159 ± 0.064	4.5	15.2	25.0	16.4	5.0
Skylark *Alauda arvensis*	835	38	14	0.271 ± 0.106	3	24.3	35.7	27.9	10.0
Tree Sparrow *Passer montanus*	351	16	10	0.108 ± 0.062	6	15.2	8.9	31.1	5.0
House Sparrow *Passer domesticus*	57	8	4	0.021 ± 0.014	10	3.9	3.6	4.9	3.3
Total	5313								

(d)

Spring 2003						% of 100m sections on which recorded			
Species	Total Count	% of census' on which recorded n = 166	Number of transects on which recorded n = 18	Overall abundance estimate /ha ± S.E.	Abund. Rank	Overall n=177	MG n=56	Mixed n=61	Pastoral n=60
Chaffinch *Fringilla coelebs*	474	81	17	0.147 ± 0.021	1	65.0	41.1	75.4	76.7
Greenfinch *Carduelis chloris*	169	43	18	0.056 ± 0.009	7	29.4	32.1	23.0	33.3
Bullfinch *Pyrrulha pyrrhula*	32	12	10	0.010 ± 0.003	9	10.2	5.4	14.8	10.0
Reed Bunting *Emberiza schoeniclus*	34	14	11	0.010 ± 0.004	9	9.0	16.1	13.1	6.7
Yellowhammer *Emberiza citrinella*	391	71	17	0.121 ± 0.026	2	55.9	46.4	82.0	38.3
Linnet *Carduelis cannabina*	381	26	15	0.119 ± 0.043	3	23.2	39.3	21.3	10.0
Goldfinch *Carduelis carduelis*	198	24	14	0.070 ± 0.025	4	19.2	33.9	18.0	6.7
Skylark *Alauda arvensis*	205	49	13	0.065 ± 0.021	6	36.2	55.4	47.5	6.7
Tree Sparrow *Passer montanus*	224	28	11	0.066 ± 0.028	5	20.3	14.3	39.3	6.7
House Sparrow *Passer domesticus*	26	13	9	0.010 ± 0.003	9	6.2	7.1	4.9	6.7
Total	2174								

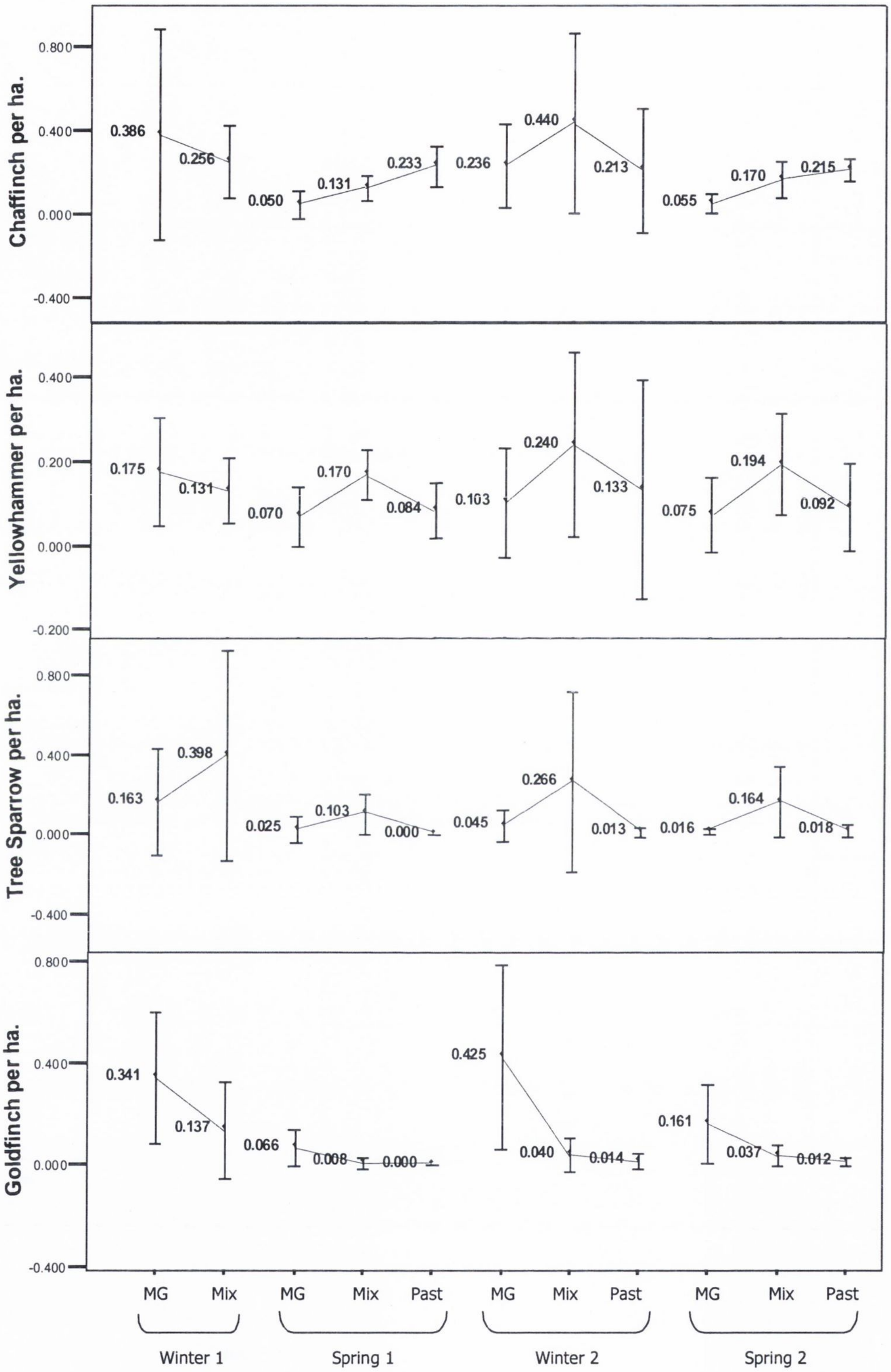

Fig 2.5. Mean species abundances ha^{-1} in strata by year and season. Estimates are based on the mean count across censuses on each transect (n = 6). Error bars represent 95% confidence intervals. Lines between points are interpretive aids only. MG = Market Gardening stratum; Mix = Mixed stratum; Past = Pastoral stratum. Winter 1 and Winter 2 were October 25th 2001 - February 27th 2002, and October 23rd 2002 – March 3rd 2003 respectively. Spring 1 was April 9th – May 2nd 2002, and Spring 2 was March 31st - June 20th 2003.

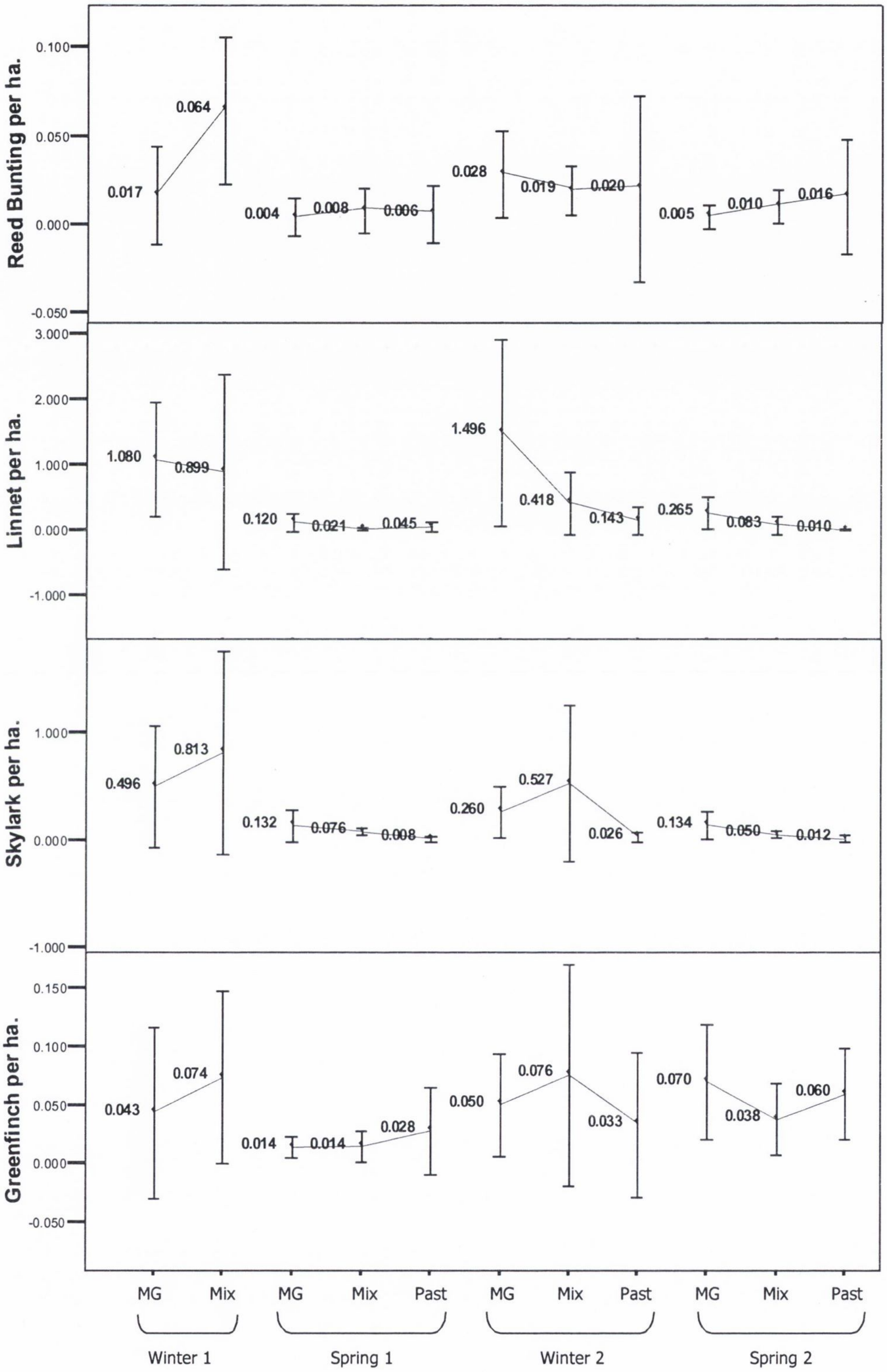

Fig 2.5. Mean species abundances ha^{-1} in strata by year and season. Estimates are based on the mean count across censuses on each transect (n = 6). Error bars represent 95% confidence intervals. Lines between points are interpretive aids only. MG = Market Gardening stratum; Mix = Mixed stratum; Past = Pastoral stratum. Winter 1 and Winter 2 were October 25th 2001 - February 27th 2002, and October 23rd 2002 – March 3rd 2003 respectively. Spring 1 was April 9th – May 2nd 2002, and Spring 2 was March 31st - June 20th 2003.

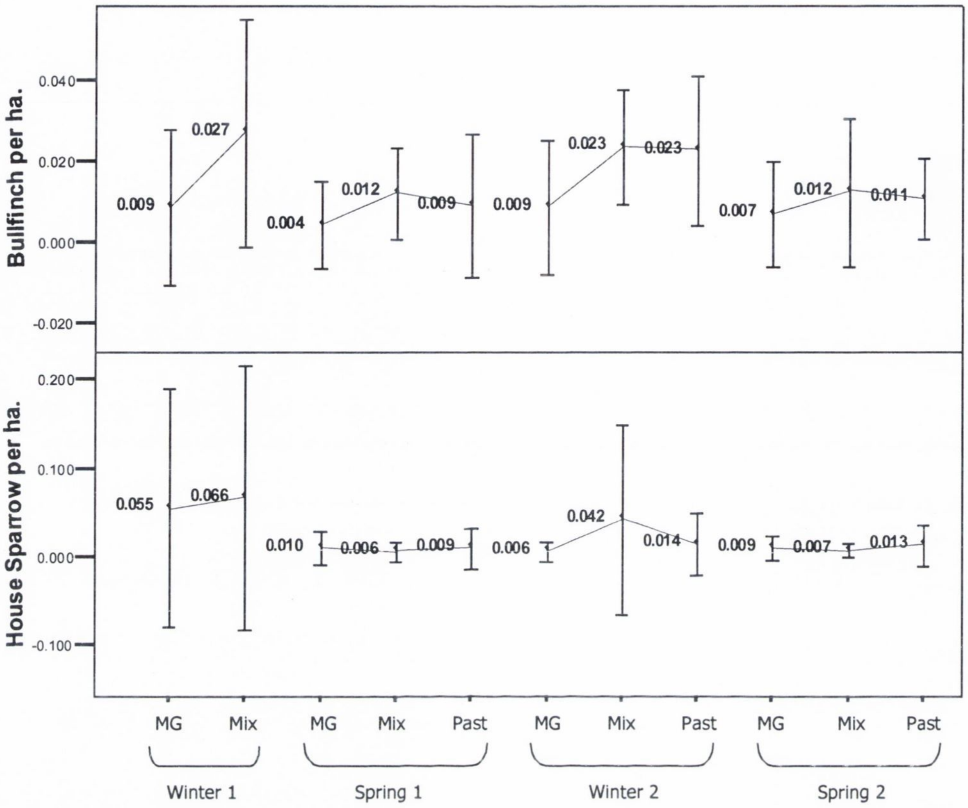

Fig 2.5. Mean species abundances ha^{-1} in strata by year and season. Estimates are based on the mean count across censuses on each transect (n = 6). Error bars represent 95% confidence intervals. Dashed lines between points are interpretive aids only. MG = Market Gardening stratum; Mix = Mixed stratum; Past = Pastoral stratum. Winter 1 and Winter 2 were October 25th 2001 - February 27th 2002, and October 23rd 2002 – March 3rd 2003 respectively. Spring 1 was April 9th – May 2nd 2002, and Spring 2 was March 31st - June 20th 2003.

among surveys in the other species, but distribution tended to be widest on transects in the Mixed stratum.

For all season/years, species' abundances were significantly positively correlated with the % of 100m sections in which they occurred i.e. the more abundant a species, the greater was its occurrence across 100m transect sections (Spearman's *rho* ≥ 0.65, *P* ≤ 0.021; one-tailed tests). Within species, abundance on transects was significantly positively correlated with the number of 100m sections in which they were recorded. Significant relationships were found for all species in all surveys (Spearman's *rho* ≥ 0.538, *P* ≤ 0.036, one-tailed tests) with the exception of Yellowhammer in the first winter. Thus, at the transect scale, abundance was positively related to the spatial extent of occurrence.

Species ranked similarly for the coefficient of variation V^* between seasons generally, despite the likelihood of seasonal differences in habitat use, and the difference in sampling intensity between the two springs. An overall mean ranking across seasons placed the species in the following order from most (higher V^*) to least specialized (lower V^*) – Tree Sparrow, Goldfinch, Skylark, Bullfinch, Linnet, Yellowhammer, Reed Bunting, Chaffinch, House Sparrow, Greenfinch.

2.6 Discussion

To begin this discussion, I first briefly qualify my use of the terms "mixed", "pastoral", and "arable", in describing the perceived farming strata. In many farmland bird studies, these terms have been used to describe the general farming context encompassing study areas, and have been applied at both broad regional scales (e.g. Perkins et al. 2000, Moorcroft et al. 2002), and finer spatial scales (e.g. Calladine et al. 2003, Wilson & Taylor 1996). They have also been used to define areas or regions as subjects of investigation (e.g. Robinson et al. 2001, Atkinson et al. 2002). It was noted in Chapter 1 that the classification of farming type landscapes in Britain is usually based on simple proportional compositional criteria (Section 1.4), and that this has typically been applied at a resolution of 10 x 10 km grid squares. It is important to note, however, that the results of any such exercise are likely to be *scale dependent* i.e. will depend on the sampling resolution. From a national perspective, the present study area falls within an area broadly designated as "mixed farmland" to characterise the agriculture of eastern and southern regions of Ireland, and presumably, this follows standard criteria being applied to 10km national grid squares. The three-way stratification, however, recognised a pronounced geographical gradient in agricultural practices across a spatial extent of approximately ~20km, and therefore, implied a finer grain of perception than that used in the classification of 10km grid squares. As results from this study are often discussed (below and in later chapters) in relation to the above-cited studies, using the terms "arable", "mixed" and "pastoral", the scale dependency of these classifications should be borne in mind. Applying typical criteria (cf. Section 1.4) to the two 10km squares broadly comprising the study area would define one "mixed' farming square (broadly covering what I have called the Pastoral stratum), and one "arable" farming square (broadly covering the MG and Mixed strata).

Notwithstanding, the cropping patterns on the sample transects broadly supported the *a priori* stratification (see below), describing east-west gradients in vegetable, cereal and grass production across the study area. This facilitated a practical and meaningful assessment of species' and community responses to these gradients. The strata were not discrete however; no broad crop class was exclusive to a stratum, and most classes were common to all three. In later analyses (Chapters 3, 4 and 5), this "gradient" perspective is emphasised.

2.6.1 *Landscape and cropping patterns*

The "intensity" of farming in the study area was underlined by the considerable proportion of land under crops observed during the winter. Overall cover of winter cereals and MG crops on transects of the MG and Mixed strata accounted for approximately 50% of the total area surveyed in Winter 1, and 25% in Winter 2. A relatively minor area of winter brassica cropping was observed on the pastoral transects. Nevertheless, the proportion of land under crop stubbles, and especially cereal stubbles, was high. The high incidence of cereal stubbles during the winter months is reflective of the continued preference in Irish cereal farming for spring cereals, especially barley. This contrasts with many regions in the UK where autumn and winter sowing has become the norm. This practice represents an extensive loss of winter foraging habitat in the form of over-winter stubble fields, and is implicated in the range and population declines observed in several granivorous species (cf. Chapter 1). The availability of other types of fallow, especially of brassica crops, is also notable. Weedy fodder brassicas and their stubbles were found to hold the highest density and diversity of wintering granivores on Scottish farmland (Hancock & Wilson 2003). It was suggested weed management might be more relaxed in these crops, relative to brassicas grown for human consumption, thereby making them more attractive to granivores. It is not known the extent to which fodder brassicas, if any, occurred on transects in this study, but it was clear that the substantial proportion was for human consumption. A considerable area was recorded under the heading "plough and till" (cultivated land) in the arable strata during both seasons. Toward the end of both winters, and in early spring, ploughing, tilling and sowing were often observed in quick succession, although a few fields were ploughed early in the winter and left for natural "curing". These substrata, and the resources they may offer in the form of exposed seeds and dislocated invertebrates, are likely to be relatively transient. Presumably, their value for foraging depends on the density of the weed seed bank, and the speed with which dislocated invertebrates bury themselves. Wilson et al. (1996) observed no strong patterns of avoidance or preference with respect to such fields in granivores, but noted a case where a single ploughed field sustained a flock of Linnets for a two-week period. In this study, foraging was observed by Greenfinches on a till over a 3-week period. Overall seasonal cover of this substrate ranged from 5% to 18% during the study, and while individual fields may exist as bare plough or till for a limited duration, area cover at any one time in the broader landscape may be considerable. Cultivated land may be of greatest importance for granivores towards the end of the winter and early spring (Lack 1992), when cultivation replenishes depleted seed food resources generally, and may boost dietary protein in the form of invertebrates, for breeding birds. Foraging habitat in the form of stubble fields was broadly available for granivores during the winter months, and was limiting only on the Pastoral transects. This thus provided ample opportunity to investigate the effects on granivores of habitat variation, both at broad scales in relation to landscape composition and structure, and at finer scales when local habitat influences could come into play.

2.6.2 *Seasonal abundance and distribution patterns*

The ranking of species' relative abundances during both springs was in general agreement with national breeding density estimates (Coombes et al. 2002, 2006) with the stark exception of House Sparrow. Data generated by the CBS indicates that House Sparrows are the second most abundant small granivore after Chaffinch. In this study, House Sparrows were infrequently encountered, especially away from buildings, and usually ranked lowest in abundance in surveys. Estimates of abundance on farmland in the UK vary considerably across studies (e.g. Arnold 1983, Parish et al. 1995, Perkins et al. 2000), and the species showed several significant relationships with agricultural practices in Siriwardena et al. (2000a). Pastoral *and* arable habitats are important (Robinson 2005, Fig. 2.6), and its scarcity in this study is curious.

Species' relative use of strata, determined by the coefficient of variation *V** of species occupancy of 100m transect sections among strata, was interpreted broadly as an *ad hoc* measure of habitat specialisation and niche breadth. The ordering of species according to *V** i.e. Tree Sparrow, Goldfinch, Skylark, Bullfinch, Linnet, Yellowhammer, Reed Bunting, Chaffinch, House Sparrow, Greenfinch, indicated that species at the head of this list were relatively more restricted in their occurrence among strata. Species at the end of the list tended to show more equitable distributions. Examination of the frequency of occurrence of these species breeding across a range of habitats in the UK (Fig. 2.6) provides several pertinent observations. In terms of a *specialist – generalist* continuum, it is clear that the species show varying degrees of specialisation. Species such as Yellowhammer and Tree Sparrow are arable farmland specialists, while Reed Buntings are highly specialised in Reed-bed habitat, and House Sparrows, in towns and villages. Chaffinch is certainly the most generalist, showing similar frequencies across woodland, scrub, and pastoral and arable habitats. It is generally apparent, that for most of the study species, farmland is not optimal habitat. Nevertheless, focusing only on "Arable" and "Pastoral" habitats in Fig. 2.6, pronounced preferences for arable over pastoral farmland (and, therefore, relative specialisation therein) can be seen in Yellowhammer, Skylark and Tree Sparrow, while no such preferences are apparent in Chaffinch, Reed Bunting, Greenfinch, Bullfinch or House Sparrow. Bearing in mind the essential arable – pastoral gradient defining the study area, these affiliations are broadly reflected in the species ordering given in Section 2.5.2: Reed Bunting, Chaffinch, House Sparrow and Greenfinch take up one end of the continuum, and Tree Sparrow and Skylark take up the other.

Fig. 2.6 is quite clear, however, in indicating that some species e.g. Reed Bunting and House Sparrow are indeed quite specialised, and their equitable distribution among strata in

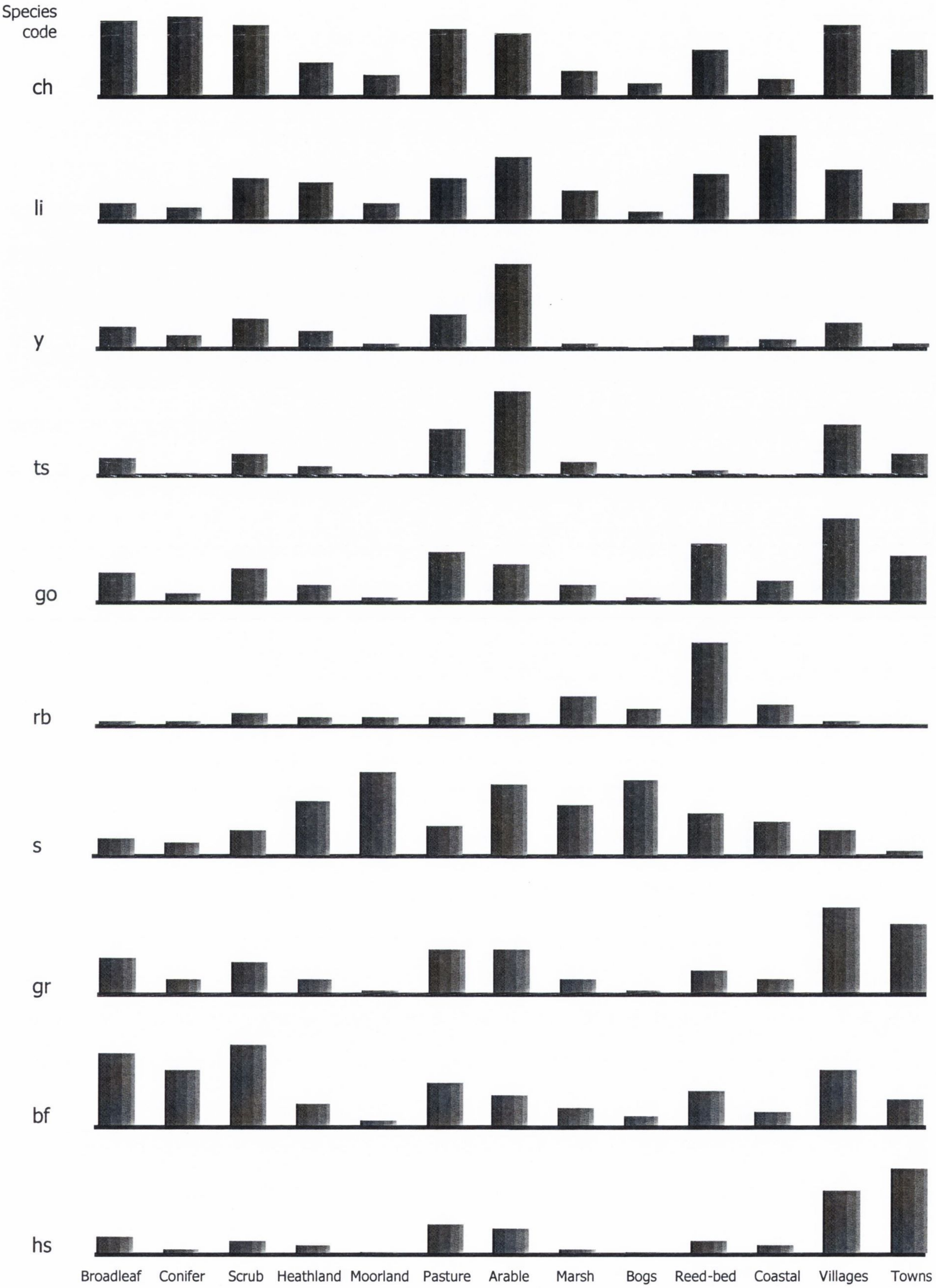

Fig. 2.6. Frequency of occurrence of the study species in a range of habitats in the UK (based on BBS data, 2000-03). Species codes are ch – Chaffinch, li – Linnet, y – Yellowhammer, ts – Tree Sparrow, go – Goldfinch, rb – Reed Bunting, s – Skylark, gr – Greenfinch, bf – Bullfinch, hs – House Sparrow. Adapted from Robinson (2005).

this study needs explanation. It is possible that the broader habitat context of observations i.e. the overall landscape composition, is important. Thus, in Fig. 2.6, Reed Bunting, Greenfinch, Bullfinch and House Sparrow all occur considerably more frequently in non-farmland habitat, with the suggestion that their frequency of occurrence in any particular farming landscape may be related to the degree to which it represents and/or accommodates this more favourable habitat. For example, species that show an association with villages and towns (House Sparrow, Greenfinch) may have been distributed relatively evenly across the strata because villages, houses and gardens, were also distributed relatively evenly. On the other hand, the even distribution of Reed Bunting may indicate a general, but low availability of favourable habitat patches across strata, which perhaps show some characteristics of more preferred habitat types (e.g. small scale riparian habitats associated with drainage channels or ditches), and which tend to be "overlooked" by the predominating farm management regimes. Unlike in Chaffinch, a "true" generalist, the abundance and distribution of these species were low (typical characteristics of species outside preferred habitats), which would be consistent with the suggestion of low levels of suitable habitat within the broader landscape mosaic.

Overall, the distribution patterns of species among the farming strata were consistent during both seasons for both years, and indicated a robust community response to underlying habitat patterns. While species' breeding habitat requirements in farmland have been well described, providing a firm basis for predicting breeding community responses, the between-season consistency in distribution is interesting in that it suggests that some aspects of breeding habitat selection and preference may apply during the winter. In the remaining chapters of this thesis, a detailed community description is undertaken for the second winter to investigate farming and habitat management correlates of species' winter distribution. However, notwithstanding the distributional similarities between seasons, there was striking variation in seasonal abundances in some species, and little in others. Below, these patterns are investigated as they pertain to the migration biology of the study species. This examination serves to highlight the importance of ecological understanding for conservation at broad scales and transnational levels.

2.6.3 *Seasonal variation in abundance – species' migratory strategies*

Bird species' geographical ranges at different times of the year are determined *inter alia* by their tolerance of the climatic extremes experienced, and movements to and from regions and areas over a broad range of distances, *Bird Migration*, are a normal response in many species to changing climatic conditions. During the Palearctic winter, severe and prolonged spells of cold weather are the major factors behind the seasonal migration and movement of a large number of species. However, climate can have other indirect effects on bird movements. Seasonal variation in day length determines the growing season and seed production in many plants, and the activity of many invertebrate prey species, so that birds must respond to this by moving or migrating to find alternative where food resources. On the other hand, food resources may instead be made unavailable by snow cover, so that even if temperatures are tolerable, broad evacuations may be forced.

Given climatic variability *per se*, and its interactions, across a range of spatial scales, with various geological attributes and processes (e.g. oceans, seas, lakes; altitude and mountain ranges; topography and biomes), it should not be surprising to see corresponding variation in species' adaptive responses to the adverse and favourable conditions (weather patterns) generated by these interactions. Both among and within the study species, a broad range of *migratory strategies* has been described, and these have been discussed for British and Irish birds in the *Migration Atlas* (Wernham et al. 2002). Migratory strategies can be viewed broadly as a continuum, along which a complex array of factors associated with a species' biology and evolution, and the climatic characteristics of regions where it occurs, interact to define patterns in species' migratory *tendency* (Wernham et al. 2002). Put simply, for a given local population, the nature and extent of seasonal movement depends, on one hand, on the likelihood and occurrence of severe climatic and weather conditions, and on local and regional altitude, topography, and/or habitat characteristics, while on the other, on a suite of species' biological, ecological and evolutionary characteristics, including diet, abundance, morphology, social organisation and breeding strategy. The range of resulting migratory strategies defines a continuum from *long*, through to *short* *distance* movements, and to *sedentary* strategies, which in turn, may be *obligatory* or *facultative*, and undertaken *partially* and/or *differentially*.

The migratory movements of the study species within many parts of their ranges are well described in the Migration Atlas. However, the atlas also highlights the specific contexts where knowledge is poor, and this varies considerably from species to species. Naturally, this will occur when data are sparse, and this is a particularly acute problem in Ireland, where very low levels of ringing activity has meant that many basic facts relating to the migratory strategies of immigrant, and especially, of indigenous populations, remain unknown. Perhaps, the most striking pattern in the abundance data (Table 2.2a,b,c,d) was the consistently higher estimates for the winter months, than for the breeding season. This occurred across all species (with the exception of Greenfinch in the second year) in both "years" i.e. in consecutive winter-spring comparisons, and it is of particular interest that the larger differences were observed for those species known to migrate, while the smaller differences were observed in the more sedentary species. In contrast to more northerly and easterly regions of Europe, where severe winter conditions often result in complete evacuation in some species, Britain and Ireland tend to receive large numbers of migratory birds because climatic conditions are increasingly benign toward western and southwestern regions. Migrants may stop to feed or rest for brief periods while on passage (*passage* migrants) to wintering grounds in southern Europe (mainly France and Iberia), or alternatively, for *regular* migrants, the islands may be their final wintering destination. An obscured picture ensues, however, because it is usually not easy to distinguish between "local" or "resident" birds, and migrants. Birds seen in the field may thus represent *residents* (birds which breed and winter broadly within the same region), a mixture of resident and migrant birds (the latter may comprise passage or regular migrants), or, exclusively, migrants.

While a full examination of the study species' migratory strategies is beyond the scope of this work, it is possible to examine the observed abundance patterns with respect to current knowledge for British and Irish populations. Much of the information presented below is from the Migration Atlas, which focuses on bird migration to and from Britain and

Ireland, but also provides much relevant detail of migratory patterns and strategies observed elsewhere across the western Palearctic. To proceed, I make practical assumptions that many of the well-described patterns in Britain are not untypical in Ireland, and acknowledge when such generalisations may not necessarily apply. In this respect, it is particularly pertinent that mean January temperatures in Ireland are typically 2° warmer than in southern Britain, and that the occurrence of severe weather conditions is far less frequent. The importance of this for local communities, and migrants, is generally not well understood. It has been suggested, for example, that woodland bird communities in the south west of Ireland may show considerable structural differences to those in southern Britain. Reasons for this have been explored by O'Connor (1986) (cited in Hutchinson 1989) who suggested that later spring migrants to this area may be at a disadvantage because the warmer winter climate of this region fosters reduced winter migration and over-winter mortality in local populations, and permits the earlier establishment of breeding territories, and an earlier saturation of habitat. By the same token, if residents also saturate habitats during the winter, this will have implications for arriving migrants, and for residents themselves, as habitat carrying capacities may then be exceeded, and competition may become important. Without a substantial increase in ringing effort in Ireland, and ring recovery data for breeding and wintering birds, the dynamics of resident-migrant patterns of distribution and potential interaction will remain largely unknown, as will the significance of the climatic differences between the two islands.

In Britain and Ireland, the wintering population is thought to be largely the same as the breeding population in Yellowhammer, Bullfinch, Tree Sparrow and House Sparrow, and these populations appear to be particularly sedentary i.e. seasonal movements are very short, or do not occur at all. In Chaffinch, Reed Bunting and Greenfinch however, resident populations are supplemented by winter immigration, and these migrant birds may or may not show ecological segregation from residents. In Chaffinch for example, for which knowledge is relatively good, the numbers across the islands are thought to approximately double, and migrants appear to show different patterns of habitat use and distribution. In other species, however, knowledge and understanding of the "profile" of wintering populations is considerably poorer, and migration strategies and patterns are considerably more complicated. For example, Skylark, Goldfinch, and Linnets are assumed to be regular winter migrants. Knowledge of the proportion of "arrivals" on passage, however, is lacking, as is data indicating their origins. To complicate matters, resident populations of these species are known to show partial migration i.e. a proportion of the population migrates, and may also show differential migration strategies i.e. certain migratory movements are typical of sex, or different age classes. Further difficulties in assessing patterns arise in some species (e.g. Greenfinch), because there appears to be no regular migration passage i.e. migratory patterns are unpredictable from year to year; flight paths and stop-over destinations vary, as does the numbers of birds, and the timing of arrivals and departures.

As noted above, the more pronounced differences in seasonal abundance occurred in those species known to migrate to and from Britain and Ireland in large numbers – Linnet, Skylark, Goldfinch, and Chaffinch. In Britain and Ireland, Linnets are partial migrants, with migrant birds flying south to winter mainly in France and Spain (although birds in eastern England show regular movement into the Low Countries). There is some suggestion that British birds (especially Scottish birds) may cross to Ireland, however the extent to which this is passage movement is unknown. Although large flocks are known to winter at coastal locations in Ireland if seed food resources are available (this was clearly exemplified in this study in the MG stratum), heavy seasonal passage (in and out) is observed at observation stations along the south coast, and it thought that the vast majority of Irish birds migrate (Hutchinson 1989) to winter mainly in the Iberian peninsula and France. The low level of Irish ringing activity, and a paucity of Irish ring recoveries means little detail is available to determine the origin/s of these birds and their migratory patterns. Several "between winter" ring recoveries indicate that migration in British populations may be facultative, with birds wintering abroad in some years and "at home" in others. More generally, such recoveries have been recorded at considerably different latitudes, again suggesting opportunistic and flexible strategies.

A similar partial strategy is apparent in British Goldfinches and Newton (1972, cited in the Migration Atlas) estimated that up to 80% migrated "overseas", mainly to Spain, with remaining birds forming "roving winter flocks", responding to food supply and local weather conditions. Although Irish data are sparse, there appears to be no substantial difference between movement patterns in Irish and British birds. Facultative and opportunistic strategies are suggested, with some multiple recoveries indicating overseas migration in one year, none in other years, and considerable geographic separation in recoveries, more generally. Irish Goldfinches have seen overall increases in population and range (cf. Chapter 1) over the last few decades, which have continued in recent years (Coombes et al. 2006). Data is sparse on the longer-term trends in this species; however, its recent expansion may be related to increases in over-winter survival (Coombes et al. 2006), perhaps because of increasing availability of food resources in sub-urban environments. This could imply an increasing proportion of Irish birds choosing a sedentary strategy, raising the interesting issue as to the degree to which migratory tendency is under genetic control. It is possible, for example, that the sedentary winter habit could increase levels of ecological segregation during the breeding season, leading to an expansion or spread of a "more sedentary" genotype. Something similar has arguably occurred in British and Irish Chaffinches, which are allopatric with their continental conspecifics, and show morphological differences (e.g. Hutchinson 1989). In any case, if environmental change in Ireland is favouring Goldfinches generally, and doing so during the winter in particular, a partial strategy has clearly been advantageous. The MG transects held considerable numbers of Linnets and Goldfinches during both winters, and regardless of their origins, the farming practices of the region appear to provide very favourable habitat.

Skylarks also showed large seasonal differences in abundance. Despite its widespread distribution within Britain and Ireland, ring recovery data is relatively scarce, even where ringing activity is high. There are no data for Ireland. Altitudinal movements are certainly normal between seasons (birds vacate upland areas for the winter), and observations of large-scale north-south movement of birds are well documented, and include movements of birds from northern Britain to Ireland. A major proportion of these flocks is likely to represent passage migrants from Fennoscandia, and notwithstanding a heavy autumnal exodus from the south coast, presumably towards Iberia, the importance of Ireland as a destination remains unknown, as is the extent of partial migration in Irish breeders (Hutchinson 1989). Large numbers of Skylarks of northern and continental origin are observed moving down the east coast of Britain, but movements inland also occur in a westerly direction. It has been suggested that Ireland may be a destination for many of these birds because of a paucity of ring recoveries at inland stations. The short duration occurrence of several large flocks on transects in the study area may reflect either of these patterns i.e. a movement of birds south, or alternatively, an arrival of birds moving west to winter further inland. On the other hand, the widespread occurrence of small numbers in favourable areas on transects, throughout the winter, probably represented sedentary Irish birds. British data, albeit sparse, suggests that British breeders may move relatively short distances within and between seasons, and several localised studies have indicated strong site fidelity across seasons and years. Partial migration strategies have been suggested for British and Irish breeding birds, however much work needs to be done (especially in Ireland) to establish the extent of this, and also to establish the conservation importance of Britain and Ireland as wintering grounds for European migrants, given the ongoing dramatic declines in European Skylark populations.

As noted, Chaffinch numbers in Britain and Ireland are thought to approximately double during the winter following the arrival of continental immigrants, and this is possibly evident in the present data; spring estimates were approximately half those for the winter (Table 2.2a,b,c,d). It is important to note, however, that winter estimates were higher also in those species whose winter populations are considered to comprise largely resident birds (e.g. Yellowhammer, Tree Sparrow). Recent work by Gillings et al. (2005) in the UK demonstrated that relative to the breeding season, species' abundances in 1km squares were higher in winter when there was more seed rich habitat available. In other words, between seasons, birds appeared to move locally toward areas with higher levels of potential foraging habitat in the form of stubble fields. Significant patterns were found in all species except Bullfinch. The authors did not comment on the possibility that continental migrants may have exaggerated the seasonal differences in their sample squares; however, this probably would not have been too important, especially for those more sedentary species whose winter populations are not supplemented by large numbers of migrants. The increases do indeed appear to represent seasonal aggregation in favourable habitats. This phenomenon is certainly intuitive for mixed farming landscapes; however it is also reasonable that it may operate across a range of spatial scales, including broad scales, as suggested in Atkinson et al. (2002). Regardless of spatial scale, it is likely that the seasonal increase in winter abundances observed in several species in the present data represents, to varying degrees, this phenomenon. Thus, in Yellowhammer and Tree Sparrow, seasonal variation in abundances was relatively low, in keeping with both the sedentary nature of the species in Britain and Ireland, and assumed low levels of immigration during the winter. The observed seasonal increases seem more likely to reflect aggregating movements, especially toward the mixed stratum, of birds resident within the study area, or from its broader hinterlands. This consideration is likely to apply also in the case of Reed Bunting, as breeding populations appear to be overwhelmingly sedentary, and immigration, mainly of Scandinavian birds, is very low. The vast majority of British and Irish Greenfinches appear to be particularly sedentary, making almost no seasonal movements. Nevertheless, in Britain, short distance winter movements do occur in a southwesterly direction, with longer distance movements apparent in females. Passage migrants from Norway are likely to pass through Ireland, while a small number of British birds cross the Irish Sea. This movement is thought to be a facultative response to food shortages or population pressure, rather than a cold weather movement, as it is irregular and usually autumnal. Greenfinch was the only species to show a higher density during the breeding season than during the winter (in Year 2), however the difference was minimal.

2.7 Summary and conclusions

- The study area provided a richly contrasted agricultural context for examining the effects of farming type and management practices on granivorous passerines at both landscape and local patch spatial scales. Study sites sampled gradients in several broad crop classes, and variation in management approaches to field boundaries.

- A strip transect methodology was used to measure variation in species abundance and distribution patterns at two spatial resolutions, in response to these habitat gradients. Surveys covered two winters and two breeding seasons.

- The study area was broadly supportive all species of farmland granivorous passerines occurring in Ireland, and most were present at most study sites. Species distribution patterns differed across the study area and this appeared to be related to aspects of agricultural management.

- The distribution patterns of species among the farming strata were generally consistent across seasons in both years, and indicated a robust community response to underlying habitat gradients. This suggested a degree of overlap in some aspects of breeding and wintering habitat selection, and that these might be related to broad farming type e.g. mixed farming versus intensive arable, or cropping regimes e.g. vegetable versus cereal farming.

- Seasonal comparisons of abundance data indicated a significant winter influx into the study area of several species, including Linnet, Goldfinch, Skylark and Chaffinch; and lesser increases in the other species. These observations probably represented two bird movement patterns: seasonal migration on one hand, especially in the above mentioned species, and movements of birds at local scales towards areas with good foraging habitat, on the other.

PART 2. THE GRANIVORE COMMUNITY OF WINTER 2002-03

Chapter 3. Community variation in space

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Preface

In this chapter, I focus on *community variation* across the study area at the transect scale during the second winter of the study. Several ordination techniques are used to elucidate this variation from three perspectives. The relationships among sample transects and species abundances are described using principal component analysis (PCA). This analysis serves as an exploratory tool to introduce the main questions addressed in the thesis. It also provides an initial test of the working hypothesis that the granivore community was structured by the management characteristics of the three farming strata. The ordination diagram reflected the geographical distribution of study sites along the farming gradient, and illustrated the extent of within-stratum and within-site variation. These patterns were further explored in a series of exploratory analyses examining their spatial nature, both explicitly and hierarchically. The latter quantifies the variation unique to each level of the hierarchical sampling design, and tests the significance of this variation. The former addresses geographical patterns in the environmental and species data sets, and includes an assessment of the spatial correspondence between community variation, and the explanatory power of two groups of environmental variables, *Boundary* and *Cover*. First, I detail the collation and treatment of the variables examined, which are relevant also to analyses performed in Chapter 4.

3.1 Data treatment

A sampling interval of approximately two weeks resulted in most sites being sampled nine times between 23rd October 2002 and 3rd March 2003. Abundance per transect of the study species was calculated as the mean count over all census visits and expressed as birds per hectare. To measure the areal proportion of different crop types, transects were treated as quadrats bisected by a central hedge/field boundary axis (the transect line). Other field boundaries were generally perpendicular to this axis and estimates of overall crop area were calculated accordingly. Over the course of the winter, fields changed: stubbles were ploughed, tilled, and sown at various times; winter crops emerged from tills to become the dominant cover, and some existing crops were harvested, especially vegetable crops. This dynamism was accounted for in an overall compositional description by weighting the cover type of each field by its duration over the 19-week surveying period. After tilling, fields were usually sown shortly afterwards. In such cases, the cover "till" was given a life span of three weeks, after which time it was classified as the emerging crop e.g. young brassica. This somewhat arbitrary distinction was based on the maximum observed duration of use of a till by the study species. Overall, the diversity of field types recognised was considerable and for the purposes of analyses, it was necessary to allocate them to a number of classes. Despite this, several field type classes and other landscape components

Table 3.1. Species, land use and boundary variables used in analyses, and normalising transformations applied to data. Power transformations were determined informally by $y = y^{\lambda}$. Also shown are sampling level and location variables. * House Sparrow was not included in analyses, and does not contribute to the variable totD

Variable code	Definition	Transformation
Species	Abundance measured as individuals/ha	Double square root
ch	Chaffinch *Fringilla coelebs*	
li	Linnet *Carduelis cannabina*	
y	Yellowhammer *Emberiza citrinella*	
ts	Tree Sparrow *Passer montanus*	
go	Goldfinch *Carduelis carduelis*	
rb	Reed Bunting *Emberiza schoeniclus*	
s	Skylark *Aluada arvensis*	
gr	Greenfinch *Carduelis chloris*	
bf	Bullfinch *Pyrrhula pyrrhula*	
hs	House Sparrow *Passer domesticus* *	
totD	Overall abundance * (Supplementary)	
Cover		
grass	% of transect under grass – including grass grown for silage	Arcsine
cerstub	% of transect under cereal stubbles	Square root
MGstub	% of transect under brassica or market garden/vegetable stubbles	none
ploughtill	% of transect under cultivated land	Square root
Boundary		
hedge1	Length of boundary in height range, 0 – 1.5m	ln squared
hedge2	Length of boundary in height range, > 1.5m – 3.0m	Power
hedge3	Length of boundary in height range, > 3.0m – 6.0m	none
hedge4	Length of boundary > 6.0m in height	Power
meanH	Transect mean hedge height	none
trees	Proportion of sampled sections with one or more trees	Square root
B/ha	Total boundary on transect / no. hectares sampled by transect	none
Location and Sampling level		
Stratum	Farming landscapes coded by 3 dummy variables	
Site	Site level coded by 9 dummy variables	
Spatial	National grid easting	

including winter cereals and winter brassica crops, patches of scrub, and buildings, occurred too infrequently across transects to be included in analyses. The practice of leaving an un-cropped boundary strip around the margins of fields was not recorded, although vehicular tracks were occasionally present.

A broad range of hedge types (Pollard et al. 1974, see Appendix 2, or Fig. 5.2) was present, usually varying considerably within transects. Other landscape scale studies (e.g. Chamberlain et al. 1999, Mason & Macdonald 2000) have classified hedges by height and width, usually in 3 or 4 categories reflecting basic management choices. For the purposes of this study, 4 height classes were identified that broadly reflected variation in management practices. Mean height for each field boundary (Section 2.2.3) was calculated, and the frequency distribution examined to detect characteristic groupings. Six distinct modes were observed and boundaries were allocated to one of the following height classes; 0 – 1.5m, >1.5 – 3.0m, >3.0 – 6.0m, and >6.0m.

The environmental variables examined in analyses in this chapter, and in the RDA analyses in Chapter 4, are presented in Table 3.1. The table also includes a description of the hierarchical nature of the sampling design *Sampling level* (transects nested within sites nested within strata) using binary (1, 0) dummy variables. Thus, the dummy variable *Site* (nine levels) specifies transect membership of sites, and the dummy variable *Stratum* (three levels) specifies transect membership of strata. *Stratum* is used in the PCA ordination of transects to calculate stratum "centroids" i.e. the mean of the axis scores of transects belonging to individual strata. Both dummy variables are used in later analyses to partition community variation among the hierarchical levels of the sampling design i.e. S*tratum, Site, Transect.* Transect location is described by the National Grid easting of transect midpoint.

3.2 Aims and objectives

- to conduct summary and exploratory analyses of abundance and distribution patterns of the wintering granivore community
- to provide initial qualitative tests of the working hypothesis of an effect of farming landscape type on community structure
- to assess the relative importance of broad and fine scale processes for community patterns
- to describe and explore the spatial dependence in the species and environmental data sets

3.3 Community ordination with principal component analysis

3.3.1 *Methods*

Ordination of ecological data (typically species abundance or presence/absence data, or descriptive environmental data, collected at a number of sampling points) is achieved by extracting from the data synthetic independent dimensions (axes) of variation. The relationship of the original data to these axes is then expressed an ordination diagram. A range of techniques has been developed to analyse different types of data that may be appropriate in different ecological situations, or to different investigative approaches (e.g. James & McCulloch 1990). Valid analyses, therefore, depend on choosing an appropriate technique. In community ordination, a broad division of techniques is based on assumptions regarding the form of the species response (the response model) to the range of variation in influential factors across samples. Do species abundances generally show linear or broadly unidirectional trends in response to these factors, or is there a peak in abundance followed by a decrease? The former indicates the species data are best described by a linear response model; the latter suggests a unimodal response model is more appropriate. As a general rule of thumb, a linear model is usually appropriate if the majority of species are present at the majority of sample sites: the samples broadly represent short sections of common (among species) influential environmental gradients (Legendre & Legendre 1998). Unimodal models become increasingly appropriate with increasing species turnover across samples, usually indicating "longer" environmental gradients are controlling species presence or absence. Samples may, however, show intermediate patterns, as the above considerations define a continuum. In this case, both models may be useful (I note that the above considerations should be applied to ecologically similar species, for example, as here, to members of a guild: it is usually of little interest to include in such analyses species that show fundamentally different ecologies or occur in fundamentally different habitats). For either response model, ordination techniques may be direct, whereby the computation of axes directly involves (is constrained by) environmental data, or indirect, whereby the ordination is unconstrained i.e. the extracted dimensions represent one set of variables only.

During the winter of 2002-03, the study species were present on most transects and varied in abundance, suggesting short environmental gradients were represented, and that a method based on a linear response model would be appropriate (Legendre & Legendre 1998). Notwithstanding, the indirect ordination technique Detrended Correspondence Analysis (DCA), as implemented in CANOCO for Windows Version 4.51 (ter Braak & Smilauer 1997), calculates the length of the community composition gradient in standard deviation units of species turnover, thus providing a measure of how unimodal the species responses are along ordination axes (ter Braak & Smilauer 2002). Sites separated by ≥ 4 units on axes will tend to have few species in common. A DCA of the winter data gave a gradient length of ~2.6 for the first axis. This is a short gradient and indicates a linear model can be assumed for the species responses. Principal component analysis (PCA), which assumes a linear response model, was therefore considered appropriate and an ordination of transects was conducted to examine the working hypothesis that habitat characteristics of the three farming strata would influence community patterns. If there was a farming stratum effect, this was likely to be evident in the resulting ordination diagram. The ordination was performed in the software package CANOCO for Windows Version 4.51 (ter Braak & Smilauer, 1997). A useful feature of PCA in CANOCO is a facility to determine the correlation relationships between supplementary or passive variables (i.e. variables of interest but which should not play a part in the ordination calculations), and the calculated axes of the PCA ordination space. A series of landscape variables believed to be of importance was, therefore, included in the analysis as supplementary variables. These were the % cover on transects of land under grass, cereal stubbles, brassica or market garden/vegetable stubbles, and cultivated land (see *Cover*, Table 3.1); and boundary variables – the length of boundary in four boundary height classes on transects, transect mean boundary height, the proportion of boundary subsections sampled with one or more trees, and boundary density per hectare (see *Boundary*, Table 3.1). Their relationships to ordination axes can be represented in the ordination diagram (a PCA biplot). A formal investigation of the importance of these variables for community variation is undertaken in the next chapter. Normalising transformations were applied to the data (Table 3.1) to reduce skew and stabilise variance, as in general, linear techniques perform better when data are normal. The normality of species' abundances was best improved using a double square root transformation (compared with square root and natural log transformations); Shapiro-Wilk tests indicated normality in all species except Bullfinch, Reed Bunting and Tree Sparrow. For these species, the transformation was best in reducing skew. The transformation also served the important purpose of striking a balance in analyses, between the contributions of very, and less abundant, species. The two-order-of-magnitude variation in the raw data among some species in transect abundance estimates, would otherwise "swamp" the ordination. The transformation instead facilitated an analysis emphasising community composition *and* structure. Interpretation of results was aided by consulting the CANOCO reference manual (ter Braak & Smilauer 2002), ter Braak (1994) and Jongman et al. (1995). For the sake of comparison, the data were also analysed by non-metric multidimensional scaling (MDS) in PC-ORD for Windows Version 3.04 (McCune & Mefford 1997). This ordination technique was developed explicitly for producing ordinations that reduce, as far as possible, the dissimilarity between the configuration of samples within a pre-defined number of axes, and the configuration of these samples in the full dimensional space. It provides a measure of this accord, "Stress", and uses Monte Carlo permutation tests to test the significance (randomness) of obtained measures.

3.3.2 *Results*

The PCA biplot (Fig. 3.1) summarised the relationships among the transect samples of the wintering granivore community. The first two principal components explained 70.1% of the community variation, $\lambda_1 = 0.507$, $\lambda_2 = 0.194$. The clustering of transects (summarised by stratum centroids) reflected the stratification of the study area and the east-west gradient in agricultural practices. PC1 was dominated by the arable-pastoral gradient and PC2 separated the MG transects from the Mixed transects. Species showed greater abundances where there was more arable farming, reflected in the preponderance of species vectors (and the direction of supplementary variable *totD*) in the left hand side of the biplot. Species scatter was greatest on PC2, characterised by Linnet and Goldfinch, and Tree Sparrow and Yellowhammer. The majority of species were most abundant among the

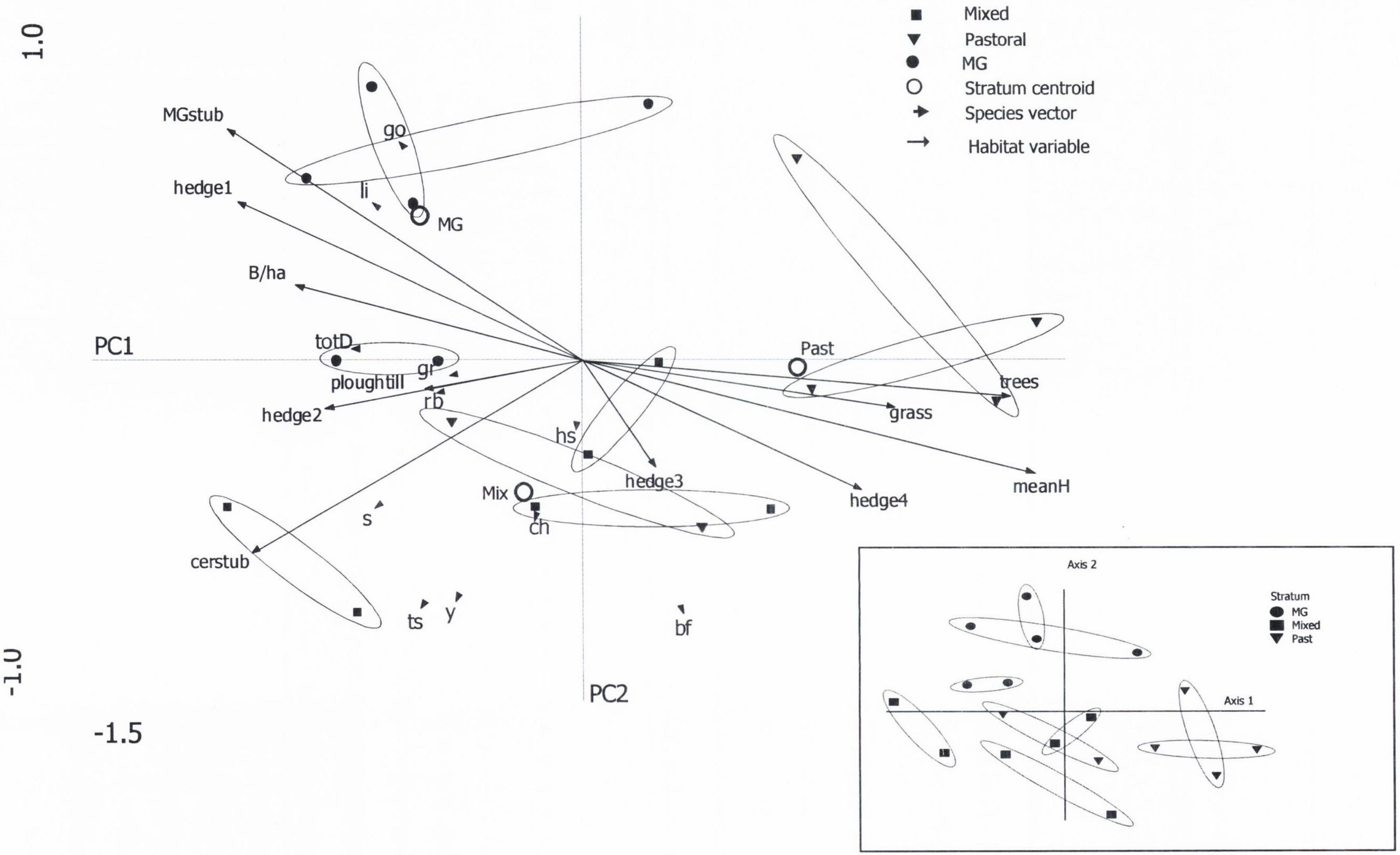


Fig. 3.1. Ordination of transects by Principal Component Analysis (correlation matrix) of species (transformed) abundances for Winter 2. $\lambda_1 = 0.507$, $\lambda_2 = 0.194$ ($\lambda_3 = 0.112$). Axis scaling focuses on inter-sample distances. Transects from different strata are indicated by symbols (see legend). Ellipses indicate transect pairs at sites. The correlation relationships of the environmental variables with the ordination axes are plotted. Inset is ordination diagram obtained from an MDS analysis of the same data, for which minimum stress was measured at ~11.3, $P = 0.01$. Species codes as per Table 3.1

mixed transects, while the greatest segregation (indicating in fact, a negative correlation) was between Bullfinch, and Linnet and Goldfinch. Greenfinch and Reed Bunting showed relatively weak relationships (short vectors) with axes suggesting more equitable distributions across the study area, with little variation in abundance. The environmental arrows indicated the direction of maximum positive correlation of these variables with the axes. PC1 was correlated most strongly with the proportion of grassland (*grass*), but mean boundary height (*meanH*), and the measure of tree occurrence (*trees*) showed similar strong correlations with this axis. Broadly, community characteristics of strata (represented by the location of transects and stratum centroids) showed strong associations with the described landscape characteristics. Increasing proportions of *MGstub* and *hedge1* were positively correlated with the MG centroid, and *Grass* was positively correlated with the centroid of the pastoral transects. A robust and significant ordination was produced in the MDS (Stress ~ 11.3, $P = 0.01$, Clarke 1993) that corresponded very well with the PCA biplot, indicating that the PCA achieved as reasonable an ordination as the MDS technique did.

3.3.3 *Discussion*

The ordination biplot clearly illustrated pattern in community structure across the study area. Species abundance rankings for strata, derived by orthogonal projection of centroids onto species vectors (applying the *Biplot Rule*), were in broad agreement with Winter 2 estimates (Fig. 2.5). Some discrepancies did result however when abundances differed little among strata (this was presumably because of differences in how variation among species abundances was explained by component axes, including the unreported axes λ_3 and λ_4 etc.). Positive relationships between granivore abundance and arable farming have been reported mostly at broad regional and national scales for the breeding season (e.g. Gates et al. 1994, Siriwardena et al. 2000a, Atkinson et al. 2002, but see Chamberlain et al. 1999 for farm scale). Several winter studies have demonstrated the importance of stubble fields of cereals and other crops as foraging habitat for granivores (e.g. Evans & Smith 1994, Wilson et al. 1996, Hancock & Wilson 2003), and demonstrated aggregation where seed densities are highest (Robinson & Sutherland 1999, Moorcroft et al. 2002). The positive associations of granivores with the MG and Mixed transects in this study almost certainly reflect the distribution of food resources available from cereal and other stubble fields. While an association with the arable strata was clear on PC1, the broad spread and spacing of the species vectors along PC2 indicated that the main gradient in species composition was among transects from these strata. Increasing abundance in Linnet and Goldfinch broadly characterised the MG transects, while Skylark, Tree Sparrow and Yellowhammer increased in abundance on the Mixed transects. The greater length of these species vectors indicated also that these species showed the greatest variation in abundance among all transects (the origin represents overall mean abundance).

Although the geographical location of study sites within strata was arbitrary, the location of transects was not, as they occurred in pairs at sites, and these were represented by ellipses in the biplot. At some sites, community structure on transects appeared quite similar (shorter ellipses), while at others, considerable differences in species abundances were suggested (longer ellipses). More generally, the looseness of the transect clusters within strata, and between transects at sites, suggested considerable variation was occurring at all levels of the sampling design. Nevertheless, the working hypothesis was well supported by the correspondence between the geographical stratification of the study area and the clustering of transects according to strata in the biplot. Questions remain regarding the variation observed within strata. It was possible that abundance estimates for the less common or more vagile species were less reliable because of sampling error, possibly resulting in an exaggeration of variation among transects. However, while species showed varying distribution patterns among strata, they did tend to co-occur on transects. The variation observed among transects within strata may well be evidence of finer scale species-specific habitat effects. In the next set of analyses, the nature of the spatial variation in community patterns is explored in greater detail.

3.4 Spatial and hierarchical perspectives on community variation

The sampling design allowed two distinct spatial perspectives on community variation to be explored. Firstly, the study sites sampled an explicit (east-west) geographical gradient in farming practices. The working hypothesis predicted spatial variation in species abundance in relation to this gradient. Such a pattern was evident in the PCA biplot, and the post-hoc projection of landscape variables in the ordination space corresponded with the observed species-landscape associations. Both data sets (describing species abundances and the farming environment), therefore, described a degree of regionalised variation, or *spatial dependence*. The extent of this is examined as it may have consequences for modelling approaches used in subsequent investigations. Secondly, the sampling design defined three spatial levels and/or resolutions (stratum and site are conceptual spatial levels, transect is a spatial resolution) that comprised a nested continuum representing a spatial hierarchy. It was possible to quantify the community variation unique to each level of this hierarchy, thereby allowing an assessment of the relative importance of broad and fine scale variation patterns. In the following analyses, these perspectives are developed by availing of specialised procedures in the CANOCO statistical package, utilising partial constrained ordination. Emphasis is placed on examining the spatially explicit structure in the data and the importance of the agricultural gradient for community patterns.

3.4.1 *Sampling level and resolution: partitioning community variation among the hierarchical levels of the sampling design*

Partial constrained ordination (Legendre & Legendre 1998) produces constrained ordinations of samples using residual variation after the effects of specified variables (covariables) have been removed (partialled out). Using this method it was possible to decompose the full community variation among the different hierarchical levels of the sampling design. The CANOCO package facilitates this analysis, and allows statistical testing of whether the variation unique to a level i.e. after accounting for variation defined at higher and lower levels, is significantly different from that which might be observed if species patterns were random. The spatial levels/resolutions considered in this type of analysis may or may not be arbitrary; detecting pattern at any spatial level is interesting in its own right, and can provide insights into the generating causes and how such patterns may manifest at different spatial scales. Ideally however, knowledge of, or hypotheses relating to, the spatial extent of processes and patterns under investigation enable more meaning to be ascribed to the results of any investigation. For an impressive example of this, see Cushman & McGarigal (2002). In the present context, the working hypothesis predicted that an important (sizeable) fraction of the community variation would be accounted for at the highest hierarchical level of the sample frame i.e. *Stratum*. Although the spatial level *Site* and spatial scale *Transect* were somewhat arbitrarily defined with respect to species' behaviour, they do represent standard and convenient sampling scales, and their value as such may be appraised. The analysis, therefore, also examines whether important community responses were evident within strata, after taking into account broad stratum effects. The ecological significance of the transect scale is addressed in the next chapter.

The procedure used is detailed in Leps & Smilauer (2003) pp. 141-144. In summary, the species data were sequentially subjected to a series of constrained and partial-constrained redundancy analyses (RDA), where each analysis quantified the variation unique to a particular hierarchical level. The analyses utilised the dummy variables defining the stratum and site levels (Table 3.1; *Stratum*, *Site*) as predictors, covariables and where appropriate, constraints in Monte Carlo permutation tests. With the exception of the highest and lowest levels where the procedure differs slightly, the variation of successive intermediate levels is determined by removing the variation accounted for by higher levels, and constraining the ordination by the dummy variable defining the level of interest. For example, to determine the variation explained at the site level, the dummy variable *Site* was used to constrain the analysis i.e. as a predictor, after specifying the dummy variable *Stratum* as a covariable. Monte Carlo tests test the significance of the levels in explaining the observed variation. Various restrictions must be applied to the possible permutations in these tests (see Leps & Smilauer 2003) by "blocking" samples and applying "split-plot – whole-plot" constraints. There is no meaningful permutation test for the lowest hierarchical level.

3.4.2 *Results and discussion*

An initial appreciation of the extent of the variation partitioned can be gained by examining the Winter 2 data in Fig. 2.5. In general, variation in species abundances was broadly distributed among strata; no stratum showed a greater or lesser tendency to produce variation. The partitioning analysis was performed on transformed relative abundances, however, so variation associated with a wide range in flock sizes was downplayed. Overall, approximately one third of the variation was explained at each level (Table 3.2), indicating abundance patterns varied considerably at broad *and* fine spatial levels/scales. Over two thirds of the variation was accounted for by the top two levels of the hierarchy i.e. by the fact that the transect samples were geographically organised. The high Mean Square value for *Stratum* (equivalent to the "among groups" mean square of ANOVA) of ~18% was significant, and underlined the strong influence of the farming gradient on community patterns. It was considerably higher than the mean variation attributed to sites within strata (*Site*) and transects within sites (*Transect*). There was some evidence of significant variation at the site level after controlling for S*tratum* and *Transect*, suggesting community patterns could vary within strata from one 1km square to the next. This result may be reflected in the PCA biplot, as each stratum shows one site that is quite separate from the other two. At any spatial resolution, however, the spatial scale of community variation is likely to be landscape specific, depending on aspects of habitat heterogeneity, and species responses to the spatial patterning of this heterogeneity. Variation observed at the transect level was slightly less than that which might have been anticipated given random species patterns (3.5% versus 5.9%). This perhaps should not be surprising, as species patterns on adjacent transects are likely to be more similar to each other, than they would be to transects from different sites. The similarity of the variation accounted for at the site and

Table 3.2. Partitioning of community variation on transects among hierarchical levels of the sampling design. The Mean Square values show the relative importance of the different spatial levels in accounting for community variation.

Hierarchical level	% Variation Explained	DF	Mean Square value	*P* (Monte Carlo Test) 499 permutations
Stratum	35.7	2	17.85	0.043
Site	33.1	6	5.52	0.061
Transect	31.2	9	3.47	n.a.
Study Area	100	17	5.88	n.a.

transect levels suggests these levels are not particularly distinguishable as descriptors of local scale of community variation.

3.5 Spatial patterns: spatial structure in the data

3.5.1 *Spatial autocorrelation*

The suggestion of spatial structure in species and environmental data creates a potential problem when it comes to testing relationships between the two (Legendre et al. 2002). This refers to the general problem of analyses of autocorrelated data. When spatial autocorrelation (SA) is present in response and predictor variables, or when there is a broad scale spatial structure in one, and SA in the other, the assumptions of classical statistical inference techniques, such as regression or correlation, are violated (Legendre 1993, Legendre et al. 2002). The data lack independence, and the variables are unlikely to be homoscedastic. If two variables show positive SA, spurious significant associations are likely (Type I errors); in the case of negative SA, genuine associations may be missed (Type II errors). SA in predictor variables, implicit, for example, in the variables describing the east-west farming type gradient in this study, can give rise to spatial dependence in a response variable that can often generate SA in the response variable. A high local abundance of a species resulting from a concentration of resources in an area may result in a "contagious biotic process", leading to a lack of independence among samples from that locale and SA in the abundance response. In birds, such an effect may be apparent at landscape scales in studies that have demonstrated an influence of landscape composition on patterns of habitat use at local scales (e.g. Arnold 1983, Best et al. 2001). If it can be correctly assumed, however, that there is no SA in a response variable, classic inference techniques remain valid regardless of SA (spatial structure) in the predictor variable (Legendre et al. 2002). Several approaches are used to take account of autocorrelation, depending on the nature of the investigation and available data. It can be described and quantified so that it can be removed (detrending), thereby allowing standard statistical analyses. Alternatively, the statistical tests themselves can be modified to allow for it. Or, it may be explicitly included in analyses or models as a process of interest.

Although data limitations in this study precluded a rigorous evaluation of possible SA in the species data, an attempt was made to describe the spatial characteristics of both the environmental and species data sets to assess potential problems of SA, and inform possible analysis strategies.

3.5.2 *Easting as a spatial predictor*

The pattern of granivore abundance across the sample transects is illustrated in Fig. 3.2. The data points, representing individual transects, were fitted by a quadratic function of transect National Grid easting, accounting for ~55% of the total variation. Clearly, granivore abundance was higher to the east where arable farming dominated, and there was little indication of difference between the two arable strata (this was also reflected in the direction of the supplementary variable *totD* in the PCA biplot; its arrow was uncorrelated with PC2, which summarised community composition differences between the two strata).

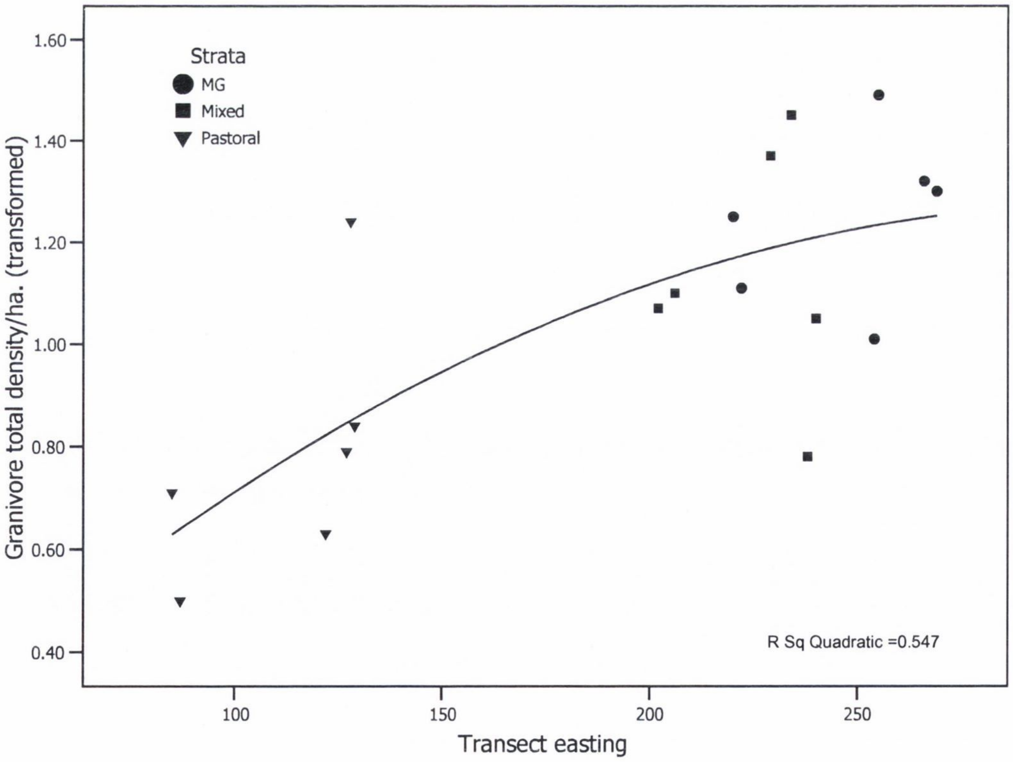


Fig. 3.2. Scatter plot of total granivore density (transformed) on transects and easting of transect mid-point for winter 2002-03. The data points are fitted by a quadratic curve. Transect membership of strata is indicated by symbols (see legend).

The east-west farming gradient was described in a similar manner. Regression analyses found National Grid easting and its square to be a significant predictor of the proportion of grassland on transects (R^2 adj. = 0.61, $P = 0.000$). It also described a considerable amount of spatial structure in the other landscape variables in Table 3.1. One variable, *hedge3*, was very poorly described (R^2 adj. –ve, $P = 0.66$). Otherwise, adjusted R-squared values ranged from 0.19 to 0.66 (mean ± SE, 0.43 ± 0.16). Only *hedge1* failed to reach significance at $\alpha = 0.05$ ($P = 0.08$). Although the performance of this simple function in describing the spatial structure in the environmental variables was quite variable (and poor for a few variables), it was decided to use it as a *spatial qualifier* in analyses. This was considered preferable to ignoring the spatial trends altogether. The alternative of modelling a *Stratum* effect on these variables accounted for less variation with fewer significant relationships. In the next analysis, easting and its square are used as a spatial qualifier of the explanatory power of community variation of two groups of environmental variables representing the "cropped" and "non-cropped" components of the farming landscapes, *Cover* and *Boundary* (Table 3.1).

3.6 Variation partitioning

A method for partitioning explained variation in species composition between two sets of variables using partial constrained ordination was described by Borcard et al. (1992). This allows comparisons of the explanatory power (%) of specified variables, or groups of variables. The method involves controlling for the effects of covariables to quantify the *pure* and *joint* fractions i.e. the independent and confounded effects, of explained variation when the groups are considered together. Borcard et al. (1992) provide examples of analyses where the method was used to examine the spatial structure in species abundances to qualify interpretations of the results of analyses using environmental data as predictors. In particular, it provided an assessment of (potential) non-environmental processes generating spatial autocorrelation in their species data. The method was extended to three sets of variables by Liu & Brakenhielm (1995) who used it to examine the relative importance of climatic, locational and environmental variables for epiphytic algae and lichens. Similarly, Heikkinen et al. (2004) examined the spatial structure of breeding density in two groups of birds (agricultural species, and all species) in considering the importance of two sets of landscape variables (*Cover* and *Structure*) in an agricultural-forest mosaic landscape in Finland. In the following analysis, I follow the procedures of Liu & Brakenhielm (1995) and Heikkinen et al. (2004) to partition explained community variation among three sets of variables – *Cover* describing field types; *Boundary* describing field boundary characteristics; and *Spatial*, relating to transect location (see Table 3.1). This was undertaken to examine the relative importance of, and patterns of overlap (confoundedness) in, the explanatory power of the environmental variable groups, and the degree of spatial structuring in their pure and joint effects.

3.6.1 *Method*

The forward selection variable test option (using 499 permutations in the associated Monte Carlo permutations test) was used in a preliminary RDA to screen the landscape variables to exclude those that were unlikely to contribute to the explained community variation. Variables that were not of potential significance at $P < 0.1$ (*hedge2*, *hedge3* and *ploughtill*) were excluded. The remaining variables explained 73.4% of the community variation. Each group of variables – *Cover*, *Boundary* and *Spatial*, was then used in a series of RDA *runs* to provide the basis for partitioning the explained variation among seven distinct fractions (Fig. 3.3). These were: *a, b,* and *c* representing the variation explained purely by the boundary, cover and spatial variables respectively; *d, e,* and *f* representing the variation jointly but exclusively explained by boundary and cover, cover and spatial, and spatial and boundary variables, respectively; and lastly *g*, representing the variation explained jointly by all three groups. Details of each run and the resulting component fraction of total explained variation are given in Table 3.3. Further solving of the following equations provided the variation of the remaining components -

$$d = (a + d + b) - (a + b);\quad e = (b + e + c) - (b + c);\quad f = (a + f + c) - (a + c)$$

$$g = (d + g + e) - d - e \text{ or } g = (d + g + f) - d - f \text{ or } g = (f + g + e) - f - e$$

3.6.2 *Results and discussion*

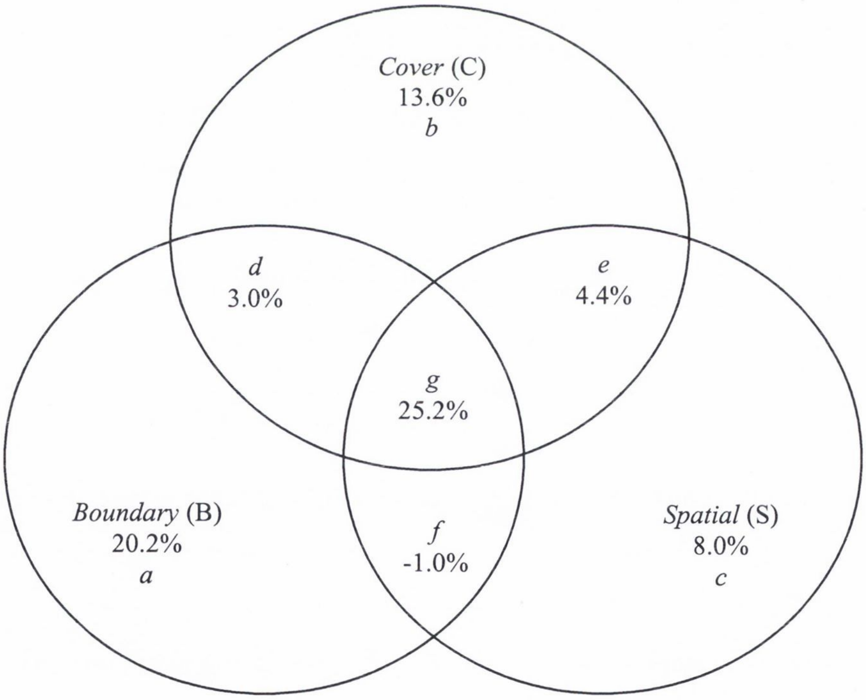
The combined explanatory power of the three groups of variables was high (Table 3.3) at 73.4%, while the purely spatial component (*c*) was low. Thus, ~90% of the explained variation was accounted for by the environmental variables. Taken separately, each group of variables acted as substantive and significant predictors. Despite the simplicity of the spatial predictor, it described over one third of the community variation. This was

Table 3.3. Outline of procedure for partitioning explained community variation (73.4%) among the different variable groupings or grouping combinations using partial Redundancy Analysis. The explanatory significance of each is tested by Monte Carlo permutation tests based on 499 permutations. Component fractions (a – g) correspond with graphic summary in Fig. 3.3.

Variable Groupings
S = *Spatial*: easting, easting squared
C = *Cover*: grass, cerstub, Mgstub
B = *Boundary*: hedge1, hedge4, meanH, trees, B/ha
} Sum of all canonical eigenvalues = 0.734

RDA run	Group/s	Covariables	%Variation Explained	*P*	Corresponding to fraction
1	Cover	Spatial+Boundary	13.6	ns	b
2	Spatial+Boundary	none	59.7	0.018	a+d+g+e+c+f
3	Spatial+Boundary	Cover	27.2	ns	a+f+c
4	Cover	none	46.2	0.004	C = b+e+g+d
	Joint effect: Cover and (Boundary + Spatial) = (59.7 - 27.2 = 32.5) or alternatively (46.2 - 13.6 = 32.6)				d+g+e
1	Boundary	Cover+Spatial	20.2	ns	a
2	Cover+Spatial	none	53.2	0.006	b+e+c+f+g+d
3	Cover+Spatial	Boundary	26.0	0.168	b+e+c
4	Boundary	none	47.3	0.008	B = a+d+g+f
	Joint effect: Boundary and (Cover + Spatial) = (53.2 - 26.0 = 27.2) or alternatively (47.3 - 20.2 = 27.1)				d+g+f
1	Spatial	Boundary+Cover	8.0	ns	c
2	Boundary+Cover	none	65.4	0.002	a+d+b+e+g+f
3	Boundary+Cover	Spatial	36.8	ns	a+d+b
4	Spatial	none	36.5	0.002	S = c+f+g+e
	Joint effect: Spatial and (Boundary + Cover) = (65.4 - 36.8 = 28.6) or alternatively (36.5 - 8.0 = 28.5)				f+g+e

confounded, however, with a sizeable proportion of the variation explained by the environmental variables. Indeed, the most striking feature of Fig. 3.3 is the high joint explanatory power of the spatial, cover and boundary variables, given by *g*. This represented over a third of the explained variation and was broadly supportive of the working hypothesis of a farming gradient effect. Much of this is likely to be represented in the variation explained at the stratum level in the hierarchical analysis (Table 3.2). Thus, a moderate degree of spatial structuring was evident in the joint effect (confounded portion) of the cover and boundary variables. The joint fraction that was not spatially structured, *d*, was small in comparison, as might be expected if there were strong spatial collinearity among environmental variables. The variation accounted for purely by the boundary variables *a*, and the cover variables *b* was considerable, however neither fraction was significant. The negative value for *f* indicated that the boundary and spatial variables together (having partialled out the effects of *cover*) explain the variation better (for various



Unexplained variation *h* = 26.6%

Fig. 3.3. Explained granivore community variation partitioned among and across different combinations of variable groups – see Table 3.3. *a, b, c* represent fractions explained purely by respective groups; *d, e, f, g* represent jointly explained fractions. *h* represents the effects of omitted environmental variables and/or undetermined spatial or stochastic processes.

possible reasons including strong correlation between the two, or opposing effects on the response variable) than the sum of the individual effects of these variables (Legendre & Legendre 1998). In this instance, it is of negligible importance. In the next chapter, a landscape-community redundancy analysis explicitly examines the importance of the individual variables for community variation. The results of the above analyses suggest this analysis will emphasise the importance of the farming gradient (a spatial process) and that, therefore, alternative unrecorded locational factor effects might be confounded with the effects of variables describing this gradient. However, if most of the spatially confounded effects are represented by *Stratum* (Table 3.2) or *g* (Fig. 3.3), there still remains a reasonable proportion of variation in each of the species and environmental data sets (*a*, *b*, and *d*) that is not spatially structured, at least at a broad scale. Analysis of this proportion of the data might reveal more local effects on community patterns, independent of location.

3.7 Main points and conclusions

- community variation was associated with the east west agricultural gradient in the PCA biplot, showing strong patterns among species, and a clear general gradient in overall abundance from pastoral to arable habitats
- community variation was evenly spread and statistically significant among the different hierarchical levels of the sampling frame. The strong effect of the farming gradient was underlined, while variation was also considerable at smaller spatial scales
- a substantial proportion of the explanatory power (%) of the environmental variables was confounded and showed spatial dependency. However, this was matched by similar proportion that was spatially independent and not confounded
- this provided a certain degree of confidence that independent effects of the tested variables could be detected in subsequent RDA analyses, and that results would not be dominated by effects of unmeasured environmental variables that also happened to be spatially structured

Chapter 4. Community-habitat relationships at the transect scale

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Preface

In this chapter, I briefly review some organisational aspects of granivore communities, particularly in relation to how habitat, predation and competition can interact to give character to local species assemblages (the local community). Then, the significance of the transect scale for sampling granivores during the winter is considered, and analyses are conducted on data summarised at this scale to identify factors associated with broader patterns in community structure. The results are discussed in relation to several farmland bird studies conducted at broad spatial scales.

4.1 Aims and objectives

- to review some aspects of the influence of vegetation structure on habitat use and selection in granivorous birds, and the possible consequences of species differences, in this regard, for community organisation
- to consider the usefulness of the 1km transect scale for sampling wintering granivore populations on farmland
- to provide a model of community patterns in relation to broad descriptors of the agricultural gradient, and assess the importance of variation in management of field boundaries

- to assess the importance of the spatial structuring in the observed community-habitat associations i.e. the importance of the agricultural gradient for community patterns

4.2 Community organisation in spring and winter

An emphasis on the breeding season in studies of lowland farmland birds in the UK has provided much detailed knowledge of the breeding ecology and habitat requirements of granivores (e.g. Parish et al. 1994, 1995, Green et al. 1994, MacDonald & Johnson 1995, Grynderup Poulsen et al. 1998, Murray et al. 2002, Moorcroft & Wilson 2000, Whittingham et al. 2001). In particular, variation in hedgerow characteristics (hedge dimensions, floristic diversity, the presence of trees or ditches, “gappiness”, field margin width etc.) has been found to influence which species use a hedge (for breeding or other activities such as foraging, roosting, cover, shelter etc.). Following niche theory, local species assemblages should reflect these characteristics, with the suggestion that the broader breeding community will be partly determined by the prevailing boundary management practices (e.g. Chamberlain et al. 1999). Such practices may be broadly characteristic of the type of agriculture practiced, and characteristic structure in bird communities is, therefore, likely to occur when agricultural practices are characteristic at landscape and regional scales. Siriwardena et al. (2000a) described such patterns among breeding granivores across farming landscapes in the UK. More generally, the broader composition and structure of bird communities is influenced by patterns in landscape composition, including the extent and nature of comprising habitats, and how this mosaic is configured. Arnold (1983), Fuller et al. (1997), Hinsley & Bellamy (2000), Best et al. (2001), Fuller et al. (2004) all highlight this general property of bird communities in agricultural land.

In contrast to the breeding season, far fewer studies have explicitly examined organisational aspects of bird communities on agricultural land during the winter. Because of this, we do not know too much about the similarities and differences between seasons in the factors that govern habitat use. For example, little is known with respect to the importance of field boundary habitat, for field feeding granivores during the winter. For non-field feeding species, the quality of the boundary habitat is of course fundamental; this is where they largely reside. Among field feeding species however, field boundaries may have a different functional importance, as they represent a structural component of a broader habitat that includes the open field. A few studies have reported overall species associations with field boundary variation (e.g. Arnold 1983, Parish et al. 1994), while others have included winter observations as part of broader studies of the effects of farming intensification on field boundary habitat (e.g. Moles & Breen 1995, Chamberlain et al. 1999, Chamberlain & Wilson 2000). Greater focus has been directed instead at the relative importance of different field types as foraging habitat (e.g. Wilson et al. 1996), and their management. The latter has implications for seed resource levels, and within-field factors affecting seed accessibility and granivore foraging behaviour (Robinson & Sutherland 1999, Moorcroft et al. 2002, Whittingham & Evans 2004). These studies have been broadly motivated by the hypothesis that the declines in population and range among granivores (Marchant & Gregory 1994) reflect reduced over-winter survival caused by reductions in the availability and quality of foraging habitat, and in seed food resources (e.g. Siriwardena et al. 2000b, Evans & Smith 1994). While this hypothesis offers convincing mechanisms for explaining declines, the negative effects of these habitat changes would be exacerbated if those remaining resources had become less accessible or unavailable. The widespread loss of hedgerows and the decrease in hedgerow quality associated with intensive farming may have placed extra pressure on species by constraining winter habitat use and, therefore, foraging opportunities.

Whittingham and Evans (2004) argued that the habitat structural effects on the behaviour of prey species observed in other taxa are also likely to apply to farmland birds. They drew particular attention to the observation in Robinson & Sutherland (1999) that the use of different parts of the field by Yellowhammers and Skylarks might relate to different escape strategies in these species to avoid predation, and how they perceive the structure of the field boundary. To Yellowhammers, the hedgerow *is* cover, in the sense that it provides a hiding place that is relatively inaccessible to predators. To Skylarks, however, which rely more on crypsis and an ability to "out-fly" avian predators (Cresswell 1994), a tall hedge may be a visual obstruction to predator detection. Other studies have suggested field boundaries and their attributes affect granivore foraging patterns. Boatman et al. (2000) suggested the use of experimental game crop plots by foraging finches and buntings was influenced by the proximity of hedgerows and trees. Similarly, Linnets and Skylarks were very rarely recorded foraging during winter food provisioning trials, possibly because feeding sites were located too close to "cover" (Siriwardena & Stevens 2004). Lima (1990) has suggested that within granivorous birds generally, a continuum of strategies exist for the use of space and cover, especially in relation to escape strategies from predators. Moreover, this continuum was a powerful organising force in a community of grassland granivores (Lima & Valone 1991). Pulliam & Mills (1977) suggested as much for nine species of sparrows wintering across a woodland-grassland ecotone at O'Donnell Canyon, Arizona, although habitat partitioning may also have been implicated. Notwithstanding, patterns of habitat use by individual species may depend also on the abundance and location of food resources; varying strategies may be utilised to avail of these resources. For example, the commonly observed foraging strategy of large multi-species flocks may ease habitat constraints relating to predation risk, which otherwise operate on smaller groups of birds, or on individual species. This is an adaptive strategy however, and may not always be possible, appropriate, or necessary; seed resources may not occur in suitable patches or at suitable densities. Some species, and some individuals, may choose to forage in "familiar" areas and rely on fine-grained local knowledge of where food can be obtained. In assessments of species habitat requirements, or habitat quality for birds, it is important to consider situations when birds are not part of large predator vigilant flocks. Habitat use patterns may be influenced by habitat aspects other than food resources and in this respect, responses among granivores to variation in field boundary structure and other attributes may be quite nuanced (as suggested above), possibly determining if particular boundaries are used at all, or how birds use the adjacent fields.

This thesis contends that variation in field boundary habitat, as a result of management affecting hedge height and the presence of trees, is important for granivorous passerines during the winter. Management choices may certainly have important implications for habitat quality in the breeding season, but they may also impose constraints on habitat use and associations during the winter.

4.3 The significance of the 1 km transect scale during winter

As described in Chapter 2, the sampling design and methodology was intended to achieve two broad objectives. Exploratory and descriptive objectives were pursued through balanced sampling within a hierarchical nested framework. This framework was intended also to provide a basis for making a comparative study of species responses to habitat variation. I adapted the standard transect methodology of the Breeding Bird Survey (BBS) (Gregory et al. 1998) to examine year round patterns in relative abundance and distribution. In particular, habitat *use* was measured by repeat census counts (details given in Section 2.2.4). The BBS protocol however, was designed for the purposes of estimating the density of breeding territories. For most passerines, these are readily identified by observing breeding and territorial behaviour during two count visits during the breeding season. Typically, a 1km transect ($0.2km^2$) accommodates several territories (within and across species), and breeding density estimates from the two transects in 1km squares are interpreted as an estimate of breeding densities in the broader vicinity, and used to produce annual indices describing population trends. A hierarchical habitat recording protocol is conducted to collect information on breeding territory requirements, and other possible habitat influences. The use of 1km transects to describe species distributions in a winter context, however, is not usual, and it is important to consider what is being sampled. Radio-telemetry work by Calladine et al. (2003) on wintering granivores in mixed farmland in Scotland, determined mean home range sizes for Chaffinch, Yellowhammer and Tree Sparrow respectively, of 149 ± 47ha, 51 ± 20ha and 20 ± 7ha (mean ± S.E.; n = 10, 10, 8 birds). These figures suggest that a 1km strip transect (equivalent to 20ha) may sample only a fraction of an individual birds home range. Inferences into the amount of resources required to sustain local populations in particular farming landscapes are, therefore, limited. On the other hand, such transects *do* sample variation in the quality and availability of habitat resources at a landscape level. Thus, assuming favourable habitat is broadly saturated, and important habitat variables have been described, analyses of species abundance and distribution on transects should provide indications of how farming type and management practices determine habitat suitability and patterns of habitat use.

Identifying such relationships should provide pointers as to how to best to manage landscapes for species during the winter.

In the following analyses, variation among transects in the variables listed in Table 3.1, is hypothesised to be associated with the observed *community level* patterns (e.g. in Fig. 3.1) It is perhaps worth reminding at this stage that the focal group comprises just nine species (data for House Sparrow were judged too sparse to be included in analyses) and that patterns of increase or decrease in abundance in just a few are likely to result in statistically significant community variation. The patterns themselves are, therefore, examined to assess which species and environmental variables might be implicated. Analyses in subsequent chapters address in detail the responses of individual species to habitat variation.

4.4 Redundancy analysis of landscape variables and community pattern

The PCA biplot (Fig. 3.1) illustrated the broader ecological question: to what extent does the distribution of transects in the ordination space (representing approximately 70% of community variation) reflect species responses to variation in field boundary habitat, preferred foraging substrates e.g. cereal versus non-cereal stubbles, and/or broader landscape effects i.e. effects of landscape composition? At the scale of the study area, the clustering of transects from the different strata supported the hypothesis that community variation was related to variation in farming practices, and Table 3.2 indicated that approximately one third was accounted for by the farming type stratification. Within strata, some sites appeared to show similar species patterns on transects, while others showed considerable differences. In the discussion of the results of the PCA (Section 3.2.3), it was suggested this variation was the result of differing responses among species to habitat variation on transects. Redundancy analysis (RDA) in the CANOCO package was used to test for associations between community patterns and the landscape variables summarising transects (Table 3.1). Data treatment is given in Section 3.1. If individual species responded differently to variation in the proportions of different field types on transects, for example, or to field boundary variation among transects, this could generate the observed patterns in the PCA biplot.

4.4.1 *Analysis protocol*

In view of the substantial proportion of spatially structured explained variation (cf. Variation partitioning analysis, Section 3.6; fraction *g* in Fig. 3.3 represented ~34% of the explained variation), and because it could not be assumed that the species data were free of autocorrelation i.e. that species' abundances on transects were solely related to local habitat and did not partly relate to a general high abundance associated with the broader landscape context, a risk of invalid ecological inferences was considered possible (Legendre et al. 2002). On the other hand, the variation explained purely by the boundary and cover variables in this analysis (fractions *a* and *b* in Fig. 3.3) i.e. which was not spatially structured and/or mutually confounded, was considerable, representing ~46% of the explained variation. This encouraged a dual modelling strategy (Standard and Control) as follows:

- A standard RDA (RDA1) was conducted on the 8 environmental variables remaining after screening (cf. Section 3.5.1).

- A second, standard RDA (RDA2) was conducted omitting the variable *meanH*. This was undertaken in view of the very high correlation between *meanH* and the spatial predictor (R^2 adj. 0.66, $P = 0.000$).

- A control RDA (RDA3) was conducted on the non-spatially structured variation in both data sets. This analysed the residual variation following a multiple regression of each data set on the spatial predictor.

This modelling strategy was intended to circumscribe two opposing assumptions regarding the species-landscape relationships. The two "standard" RDA analyses assumed there was no spatial autocorrelation (SA) in the species data, and that species responses reflected genuine ecological considerations. On the other hand, if there was SA in the species data (as a result of a possible lack of independence of transects within strata or at sites, and more generally, because of the broad scale spatial structure apparent in *both* the species and environmental data sets), some results from theses analyses might be spurious (Legendre et al. 2002). As noted in Section 3.4.1, it was felt that a reliable evaluation of SA in the data was not possible, precluding formal attempts to account for it. It was decided, therefore, to conduct a "control" analysis on an alternative data set (the "control data") that excluded the broad scale spatial structuring in the environmental and species data. This data comprised the residuals after regression of the individual variables (species and environmental) on the spatial predictor (Easting and its square). Essentially, the broad scale environmental and community patterns (e.g. farming landscape effects) were removed from the data to search for more *local scale* influences. This "standard-control" framework thus provided a series of qualified results that circumscribed the actual patterns i.e. the ecological relationships of species with farm management variables. Notwithstanding, the results of the different analyses (standard versus control) could be interpreted as a test of the hypothesis that important proportions of the variation in both the species and environmental data sets i.e. proportions that contributed to the significant associations observed in the standard analyses, were spatially structured, supporting (or not) the hypothesis of an effect of the farming gradient on granivore community structure.

4.4.2 *Results*

RDA1 identified *meanH* as having the strongest association with community variation (Table 4.1). This association disappeared completely, however, when the spatial predictor was included as a covariable, highlighting the strong spatial correlation between *meanH* and the spatial predictor (R^2 adj. 0.66, $P = 0.000$). Clearly, *meanH* was associated with the agricultural gradient; however it was possible that alternative aspects of farming type, or alternative unmeasured variables or locational factors (e.g. proximity to the coast, or to housing estates) may have been influential. When it was omitted from RDA2, several other variables became important (*MGstub, trees*, and *hedge4*) which better expressed landscape variation associated with the farming gradient, and accounted for increased community

Table 4.1. Main results from the RDA analyses. Analyses 1 and 2 differed in the omission of *meanH* in the latter. Analysis 3 modelled the residual variation in the species and environmental data, after removing the spatially structured variation in both, as estimated by the spatial predictor. Manual forward selection of variables was used to identify important variables.

Analysis	Variables	%Variation Explained	P (Monte Carlo test, 499 permutations)
1. Standard (8 variables)	*meanH*	28.9	0.002
	cerstub	13.6	0.012
	MGstub	4.7	0.3
	Axis1	37.8	0.048
	Axis2	14.2	0.16
	All canonical axes	65.4	0.012
2. Standard (without meanH)	*trees*	25.4	0.004
	cerstub	12.4	0.008
	MGstub	12.0	0.016
	hedge4	6.3	0.102
	Axis1	37.8	0.04
	Axis2	14.2	0.092
	All canonical axes	63.7	0.006
3. Control	*cerstub*	13.0	0.034
	MGstub	8.0	0.18
	Axis1	27.1	0.192
	Axis2	14.0	0.328
	All canonical axes	58.0	0.074
Spatial predictor	Easting	27.4	0.002
	Easting^2	9.1	0.05

variation. Notwithstanding, *meanH* remained the best individual predictor, and its association with community variation is illustrated in Fig. 4.2a. It was not significant in the control analysis (RDA3), where only *cerstub* remained significant at the $\alpha = 0.05$ level. The influence of this variable on the community, for both the standard and control analyses, is also shown (Fig. 4.1b, c). Species showed varying associations with these variables, which included positive and negative monotonic (unidirectional) trends, and apparent optima. Change in community structure was most clear for *meanH*, although as mentioned, it is unknown the extent to which this variable was causal. With the exception of Bullfinch, the ordination of species on *cerstub* was the same in standard RDA2 (without *meanH*) and

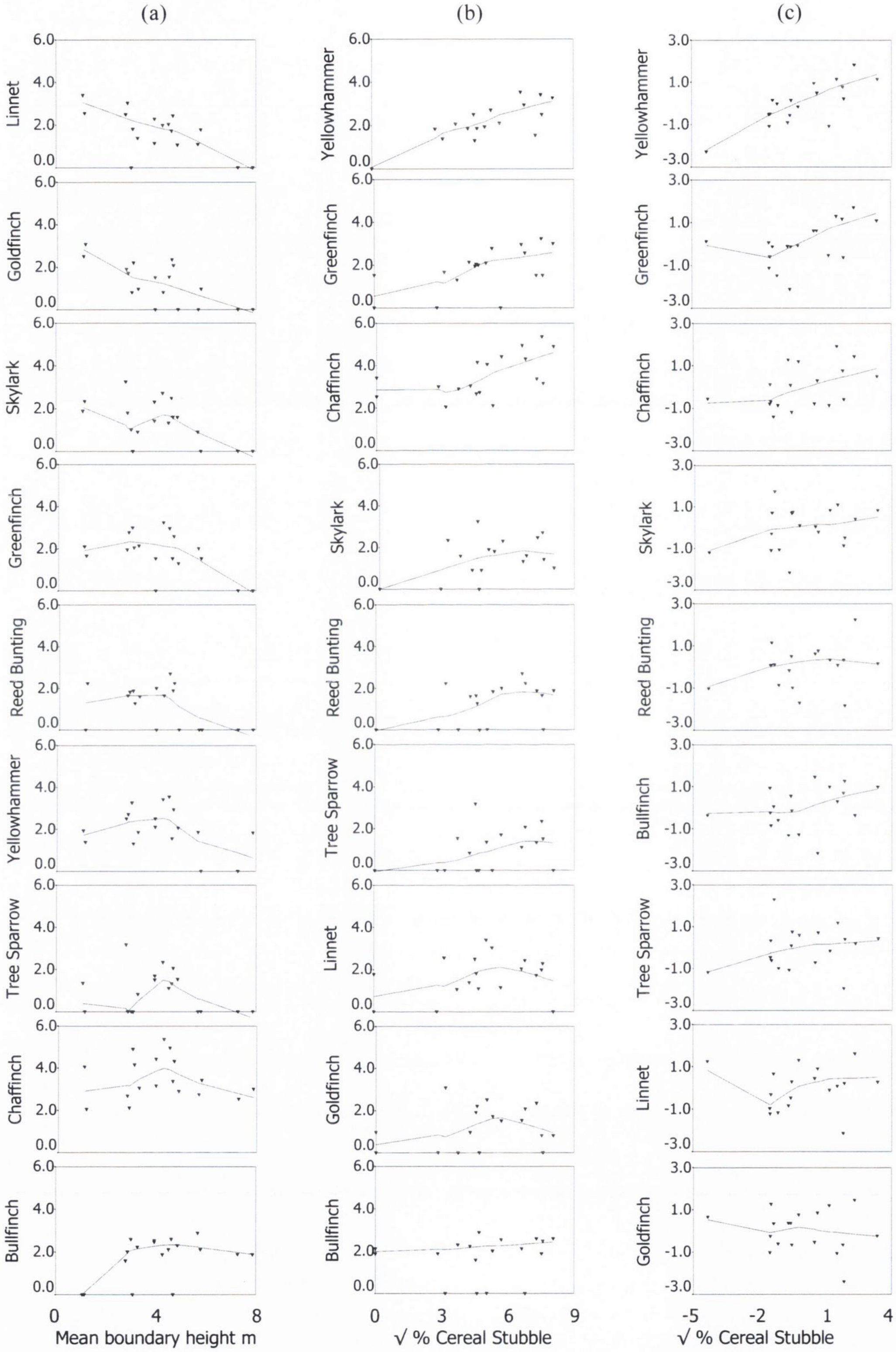

Fig. 4.1. Species and community response to gradients in (a) mean hedge height, (b) (transformed) % cereal stubble on transects – indicated by standard modelling. (c) represents the same as (b) but for residual values after fitting the spatial predictor. The y-axes are (a, b) species (transformed) densities, and (c) residuals thereof after fitting the spatial predictor, all standardized by sample standard deviation. The vertical order of plots corresponds to species ordination on the respective variables in (a) RDA1, (b) RDA2 and (c) RDA3. The trend line is a LOWESS smoother.

control RDA3 (Fig. 4.2). After removing the spatially structured variation in the data, response curves for *cerstub* did change; unimodal responses were neutralised (Linnet,Goldfinch), and stronger positive relationships appeared (Tree Sparrow, Bullfinch, Skylark). In both standard RDAs, the general test of significance for "all canonical axes" was significant, indicating that community structure was not independent of the variation in the measured landscape variables. Tests of individual canonical axes were significant for Axis 1 only in the two standard analyses, although some evidence exists in RDA2, of an effect for Axis 2 ($P = 0.09$). There was slight evidence of structure in the residuals (RDA3 Axis 1, $P = 0.19$) after eliminating the broad scale spatial patterns.

The triplot for RDA1 (Fig. 4.2a) represented just over 50% of the community variation, and was generally reflective of the patterns suggested in the PCA biplot (Fig. 3.1). The distribution of transects, and patterns in species relationships with environmental variables were similar, although there was greater overlap of transects from different strata. Axis 2 described relatively more community variation than its counterpart, PC2, in the PCA. The environmental associations of species in the triplot for RDA1 were broadly conserved in the triplot for the control analysis (RDA3), although there were some suggestive differences. The arable-pastoral "effect" suggested in RDA1 was arguably refined to a "stubble – non-stubble" dimension; the positive effects of the area of the two stubble types remained, despite accounting for the "negative effects" of the area of grass. The (residual) grass cover was no longer strongly negatively correlated with the remaining proportions of stubbles (MG or cereal) and showed little association with species patterns. Several species' responses did appear to differ between analyses, however. Tree Sparrow abundance was positively correlated with Linnet abundance in the control RDA whereas they were largely independent in the standard RDA. The same applied to Bullfinch, which became positively correlated with several species e.g. Yellowhammer. The significance of *cerstub* has already been noted. The general aversion to areas with more trees was maintained. The short length of most of the environmental arrows, however, indicated that they were not important influences in the control data. It must be stated that interpretations of the control RDA should be treated cautiously as the spatial predictor performed variably,

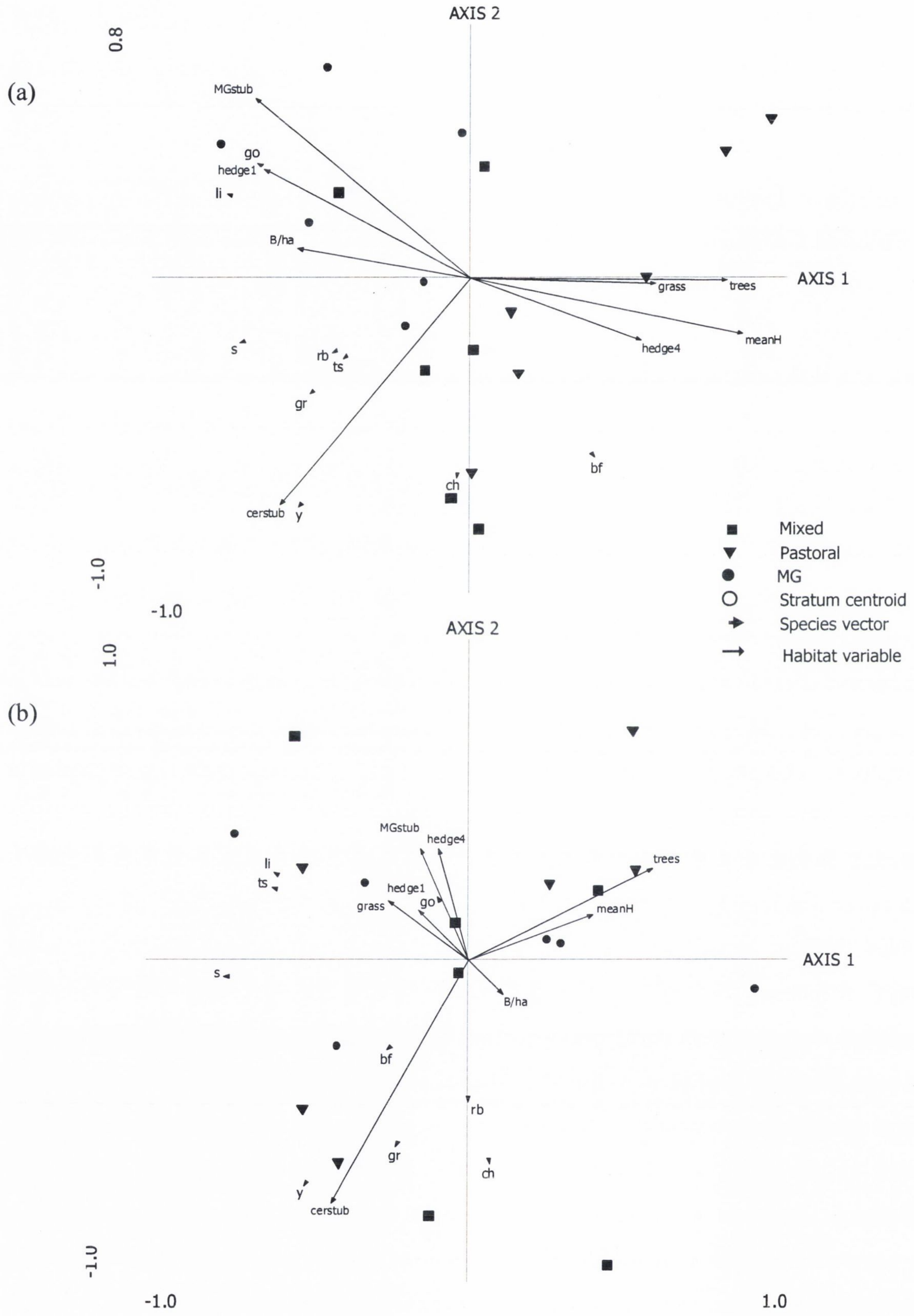

Fig. 4.2. Ordination triplots of (a) RDA1 and (b) RDA3. Axis scaling focuses on inter-species correlations. Transects from different strata are indicated by symbols (see legend). (a) λ_1 = 0. 373, λ_2 = 0.142. (b) λ_1 = 0.271 ≡ 17.2% of full data set, λ_2 = 0.14 ≡ 8.9% of full data set. Species codes as per Table 3.1.

and in some cases poorly, in modelling the environmental variables. It may, therefore, be wisest to interpret it as a simple test of the importance of the spatial patterns in the standard analyses, although this also relies on the accuracy with which the spatial predictor summarised spatial structure in the data.

4.4.3 *Discussion*

The sample transects captured considerable variation in granivore community structure and environmental patterns associated with the farming gradient, and the RDA analyses revealed several significant community-landscape relationships. RDA1 identified mean hedgerow height (*meanH*) of transects as the most important variable associated with community structure. This variable was strongly correlated with the *hedge4* and *hedge1* (cf. Fig. 4.2a) i.e. the length of hedge in the tallest and shortest height classes, suggesting species may have shown different responses to tall and short hedges. Indeed, species response curves (Fig. 4.1a) suggested Linnet, Goldfinch and Skylark preferred transects with lower hedges. An association with low hedges for Linnet and Goldfinch was suggested in Chamberlain et al. (1999), and a negative effect of hedges and trees in general on Skylark abundance was described by Chamberlain & Gregory (1999) in the breeding season. Hancock & Wilson (2003) corroborated this negative pattern for Skylarks wintering on Scottish farmland, but also found that Linnet, Reed Bunting and Tree Sparrow preferred landscapes (1km squares) with lesser amounts of woody habitats, including woodland, hedgerows and scrubby field boundaries. These observations related to spatial scales broadly commensurate with the transect units in this study, and raise interesting questions as to the ecological traits reflected. Such questions are explored further in following chapters. Other species showed abundance optima on transects with mean hedge height between 3m and 5m. Bullfinch abundance peaked when *meanH* reached 2.5m and remained relatively constant thereafter. Although this species is usually described as a granivore, during the winter it tends to rely more on the fruits and buds of hedgerow species as a food source. During Winter 2, it was observed foraging on the ground on only one occasion. Its generally even abundance on transects with mean hedge height of 2.5m or greater suggested a broad consistency in the quality and availability of habitat resources on these transects.

When *meanH* was omitted in RDA2, *MGstub, trees*, and *hedge4* became important. This model explained more significant variation than RDA1 (49.8% compared with 42.5%) perhaps by providing a more explicit description of the farming gradient. For example, the availability of trees (*trees*) was almost as important as *meanH* (25% against 29%), and the omission of the latter in RDA2 might have revealed "extra" independent effects of *trees* and *grass* (the latter avoided by most granivores), which may have been confounded with *meanH*. As tree height played no part in estimating the mean height of hedges (except in the few cases where the hedge was a tree-line; usually very tall Ash hedges), the correlation between *trees* and *meanH* (Fig. 4.2a) reflected the fact that areas with tall hedges also had more trees. From a management point of view, this might be expected.

While species response curves for *meanH* showed a clear pattern, it was also clear in Fig. 4.2a that the proportion of cereal stubble (*cerstub*) on transects was important for Yellowhammer, Greenfinch, Reed Bunting and Tree Sparrow. As the effects of this variable were broadly independent of those of *meanH* (see the orthogonal relationship of the respective environmental arrows in Fig. 4.2a), it is suggested that cereal stubbles were particularly important for these species (this does not mean hedge height was unimportant; rather, the response curves for these species in Fig. 4.1b may be dominated by the effect of *cerstub*). In eastern England, Parish et al. (1995) found land use adjacent to 200m hedgerow transects to be important for winter abundance (mean count across 5 survey visits) within their "Finches" grouping (broadly similar to the species examined in this study, but omitting Yellowhammer, and including Corn Bunting). In stark contrast to this study, higher abundances were found on transects running through pasture (with the exception of Corn Bunting and Skylark), compared with those running through "small arable fields" or "large arable fields". This disagreement might be explainable if their "arable" transects sampled few stubbles or fallows (they do not provide this detail). Alternatively, hedgerow quality may have been so poor on their arable transects that species tended to avoid arable areas. Although the land use association remains somewhat puzzling, their Finches group as a whole responded positively to greater length of hedge, increasing hedge height and volume, verge width, and the presence of trees. Indeed, the measure of hedge length *within* their 200m transects suggests there was some degree of variation in the integrity or "gappiness" of their hedges. This was a feature of some of the hedgerows in this study, especially in those of the MG stratum. The importance of cereal stubbles for wintering granivores (e.g. Wilson et al. 1996, Moorcroft et al. 2002, Calladine et al. 2003) was highlighted in all three RDAs, and was underlined by RDA3; despite removing the broad scale spatial trends in habitat variation and species abundances, species' responses to this variable remained generally consistent with those observed in RDA1 (compare Fig 4.2a, b), and the community response remained significant. Of greater interest however, was that the availability of cereal stubbles appeared to be of varying importance among species (Fig. 4.1b, c). Strong positive responses were apparent in Yellowhammer, Greenfinch and Chaffinch in the standard and control data sets. On the other hand, Goldfinch and Linnet occurred at similar abundances irrespective of cereal stubble availability in the control data, or tended to decrease at higher values in the standard data. It is possible that dietary specialisation and/or breadth were behind these patterns. Linnets may show a preference for the seeds of *Brassicaceae* (Wilson et al. 1999, Moorcroft et al. 2000), which include cabbage varieties, the dominant crop of the MG stratum. Incomplete harvesting and tardy cultivation resulted in much seed set in these crops, perhaps providing particularly rich supplies in stubbles. Goldfinch on the other hand, may be specialised in foraging for the very small seeds of *Asteraceae*, which are characteristic of high disturbance (staggered cultivation practices and ongoing harvesting of vegetables were a general characteristic of the MG stratum farming practices), and include Lettuce, which was restricted to the MG transects. Notwithstanding, the association of Linnet and Goldfinch with the MG stratum was one of the stronger patterns observed. Their association with lower hedges in other studies has already been noted, but it is perhaps significant that large flock size was a characteristic of observations (personal observation). In comparison, other species occurred in smaller flocks, reaching highest abundances in the Mixed stratum. It is arguable that this pattern reflected fundamental ecological differences in relation to hedgerows. Total density of birds was slightly higher in the MG stratum, suggesting seed resource levels were an unlikely factor determining patterns. Rather, species with a greater tendency to occur in larger flocks (i.e. Linnet and Goldfinch) were able to exploit the more exposed and open habitats characteristic of the MG transects. The other species (excepting Skylark) were more often observed in smaller groups, rarely foraging beyond 30 metres of a hedge, and frequently retreating to the cover of the hedge. For these species, hedgerows were *functional* in providing cover and, therefore, access to seed food resources that may otherwise have been unavailable (cover dependence). In very open landscapes, large mixed-species foraging flocks may form as an adaptive response to patchily distributed resources, which engenders increased vigilance against predators. Seed resources must be sufficient, however, to justify this strategy; if they are not, alternative foraging strategies and patterns of habitat use may result. In such situations, hedgerows may permit species to exploit more thinly distributed seed resources. Smaller flocks of birds might then be dispersed more generally across patches with lower seed abundance, with the compensation being the safety of the cover afforded by (suitable) hedges.

After removing the broad scale spatial trends in the data, RDA3 (Table 4.1) showed non-significant relationships between community patterns and the canonical axes. This result confirmed that an important fraction of the significant variation in community structure and environmental variation i.e. the variation significantly associated with axes and variables identified in RDA1 and RDA2, *was* spatially structured, and supported the hypothesis that observed community patterns were associated with the farming gradient. Two studies based on breeding and winter atlas data are of interest with respect to this hypothesis. For practical reasons, bird atlas data is coarse, describing species national abundance and distribution patterns at a resolution of $100km^2$ (10 x 10 km grid squares). Briefly, for the breeding atlas (Gibbons et al. 1993), a frequency index was calculated for each species in each 10km square based on the proportion of a minimum 8 sampled tetrads (2 x 2 km squares; 25 tetrads per 10km square) recording a species presence. For the winter atlas (Lack 1986), species abundances per 10km Square were estimated by considering total counts for species during a standardized 6-hour day. Siriwardena et al. (2000a) modelled granivore frequency index data (breeding atlas) with contemporaneous agricultural data (crop type and diversity, total agricultural land, grazing characteristics etc.) and found strong species-specific associations with a variety of agricultural variables. These, they suggested, were related to ecological differences in habitat preference and sensitivity to environmental variation. The present study area is broadly equivalent to two atlas grid squares and the analyses in this study have suggested species-specific responses to changing agricultural landscapes (defined as strata) across these squares. This grain of variation (in agriculture and community structure), if representative, could easily produce the types of relationships observed in Siriwardena et al. (2000a). In the second study, Atkinson et al. (2002) compared species seasonal abundance and distribution patterns using data from the two atlases, and found granivores tended to maintain an association with arable habitats throughout the year. Although this implicated the importance of the availability of seed food resources in these habitats, three species (Skylark, Linnet and Reed Bunting), appeared to show shifts away from more arable areas to mixed farming areas. Quite why these species might move in this way is not clear, but it may be related to the general quality of non-cropped habitats associated with mixed farming. They called for greater understanding of the year round importance of this habitat, especially in relation to hedgerows. In the present study, field boundary attributes, especially hedgerow height, appeared to be important factors structuring the winter granivore community.

Much is known of the breeding ecology of the study species, providing information for devising conservation measures for maintaining or enhancing habitats for breeding birds (e.g. Lack 1992, Boatman et al. 2000, Hinsley & Bellamy 2000). By comparison, their winter ecology has been less well studied. For a variety of reasons, winter studies are relatively rare, not least because there has been no tradition of winter surveying (unlike the breeding season) and, therefore, less information with which to generate hypotheses. They also tend to be difficult to conduct, and are all the more so because species (and granivores in particular (Wiens & Johnston 1977)) tend to be very vagile during the winter, as they do not defend territories as they do in the breeding season. While the conspicuous selection of stubble fields by granivores for foraging has provided a focus in several studies, little is known of broader patterns of habitat use ("whole landscape use" – Fuller et al. 2004). Unless sufficiently intensive, sampling may fail to detect patterns when confronted with such high mobility, or may create an impression that if detected at all, they are so loose as to be unimportant. In this respect, the work of Calladine et al. (2003) is highly pertinent. Using radio telemetry, they described different winter movement patterns among Chaffinch, Yellowhammer and Tree Sparrow within a 5 x 5 km square on mixed farmland in Scotland, and suggested these reflected degrees of specialisation. While the ecological interpretations of the community patterns detected in the analyses above were based on broader landscape associations, the finer grained processes alluded to by Calladine et al. (2003) may be operating. In the next chapter, species distribution and habitat use is considered at a fine spatial resolution to examine the hypothesis that habitat use varies among species in relation to variation in the attributes of the hedgerow habitat.

4.5 Main points and conclusions

- relative to the breeding season, studies on the winter importance of field boundary habitat for farmland birds are rare
- transects sampled variation in the cover of different field types associated with the agricultural gradient during the winter, and the broad characteristics of field boundary management patterns
- multi-collinearity was apparent in these landscape variables; however, species appeared to respond differently to the area of cereal stubbles, and to the mean height of field boundaries on transects
- the three farming landscapes showed characteristic species patterns which are likely to reflect species-specific responses to broad management patterns. Skylarks, Linnets and Goldfinches used open areas of habitat, with fewer trees and lower hedges. Chaffinches and Bullfinches showed the strongest associations with increasing field boundary height and the presence of trees. Yellowhammers, Reed Buntings, Tree Sparrows and Greenfinches responded most strongly to the availability of cereal stubbles.

Chapter 5. Species habitat use at the section scale

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Preface

The transect analyses described strong winter patterns; the change in community structure across the agricultural gradient was appreciable as species abundances on transects responded to broad variation in several landscape descriptors. This community variation was quite clear in the clustering of transects from individual strata in the PCA biplot (Fig. 3.1). However, when the ordination was constrained to reflect environmental variation (Fig. 4.2a), the stratification became less apparent; transect clusters were considerably more diffuse, and showed substantial overlap. It was noticed that the transects could be divided into two broad groups with respect to the ordination axes. One group contained transects that were clearly separated on Axis 1, and represented the extremes of the arable-grassland gradient. The other, containing the majority of transects, showed a strong alignment on Axis 2 with little variation on Axis 1. It was noticed for this group that the Mixed transects spanned this axis, while Pastoral and MG transects tended to separate. This axis also represented the main gradient in community composition, and it was felt, therefore, that it was rather the more interesting. It was also felt that the "outlying" nature of the three pastoral sites on the right hand side of Fig. 4.2a had a disproportionate influence on the ordination. They were only important for Bullfinch, and other than suggesting granivores showed low abundances on pastoral landscapes relative to arable, contributed relatively little to an understanding of granivore community patterns. It was decided to eliminate them in a further exploratory RDA. The triplot for this analysis is presented in Fig. 5.1.

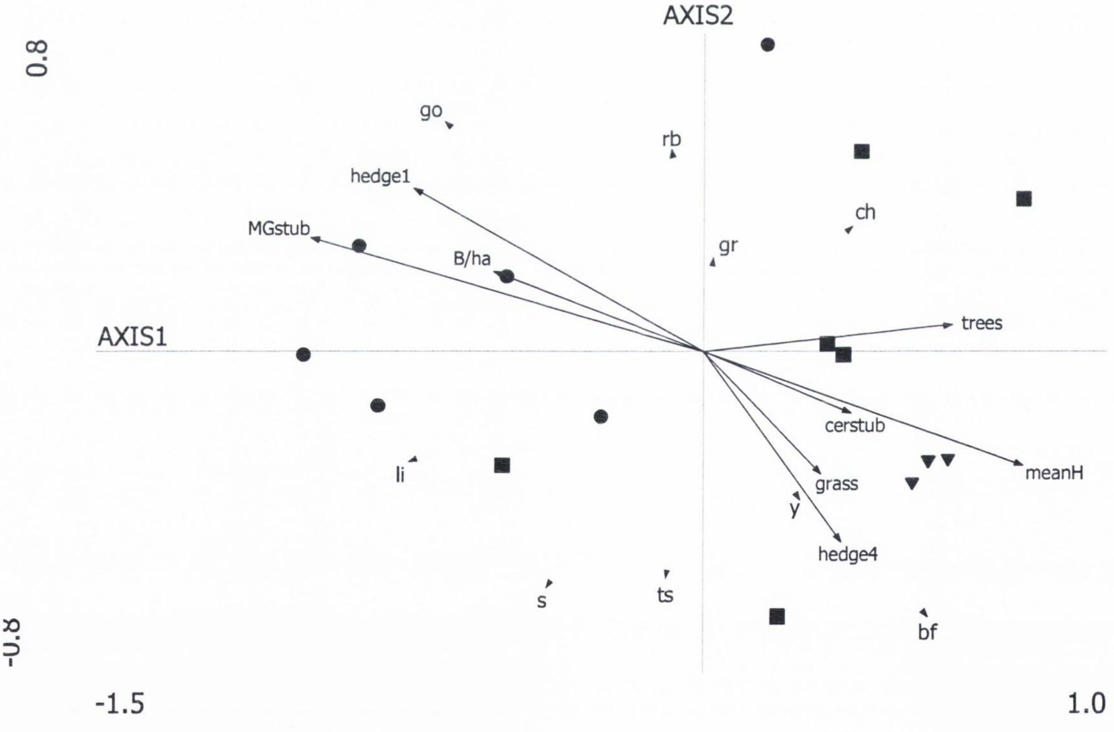


Fig. 5.1. Ordination triplot of exploratory RDA omitting three "outlying" pastoral transects and showing diverse responses among species to gradients in measured environmental variation. λ_1 = 0. 327, P = 0.086; $\lambda_2 = 0.126$. Symbols as per legend Fig. 4.2. Species codes as per Table 3.1

The effect of omitting these transects was quite revealing. Briefly, the principal gradient now emphasised landscape and species variation across the MG and Mixed transects (more like Axis 2 in RDA1). The purpose of presenting the biplot, however, was to illustrate the considerable differences among species in responses to the habitat gradients, as suggested by the omni-directional species vectors. This observation was supported by the results of Spearman's rank correlation tests among species abundances across transects, where only one third of all pair-wise comparisons were significantly correlated at the 5% level. In this Chapter, I examine patterns of habitat use among species at a fine spatial scale to investigate these species-specific responses.

5.1 Introduction

In Chapter 4, references were made to a range of studies addressing various aspects of species' winter niches. These included assessments of the effects of within-field microhabitat factors that operate once a bird has alighted in a field; the implications of different crop management practices; studies examining species-hedgerow/field boundary associations; and several studies describing effects of landscape composition on communities. This range highlights the multi-scale nature and potential interactive complexity of factors determining species distribution patterns. Studies that observe phenomena at a variety of scales are, therefore, likely to provide fuller understanding of deterministic and regulatory processes. Up to now, investigations have considered patterns in community and landscape described at the spatial scale of the transect, and the RDA analyses in Chapter 4 were broadly successful in revealing associations amongst these patterns. Briefly, analyses identified several landscape descriptors that were significantly associated with community variation (RDA1 and RDA2). However, stronger general inference (i.e. greater *external* validity) was predicated upon accounting for the broad scale spatial dependence (RDA3) in the data sets, which could otherwise have led to erroneous observations based on the standard analyses alone. Thus, the area of cereal stubble on transects was the only variable to show significant effects on community pattern independent of location, and this probably represents the most generally reliable inference from these analyses. Species response curves (Fig. 4.2b,c) for this variable suggested, nevertheless, that it was of varying importance among species, or that other factors, such as hedge height, modulated its importance. As mean hedgerow height on transects was the strongest individual predictor of community variation, it was suggested that species showed habitat preferences with respect to the extent of taller and shorter hedges, and/or varying levels of dependence on hedges in general. To elucidate these patterns further, fine scale distribution and habitat use among species was investigated in relation to fine-scale equivalents or analogues of those variables analysed at the transect scale. By examining fine scale distribution over time, it was hypothesised that observed patterns would indicate important habitat components, and enable a greater understanding of species functional integration into the landscape. Thus, community patterns described at the transect scale could be examined in light of observed fine scale patterns (this is the subject matter of Chapter 6). Analyses focus on whether variation in field boundary structure has any bearing on patterns of winter habitat use in granivores, an area that has received little attention (Robinson & Sutherland 1999, Whittingham & Evans 2004).

5.2 Aims and objectives

- to elucidate fine scale patterns in species distribution and habitat use on transects
- to determine fine scale habitat correlates of these patterns
- to summarise findings in terms of the fundamental farmland habitat mosaic

5.3 Methods and data treatment

5.3.1 *Methods*

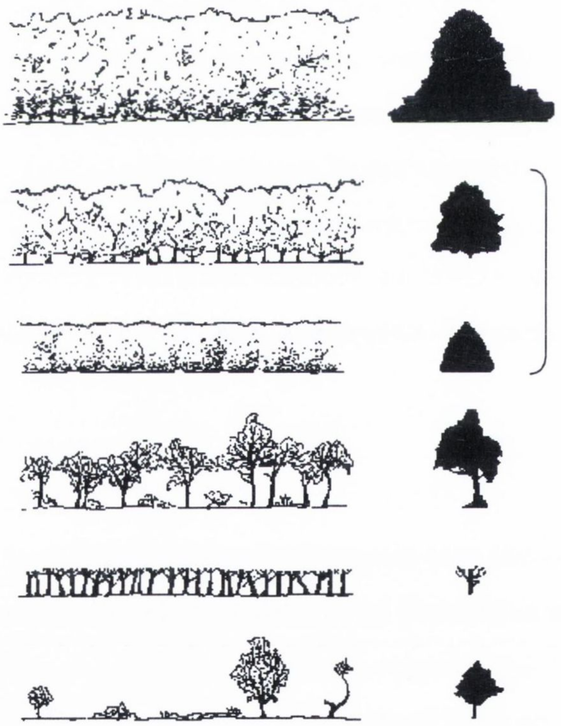
Fine-scale patterns of habitat use over the survey period were described by overlaying a grid (cell dimensions (length by breadth) representing 100m by 200m) on the mapped location records for each transect count (cf. Fig. 2.3), and deriving species "use scores" for each transect section – the number of times a species was recorded in a section as a proportion of the total visits to the section. The relationship between species use scores and habitat variation summarised at the section level was analysed using univariate and multivariate logistic regression in MINITAB Release 14.2 (2003). The analyses availed of the "success/trials" polychotomous response variable option, with each census count recording a presence treated as a "success", and the total number of counts as the number of "trials". This approach has been used to circumvent difficulties associated with choosing an appropriate response model due to the error structure typical of count data for gregarious species, such as flocking birds (e.g. Perkins et al. 2000, Moorcroft et al. 2002, Hancock & Wilson 2003). These studies modelled species *frequency of use* of individual fields or habitat compartments because the frequency distribution of their bird count data was highly skewed and contained a large number of zero counts, making it difficult to transform to normality. This was also the case in the present study. The aggregated nature of the occurrence of individuals within sections was indicated in six of the nine species by variance to mean ratios appreciably greater than 1 (ranging from 1.98 in Yellowhammer to 16.8 in Linnet). Species whose individuals tended to occur singly or in small numbers e.g. Bullfinch and Reed Bunting showed ratios less than 1. Thus, analyses using Ordinary Least Squares regression, or regression based on a Poisson model would be inappropriate. Notwithstanding, I wished to emphasise *frequency of use* over the winter as the measure of section importance for species, as it reflected fine scale patterns of landscape use, and provided a basis for examining relationships between patterns in habitat use and species abundance on transects. It also facilitated a comparison of species in this regard. All species showed a highly significant correlation between frequency of use and total count in sections, for the whole data set, and for the subset of sections analysed (see below), suggesting that factors associated with frequency of use were also likely to be associated with abundance (Moorcroft et al. 2002).

5.3.2 *Data treatment*

For each 100m section, area of crops (weighted by duration as per the transect summaries, see Section 3.1), boundary length according to height class (Table 3.1), and the *number* of hedgerow sub-samples occurring in each section with one or more trees, were determined. While the transect scale analyses allowed variables to be expressed on a continuous scale, the reduced area of sections tended to sample the presence or absence of features. Also, continuous measures such as overall boundary length, or the length of particular boundary height classes, for example, showed multi-modal distributions, and

Table 5.1. Variables used in Logistic Regression Analyses of species occupation frequency of 116 100m transect sections. *n* = number of sections relating to given factors.

Variable	Description	*n*
Cerstub	2-Level factor: Reference level - cereal stubble present	87
Treeline	2-Level factor: Reference level - tree-line absent	85
Trees	3-Level factor: Number of sampled subsections with at least one tree – range 0 – 8	
	No sections	46
	1 – 2 sections – Reference level	55
	> 2 sections	15
Boundary	3-Level factor: Boundary length categories. Range 100m to 400m	
	100m to 150m	27
	> 150m to 250m – Reference level	53
	> 250m	36
Index B	Covariate: Calculated Index analogous to weighted mean of boundary height	
Index M	Covariate: Calculated Index expressing perceived management intensity of boundary	
Easting	National Grid Reference easting for mid-point of transect providing section	
AutoC	Linear correction factor for autocorrelation in bird data due to section adjacency	



Unmanaged Boundaries. Hedges – tall, dense, bushy, variable, voluminous. Strong undergrowth of non-woody species. Proportion of all boundaries ~ 41%. Proportion in analysed sections ~ 37%. Management score 4

Moderately managed Boundaries. Hedges show obvious signs of management. Frequency of management variable. Rather uniform, dense. Undergrowth not as strong as above. Proportion of all boundaries ~ 22%. Proportion in analysed sections ~ 24%. Management score 3

Characterised by openness. Usually narrow, tall, "leggy" and "gappy". May result from grazing pressure at base, or intensive management at base. Proportion of all boundaries ~ 10%. Proportion in analysed sections ~ 9%. Management score 2

Intensively managed, boundaries tidy, hedges short, neatly squared, narrow. Proportion of all boundaries ~ 8%. Proportion in analysed sections ~ 9%. Management score 1

Boundaries with remnant hedge – large section of hedge missing. Often stretches of low bramble, many isolated bushes. Proportion of all boundaries ~ 19%. Proportion in analysed sections ~ 21%. Management score 0

Fig. 5.2. Structural and morphological attributes recognised to classify hedges and field boundaries into 5 management classes. Classes are scored according to a broadly *perceived* gradation in management intensity. Adapted from Pollard et al. 1974.

high counts in zero classes. Modelling such data as continuous variables is problematic, and it was considered appropriate to re-code measures for several variables into factors with 2 or 3 levels, or compute alternative summaries (Table 5.1). Factor levels were determined by examining the frequency distribution of respective variables. It seemed reasonable that species, if they responded at all, would do so to coarser differences among sections. Using factor levels, therefore, geared the analyses more towards detecting effects, rather than quantifying responses. A boundary height index (Wilson et al. 1997), *Index B*, was calculated for each section. Each of the four boundary height classes was given a score (0 – 3) in order of increasing height. The length of boundary in each height class was then multiplied by this score, and the sum over all classes divided by the total boundary length for the section. This index is analogous to a weighted mean height. Approaches to boundary management varied both within farms, and across the study area, producing a diversity of hedge types. These are well characterised by the scheme of Pollard et al. (1974) (Fig. 5.2), and it was decided to classify field boundaries accordingly. This scheme can arguably be interpreted as a gradient in management "intensity", and increasing management severity is likely to impact on the related aspects of floristic diversity, structural complexity, and broader habitat quality. The allocation of boundaries to classes was somewhat subjective; however, the process was aided by considering boundary and hedge dimensional data, and the scores given to hedgerow sub-sections (Chapter 2) for two aspects of structure. Thus Doogue (1996), in a botanical study that encompassed the study area, scored 30m hedge sections for "management level", to reflect the intensity of trimming, and hedge "tightness", incorporating aspects of density, "stockproofness" and width, both on a scale of 1 – 5 (cf. Appendix 2). An index similar to *Index B* above, *Index M*, was calculated for each transect section, with classes scored in order of decreasing management intensity (0 – 4). Generally, the more intensive the management, the more likely the hedge was small, narrow, "gappy" or porous. The broad characteristics of the hedge classes are noted in Fig. 5.2. Although it is not immediately clear how hedge morphology (largely the result of management) might influence species, the main considerations were its potential importance for predation risk and predator avoidance, as shelter, and the simple possibility that species responses may reflect more fundamental habitat preferences. The presence or absence of a tree line, *Treeline*, and whether the section sampled cereal stubble, *cerstub*, were coded using binary dummy variables. The variables analysed are presented in Table 5.1. For all factors, the modal category was selected as the reference level in analyses.

Although all 178 transect sections could have been included in analyses, it was decided to exclude those that sampled only improved grassland (37 sections), as granivores generally avoid this habitat during the winter (Hancock & Wilson 2003, but see Parish et al. 1995b and Arnold 1983) in the presence of arable habitat. Certainly in this study, species observations in grassland sections were uncommon, with the exception of Chaffinch and Bullfinch. The data were further screened to exclude sections that provided potential foraging habitat (crop stubbles) for only a limited duration. A management characteristic of the latter part of the survey period was an increase in the area of cultivation as stubbles were ploughed in preparation for spring crops. It was decided, therefore, to include only sections that provided at least 0.5ha of crop stubble for at least two thirds of the survey period, termed "full term" stubbles. Thus, a further 25 sections were excluded. This resulted in 116 eligible sections, most of which were from transects from the market gardening and mixed strata. These were affected by the loss of stubble habitat to the following degrees: 26% of sections for the final census, 16% for the second last census, and 9% for the third last. If the strength of species responses is ultimately based on the presence of foraging habitat (stubble fields), resulting errors (due to an inflated denominator in the multinomial response variable) are likely to be conservative. Overall, only 6% of the total bird-count visits analysed (i.e. 60 out of 998) were affected by a change from stubble to a cultivated substrate.

5.3.3 *Spatial dependence and spatial autocorrelation*

The problems associated with statistical inference from spatially autocorrelated data were discussed in Chapter 3 in relation to the transect scale community analysis (Chapter 4), and the east-west gradient in farming type. It was felt the data precluded a reliable quantification of possible spatial autocorrelation (because of the small sample size and irregular location of sites), and therefore, any formal approach to accounting for it. Instead, a dual modelling strategy involving a simple trend surface (the data was modelled *with* and *without* its broad scale spatial structure) provided a frame of reference for examining the importance of the farming gradient and individual landscape descriptors. In the present analysis, the potential for spatial autocorrelation (SA) in the species data resulting from the broad scale spatial dependence in the data remained. In addition, fine-scale SA was anticipated in the section data, as sections selected for analyses were generally contiguous within transects. Specifically, the presence of a species in a section may simply have been a consequence of its presence in an adjacent section, notwithstanding the fact that habitat in both was favourable. Thus, two potential sources of SA had to be considered. Once again, a dual strategy was adopted: modelling was carried out with, and without, spatial controls applied to the data. However, unlike the approach taken in the transect scale analyses, where the spatial predictor (easting and its square) was used to remove the broad scale spatial structure (detrending) in the data in a "control" analysis (RDA3), to *qualify* findings from "standard" analyses (RDA1, RDA2), the spatial predictor was retained in a set of "control" logistic regression analyses to *account for* potential SA in the modelled response (section use) resulting from the broad scale spatial structuring in species abundances. In addition, these models included an *autocovariate* term (Augustin et al. 1998) to account for potential SA at the section level. This term corrects for the non-independence of adjacent samples, and is represented by a function of the species response in transect sections adjacent to the focal section. This function may be defined somewhat arbitrarily, but it should be based on ecological considerations. For example, spatial aspects of environmental resources, or contagious biotic characteristics of the study species (e.g. flock size and dispersion) can be considered in estimating a "zone of influence" of the autocorrelated process. Siriwardena et al. (2000a) controlled for the possibility of SA in frequency index data for farmland granivores due to species associations with regional agricultural practices, and the consequent lack of independence among adjacent study units (10km grid squares). They used an autocovariate based on the frequency of occurrence of species in all sampled tetrads (2 by 2 km squares) from the nine grid squares neighbouring the focal square. They could have similarly computed a value based, for example, on all tetrads within a 50km radius. In the present analysis, an autocovariate (*AutoC*) was determined by computing the average frequency of occurrence of a species across survey visits, in the two sections adjacent to the focal section (or one adjacent section for sections at the end of contiguous blocks). For example, if Chaffinches were recorded in section A three times, and in section C six times, over the course of nine surveys, the autocovariate for section B was (3 + 6)/18. A zone of influence of 1 section was considered sufficient. Forced into models, this term was intended to explicitly account for patch-like patterns in habitat use that spanned adjacent sections. Associations between the residual species data and the environmental variables could then be interpreted with greater confidence. The effect of forcing the spatial controls, and particularly the spatial predictor, into models, ran the risk of accounting for some real effects of variation in agricultural management. The data were, therefore, also modelled to derive an alternative set of models (hereafter referred to as "regular" models), which excluded the spatial predictor and the autocovariate term.

5.3.4 *Analyses*

Model building was undertaken to describe species responses to fine-scale variation in qualitative and quantitative aspects of the field boundary infrastructure, and test for possible preferences for cereal or market gardening (overwhelmingly brassica) stubbles. As with the transect scale analysis, House Sparrow was not considered due to a dearth of data. Four models were produced for each species: univariate and multivariate, with, and without, the spatial controls described above. First, univariate models were constructed to test the significance of individual variables using likelihood-ratio tests. Then, the most significant variable found was the first entered into a multivariate model. Model building then followed a forward selection procedure until the most parsimonious model was obtained i.e. the minimum adequate model (MAM). At each step, the term that had the most significant effect (resulting in the largest decrease in deviance – a measure of relative fit), as assessed by the likelihood-ratio test, was added. The decrease in deviance, on the addition of the variable to be tested, times –2, follows a chi-square distribution with one degree of freedom for continuous (covariates) and binary variables. When factors with more than 2 levels are tested, allowances must be made for the extra degrees of freedom. The change in deviance is therefore tested against chi-square with n-1 degrees of freedom, when n is the number of levels in the factor. MAMs were obtained when no further term could be added that caused a significant decrease in deviance at the 10% level. Minitab, in addition to the global test of a factor, tests the significance of different factor levels against the reference level, to identify which is responsible for the significant effect identified in the global test. Interaction terms were not considered.

The significance of all pair wise correlations between predictor variables was determined (Table 5.2) to qualify findings from the modelling process. Tests undertaken included Spearman's rank correlation (for continuous versus continuous variable), Mann-Whitney (for 2 level factor versus continuous variable), Kruskal-Wallis (for 3 level factor versus continuous variable) and Gamma (for ≥ 2 level factor versus ≥ 2 level factor). The implications for the MAMs, of intercorrelations between the modelled habitat variables were considered by examining the effect of replacing selected variables with those showing a significant intercorrelation. Reference was also made to the results of univariate tests: because variables are correlated does not imply they will both show significant effects; also, a variable may become significant in a MAM even though it does not show significance in a univariate test.

5.4 Results

5.4.1 *General patterns in habitat use*

The overall patterns of species section use are presented in Fig. 5.3. Three spatial levels or resolutions are depicted in the graphic - section, transect and stratum; however each pair of transects (reading vertically) are approximately 0.5km apart, providing an extra spatial qualification. The grey-scale tones indicate the observed "intensity" of use, and this varied among species, especially across strata. Transects in the mixed stratum were most supportive of species generally while the MG and Pastoral strata tended to be supportive of particular species e.g. Goldfinch, Skylark, Bullfinch. This general pattern was reflected in species % section occupancy per stratum, in Table 2.2c, and is consistent with the findings from the community analyses in Chapter 4. The graphic, however, explicitly shows fine scale variation in species use of sections within transects, indicating more and less favoured sections, and those that were apparently avoided. It also illustrates the variation among

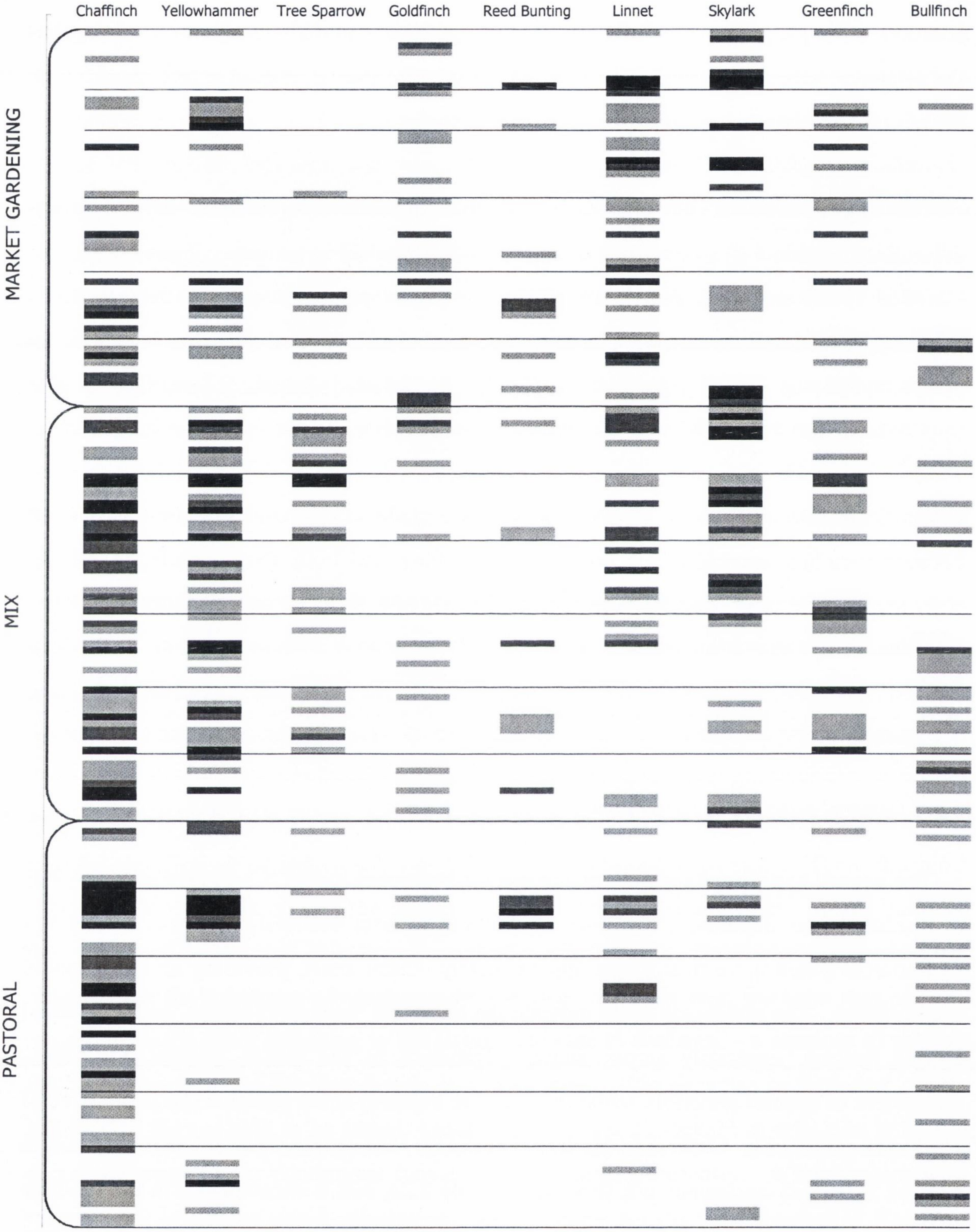


Fig. 5.3. Graphic illustrating species frequency of occurrence in 178 100m transect sections during Winter 2002-03. Individual transects are demarked by horizontal lines, ordered according to easting, paired according to site, and bracketed by stratum. Frequency of occurrence across surveys in individual sections is grey-scale coded: Black – species occurred 3 times or more; Dark Grey – 2 times; Light Grey – 1 time; White – not recorded.

species in fine scale distribution. Irrespective of species, ~75% of sections were used 5 times or less, while ~10% of sections averaged one observation or more, per visit. Species were absent from 11% of sections, and 5 or more species were recorded from only 15% of sections. Thus, habitat use was quite concentrated, and relatively few sections were speciose. Most species were absent from most of the pastoral transects, although one transect was exceptional. Approximately half of this transect was under cereal stubble. Understandably, high use (3 or more times) tended to be observed for the more abundant species i.e. for Chaffinch, Yellowhammer, Linnet and Skylark. High use was also associated with broader within-transect distribution; transects with more high use sections tended to show a greater number of used sections. For less abundant species (e.g. Greenfinch, Bullfinch, Reed Bunting), favoured sections were not so apparent, but this may represent sampling error i.e. less abundant species were more likely to be absent from preferred habitat patches during counts, and does not imply weak associations with sections.

5.4.2 *Associations among predictors*

Significant associations among the section habitat variables (Table 5.2) and their individual correlations with easting highlighted boundary management differences across farming types. Management was generally more severe on the MG transects, resulting in fewer tree lines and lower hedges, hence the negative correlation of these variables with

Table 5.2. Significant correlations between all pair wise combinations of variables used in analyses. Correlation tests included Spearman's rank correlation (continuous variable versus continuous variable), Mann-Whitney (2-level factor versus continuous variable), Kruskal-Wallis (3-level factor versus continuous variable) and Gamma ($\geq$ 2-level factor versus $\geq$ 2-level factor). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Cerstub	*Treeline*	*Trees*	*Boundary*	*Index B*	*Index M*	*Easting*
Cerstub							
Treeline	+ *						
Trees							
Boundary			+ **				
Index B	+ *	+ ***					
Index M		+ *			+ ***		
Easting	– ***	– ***			– ***		

easting. The correlation between *Index B* and *Index M* was expected, as unmanaged hedges were usually tall, although not all intensively managed hedges were short. The moderate positive association between *Trees* and *Boundary* (Gamma Index for association between ordinal variables = 0.47) was not anticipated. If, however, management efforts tend to be directed away from areas that may be more difficult (machinery access to field corners), or less cost effective (less crop in corners) to manage, this relationship might be expected. *Boundary* served as a surrogate measure for the number of hedges and hedge intersections per section, and the complexity represented by high levels of this factor may discourage intensive management. A complex of positive associations was found for the presence of tree lines, taller, and less intensively managed boundaries, probably reflecting preference for less intensive management, in general, within the sections concerned.

5.4.3 *Logistic regression analyses - univariate*

Tables 5.3a and 5.3b present the results of univariate tests of regular and control models, respectively. *Easting* had positive and negative effects on species reflecting the broader patterns highlighted in the Fig. 5.3. Frequency of occurrence in sections increased significantly in an easterly direction for Linnet and Skylark, but decreased significantly for Chaffinch and Reed Bunting. The autocovariate *AutoC* was important among the more abundant species indicating that habitat use and spatial occurrence was often "patch-like" across adjacent sections. The inclusion of the spatial control terms (Table 5.3b) did not change significance levels for most variables, however spatially confounded effects were indicated for several variables. A positive effect of increased boundary density, *Boundary*, was revealed for Chaffinch and Yellowhammer in control models, while a positive association with taller boundaries, *Index B*, disappeared for Yellowhammer. Similarly, management intensity, *Index M*, increased in importance for Reed Bunting, and the negative effect of treelines, *Treeline*, became insignificant for Linnet. *Index B* was the most important variable across species, with 7 and 8 significant associations respectively, in the control and regular models. Positive associations were most common. Despite a strong correlation with *Index M* (Spearman's *rho* = 0.683), it was not always the case that an association with one variable implied an association with the other. Four species

(Linnet, Tree Sparrow, Goldfinch, Reed Bunting) showed an association with one, or the other, in the control models (indeed, Tree Sparrow showed opposite relationships with both, in the control and regular MAMs, see below). Contrasting associations were found across species with the variables describing boundary density and the occurrence of trees (*Trees*). Increasing boundary density favoured Chaffinch, Yellowhammer and Greenfinch, and lower values favoured Skylark. Low tree occurrence had negative effects on Chaffinch, Yellowhammer, Tree Sparrow and Greenfinch, but favoured Skylark. Higher occurrence was positively associated with Chaffinch, Goldfinch and Reed Bunting.

5.4.4 *Logistic regression analyses - MAMs*

After forcing the spatial control terms into models, the significance and direction of associations remained essentially unchanged in the control and regular MAMs for Greenfinch, Bullfinch, Goldfinch, Tree Sparrow and Linnet (Table 5.4a, b). For the remaining species (excepting Skylark for *Easting*) *Easting* was significant at the 10% level and *AutoC* showed high significance, resulting in several differences between control and regular models. As in the univariate models, inclusion of the control terms revealed a positive effect of increased boundary density in Chaffinch and Yellowhammer; in the latter, the positive effects of increased availability of trees and increasing hedge height disappeared. For Skylark, a negative effect of increasing boundary density was found in the control model, and cereal stubble showed a negative influence. *Index B* was the most important variable across species, showing contrasting effects, and *Trees* and *Boundary* also showed a mixture of positive and negative effects. Models for Chaffinch, Yellowhammer, Skylark and Greenfinch had the greatest number of significant associations, while only one significant effect was observed for Linnet and Bullfinch.

Table 5.3. Results of univariate tests of species section use with, and without, spatial control terms. (a) Shows the significance of the broad-scale control term, E*asting*, and the fine scale control term *AutoC*, ($P < 0.05$ in bold), in addition to significant associations with the considered landscape measures. (b) Shows significant associations after forcing the spatial control terms into univariate models. Associations significant at 10% level, assessed by likelihood-ratio tests, are reported. Plus (+) and minus (–) signs indicate the direction of the effects with respect to variables (cf. Table 5.1).

(a)

Variable	**Chaffinch**	**Linnet**	**Yellowhammer**	**Tree Sparrow**	**Goldfinch**	**Reed Bunting**	**Skylark**	**Greenfinch**	**Bullfinch**
***n* present**	67	41	55	25	23	19	40	31	28
Cerstub	– 0.000		– 0.057		+ 0.001			– 0.108	
Treeline	+ 0.000	– 0.094					– 0.000		
Trees									
none	– 0.006		– 0.000	– 0.001			+ 0.004	– 0.003	
> 2	+ 0.003				+ 0.057	+ 0.013			
Boundary									
< 150m	– 0.000		– 0.016				+ 0.000	– 0.109	
> 250m								+ 0.000	
Index B	+ 0.000	– 0.007	+ 0.026	+ 0.051	– 0.005		– 0.000	+ 0.005	+ 0.017
Index M	+ 0.003	– 0.040			– 0.052		– 0.000	+ 0.079	+ 0.059
Easting	**– 0.000**	**+ 0.025**	+ 0.111	+ 0.624	+ 0.127	**– 0.028**	**+ 0.007**	+ 0.521	– 0.201
AutoC	**+ 0.000**	**+ 0.035**	**+ 0.000**	+ 0.247	+ 0.077	**+ 0.000**	**+ 0.000**	+ 0.221	+ 0.312

(b)

Variable	**Chaffinch**	**Linnet**	**Yellowhammer**	**Tree Sparrow**	**Goldfinch**	**Reed Bunting**	**Skylark**	**Greenfinch**	**Bullfinch**
Cerstub					+ 0.007			– 0.102	
Treeline	+ 0.006						– 0.020		
Trees									
none	– 0.010		– 0.001	– 0.002			+ 0.034	– 0.004	
> 2	+ 0.007				+ 0.072	+ 0.042			
Boundary									
< 150m	– 0.000		– 0.015				+ 0.000	– 0.103	
> 250m	+ 0.053		+ 0.059					+ 0.001	
Index B	+ 0.000	– 0.089		+ 0.033	– 0.027		– 0.000	+ 0.001	+ 0.040
Index M	+ 0.014					– 0.079	– 0.000	+ 0.057	+ 0.109

Table 5.4. Results of multivariate analyses of species section use with, and without, spatial control terms. (a) Final models without spatial control terms, (b) final models with spatial control terms. Associations significant at 10% level, assessed by likelihood-ratio tests, are reported. Plus (+) and minus (–) signs indicate the direction of the effects with respect to variables (cf. Table 5.1).

(a)

Variable	**Chaffinch**	**Linnet**	**Yellowhammer**	**Tree Sparrow**	**Goldfinch**	**Reed Bunting**	**Skylark**	**Greenfinch**	**Bullfinch**
***n* present**	67	41	55	25	23	19	40	31	28
Cerstub	– 0.020				+ 0.003				
Treeline			– 0.041				– 0.094		
Trees									
none			– 0.001	– 0.002				– 0.011	
> 2	+ 0.009		+ 0.107			+ 0.002			
Boundary									
< 150m	– 0.022						+ 0.007		
> 250m						– 0.098		+ 0.000	
Index B	+ 0.000	– 0.007	+ 0.008	+ 0.001	– 0.017			+ 0.004	+ 0.017
Index M				– 0.002			– 0.001		

(b)

Variable	**Chaffinch**	**Linnet**	**Yellowhammer**	**Tree Sparrow**	**Goldfinch**	**Reed Bunting**	**Skylark**	**Greenfinch**	**Bullfinch**
Cerstub					+ 0.009		+ 0.070		
Treeline			– 0.107						
Trees									
none			– 0.015	– 0.002				– 0.012	
> 2	+ 0.040					+ 0.049			
Boundary									
< 150m	– 0.009						+ 0.001		
> 250m	+ 0.083		+ 0.076				– 0.046	+ 0.000	
Index B	+ 0.000	– 0.089		+ 0.000	– 0.031			+ 0.002	+ 0.040
Index M				– 0.003		– 0.087	– 0.001		
Easting	– 0.062		– 0.080			– 0.098			
AutoC	+ 0.007		+ 0.000			+ 0.013	+ 0.000		

5.5 Discussion

The aim of the regression analyses was to determine if stubble type, structural, and infrastructural attributes of the field boundaries influenced patterns of habitat use among species. The results suggested that far from being a functionally homogeneous group during the winter, species differed in their associations with finer scale "landscape" variation. This finding is broadly consistent with those from several recent winter studies of granivores (e.g. Siriwardena & Stevens 2004, Calladine et al. 2003), and highlights the need for greater autecological understanding of these species during the winter, as species differences may have important implications for winter conservation measures. In discussing the observed distribution patterns, it is important to acknowledge the limitations associated with the observations made at the 100m resolution. These are likely to represent the influences of a hierarchy of factors i.e. important components of habitat are found, and act, at different spatial scales. For example, within field factors (e.g. Robinson et al. 1999, Moorcroft et al. 2002) were not measured, and if very variable from section to section, could have generated much "noise" and confounding in the results of analyses. Similarly, features of broader landscape composition (e.g. the prevalence of other habitat types, the configuration of habitat components) were not measured, which could have affected species regional patterns. It is arguable, however, that these influences pertain to different hierarchical levels in habitat effects, to the one considered, so that their effects were broadly general - in the case of higher level broad scale factors, and generally subordinate – in the case of within-field scale factors, to the *mesoscale* influences of field boundary structure. The results are discussed in light of such considerations, and broadly in relation to the range of processes considered in the studies cited in the introduction to Chapter 4.

5.5.1 *The significance of the section scale*

As already discussed (Chapter 4), the choice of 1km transects as sampling units in a winter context was made somewhat arbitrarily. However, they were found to capture regional variation in landscape components that appeared to be important influences on community structure. Their sub-division into 100m sections represented an attempt to identify finer scale influences on species distribution patterns. This spatial resolution was considered useful for capturing fine-scale landscape structural variation, as much as for investigating an *a priori* notion that species responded to habitat patchiness at this scale. The hypothesis that patterns of winter habitat use are influenced at this scale, by variation in field boundary attributes is, however, reasonable. For example, a common behavioural observation during fieldwork was of birds foraging up to 30m into the field, and repeatedly retreating to the boundary in a skittish manner. Several birds were usually present in boundaries, while others foraged. This behavior is largely related to vigilance against actual and perceived predation risks, principally from avian predators such as Sparrowhawks *Accipiter nissus*. In this respect, variation in the structural attributes of field boundaries and spatial patterning, within 50m of a foraging flock may influence patterns of habitat use. Notwithstanding, the resolution is broadly commensurate with the spatial scales considered in Arnold (1983), Parish et al. (1995a,b), Calladine et al. (2003) and Siriwardena & Stevens (2004), allowing reliable comparison of observations.

5.5.2 *Methodological issues*

Most studies of finer scale community processes of farmland birds have focused on species relationships with, and within, discrete habitat components, such as individual fields or 200m stretches of hedgerow. As has been pointed out (e.g. Wiens 1989, Fuller et al. 2004), habitat selection cues used by birds may not necessarily coincide with such units (i.e. habitat definitions often used by humans). The restricted focus of these studies may certainly determine important functional qualities of these units, but it often ignores influences that may be of proximate importance for observations. A grid sampling approach, on the other hand, may address this problem by allowing a broader range in variation of possible influences governing processes of interest to be sampled. The starting point of the grid arbitrarily determines what each cell-sample represents, and provided grid cells (in this study, transect sections) are of an appropriate size to capture "working" variation in the processes under investigation, and sample sizes are adequate, a more comprehensive picture of important factors is possible. However, the ability to make inferences regarding the effects of factors acting at finer or broader spatial scales depends on the resolution and extent of the grid. Drawbacks of the approach are a loss of experimental control of samples, for example, when an "event" is divided between adjacent cells, resulting in pseudoreplication (cell samples are certainly not independent observations of the process of interest), or when a factor identified in one cell influences events in an adjacent cell or cells. Nevertheless, the approach explicitly compared the use of space among species, and provided a basis for identifying correlates of section use. This could thus provide useful details for explaining the broader community patterns observed at the transect scale.

The tested habitat variables described coarse variation in structural and infra-structural attributes of the boundaries associated with stubble fields. Analyses of species relationships with this variation, however, unrealistically assumed that each sample section provided similar levels of seed food resources during the study. It was beyond the scope of the study to measure these resources, and although it was anticipated that areas with more seed should attract higher numbers of birds (Robinson & Sutherland 1999), perhaps more frequently (Moorcroft et al. 2002), there was no reason to expect such patches to be correlated with the analysed variables (a moot point is a possible association with boundary density – discussed below). In light of the above, and the omission from analyses of other possible influences such as the width of boundaries (Parish et al. 1995) or within-field vegetation cover (Moorcroft et al. 2002), there was little expectation that derived models would show good fits in terms of some pseudo r-squared measure, so no attempt was made to estimate fit. Rather, it was considered the approach would yield additional or alternative insights into more general patterns of winter habitat use (not just restricted to foraging behaviour), not addressed by more traditional "field oriented" approaches.

5.5.3 *The effects of habitat variation at the section scale*

The simplest models obtained were for Linnet and Bullfinch, for which boundary height appeared to be the only important factor (although an unfavourable effect of treelines was suggested for Linnet in the regular univariate analysis). The community ordination (Figs. 3.1, 4.2a) indicated a negative correlation between these species on transects, and this was consistent with the opposing effects observed at the section scale. Indeed, the only negative correlation among species section use scores was observed between these species (Spearman's *rho* 0.22; $P < 0.05$). Bullfinches were invariably recorded in taller, broader and bushier hedges (associations with *Index B* and *Index M*). In contrast, Linnets are regarded as "open field" species, and although they were occasionally observed foraging close to taller hedges during field work, the observed tendency was for sizeable flocks to range and forage in the more open areas. They were often seen "outside" transects i.e. beyond 100m, foraging in field centres, however the negative relationship with taller boundaries suggested such observations did not simply represent independence of boundaries *per se*. Siriwardena & Stevens (2004) rarely observed Linnets at supplementary feeding sites that were specifically located close to cover, and an association with "open" 1km squares was found on Scottish farmland (Hancock & Wilson, 2003). Linnets, above all other farmland granivores, show a tendency to form large flocks, and it is arguable that this behavioural trait becomes of diminishing value and efficiency, from the point of view of anti-predator vigilance, in the presence of visually obstructive cover (e.g. tall dense hedges or treelines). Larger flocks, on the other hand, can forage in exposed areas while maintaining a high level of vigilance, and exploit resources generally unavailable to smaller flocks. The perception that Goldfinch habitat use was similar to that of Linnet was borne out by a positive section use correlation between these species (Spearman's *rho*, 0.247, $P < 0.05$). The general observation was of reasonable sized flocks ranging in more open habitat, often in the presence of Linnets, and showing no particular affinity for field boundaries. The multiple regression models suggested an avoidance of taller boundaries, independent of the preference shown for non-cereal stubbles, despite the broad negative correlation between these factors.

A more explicit avoidance of hedgerows was apparent in the models for Skylark, although this was not related to flock size. Several large flocks were recorded (100+ birds), but most observations were of smaller groups of less than 5 birds. Their use of stubble fields was restricted by boundary attributes that decreased habitat openness, and their tendency to use central areas of fields (Robinson & Sutherland 1999, Hinsley & Bellamy 2000) was reflected in a negative relationship with increasing boundary density i.e. they avoided field intersections (a positive association with lower presence of trees found in the univariate analyses may reflect confounding in these variables – *Trees* was positively correlated with *Boundary* (Table 5.2)). As with Linnets, many observations were of birds outside transects limits. Increasing intensity of management of boundaries was more important than decreasing hedge height and this pattern was observed also in Reed Bunting and Tree Sparrow. Tree Sparrows were rarely encountered on the MG transects (Fig. 5.3), so the results for this species are derived primarily from the Mixed transects. The contrasting directions of effects of increasing boundary height and management intensity suggested that sections with taller but well-managed hedges were preferred over those with unmanaged hedges. While Reed Buntings were also associated with more managed hedges in the control models, a greater presence of trees also appeared favourable. This species may have been associated with more exposed ditches resulting from more intensive hedge management; in unmanaged hedges, branches and undergrowth often covered over ditches to the point of concealment. Isolated bushes/trees may have been important as perches or vantage points. The presence of trees was important also for Yellowhammer, Tree Sparrow and Greenfinch; however these species did not show the positive association with increasing availability of trees in sections shown by Chaffinch. This difference probably reflects the woodland affiliation in Chaffinch (Gibbons et al. 1993, Whittingham et al. 2001). The importance of trees in providing cover, a perch or vantage point, for the other species is suggested. Indeed, in the control MAM, Yellowhammer was found to be independent of hedge height while showing a negative response to the absence of trees, suggesting that it may not have been constrained by low hedge height in sections provided there were a few trees around. Interestingly, it showed a negative association with the presence of tree lines, a pattern observed during the breeding season in Bradbury et al. (2000). Across much of its range, the Chaffinch is regarded primarily as a bird of woodland (Hagemeijer & Blair 1997); however, it is common and widespread in farmland habitats during the breeding season in Britain and Ireland (e.g. Fig. 2.6, Robinson et al. 2005). Whittingham et al. (2001) attributed this to its relative independence of land use practices, and the presence of trees in this habitat (particularly Oaks *Quercus* spp. and Willows *Salix* spp.), important in providing foraging resources. The patterns emerging from the present study suggest these considerations may also apply during the winter;

Chaffinch habitat use was positively associated with the availability of trees, and its distribution appeared to be limited more by the qualities of the boundary habitat than by land use. Section use patterns across the strata (Fig. 5.3) show it was well supported on the pastoral transects (in contrast to the other species), and less supported on the market gardening transects, where field boundaries were subject to more intensive management. A similar distribution pattern was observed for Bullfinch, although this more obviously implicated its dietary difference (noted in Chapter 4) from the other species during the winter. It is noteworthy that approximately 30% of sections recording Bullfinch were eliminated in the section screening process, underlining its independence of arable habitat.

The easting term served as a proxy for several variables that were correlated with the farming type gradient, including hedge height, the prevalence of treelines, and of cereal stubbles. It was hoped that its inclusion as a control factor would dampen broader landscape effects (landscape composition effects related to the farming gradient) on species abundances that may have generated autocorrelation in the species data. Its inclusion in models appeared to elucidate some spatially confounded responses; however, it is difficult to assess the appropriateness of the measure. It was most instrumental in suggesting interactive effects of boundary density and boundary height in Skylarks, Chaffinches and Yellowhammers, by accounting for the effects of the general west to east trend in boundary height. Thus, there would be no relationship with boundary density in Chaffinch if boundaries were very low. Similarly, Skylark only showed a significant aversion to a higher density of taller boundaries. It is possible that the positive association with higher boundary density for some species was related to a greater accessibility to seed resources. Thus, for cover-dependent species, a greater area of potential foraging substrate is available in sections with hedge intersections. It is also possible intersections themselves will be richer in seed resources because of management difficulties. Lack (1988) and Hinsley & Bellamy (2000) discussed several functional advantages of hedge intersections over equivalent (in terms of length, and habitat composition e.g. the number of trees) straight-hedge sections in terms of energy efficiency and edge to area ratios, and noted the increased options afforded for shelter and escape from predators. Lack (1988) found greater territorial activity at intersections compared with straight sections in several species of farmland birds. However, of the three granivore specie he considered – Chaffinch, Yellowhammer and Tree Sparrow, only Chaffinch suggested an association with intersections ($P < 0.1$, paired *t*-test). Notwithstanding, a strong case remains for the importance of species fundamental habitat affiliations, to woodland or scrub for example. Intersections provide a general increase in structure and complexity that may approximate primary (or preferred) habitat conditions.

The effects of variation in boundary height and management intensity on species were not affected by the inclusion of control terms (univariate and MAMs generally), with the exception of Reed Bunting – an avoidance of less managed hedges was suggested, and Yellowhammer – when the positive association with hedge height was no longer significant. The significance of the autocovariate term in several of the MAMs indicated that for these species, frequency of occurrence in sections was positively correlated with their occurrence in neighbouring sections. This suggests that favourable habitat frequently occurred at scales broader than 100m, indeed, at scales broadly commensurate with that of the individual field. This may indicate quality differences among fields relating to seed resource abundance or accessibility. Nevertheless, section use remained associated with the structural and infrastructural aspects of the boundaries, after controlling for this patchiness.

Hancock and Wilson (2003) highlighted a broad dichotomy within granivorous passerines wintering on Scottish farmland, based on their responses to variables implying habitat "openness". In their study, Skylark, Linnet, Tree Sparrow and Reed Bunting showed associations with 1km squares with lower cover of woodland and scrub compared with other granivores. This pattern was also described at the field scale, with lower densities being found in fields with some woodland or scrub around them. The section scale analyses of this study suggested similar associations in relation to habitat use for Linnet and Skylark. The results for Reed Bunting and Tree Sparrow showed less agreement. The patterns observed for Goldfinch suggested preferences for locally open areas (although the availability of trees was favourable in the univariate models), agreeing generally with Siriwardena & Stevens (2004), who found a preference for experimental feeding sites located at greater distances to cover, and an avoidance of high and deep cover (large hedges and trees).

The various associations reported in Tables 5.2a and 5.2b provide a reasonably clear picture of species use of the fundamental mosaic comprising the farmland of the study area. This mosaic was most clearly reflected in the contrasting habitat use patterns shown by Skylarks and Chaffinches, while other species showed varying levels of dependence on, and relationships with, structural and other attribute variation of field boundaries. Thus, at the 100m resolution, the landscape varied locally (within transects) and more broadly (across strata), in terms of hedgerow type, height and density, and in the availability of trees. Species appeared to respond to this variation (patchiness) irrespective of other unmeasured influences. The associations observed may allude to more fundamental habitat preferences and/or differences in habitat use, as there is little in the literature to suggest that competition is important for granivores during the winter, which could otherwise result in habitat partitioning. Replicate studies from different regions would shed further light on the importance of the observed patterns. In this respect, Siriwardena & Stevens (2004) found several inconsistent results between two very similar studies of the influence of local habitat on winter use of supplementary foraging sites, conducted across different regions (one study was conducted within a region, and the other conducted across several regions). In both studies, a prevailing pattern of species-specific responses to habitat variation was observed, and this discouraged them from deriving general prescriptions for the location of supplementary feeding sites. The results of the present analysis also point to species-specific responses to local habitat variation, although in a more general and "natural" context i.e. responses to habitat variation were not restricted to observations of foraging activity at artificial foraging stations.

5.6 Main points and conclusions

- the tested habitat variables described coarse variation in structural and infra-structural attributes of the boundaries associated with stubble fields

- a range of contrasting and species-specific relationships were identified, which may have important implications for the design of winter conservation measures
- many of these relationships alluded to a broad dichotomy in farmland granivores based on species preferences for open and closed landscapes
- these patterns probably reflect more fundamental habitat preferences, as competition does not appear to be a strong organising force among farmland granivores, at least during the winter

Chapter 6. Community integration – from habitat use to community structure

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Preface

In the preceding chapters, distribution and abundance patterns have been described at three spatial levels or resolutions in relation to a 20km geographical agricultural gradient. Analyses were conducted to determine species-habitat relationships at two spatial resolutions; the transect level (0.2km^2) and the transect section level (0.02km^2). The schematic in Chapter 5 (Fig. 5.3) provides a useful representation of the analysed species patterns. The differential effect of the gradient among species is quite clear at the landscape scale, while finer scale variation in habitat use is also apparent. The intention of this chapter is to bring together the ecological patterns described by the analyses at the two scales. In particular, I consider the extent to which local assemblages (i.e. species patterns at the transect scale) represent the aggregation of fine scale habitat use processes, the possible habitat factors involved, and how this manifests at broader community scales.

6.1 Introduction

Redundancy analyses in Chapter 4 found community structure (summarized at the transect scale) varied in a significant way with quantitative measures of crop type and field boundary attributes. In Chapter 5, it was suggested that this variation reflected (in part) species-specific responses to finer scale habitat variation. This was investigated by conducting logistic regression analyses on data that summarized habitat and patterns of habitat use among species at a spatial level of 100m transect sections. Modelling of these data found statistically significant associations between species' frequency of occurrence in sections, stubble type, and the structural and spatial variation in the field boundary habitat. Although it was possible to simply examine community patterns (described by the RDA analyses) in light of these results, a supplementary "bridging" analysis was conducted which took advantage of the fine scale variation described by the section data, providing additional information and perspective. Thus, an alternative transect level data set was derived from the section scale data which implicitly incorporated a measure of the spatial extent of the fine scale processes (section level habitat attributes and species section use). The correspondence in the results from the different sets of analyses was then examined. In particular, the implications of the results from the fine scale analyses are explored in terms of the hypothesis that granivore community structure during the winter reflects species-specific responses to fine scale variation in field boundary habitat, and preferences for different stubble types. It is argued that variables that showed consistent significant effects across analyses are particularly important determinants of community structure in farming landscapes.

6.2 Aims and objectives

- to investigate if correlates of species' habitat use at the sections scale were manifest at the transect scale
- to explore the consequences for community structure across the study area, of any such correspondence

6.3 The bridging analysis

6.3.1 *Data treatment*

As explained in Chapter 5, to conduct the logistic regression analyses of section use by species, alternative expressions of the quantitative habitat data used in the transect summaries were necessary. Thus, attribute presence or absence, factors with 3 levels, and field boundary indices were derived for each section. For the purposes of the "bridging analysis", transect summaries were derived from the section level data simply by enumerating sections pertaining to particular factor levels and attributes (Table 6.1). To compute summaries for the sectional boundary (*Index B*) and management (*Index M*) indices, sections were allocated to 3 and 4 index intervals respectively, and counted accordingly. Additionally, a new index of *B* and *M* was calculated for each transect as follows. Each section was allocated to one of 6 or 8 equal classes, for *B* and *M* respectively, and the number of sections in each class was multiplied by the class number (i.e. 1 to 6 for *B*, and 1 to 8 for *M*). These values were then summed to give a value for each transect.

Table 6.1. Transect summary variables for section level data (see Table 5.1) analysed in "bridging" analysis.

- Number of transect sections
    - with "full term" stubble of Brassica or MG crop
    - with "full term" stubble of Cereal crop
    - belonging in each class interval for factors -
        - *Trees* for factor level details see Table 5.1
        - *Boundary* "
    - belonging in each class interval for indices -
        - *Index B:* 0 to < 1: 1 to < 2; 2 - 3
        - *Index M:* 0 to < 1: 1 to < 2; 2 to < 3; 3 - 4
- New indices for whole transect derived from sections scores for *Index B* and *Index M*
    - Index B *overall*
    - Index M *overall*

This alternative environmental data set was broadly analogous to the "quantitative" data set describing transects, however several differences should be noted. Stubble types in the logistic regression were either cereal or non-cereal, with the latter including the minor cover of potato stubbles. This cover, therefore, made a minor contribution in the tallies of sections with "full term" brassica or MG stubbles. In the "quantitative" data set, potato stubbles were not considered (when tested in preliminary analyses for Chapter 4 as a quantitative variable and as a present/absent attribute, no effects were suggested). The effect of the presence of treelines was tested at the section level, but the overall length of treelines on transects was not considered in the "quantitative" analyses. Possible effects tested for at the transect scale, but not at the section scale, included those related to the cover of cultivated land (till and plough), and of grass. The most pertinent aspect of the new data set was that it implied a measure of the spatial extent of fine scale habitat variation, which was not specifically addressed in the "quantitative" approach. All sections comprising transects included in analyses (see below) were used to derive this new data summary.

Similar consideration was given as to how to best use the fine scale detail of the species section use data, in a transect summary. Although abundance is the most frequently used measure of importance in "gradient" type studies, it says nothing specific about how species are distributed within sampling units. The mapping of species' occurrences in transect sections provided fine scale detail of distribution patterns implicit in the abundance estimates for transects. Thus, Chapter 2 noted strong positive correlations between species' occurrence among sections and their abundance on transects (Spearman's *rho* 0.82 ± 0.11, mean ± SD). Further, subsequent tests found a tendency (albeit weak for the less abundant species) for greater use of individual sections to be significantly positively correlated with mean abundance per observation i.e. more frequently used sections tended to attract more birds generally. Strong patterns were observed in Chaffinch, Linnet and Yellowhammer, while significant associations were observed in Tree Sparrow, Goldfinch and Bullfinch (Spearman's *rho*, $P < 0.05$). Given these relationships, if a measure of transect use by a species, incorporating aspects of both spatial distribution and frequency of use (a "weight of use" measure) was possible, this provides a refined alternative to the transect scale abundance measure, density per hectare.

Several transect "weight of use" (WOU) measures were considered including the number of sections used at least once, and the total proportion of section/visits recording a species. However, these were perhaps not as informative as some of the *information-theoretic* indices (Magurran 1991) that could be used to describe the data. Usually in ecology, these indices are used for comparative purposes to measure the diversity of species assemblages among different samples. In theory, however, they measure the diversity of particular *states* and vary in the extent to which they emphasise the number of states – *richness* (e.g. the number of species in a sample), and the measure of relationship among the states expressing *evenness/dominance* (e.g. species relative abundances). They are often used to measure heterogeneity in data e.g. habitat or land use heterogeneity in an area. In the current context, the intention was to find a measure of transect use by a species that would emphasise the number of sections used *and* the frequency with which they were used. Thus, a useful index would increase as the spatial distribution of a species i.e. the number of sections used on each transect, increased. It would also increase as the frequency of use of these sections increased generally, and more specifically, when this increase in frequency was more equitable among sections. It was not the purpose to make comparisons among transects (in which case different numbers of sections and counts among transects would be problematic), but rather to explore possible associations between WOU and the transect summaries of sectional habitat.

The qualities of several diversity indices were considered including the Shannon-Weiner, Simpson, and the Brillouin. The latter was chosen over the Shannon Index, because the Brillouin index, unlike the Shannon, is sensitive to an increase in frequency of use while evenness remains constant (In general, the Shannon Index is not sensitive to increase in abundance if the proportional abundance (or other measure of relationship among states) remains constant). The performance of the index on an artificial data set, which broadly circumscribed the patterns found in the actual data, is summarised in Table 6.2. Calculated index values increased as the number of sections used, and the frequency with which they were used, increased. When the number of sections used, and overall "use" were kept constant, the index increased with evenness i.e. with increasing equitability of observations among sections. Several examples will clarify these results. Say on two

Table 6.2. The behaviour of the Brillouin Index (vertical arrows indicating increasing or decreasing calculated value) when applied to an artificial data set describing covarying patterns in the frequency of use, and the number of sections used, by species on transects.

		As the frequency of section use		
		Increases	Stays constant	Decreases
As the number of sections used on transects	Increases	↑	↑	↑
	Stays constant	↑	↑ with evenness	↓
	Decreases	↓	↓	↓

transects, A and B, each having 10 sections, a species occurs during the course of 10 count visits twice in each section on A and three times in each section on transect B i.e. A – 2222222222, B – 3333333333, it is clear that B should have a higher WOU than A. The Brillouin Index scores B higher than A, unlike the Shannon, which gives an equal score to both. These observation patterns also suggests that favourable habitat is evenly distributed across sections of both transects, and that the habitat on B is slightly more favourable than that on A. Again, on two more transects (C and D), if a species occurrence was recorded giving a pattern of 0404040404 (20 occurrences) on C, and 2222222222 (again 20 occurrences) on D, it is arguable that transect D, as a whole, shows a higher WOU than C, as more of the transect is being used, even though the frequency of observations is the same. The Brillouin Index scores higher for transect D than for transect C. Importantly, this pattern of observations suggests that favourable habitat is generally present on D, but only present in every second section on C. If, on two more transects (E and F), 30 occurrences were distributed across all sections of the transects according to the pattern 1351351353 on E, and 3333333333 on F, it is again arguable that WOU should be higher for F, and that favourable habitat is more available generally on F. In this case, the Brillouin Index scores higher for F, despite the similar number of occurrences on transects, and the fact that all sections record a species; the index gives weight to the equitability of occurrences among sections. It is notable also, that within the covarying patterns examined in the artificial data, proportionally more weight was given to increasing *number* of sections used, even though overall *frequency of use* declined (top right hand arrow in Table 6.2). More generally, most diversity indices increase as the number of "states" (here, sections recording a species) and their evenness (equitability of records among sections) increase. The Brillouin Index can, therefore, be used to derive a robust WOU measure, which scores the spatial extent and equitability of species use of transects during the winter, while also scoring for variation in the frequency of occurrence in used sections.

Brillouin indices were determined for each species for each transect. All sections comprising transects included in analyses (see below) were used to derive this new data summary. In effect, the index scores the overall "darkness" of transects depicted in Fig. 5.3. A minor problem in the use of the index as a WOU measure was that the score for a transect which records a species in only one section is zero. To distinguish "true" absence from cases when only one section recorded a species, an arbitrary value was given to the latter equal to half the lowest possible score, obtained when a single observation is recorded in two sections. In practice, calculated Shannon and Brillouin index values were very highly correlated for all species (Pearson's correlation ≥ 0.98).

6.3.2 *Analysis rationale*

The purpose of conducting the bridging analysis was to examine whether the results obtained in the section scale analyses of habitat use (Chapter 5) were apparent at broader scales. Firstly, Spearman's rank correlation tests were used to test for associations between the two new data sets described above. The significance of these data is their implicit spatial dimension: both summarise transects in terms of the extent of fine scale species and habitat processes i.e. habitat *use* and *variation* occurring at a resolution of 0.02km^2. The results of these tests are then compared to the results from the section scale analyses of Chapter 5 to identify those factors which showed significance in both, indicating an aggregated effect at the transect scale i.e. an effect across spatial scales. It is arguable then, that these factors are particularly important determinants of community structure because a link is established between broader community and habitat patterns on one hand, and fine scale correlates of species distribution and habitat use, on the other.

The following assumptions and considerations are proposed for the interpretation of the results:

- it is assumed that suitable habitat on transects is broadly saturated and therefore, that WOU corresponds to the availability and quality of this habitat
- important habitat attributes determine the extent and frequency of habitat use, and these will be especially reflected in WOU
- community variation will reflect the availability of important habitat attributes

In other words, transects with higher or lower "amounts" of important section scale habitat attributes should show corresponding patterns in WOU. Also, community diversity or species richness on transects should reflect heterogeneity in the various habitat components identified as important for habitat use in individual species.

6.3.3 *Analysis and comparison tables*

For all intents and purposes, the logistic regression analyses drew from the data represented in RDA Fig. 5.1, as the three transects omitted from this analysis contributed just three samples (out of 116) to the logistic regression data. For consistency, and for the same reasons given at the start of Chapter 5 for omitting these transects in the RDA, the bridging analysis considered just the same 15 transects. Species WOU was tested (two-tailed) for correlation with the transect summaries of the section scale habitat descriptions using Spearman's rank correlation, and results significant at $\alpha = 0.15$ are reported in Tables 6.5a and 6.5b. All numerical information in these tables relates to this analysis. The tables also include another layer of information summarising the performance of variables and factors tested and modelled in the analyses of section use (see Tables 5.3a, b; 5.4a, b). Table cells are formatted with respect to the direction and significance of effects in the univariate tests and in the MAMs (see Table 6.4 for interpretive guide). Several transect summaries in Table 6.5b do not relate directly to factors and covariates tested in the logistic regression, however, they provide additional relevant information. The tables thus summarise species responses at the two scales of enquiry, and highlight instances when relationships found at the section scale were apparent at the transect level.

6.3.4 *Additional considerations and analyses*

Since positive associations were found between species abundances and number of sections used on transects, and between frequency of use of sections and mean abundance per observation, it was predicted that WOU would be positively correlated with abundance. Correlation tests (Spearman's *rho*, one-tailed) were conducted to assess the association between species abundance and WOU for transects. It was necessary, however, to first standardise the calculated WOU values to make them comparable in these analyses. This is because the values taken by the index are case specific i.e. they pertain to specific combinations of the number of sections comprising transects, and the number of counts each received. This created the potential problem that similar values among transects could have resulted from quite different section occurrence and frequency data, yet the intention was to correlate these values to standardized abundance data. To ameliorate this, WOU values were standardised according to a transect specific maximum possible value (obtained if all sections are occupied by a species on all census counts). (This was not a problem in the WOU – transect section summary correlation tests because the correlations being evaluated related specifically to variation in the number of sections on transects with particular habitat attributes.)

It was also considered informative to compare among species, the correspondence between WOU and abundance estimates. The standardized value of WOU was proposed and tested as a predictor of raw abundance in simple linear regression analyses. Given the positive association between abundance on transects and number of sections used, and between mean abundance in sections and frequency of use of sections (increases in both number and frequency cause WOU to increase), the derived r-squared values broadly characterised the equitability of a species distribution among used sections. Higher r-squared values indicated abundance covaried more closely with WOU, so that across transects generally, abundance estimates were more likely to be derived from a more equitable distribution of observations (of flocks or individuals) among used sections. Conversely, lower r-squared values indicated abundances were less evenly distributed with respect to WOU. The r-squared values thus provided a basis for comparing species in terms of the "distribution of individuals" (more even or more variable), alluding, therefore, to flocking characteristics. Further insight in this respect was provided by calculating "Variance to Mean" ratios for species *abundance per observation* i.e. mean across counts recording the species, across sections. These broadly reflected the range in flock size occurring across sections.

6.4 Results and discussion

6.4.1 *Abundance and distribution patterns*

The statistics in Table 6.3 reflect differences in abundance and distribution patterns, and may allude to important ecological differences in habitat use. With the exception of Reed Bunting, WOU was strongly correlated with transect abundance (column a). As a predictor of abundance however, it varied considerably in accuracy among species, from 0.31 in Linnet to 0.63 in Bullfinch (column b). In Bullfinch, Reed Bunting and Greenfinch

Table 6.3 (a) Spearman's *rho* for standardized WOU and species transect abundance estimates (one-tailed tests). (b) r-squared values for standardized WOU as a linear predictor of species transect abundance estimates. (c) Variance to Mean ratios for species abundances in transect sections from the 15 transects considered in analyses. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Species	(a) *rho*	*P*	(b) r-squared	*P*	(c) Variance : Mean
Chaffinch	0.70	**	0.41	**	16.2
Linnet	0.73	**	0.31	*	38.7
Yellowhammer	0.87	***	0.58	***	3.2
Tree Sparrow	0.81	***	0.47	**	14.2
Goldfinch	0.78	***	0.40	**	16.9
Reed Bunting	0.62	**	0.58	***	0.3
Skylark	0.81	***	0.37	**	18.8
Greenfinch	0.72	**	0.49	**	1.6
Bullfinch	0.81	***	0.63	***	0.3

(relatively uncommon species), and Yellowhammer (a relatively common species), the lower variance to mean ratios (column c) indicated a smaller range in abundance (measured as mean per observation) across sections in which they occurred. In such cases, WOU should be a better predictor of abundance on transects; this was confirmed by higher r-squared values in column b. On the other hand, WOU was a poorer predictor of transect abundance for species that showed a greater range in abundance across sections i.e. species with greater tendency to occur in more variably sized flocks, evidenced by higher variance to mean ratios. This group included the more abundant species such as Linnet, Chaffinch and Skylark, but also the moderately abundant Tree Sparrow. Species thus showed differences in how individuals were distributed that may relate to habitat use strategies. In the following discussion of species – environment relationships observed in the bridging analysis, and their correspondence with the section scale correlates of habitat use, it was possible to qualify observations in terms of apparent differences in habitat use strategies suggested in Table 6.3.

6.4.2 *Bridging analysis results and correspondence with fine scale patterns*

Below, the information summarised in Tables 6.5a and 6.5b is considered to determine the extent to which patchy variation in the main structural components of the farming landscape (stubbles, trees, hedges and field boundaries) identified as important fine scale correlates of species habitat use, had broader effects on community structure. Implicit in this information is the 0.02km^2 resolution of the transect sections, so that observed correspondences strengthen suggestions that species were sensitive to spatial variation in habitat at local scales. It should be borne in mind, however, that many of the reported results are from univariate tests, and should be interpreted as suggestive or corroborative. The strongest and most convincing patterns for each species are identified and considered in relation to community variation observed at broader scales.

6.4.3 *Patterns in species use of sections* and *transects*

WOU in Chaffinch was strongly positively associated with the extent of stubble types on transects (Table 6.5a). This pattern was also evident at the section level in both univariate models, and one MAM (without controls), where the absence of cereal stubble had a negative effect on section use. It is important to note, however, that the distribution of this species was not limited to transects with cereal stubbles (see Fig. 5.3); for example, one of the omitted pastoral transects showed high WOU and median abundance. WOU was also associated with several boundary variables. It showed a strong positive correlation with transect scores for *Index B* (Table 6.5b), and the results for the interval data elucidated this response: transects with more sections with hedgerow taller than 4m showed a significant weak positive response in WOU, while transects with more sections of hedgerow 2m or shorter showed a significant weak negative response. *Index B* measured at the section scale had a positive effect on the species in all logistic regression models. Transect scores for management intensity (*Index M*) showed a considerably weaker association with WOU, while in the MAMs, the effect of *Index M* was confounded to a significant degree with that of *Index B* (compare Table 5.3a, b and Table 5.4a, b). At the section level, the availability of trees (*TreeCat1* to *TreeCat3*) was an important factor determining frequency of use, with both MAMs indicating a positive effect of "more" trees i.e. there was a significant positive effect for *TreeCat3*. The univariate models found negative effects for low tree occurrence. These relationships were not detected in the WOU analysis. If the availability of trees were critical i.e. limiting, it would be reasonable to expect a significant effect of *TreeCat1* on WOU. This relationship was not observed, and the above suggestion that the influence of trees was a positive rather than limiting factor is consistent with this. The positive effect of trees may also be reflected in the weak evidence that WOU and section use (univariate models only) responded positively to the presence of treelines. Although the fine scale models suggested boundary density was important for section use (*BCat1* negative, *BCat3* positive), this effect did not propagate to the transect scale for WOU. It is possible that the range in boundary density across transects was too small to detect effects for the given sample size. In Chapter 5, it was suggested that the inclusion of the easting term in models revealed an interaction between boundary density and height; this possibility could not be

Table 6.4. Interpretive guide for Table 6.5a and 6.5b.

Attention should first be directed at the numerical information in cells. This is the results of the Spearman's correlation analyses between transect WOU for species, and the transect summaries of section habitat attributes. For reporting purposes, *rho* values are described as strong (≥ 0.7), moderate (≥ 0.6 *rho* < 0.7) or weak (< 0.6). The indicated relationships are then considered in relation to the results from the logistic regression analyses of habitat use (see Tables 5.3a, b; 5.4a, b), which are represented in the tables according to the formatting below. Table cells are given a single or double border, and are grey-scale coded using white, medium grey, and dark grey, to indicate, respectively, whether the factor/variable was significant in a univariate and/or multivariate logistic regression model, and the general level/s of significance attained in these models. Some cells are information rich and vice versa, and the ecological significance of this is examined.

Cell Border	Interpretation	Grey-scale Fill	Interpretation
Single	Bird/environment relationship shows a degree of significance in univariate (usually) *or* MAM logistic regression model	▓	Level of significance achieved in logistic regression model/models $P \leq 0.05$. Direction of effect indicated +ve or -ve
Double	Bird/environment relationship shows a degree of significance in univariate *and* MAM logistic regression models	░	Level of significance achieved in logistic regression models: $P \leq 0.05$ in one model, and $0.05 < P \leq 0.1$ in the other. Direction of effect indicated +ve or -ve
rho value *P* value	Numerical information - (top) Spearman's *rho*; (below) *P* for two-tailed test. **Bold type - $P \leq 0.05$**; regular $0.05 < P \leq 0.1$. All *Italics* indicate $0.1 < P \leq 0.15$	No fill	Level of significance achieved in logistic regression model/models $0.05 < P \leq 0.1$. Direction of effect indicated +ve or –ve.

Table 6.5a. Results of Spearman’s correlation analyses of species WOU and transect summaries of section habitat attributes, and summaries of the correlates of species transect section use obtained from logistic regression analyses conducted in Chapter 5.

	No. sections per transect with “full term” stubble		No. sections per transect pertaining						
	Cereal	Brassica or MG	Treeline present	TreeCat1	TreeCat2	TreeCat3	BCat1	BCat2	BCat3
Chaffinch	**0.63** **0.012**	**-0.575** **0.025**	*0.438* *0.102*	- ve		+ ve	- ve		+ ve
Linnet			- ve						
Yellowhammer	*0.404* *0.135*	-0.485 0.067	- ve	- ve		+ *ve*	- ve		+ ve
Tree Sparrow	**0.584** **0.022**			- ve				-0.496 0.06	**0.544** **0.036**
Goldfinch		**0.634** **0.011**				+ ve			
Reed Bunting						+ ve	-0.472 0.076		+ ve
Skylark		+ ve	- ve	+ ve			+ ve		- ve
Greenfinch	+ *ve*			-0.604 0.055	0.498 0.059		- *ve*		+ ve
Bullfinch		-0.492 0.062							

Table 6.5b. Results of Spearman's correlation analyses of species WOU and transect summaries of section boundary height and management levels, and summaries of the correlates of species transect section use obtained from logistic regression analyses conducted in Chapter 5.

	Overall transect score		No. sections in index class interval						
	Index B	Index M	Index B			Index M			
			0 to < 1 (0.5 to 2m)	1 to < 2 (2m to 4m)	2 to 3 (> 4m)	0 to < 1	1 to < 2	2 to < 3	3 to 4
Chaffinch	**0.706** **0.003**	0.588 0.089	**-0.585** **0.022**		**0.595** **0.019**	*-0.429* *0.11*			
Linnet	- ve	- ve							
Yellowhammer	*0.435* *0.105*		**-0.564** **0.028**		0.513 0.051	*-0.407* *0.133*			
Tree Sparrow	+ ve	- ve							
Goldfinch	**-0.614** **0.015**	**-0.608** **0.016**	**0.611** **0.015**		**-0.556** **0.031**	**0.678** **0.005**		*-0.41* *0.129*	-0.472 0.075
Reed Bunting		- ve				*-0.417* *0.122*	*0.437* *0.104*		
Skylark	- ve	- ve							
Greenfinch	+ ve	+ ve							
Bullfinch	*0.416* *0.123*	+ ve						**0.599** **0.018**	

examined in the Spearman's *rho* analysis. A relatively high variance to mean ratio (Table 6.3) indicated considerable variation in abundance among sections, and this appeared to be the result of two habitat use strategies. Where hedgerows were of an appropriate height, Chaffinches were regularly recorded; this is well illustrated in Fig. 5.3. Often, individuals and small flocks of two or three birds were observed foraging on fields close to the hedge, and in field margins and ditches. Where there were trees, such observations were frequent. Alternatively, larger flocks (e.g. 8 or more birds) could be observed foraging up to 30 metres into stubble fields, often in the company of other finches. It has been suggested that this division, particularly in the case of larger flocks, may represent differences in behaviour between migrant and local birds (e.g. Hutchinson 1989). There were only two occasions, however, when I suspected I was observing migrant birds, when flocks of 45 and 60 birds were recorded. It is possible that some of the smaller flocks observed were of migrant birds, perhaps representing the disintegration since arrival, of larger flocks. If this was the case, this begs the question that such an effect is a general response to habitat; larger flocks may have been at a disadvantage in the more closed landscape conditions typical of much of the Mixed stratum. Alternatively, available food resources may have been so sparse or distributed in small patches so as to discourage large flocks.

In contrast to Chaffinch, two species that were very rarely recorded singly were Linnet and Goldfinch. These species usually occurred in sizeable flocks, especially Linnet. The high variance to mean ratios for both reflected considerable variation in flock size. Among all species, Linnet WOU was the weakest predictor of transect abundance (r-squared 0.31), and this may be related to the general lack of significant results in the various tests (see below). Habitat characteristics significantly associated with occurrence were restricted to negative effects at the section scale for increasing boundary height and/or lack of management. Despite this, there was no suggestion of a general avoidance (negative response in WOU) of transects with more sections in the higher *Index B* or *Index M* intervals i.e. sections with taller or less managed hedges. Conversely, the lack of a positive response in WOU for transects with more sections in the lower intervals of *Index B* or *Index M* reflected the fact that birds were not evenly distributed across the more open areas. This lack of correspondence may of course be related to the distribution of food resources.

If these were patchily distributed, many otherwise suitable sections would not be used. Alternatively, unaccounted for habitat attributes in adjacent sections, or beyond the 100 metre transect bounds might have been influential. A tall hedge or treeline, for example, falling just outside the transect bounds may have discouraged use of apparently suitable sections. Thus for Linnet, interactions with habitat may have been governed at spatial scales broader than 200m. Nevertheless, regardless of how food resources were distributed or the sampling limitation of the 100m "range" of transect sections, the species appeared to respond to habitat "openness" at local scales. It was suggested in Chapter 5 that the avoidance of taller hedges was a behavioural consequence of the tendency to form large flocks. This was consistent with the many observations of their use of field centres "outside" transects. Fine scale openness, perhaps at a spatial scale of 2 or 3 hectares, might be a limiting factor of habitat use. Linnets may be associated with more open landscapes generally, because they comprise more fine scale openness associated with food resources. While it is possible that important variables influencing Linnet habitat use were not considered in analyses, or were considered at inappropriate spatial scales, the general lack of pattern observed may instead reflect confounded behavioural strategies related to flock size. An approach where habitat use is modelled for different flock size levels may be illuminating.

Although Goldfinches regularly occurred with Linnets on the MG transects, this was not the case generally; Goldfinch observations were infrequent on the Mixed transects (see Fig. 5.3). WOU showed a moderate positive correlation with the number of transect sections with Brassica/MG stubble, and this corresponded broadly with the fine scale preference for sections without cereal stubbles evident in all logistic regression models. As with Linnet, occurrence in sections was positively associated with low stature boundaries (both MAMs and univariate models). However, unlike Linnet, this relationship was apparent at broader spatial scales in the significant negative correlation between WOU and *Index B*, and in the significant opposite effects on WOU of the number of sections in the higher and lower *Index B* height intervals.

Perhaps the most convincing evidence of a preference for "openness" in landscapes, at least at a local scale, came from the section use correlates for Skylark. Reduced boundary density and increasing boundary management showed positive effects, while the presence of treelines had a negative effect. The association with *Index M* (or *Index B*), however, was not evident at the broader transect scale: there was no relationship between WOU and the transect level indices, or between WOU and the more explicit class interval measures for these indices. Nor was there any indication that the number of sections with treelines was important, or that Skylarks preferred field centres (interpreted at the section scale in the positive response to *BCat1*), when WOU might have shown a positive response to low boundary density on transects (represented by an increasing number of sections in the *BCat1* class interval). As with Chaffinch (but in reverse), the inclusion of the spatial predictor in the MAM for Skylark suggested an interaction in the effects of boundary density and height, which could not be addressed in the WOU analysis. Notwithstanding, birds were often seen using field centres beyond the transect bounds. A high variance to mean ratio indicated a large range in flock sizes; several large and moderate sized flocks were observed, however, over 50% of used sections recorded a mean of 3 or fewer birds per observation. As with Linnet, WOU was a poor predictor of abundance and similar considerations might apply in explaining the lack of pattern. Observed distribution patterns may certainly reflect patchiness in the availability of food resources across stubble fields, however "openness" at scales broader than 200m may also be important.

For Tree Sparrow, the other flocking species, WOU was weakly positively correlated with the extent of cereal stubble on transects. This association was not observed at the section scale, thus a significant number of sections with cereal stubbles did not record Tree Sparrows. Observations were broadly restricted to the Mixed transects (see Fig. 5.3), and results for this species may be more reflective of the spatial covariance in the environmental factor levels and variables. Thus, cereal stubbles occurred to greater extent in the mixed stratum, probably generating the positive association observed in WOU. At the section level, the logistic models suggested an avoidance of treeless sections, a positive response to increasing boundary height, and a negative response to decreasing levels of boundary management. The first two of these factors were also spatially dependent; there were more treeless sections in transects of the MG stratum than in the Mixed, while hedge height increased from the MG to the Mixed stratum. (A converse pattern may be evident for Goldfinch; this species was broadly restricted to the MG stratum, so while WOU was positively associated with the extent of MG stubbles, it was negatively associated with the co-varying *Index B*). Nevertheless, these finer scale patterns emerged despite the dampening effects of the spatial predictor in the control MAM. Cereal stubbles in the MG stratum may not have provided suitable habitat because of a lack of taller hedges. WOU was positively associated with transects with more high boundary density sections (*BCat3*), although this association was not suggested for section use. The contrasting effects on section use of the positively covarying indices for boundary height and management remain curious.

At this point, it is timely to highlight the fact that compared with the above, the remaining species (Bullfinch, Greenfinch, Reed Bunting and Yellowhammer) showed much smaller variance to mean ratios (Table 6.3) indicating smaller variation in mean abundance per observation per section, and smaller flock sizes generally. Consistent with this, WOU was more successful in predicting abundance on transects. These results may reflect the general low abundance in the study area of Greenfinch and Reed Bunting, or in the case of Bullfinch, habitat use associated with a different winter diet. The results for Yellowhammer, however, suggest a habitat use strategy distinct from that used by the species that demonstrated a tendency to form larger flocks. This accorded with field impressions of a relatively even distribution of small flocks, pairs and individuals. Among all species, Yellowhammer was the easiest to approach. This contrasted with the flighty behaviour of single species and mixed flock assemblages. While some studies have suggested Yellowhammers prefer to forage close to hedgerows (Robinson & Sutherland 1999, Siriwardena & Stevens 2004), in this study, small flocks were observed foraging in fields at distances of 100m or more from hedges. These observations suggest the species does not rely particularly on flocking as part of a habitat use strategy. WOU in Yellowhammer was weakly correlated with the extent of the two stubble types, notably showing a negative response to Brassica/MG stubbles. This was consistent with the section level univariate model *without* spatial controls (Table 5.3a), where the absence of cereal stubbles (*cerstub*) had a negative effect on section use. This factor did not, however, enter either MAM, despite the strong correlation between Yellowhammer abundance and the area of cereal stubbles on transects (Fig. 4.2a, b, Fig. 5.1). WOU showed similar field boundary associations to those identified as important for Chaffinch. The extent of taller hedges showed a weak positive effect, while the extent of shorter hedges showed a weak negative effect. This relationship was suggested at the section level when section use was significantly positively associated with hedge height (*Index B*) in the models without spatial controls. In contrast to Chaffinch, however, the presence of a treeline in sections had a negative effect on habitat use in the MAMs, although it was not significant in the univariate models. An effect for the extent of treelines on WOU was not indicated.

Reed Bunting WOU responded similarly to the extent of cereal and Brassica/MG stubbles on transects as did Chaffinch and Yellowhammer WOU; cereal stubbles appeared to represent preferred habitat. It was also positively associated with the number of transect sections with "some" trees (*TreeCat2*), as opposed to "more" trees (*TreeCat3*). This result differed slightly from the logistic regression results where sections with "more" trees were associated with increasing section use. Nevertheless, the broad suggestion was that Reed Buntings favoured sections with trees over those with no trees. The interesting suggestion that sections with some degree of hedgerow management were favoured (in the control logistic models, use was deterred by decreasing levels of management) was elucidated further in the WOU responses in Table 6.5b. Where the management was most severe (*Index M*, 0 to 1), an avoidance was suggested, while where it was moderate (*Index M*, 1 to 2), a positive response was indicated. A negative response to the extent of unmanaged sections was not apparent.

The availability of trees was the only factor associated with WOU in Greenfinch; transects with more treeless sections were used less. There was no suggestion that "more" trees had extra positive effects; rather, "some" trees were essential. At the section scale, the absence of trees had negative effects in all models, and this was consistently translated to the transect scale. A weak negative WOU response to the extent of MG stubbles was suggested for Bullfinch, while treelines and increasing boundary height showed weak positive effects. For the latter, the fine scale association was strong, and there was a suggestion that decreasing management intensity was also favourable. WOU showed a weak positive association with an intermediate management level (Index M interval 2 to 3).

While there was considerable collinearity among the variables and factors associated with the farming gradient, several considerations mitigated against inferring incorrect associations. Firstly, collinearity was not too severe in the fine scale factors and variables (Table 5.2) and contrasting independent effects were found across MAMs, even for positively covarying variables (e.g. in MAMs for Tree Sparrow, Reed Bunting, Yellowhammer). Secondly, most of the species occurred in samples (sections and transects) from across the region. The results for Tree Sparrow and Goldfinch, which showed strong associations with particular strata while remaining broadly absent in others, are likely to be the least reliable. Thirdly, most of the relationships described were consistent with findings from studies of habitat relationships during the breeding season, and from the few studies conducted during the winter. In addition, the small spatial extent and regional integrity of the study area arguably meant that the broad scale distribution patterns reflected *landscape preferences*: species responded to characteristic habitat variation resulting from management practices associated with the different cropping systems i.e. vegetable and market gardening, as opposed to cereal production, or grass production. These general patterns of landscape association usually corroborated the suggested fine scale habitat use patterns.

6.4.4 *Community synthesis*

The bridging analysis tested whether the measure of transect use (WOU) could be correlated with the (spatial) extent on transects, of the various habitat attributes considered important in the section scale analyses. The latter identified correlates of occurrence, which provided a broad and sometimes detailed picture of species' associations with the main structural components of the farmland mosaic. It would, however, be overly presumptuous to simply extrapolate these patterns to explain community variation at broader spatial scales. Instead, the bridging analysis tested for aggregate patterns in section scale effects; the implied "capacity" in the variables tested was of particular interest. WOU measured the spatial extent of occurrence and the frequency of occurrence of species, both of which were significantly related to abundances (albeit with varying levels of correspondence), while the transect summaries described the spatial extent of finer scale habitat attributes on transects. As suggested in Section 6.4.2, variables that showed significant effects in both sets of analyses are considered likely to be among the more important *macrohabitat* determinants of distribution and, therefore, of community structure.

Overall, there were few results in the bridging analysis suggesting habitat use relationships that had not already been suggested in the logistic regression analyses. Local granivore assemblages (species patterns on transects) were structured by the extent of taller and shorter hedges, the extent of the different main stubble types (vegetable or cereal), and the general availability of trees. A feature of the bird data was that it did not differentiate different types of habitat use. Many observations were of foraging birds, many were suggestive of foraging, but for many others, the specific behaviour could not be ascertained. Thus, the distribution patterns described were general in nature, and the described habitat associations are, presumably, also general in nature. While consequences of management decisions affecting field boundary habitat have been well described for breeding birds, the results of the above analyses provide indications as to how such management affects granivore distribution and habitat use during the winter.

Two winter studies discussed in Chapter 5 have particular relevance to these results. Siriwardena & Stevens' (2004) analyses of the effects of local habitat on use of supplementary feeding sites (habitat was described within 50m of feeding sites) described contrasting and species-specific responses to variation in cover height and depth, the presence of trees, and distance to cover of the feeding site, among species in a group similar to that considered in this study. In addition, they suggested Linnets and Skylarks avoided their feeding sites, probably because they were too close to cover. It is reasonable, then, to suggest that more general patterns of habitat use and distribution might also reflect these preferences. If true, the clumping or absence of such habitat components would generate spatial variation in species assemblages. The bridging analysis in this study provided simple tests of this suggestion by searching for aggregate responses on transects, to section scale correlates of occurrence. The propagation to broader scales of such relationships would begin to define local assemblages, while characteristic community patterns would emerge at broader scales in uniformly patterned landscapes. In their extensive study of granivore habitat associations on Scottish farmland, Hancock and Wilson (2003) detected a dichotomy in species based on associations with variables that were interpreted in terms of landscape "openness". Skylark, Linnet, Tree Sparrow and Reed Bunting showed a decreasing probability of being recorded in 1km squares as woodland and scrub cover increased from 0% to 5-10% to 10-15% (the availability of seed rich habitat was roughly equal between the latter two groups of squares). This pattern was also suggested at the field scale; densities of these species tended to be less in fields with some woodland or scrub around them, than in totally "open" fields. Chapter 5 noted the agreement of patterns observed at the section scale for Skylark and Linnet, with these findings. The present study area was essentially devoid of woodland, while scrub cover on transects was minimal. Landscape "openness" was interpreted instead, in terms of hedge height and hedgerow density, the abundance of trees in hedgerows, and the prevalence of treelines in general. It was suggested that *fine scale* openness was limiting for these species, perhaps at a scale of a few hectares. If this suggestion holds i.e. fine scale openness determines patterns of habitat use, the spatial distribution of habitat components that reduce openness becomes critical, as increasing edge to area ratios will increasingly exclude such species. For example, a single woodland (or area of closed habitat) located at the centre of a 1km square, with a coverage of 10-15%, will reduce the amount of available habitat. However, if this amount of woodland were distributed in say, ten evenly distributed woods, available habitat would be reduced even to the point of excluding species. Such effects would become even more critical if food resources were not generally available within otherwise suitable areas. The converse pattern observed by Hancock and Wilson (2003) was of an increasing association shown by species, including Yellowhammer, Chaffinch and Greenfinch, with 1km squares that comprised increasing cover of scrub and woodland from 0% to 10-15% (decreasing slowly thereafter, presumably because to decreasing availability of foraging habitat). Consistent with this, WOU for these species generally responded positively to the extent of taller hedgerows, trees and treelines on transects. In summary, the broader dichotomy of species based on habitat preferences observed in Hancock & Wilson (2003) was generally observed in the data in this study, however, the observed patterns were related to a relatively fine scale mosaic of open and less open areas determined by the management of field boundaries.

This study was intermediate in resolution to the studies of Siriwardena & Stevens (2004) and Hancock & Wilson (2003), and provided suggestions as to how broader scale patterns (e.g. those described in the latter) may result from the finer scale processes related to species habitat preferences and habitat use (Chapter 5 this study, Siriwardena & Stevens 2004). Management of the structural attributes of field boundaries, and its variation in space, had important consequences for wintering granivores. Moreover, this was related to the predominating cropping regimes. The positive and negative effects on species of more intensively managed boundaries, especially those of fields associated with intensive vegetable production are highlighted, while increased species diversity was associated with the areas where agricultural practices were more mixed i.e. on the transects of the Mixed stratum.

6.5 Main points and conclusions

- a transect "weight of use" measure (WOU) was derived from species' use scores for individual transect sections, that incorporated the spatial extent of occurrence, and the frequency of use of individual sections
- species' WOU on transects was proportional to the spatial extent of particular qualities and attributes of the field boundary habitat
- local granivore assemblages were structured by the extent of taller and shorter hedges, the extent of the different main stubble types (vegetable or cereal), and the general availability of trees
- broader community patterns reflected a relatively fine scale mosaic of open and less open areas determined by variation in the management of field boundaries

Chapter 7. Theoretical models, habitat use, and winter conservation: a general discussion

Given the premise that the study area represented one of the most intensively farmed regions in the country, a broad aim of the study was to make an appraisal of the impact of agricultural intensification on granivorous passerines on Irish farmland. A comparative ecological study of ten species was undertaken to assess their responses to the intensive practices in the region, especially those related to arable agriculture. However, interpretation of the survey results and broader findings in this respect must acknowledge that the agricultural patterns and activities in the study area were also likely to be characteristic of "urban fringe farming" (e.g. Ilbery 1992). While many intensive practices are undoubtedly characteristic of the area, urban fringe farming may mitigate some of the more damaging effects of intensification. In particular, the broad scale homogenisation of landscapes and habitat that may affect landscape ecological processes was not a concern. The varying demands of a large local market (the city of Dublin) for a variety of produce have fostered a diversity of farming types and enterprises, thereby maintaining a considerable degree of habitat heterogeneity. Notwithstanding, uncertainty of longer-term land use, and the potential for land use conflicts (e.g. the rezoning of land for sub-urban expansion or other infrastructural developments e.g. motorways or municipal dumps), in the urban fringe, means farmers tend to eschew farm expansion and large long-term capital-intensive activities (typical components of intensification), and instead pursue more flexible, short-term strategies. Little may be gained by farm restructuring or expansion, and indeed, areas around Dublin have bucked national trends in this regard (Crowley et al. 2004). Thus, the area does not represent the effects of intensification on processes occurring over broader spatial scales in more uniform landscapes (e.g. whole regions devoted to cereals, or intensive beef production), and may be limited as an indicator of possible wider problems.

Nevertheless, advantage was taken of a characteristic west to east agricultural gradient that exhibited several management patterns that could be interpreted as gradients in farming intensity. Specifically, these related to the management of the field boundary habitat, and a gradient in farming heterogeneity. An advantage of the study area was the sharp habitat gradient that occurred over a relatively small spatial extent of 20km. It was likely, therefore, that the observed species' distributions largely reflected their responses to agricultural management practices. Such agricultural gradients are usually recognised over broader spatial extents, and usually represent several agricultural regions. If samples are drawn from different regional contexts however, different landscape characteristics associated with these regions may have confounding effects on species relationships with agricultural practices. In any case, there were clear associations between the agricultural gradient, notionally described in a stratification of the study area into three sub-regions (Pastoral, Mixed, and Market Gardening), and habitat patterns, which provided a rich context for examining effects of different management practices. The use of geographical environmental gradients to study ecological processes has been advocated generally by McDonnell & Pickett (1990), and the approach has been used to examine bird community patterns in relation to gradients in, for example, urbanisation (Blair 1996) or, altitude and vegetation (Estades 1997). It has also been used to study effects of agricultural intensification, at scales both considerably broader (Filloy & Bellocq 2007), and finer (Burel et al. 1998), than here. Critics of the approach (e.g. Dawson 2002) have urged caution when inferring cause and effect from statistical analyses because of the high levels of multicollinearity in landscape descriptors usually applied in describing gradients in landscape variation or type (e.g. % habitat cover). Instead, a case study perspective is advised: patterns may be valid *internally*, but broader inference should be based on agreement among the results of replicated studies, using, for example metareplication methods (Johnson 2002). In the broader scale analyses in this study (Chapter 3 and 4), multicollinearity and spatial dependence were identified in the data, so it was especially important to consider the results of analyses in relation to findings from other studies.

An intensive transect sampling methodology enabled a detailed description at two spatial scales, of the breeding and wintering distribution and abundance patterns for ten species of granivorous passerines, in relation to habitat variation associated with the agricultural gradient. Part 1 of the thesis summarised the results for two winter and two spring bird surveys, conducted between October 2001 and June 2003, and seasonal estimates of the relative cover of grassland, cereal, and vegetable/market gardening fields on sample transects. The study area was broadly supportive of all species of granivorous passerines occurring on lowland farmland in Ireland, and most of these were present at most of the study sites. Notably, Yellowhammer and Skylark, species of national and international conservation concern, were well represented, as was the precariously distributed Tree Sparrow. Nevertheless, two species of high conservation concern in Britain and Ireland have vanished from the area over the last 50 years (anecdotal evidence) – the Corn Bunting (probably extinct as a breeding species in Ireland), and the endangered Grey Partridge, suggesting detrimental changes in farming practices may have occurred in the area.

Comparisons of seasonal abundance data indicated a significant winter influx into the area of several species, including Linnet, Goldfinch, Skylark and Chaffinch. Lesser, but nonetheless important increases also occurred among the other species. These observations probably represented two bird movement patterns; seasonal migration on one hand (especially in the species mentioned above), and movements of birds at local scales towards areas with good foraging habitat (Gillings et al. 2005), on the other. Species' abundances responded varyingly to the agricultural gradient. Consistency between years and between seasons in abundances and fine scale distribution patterns, within the farming strata, were suggestive of a robust community structure that was likely to have been a reflection of habitat suitability. The patterns appeared to be related to aspects of farming type and intensive management, and provide a reference for studies in other areas of Ireland, or elsewhere, where intensive farming may be of conservation concern.

In Part 2 of the thesis, attention was focused on species abundance and distribution during the second winter of the study. As noted above, the arable grassland gradient of the study area exemplified two component characteristics of agricultural intensification. These were a decrease in habitat heterogeneity as a consequence of the predominance of particular farming types at the ends of the gradient, and a related gradient in the management intensity of field boundary habitats. For the study species, the farming type gradient also represented variation in the availability of foraging habitat and resources, and species responses were apparent in Fig. 3.2 and Fig. 5.3. These broad scale patterns, however, overlay a considerable amount of patchy habitat variation, even towards the more homogeneous "ends" of the gradient i.e. within the Pastoral and MG strata. The thesis pursued the working hypothesis that such patchiness was important to species during the winter. Modelling their distribution and abundance patterns would, therefore, test this hypothesis, and reveal details of species-environment relationships. It would also reveal if ecological differences existed among the species in their responses to this heterogeneity. It was further proposed that the more important fine scale habitat associations observed should manifest at broader spatial scales to generate local assemblage patterns among transects, and thence, broader community pattern across the study area.

Community level patterns were described and interpreted using ordination techniques (mainly RDA, Chapters 3 and 4) to model data describing habitat and granivore assemblages on 1km transects. These patterns were then elucidated using logistic regression analyses of data describing species use of 100m transect sections, and the structural and infrastructural variation of field boundary habitat (Chapter 5). These spatial resolutions i.e. 1km transects ($0.2km^2$) and 100m transect sections ($0.02km^2$), proved successful for capturing variation in influential habitat processes both across the study area, and within transects. Fig. 5.3, which summarised the species *section use* data, was especially useful in illustrating the strong spatial variation in distribution patterns among species, both across the farming strata, and at the finer spatial scales of site, transect, and transect section. The scores presented in Fig. 5.3, however, also implied a temporal measure of habitat use, and it was possible to derive a broader measure of transect use, transect "weight of use" (WOU, Chapter 6), which combined this temporal dimension, and the spatial extent of species occurrence. The temporal dimension was particularly interesting because it alluded to species functional integration into the landscape i.e. whereabouts they tend to spend most time. The results of these two sets of analyses were considered in tandem to link and integrate aspects of abundance, distribution, habitat use, and habitat characteristics, and this was attempted formally in the "bridging analysis" of Chapter 6.

These analyses thus considered species distributional, temporal and abundance patterns, and in the various chapters, these were examined in applied terms of species' autecologies and their responses to the agricultural management patterns present. At the same time, organisational and theoretical views of community ecology were touched upon, including the generalist-specialist continuum and niche breadth, habitat heterogeneity and habitat partitioning, the importance of predation, and community diversity.

In this final section of the thesis, I draw together some of the applied themes of habitat use and preferences, and species conservation, within a broader theoretical consideration of landscape ecology and patch dynamics. Several general models of habitat and patch structure, and landscape ecological processes, are considered in terms of how they might apply to the species and environmental patterns described. The implications of these observations for conservation approaches during the winter are then considered. For the purposes of this discussion, it is convenient and helpful to summarise again, the habitat patterns sampled, as below, these are discussed using various conceptual and theoretical terms employed in the models (jargon). The summary helps to clarify my interpretation of these terms by making direct references to the real habitat and ecological processes observed. The summary is also intended to remind the reader that the habitat variation (patchiness) observed was detected using a spatially hierarchical sampling frame, and that the results from the various analyses should be considered simultaneously to develop an integrated picture of the patterns at both scales.

Landscapes, habitats, patches and models

Notwithstanding the broader geographical trend in farming type, the study area constituted a patchy environmental mosaic. Elements of this patchiness were described at a spatial resolution somewhat finer than "field scales" (fields usually being quite a bit larger than $0.02km^2$ resolution of 100m transect sections), and the typical variation patterns were summarised in Table 5.1. Species' responses to this patchiness were suggested in Fig. 5.3, and Chapter 5 was concerned with identifying the environmental correlates of these responses. From a qualitative point of view, it is useful to examine the various habitat characteristics in the site photographs in Appendix 1. Patchiness occurred at a range of spatial scales, clearly among fields, but it also occurred from farm to farm. Furthermore, farm sizes were sufficiently small for individual transects to sample several (two to four per transect, cf. Table 2.1), and these were generally either arable or pastoral enterprises. The landscape mosaic, therefore, reflected choices among farming type (arable or pastoral) and cropping patterns (cereal, vegetable, market gardening etc.). This however, was nuanced by the management preferences of individual farmers, especially in relation to field boundaries. Thus, while a range of field types could occur within and among farms (cf. Chapter 2), these were associated with a considerable range of boundary types (Fig. 5.2), ranging from short intensively managed hedges with few trees, to taller unmanaged hedges with many trees. On some farms, the various types were often contiguous, while on others, management was far more uniform. At some sites, sample transects ran along farm boundaries, and differences in management were often quite stark, especially when pastoral operations bordered arable operations. Where mixtures of management occurred within farms, hedge orientation may have been a factor in deciding which hedges to keep short, to maximise crop exposure to the sunlight for crop growth. On the other hand, low intensity management may have reflected sympathetic attitudes to wildlife in general, or simply old-fashioned less intensive approaches. Regardless, fine scale heterogeneity occurred in a rather unpredictable way on transects. Nevertheless, the east-west gradient in farming practices (Section 2.5) meant that this patchiness was not uniform across the study area, and Chapter 3 and Table 5.2 reported significant spatial dependency in values taken by the cropping and boundary variables. This then was the sampled landscape, and the environment that exhibited the various patterns of species abundance and distribution described.

To further explore some of the species-environment relationships found in these analyses, it was decided to consider them in relation to the landscape ecological framework models of Kolasa (1989), and Kotliar & Wiens (1990). These models address the ecological implications for species of the spatial characteristics of mosaics of habitats and *patches* (the latter interpreted broadly as favourable areas a species distinguishes from other areas within a habitat type or landscape). In particular, they consider the ecological significance of the *extent* and *physiognomy* (contrast, dispersion, configuration; cf. Dunning et al. 1992) of habitats and patches, and recognise spatial and hierarchical patterns in the organisation in these attributes.

Kolasa's model of species and habitat in a heterogeneous landscape proposes a hierarchical distribution of constituent habitats that corresponds with patterns of species abundance and distribution. Kolasa recognised empirical patterns in how species in various taxa distributed themselves among increasingly finely divided habitat sub-divisions, and suggested this represented a "natural" hierarchical structure within habitats. Thus, the broad habitat type, representing the top hierarchical level, contains increasingly partitioned and refined finer scale habitat sub-divisions, micro habitats and/or patches, which are distinguishable especially in terms of their "amount" (usually represented in terms of areal *extent*). In more theoretical terms, the full dimensional habitat space comprises increasingly refined and nested sub-regions, akin to the Hutchinsonian niche, which take up diminishing proportions of the full landscape "hypervolume". His model, therefore, can be extended in a more general way to patchiness *per se*, recognising that the organisms' perception of its environment implies qualitative (habitat types) *and* quantitative (preferred values along environmental dimensions within habitats i.e. niche characteristics) discrimination. A simple application of his model explains how "habitats" accommodate generalist and specialist species by assuming characteristic niche relationships and an "ideal situation" where the abundance structure of the community is a strict reflection of the availability of suitable conditions. He notes, however, that he interprets the terms "specialist" and "generalist" in *real* terms, so that species are specialists or generalists relative to the area under consideration, downplaying the more usual emphasis on niche breadth implied in the terms. In the present study, Chapter 2 considered the relative affiliations of the study species to a range of UK habitats (cf. Fig. 2.6), and noted their general tendency towards being "generalist" or "specialist" with respect to these (niche breadth interpretation). The study area was then considered in terms of the extent to which species preferred habitats (several types in the case of generalist species e.g. Chaffinch, or a few to single types, in the case of specialists e.g. Reed Bunting, Tree Sparrow) might be represented or approximated. It was suggested that the observed distribution patterns among species were broadly consistent with this i.e. that the study area appeared to accommodate species to the extent that it accommodated or approximated their more broadly preferred habitats. For example, Greenfinches, Reed Buntings and House Sparrows were fairly evenly distributed among the farming strata possibly because the occurrence of the patches they used was relatively independent of the predominant management practices: the farming regimes accommodated favourable habitat patches. On the other hand, farmland specialists *per se* i.e. Tree Sparrow, Yellowhammer responded more directly to how the farmland was managed, for example, by occurring where cereal growing was a major land cover. In Kolasa's model, specialists use the lower level divisions of the habitat hierarchy, and generalists use the higher levels. Thus, assuming a positive relationship between the "amount" of suitable habitat for a species, and its general abundance, this would generate a similar relationship between distribution and abundance. Such a relationship was observed among the study species (Spearman's $rho \geq 0.65$, $P \leq 0.021$; one-tailed tests, Chapter 2).

The "quantitative" emphasis in Kolasa's model can be complemented by a more conceptual "spatially aware" model of habitat heterogeneity and patches developed by Kotliar & Wiens (1990). Their framework recognises that environmental patchiness occurs at a range of spatial scales which can be recognised and responded to by individuals and populations, and proposes that these (associations) can be represented as hierarchical levels in a *patch structure* hierarchy. This model is appropriate for vagile organisms such as birds, and may be especially useful when applied to ranging species that sample patches in "landscapes" (the quotation marks emphasise the fact that different species may be constrained to operate within particular spatial limits). Although Kolasa demonstrated a theoretical negative effect on a specialist species as a consequence of increasing dilution of its habitat within the more ubiquitous habitats of higher hierarchical levels, Kotliar & Wiens' model can provide more intuitive *process* based explanations of how patchiness affects individuals (or populations). They recognise in particular that species may require habitat or niche components to be available at particular spatial scales or within particular spatial domains, and that this may vary among species. It is pertinent here to introduce the "ecological neighbourhood" construct of Addicott et al. (1987), which underlines the fact that among and within species, particular ecological processes (foraging behaviour, habitat selection, competition, breeding territory selection etc.) have specific spatial and temporal ambits. Thus, Kotliar and Wiens illustrate their model using the ecological neighbourhood of optimal foraging in humming birds. They consider an individual's responses to the availability and quality of flowers in terms their distribution in space, and how typical patterns in the spatial distribution of flowers may represent levels in a foraging patch structure hierarchy. Each level in this hierarchy defines a new patch *order*, and the nature of the patchiness at each level may have important consequences for foraging decisions. To parallel their example, a granivorous bird in a farming landscape may sample and respond to seed density in a patch of seeds within a stubble field (a first order patch). It may then sample several seed patches within the field (a second order patch), and respond to differences amongst them (e.g. Robinson & Sutherland 2002). Variation in the seed availability among nearby stubble fields (third order) may then be sampled (e.g. Robinson et al. 2004). At a higher level still, the bird may range over a broader area (e.g. its home range, Calladine et al. 2003) to sample the patchy availability of foraging habitats caused, for example, by variation in cropping and management practices among individual farms. At each of these levels, decisions relating to if, and/or how, "patches" (which are now defined for each hierarchical level) are likely to be used may depend on characteristics pertaining at each level. Kotliar and Wiens consider spatial and contextual criteria (principally relating to the aggregation/division of patches, and varying levels of patch contrast, mixing and quality) to be important for patch selection at each level. It is this heterogeneity that individuals respond to. While the focus of their model is on individuals' responses, it should be possible to apply the model to patch use by gregarious species that form groups, as to a large extent this behavioural trait suppresses individualistic behaviour i.e. the group (herd, flock etc.) may be broadly considered as a whole. This allows the model to be applied to the landscape context of the present study area, to examine aspects of granivore distribution patterns (patch selection). It is important to note that the patches to be considered are not confined to discrete foraging resources, e.g. flowers, or patches of seeds. Rather, they represent the "patches" or habitat sub-divisions described in Kolasa's construct. In the study, a range of spatial levels and/or resolutions was considered which shed light on broad and fine scale patterns of community variation and organisation. I now consider if and how the model of Kotliar and Wiens might apply to these patterns, and whether they may indicate hierarchical patterns in the distribution of (preferred habitat) patches.

Species' broad habitat preferences were apparent among strata, and these may represent choices made among higher-level patch *types*, by applying criteria at broad spatial scales e.g. general patterns of landscape composition. Variation in occurrence among transects within strata is likely to represent lower level criteria related to cropping patterns and farm type. Patch selection at a similar level was perhaps implicit in the dichotomy observed by Hancock & Wilson (2003) in species' responses to habitat "openness" on Scottish farmland (cf. discussion to Chapter 5). At the finest level considered in the study, transect sections were clearly being differentiated. At this level, the patterns of distribution in Fig. 5.3, and the results of the logistic regression analyses in Chapter 5 can be examined in tandem to try to get a feel for how the spatial distribution of *section use* varied with respect to the habitat gradients associated with the different farming types. It is acknowledged here, that a rather broad ecological neighbourhood of *general* habitat use is being considered, precluding an examination of specific processes or behaviours such as foraging, shelter, or social activities. The viewpoint taken, however, posits the notion that these activities will tend to take place in characteristic favoured locations. So for example, according to Table 5.4b, good patches for Yellowhammers appear to be where cereal stubble is located nearby to a hedge intersection that contains a tree or tall shrub. Alternatively, Greenfinches might be attracted to the same attributes, but may show an additional preference for areas where hedges are taller or less managed, and occur at a higher density (Table 5.3a, 5.4b). According to the analyses, this is where these species tended to spend their time, regardless of what exactly they were doing. The general question to be considered is, if the study species were differentiating among transect sections on the basis of section scale habitat attributes, is it right to assume that the broader patterns of absence among strata, suggested in Fig. 5.3, resulted simply from a lack of suitable habitat at the section scale? Considering the model of Kotliar & Wiens, it is possible to speculate that Tree Sparrows, or Greenfinches, for example, were absent from potentially suitable patches that occurred on transects in the pastoral stratum, because these patches were generally not abundant or aggregated enough in the general landscape to meet winter habitat requirements. Small areas of arable habitat were sampled by all pastoral transects, but in many cases, species were not recorded using these areas. Similarly, the absence of Tree Sparrows from rich foraging resources (cereal stubbles) on transects in the MG stratum, may, in part, reflect the hostility of the MG landscape to a species that may require hedgerows and trees to be generally present (Table 5.4a, b), notwithstanding the specific requirements for habitat use at finer scales. Theoretically, Tree Sparrows and Greenfinches may have been absent from transects in the pastoral stratum because suitable patches were too few and isolated to sustain local populations (birds may have continually entered areas in the stratum but these areas did not become part of a regular home range). Lower order patch structure was inadequate (parches were not abundant or aggregated enough) for defining a higher order patch that would attract birds. On the other hand, Tree Sparrow absence from the MG landscape may reflect a combination of an unfavourable matrix at higher levels (a patch contrast consideration) and a high isolation of favourable patches; the species may have been deterred by patch structure at high *and* low levels. More generally, if granivores searching for new habitat use a top down selection process, the qualities of higher levels in a patch structure hierarchy will be particularly important. If, however, an area is recognised at higher levels as generally favourable, birds may then explore it and use lower level criteria in decisions as to whether to remain in a particular area, or search again. This may, of course, have been the case in this study: the vagility of the study species may have been sufficient for them to sample local scale habitat conditions across the study area, so that the above-mentioned higher-level considerations were not at issue.

Whatever the actual mechanisms in operation were, this discussion is intended to highlight the possible importance of patch structure hierarchies for farmland granivores when habitat selection is a hierarchical process. To this end, a more general question may serve this purpose: would the same patterns of habitat use and species distribution among transects be observed if the different farming types were uniformly distributed across the study area? That is to say, are the observed patterns solely reflective of processes operating at smaller spatial scales? If this were the case, it would not matter too much how farming practices were distributed, and the observed species patterns would be generally maintained. If landscape structural effects were important however (implicating effects of higher levels in a patch structure hierarchy), then distribution patterns, at least among transects might be different. Species could occur more frequently on transects that did not record them, or less frequently on those that did.

Winter movement and conservation strategies

An important implication for species of the spatial organisation of resources is their ability to move between them and the spatial scales over which they tend to sample their environments. These are likely to differ both among species, and among landscape types, and it has been suggested that in farmland granivores, they relate to the extent of between season movements (Robinson et al. 2004). Long and short distance migrants may sample their wintering grounds over broad scales, and are likely to respond to coarse aspects of landscape structure. For sedentary species, local habitat characteristics are likely to be more important, and required habitat resources may need to be in relative close proximity. Thus, depending on the vagility of the species, there are likely to be spatial thresholds within which required resources must be available, and beyond which, individuals and local populations should incur costs, or may not occur at all.

Recent research in the UK has focused on elucidating this aspect of granivore winter ecology, as the principal aim of winter conservation efforts (deliverable through Agri-environment schemes (AES)) is to improve overwinter survival by supplementing and enhancing winter foraging resources. Given the enormous costs involved, key to the success of such AES is efficiency and cost effectiveness, and this requires understanding of the spatial scales at which granivores can operate during the winter. In arable landscapes in eastern Britain, Siriwardena et al. (2006) conducted a landscape scale experiment to investigate consequences for several granivore species of spatial separation between artificial foraging stations (10 replicates, with separation distances ranging from 100m to 10km). In another large-scale experiment (3 replicates), Robinson et al. (2004) examined population responses to the manipulation of seed resources in 1km^2 blocks of arable land located within grassland counties of the UK (where foraging habitat is typically sparse).

Calladine et al. (2003) conducted a pilot study using radio telemetry and various mark-recapture/re-sighting approaches to describe the ranging behaviour and habitat use patterns of three granivores wintering within a 5km by 5km square of mixed farmland in southern Scotland. These studies have provided basic information helpful in the design and implementation of measures to supplement winter foraging resources.

The observations of Calladine et al. (2003) enabled estimates of home range size, and described patterns of habitat use in Chaffinch, Yellowhammer and Tree Sparrow within a habitat rich 5 by 5 km block of mixed farmland (the area included several potentially important non-farmland habitats, including areas of woodland, scrub, and riparian habitat). Species' home range sizes were markedly different, and it was suggested that this reflected varying degrees of habitat specialisation. Tree Sparrows tended to range more broadly than the other two species and this was put down to their specialised use of cereal stubble fields. The other species ranged over shorter distances, and used a broader range of habitats, including pastoral, arable, scrub, and woodland areas. Species' abundance estimates also accorded with theoretical expectations; the most generalist species, Chaffinch, was the most abundant, and the most specialised, Tree Sparrow, was least abundant. The authors drew particular attention to the UK population trends for these species on farmland, and the generally observed positive association (e.g. Fuller 2000) between increased ecological specialisation and increased population and range declines. This study scenario shows broad parallels with Kolasa's model of a hierarchically sub-divided habitat, and may exemplify how increasingly specialised species are accommodated with increasing levels of habitat refinement. Arguing "costs" to species (e.g. energy required to move between patches, increased predation risks in doing so etc.) are relatively higher when patches are increasingly divided and rare, and that isolated local populations are more susceptible to deleterious stochastic events, Kolasa demonstrated a theoretical disadvantage to specialists as a consequence of habitat "dilution" within the more ubiquitous mosaic used by generalists. The home range characteristics and patterns of abundance and habitat use among the species observed by Calladine et al. (2003) accorded with Kolasa's model, and species' national trends were consistent with the theoretical "disadvantage" of specialists. The broader implication is that where environmental changes have had negative effects on granivores generally, these will probably have been more critical for "naturally" disadvantaged specialist species.

Patch aggregation/separation is one of the main characteristics of habitat considered by Kotliar and Wiens (1990) in defining their patch structure hierarchy model. They propose that species may show differing "grains of perception" with respect to the spatial organisation of patches characterising hierarchical levels. I speculated above as to whether this consideration was apparent with respect to Tree Sparrow and Greenfinch distribution patterns in the pastoral stratum i.e. whether small isolated patches of potential foraging habitat were not used because they were not recognised or not sampled by birds. Habitat suitability for these species may have required aggregations of lower level patches that were not sampled by transects in the pastoral stratum. Other species, on the other hand, may have recognised and used these lower level patches, regardless of their isolation (or position in a patch hierarchy). Siriwardena et al. (2006) found evidence that variation in the isolation of foraging sites was important for Yellowhammers, Reed Buntings, Chaffinches and House Sparrows. Yellowhammers and Reed Buntings were more abundant at foraging sites that were in close proximity to each other (count data at 3 patches within 500m of each other), than they were if foraging sites were separated by greater distances. In contrast, Chaffinches and House Sparrows were more abundant at sites that were more isolated (count data at 3 patches within 10km of each other, but no closer than 500m). This finding, they suggested, alluded to two foraging resource use strategies that might be expected where species showed differences in vagility, or in their tendencies towards gregariousness. Higher use of clumped foraging patches (or clumped habitat in general) would result where species were more mobile and/or gregarious, so that abundances and patch use would be either proportional to, or exceed resource availability, relative to more isolated patches. Higher use of more isolated patches, on the other hand, should occur when birds are more evenly distributed across a broader area, and congregate at more isolated patches. Where patches are less isolated, a similar number of birds would be distributed among patches, so that use and abundance would be relatively less per patch. Although these observations allowed the authors to recommend a compromise spatial distribution for introduced winter foraging habitats that would suit most species, *and* cater for discrete local communities, the behavioural patterns observed may exemplify Kotliar & Wiens' proposal that species may respond differently to different levels in patch structure hierarchies, and therefore, operate at different spatial scales within environments. These differences are likely to result in different patterns of scale dependent habitat selection. Interestingly, scale dependent habitat effects were found at quite large scales during the breeding season by Robinson et al. (2004). Densities among Corn Bunting, Yellowhammer and Grey Partridge in 1km^2 focal BBS squares responded most strongly to the area of arable habitat within various radii, ranging from 1 – 4 km of focal squares, and did so in a species specific way. It was suggested that this might reflect characteristic differences in the extent of between season movements. Notwithstanding the ecological mechanisms reflected, these relationships indicate differences in the scales at which these species respond to landscape composition, and suggest rather high hierarchical levels of habitat organisation (we have clearly moved into the domain of landscape ecology) can effect species differently. The importance of context for the focal "patch" is again underlined. Patterns observed at any patch level, or scale of resolution, are unlikely to be independent of the influences and processes operating at different levels in patch/habitat hierarchies, if they are present.

In more general terms, species' abundance and distribution depends on the availability of favourable environmental conditions (habitats and patches), and as this increases or decreases, species may adapt their behaviour accordingly. In many environments, species exist at the extremes of their ecological range (they "eke out a living" where conditions may be testing), and this is where subtle environmental changes may be sufficient to cause "catastrophes" (e.g. local extinctions, changed habitat carrying capacities). In the context of agricultural management and the sustainability of granivorous bird populations during the winter, much has depended on how environmental change has influenced not just the nature and extent of habitats and resources, but also, how such change has affected their organisation in space. Chapter 1 highlighted how agricultural polarisation (engendering habitat loss and homogenisation), at a broad range of scales, has had direct effects on populations through habitat loss. However, it has also affected species indirectly, in particular by interrupting important ecological mechanisms (e.g. Dunning et al. 1992). At smaller scales, for example, particularly sedentary species e.g. Corn Bunting, Cirl Bunting (Evans 1997), may be affected by the loss of fine scale habitat mosaics. On the other hand, broad scale seasonal movements (not including migratory movements), are likely to indicate that landscapes that are suitable during one season, do not meet habitat requirements during the other (e.g. Atkinson et al. 2002, Gillings et al. 2005). Indeed, it is possible these movements reflect an adaptive response to polarisation. At particular stages in any habitat polarisation or fragmentation process, minimum threshold criteria may apply at any level of a patch structure hierarchy, so that species may be absent from apparently favourable locales, areas or regions because of unfavourable conditions at another habitat organisational level.

Conservation management for farmland birds is implemented at the farm level through agri-environment schemes (AES), whereby farmers and managers enter into agreements to implement specific conservation measures. The studies of Calladine et al. (2003), Robinson et al. (2004) and Siriwardena et al. (2006) have provided much useful information on aspects of winter movements and the spatial scales at which granivorous passerines sample habitat resources, for informing the design and implementation of measures intended to supplement winter foraging resources. In particular, the work of Siriwardena et al. (2006) has provided the first concrete suggestions for a practical and effective spatial pattern for the distribution of introduced foraging habitats that will benefit a range of species. The success of the basic measures, however, will depend on other aspects of species ecologies, and may require a degree of modulation depending on regional management and habitat characteristics (e.g. Atkinson & Robinson 2002). For example, whether measures are aimed at enhancing habitats to boost overwinter survival, or whether the broader intention is to promote the expansion of species back into areas from which they have disappeared, these differing circumstances may require different overall strategies. Robinson et al. (2004) have suggested that habitat introduction, for example, in grassland dominated areas should be coordinated among adjacent farm units over areas as large as 80km^2, in light of the strong scale dependence they observed in breeding responses to the availability of arable habitat at such scales. If measures are too diluted, they may be less effective because of movement limitations. Alternatively, if the intention is to benefit a range species, for example, in the more homogeneously managed arable landscapes in Siriwardena et al. (2006), local habitat considerations may be important. In this respect, Siriwardena & Stevens (2004) found species specific responses to local habitat surrounding the experimental foraging sites used in Siriwardena et al. (2006), and results from the present study (Chapter 5) described differences in species use of 100m transects sections that were related to aspects of field boundary management. In addition, Chapter 6 suggested that some of these fine scale patterns were also evident at the 1km transect scale, generating characteristic variation in local granivore assemblages. Thus, consideration should be given to how habitat context might affect species' use of introduced habitats, and this will be particularly important for species that differ in their preferences for more open, or more closed, habitats.

As the most likely means of delivery of winter foraging habitat through AES will be through the retention or introduction of seed rich stubble fields, the choice of which field to enter into schemes should be optimized depending on the habitat preferences of target species. Thus, the work of Siriwardena et al. (2006) suggested that in arable landscapes, the location of winter foraging habitats separated by distances of 1km or so, could be effectively "reached" by most species. Resources dispersed at this level would tend to cater for discrete local populations, and also represent the best compromise for species that preferred to use clumped resources, and those that did not. In the present study, local granivore assemblages were structured by the extent of taller and shorter hedges and the general availability of trees. Especially important was the suggestion that the responses of species to the open or closed nature of landscapes found by Hancock & Wilson (2003), appeared to be expressed at the finer scales of transect and transect section. When the aim of a scheme is to benefit as many species as possible, including those species which prefer open or closed habitat, the best field would be one that straddles or abuts the steepest gradient in boundary structural characteristics. The broad idea is to associate the field with the best semi-natural ecotone from closed habitat to open habitat. For example, one end of the field might adjoin a small woodland, or an area with a relatively high density of taller hedgerows. This "end" of the field could be managed to maintain hedgerows in a relatively "unmanaged" state, and encourage trees. The other end of the field should merge with the most open area in the vicinity. At this end, and within several hectares, management could involve maintaining or promoting habitat openness by keeping hedgerows relatively short, and limiting the availability of trees. Although this may not be possible all the time, choosing a field that incorporates a gradient in vegetation height and structure, and is amenable to practical management, would provide a heterogeneous patch that could benefit a range of species (and not just granivores) with different preferences for open and closed habitat conditions.

Many aspects of habitat, which could have been important for the observed distribution patterns, were not investigated in this study. Chief amongst these was likely to have been the effects of variation in abundance of seed resources among and within stubble fields (e.g. Robinson & Sutherland 1999). This is likely to depend on field management history. Nevertheless, seed resources generally available in stubble fields are thought adequate to attract granivores (Robinson et al. 2004), and the more important consideration is usually the availability of stubble fields *per se*. The analyses in Chapter 5, which only considered transect sections where there was a minimum of (0.5ha) of stubble for the main part of the winter, found differences among species in their associations with attributes of the field boundary habitat, despite possible variation in the quality of stubble fields, or the distribution of seed rich patches within them. It is also noteworthy, that the data did not differentiate between habitat use types (e.g. foraging in fields, foraging within hedgerows, social aggregation, shelter, or behaviour related to how species move between favoured patches), so that observed results suggested preferred habitat conditions in a general sense. In this respect, the use of presence absence type data (in Chapter 5 and Chapter 6) placed a greater emphasis on identifying these conditions, and downplayed effects of variation in seed resource levels. The study helped to identify field boundary management practices beneficial to different species in a winter context. The best patches for species, therefore, are likely to be where favoured boundary habitat conditions coincide with good foraging resources. More general management of arable habitats for granivores during the winter should strive for adequate availability of such patches within the spatial domains typical of species' home ranges.

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Appendix 1

Plates of sites, survey transects, and landscape and habitat characteristics (pp. 174-191)

Market Gardening stratum sites

Plate 1. Loughshinny 174-175
Plate 2. St. Maur 176-177
Plate 3. Balleally 178-179

Mixed stratum sites

Plate 4. Tyrellstown 180-181
Plate 5. Ballaghstown 182-183
Plate 6. Ballymaguire 184-185

Pastoral stratum sites

Plate 7. Damastown 186-187
Plate 8. Rowlestown 188-189
Plate 9. Baldwinstown 190-191

Plate 1. Market Gardening stratum. Site Loughshinny. Transects, right – "Coast", left – "Inland". Strip cropping of vegetable and market gardening crops. Extensive areas of type A, B and C hedges. Very few trees. Visible is the only substantial woodland seen during surveying.

1. Maximising land use against a type F hedge.

2. Looking east.

3. Foreground brassica crop; beyond, almost total weed cover.

4. Tall type B hedge.

5. Low scrubby field boundary; very open landscape

6. Spring. Recent severe mechanical flail management of low type C hedge.

Plate 2. Market Gardening stratum. Site, St. Maur. Transects, top – "Open", bottom – "Wall". Strip cropping, glass housing, and produce processing depots. Poor hedgerow infrastructure apparent, few trees. Strong contrast between "Open" and "Wall" hedge/boundary characteristics.

1. Early spring. Boundary largely type A. Isolated Hawthorn and Gorse; Bramble emerging from ditch.

2. Recent severe management of low type F hedge.

3. Old brassica fallow and plough. Low scrubby type A boundary to left.

4. Long term grass setaside with woody copse.

5. Heavy weed infestation of salad crop.

6. Full weed cover and un-harvested brassica crop flowering.

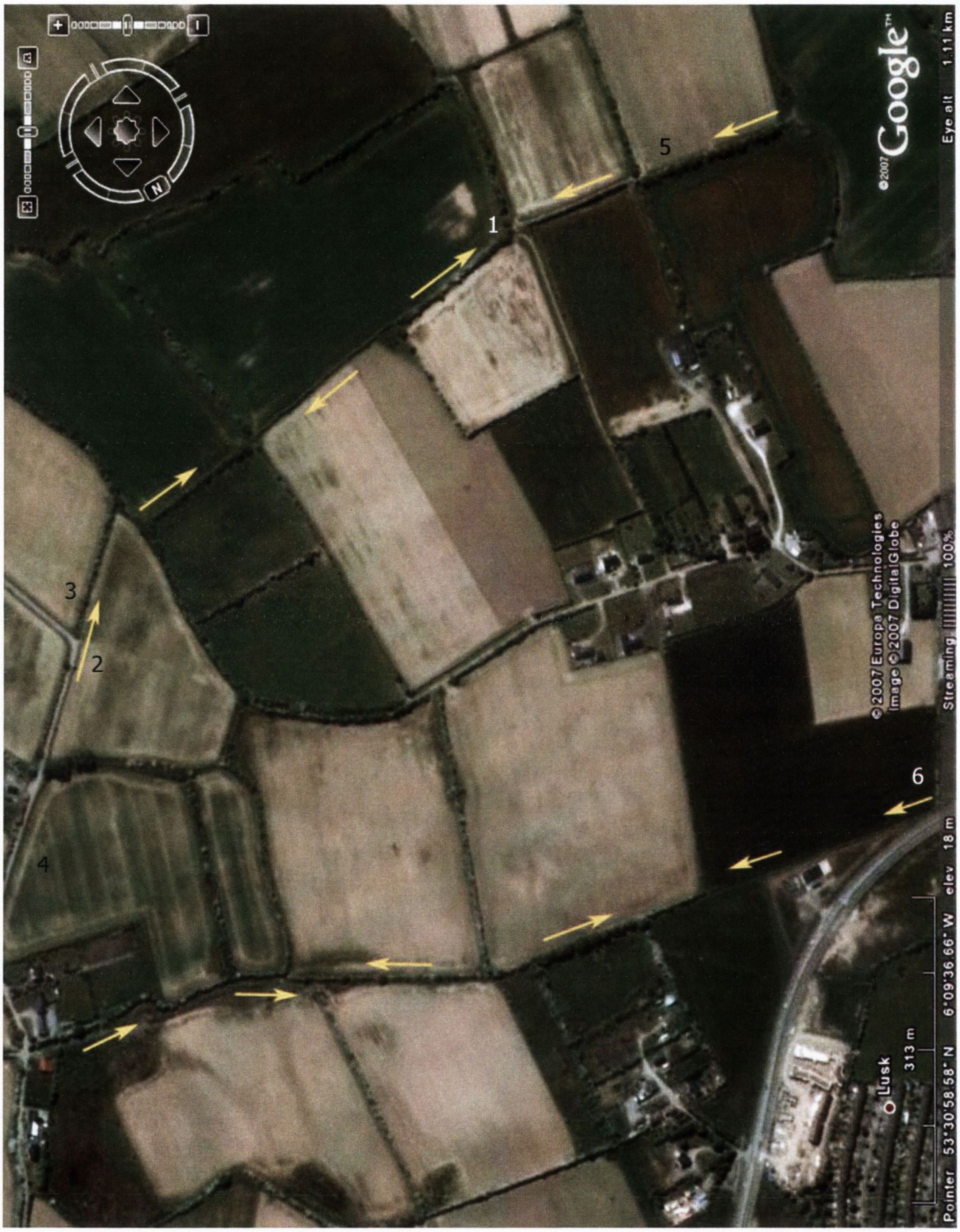


Plate 3. Market Gardening stratum. Site Balleally. Transects, top – "Dump", bottom – "Boylan". Transects sample several farms and individual parcels of land. A particularly heterogeneous site, rather atypical of the MG stratum, with pasture, cereal farming, vegetables and market gardening. Most hedge types represented. Trees and tree lines are visible, also an area of scrub (bottom left) and a Lusk housing estate. The road, bottom right, postdates the survey period.

1. Tall F type hedge along cereal stubble. Similar hedge in distance.

2. Market Gardening cropping – lettuce and herbs.

3. Leeks and a brassica stubble (beyond). Tree line in distance.

4. Till.

5. Market Garden cropping.

6. Porous, tall, thin type B hedge. Young brassica crop.

Plate 4. Mixed stratum. Site Tyrrelstown. Transects, top – "Clinton", bottom – "Hooey". Transects sample 3 farms. Predominantly Arable farming. Glass housing bottom left. Variable hedges and several tree lines. Scrubby area top right. Isolated bushes and trees visible. Top left area relatively open.

1. Two hedge types (distance and middle distance) and tree line in close proximity.

2. Tall narrow type D hedge. Maximised land use.

3. Open area with type A hedge. Recently managed boundary (note cutting of ditch vegetation).

4. Spring cereals and "gappy" type D hedge.

5. Spring vegetables and "gappy" hedge.

6. Low "gappy" type F hedge with signs of recent management.

Plate 5. Mixed stratum. Site Ballaghstown. Transects, top – "Railway", bottom – "Baldongan". Generally open landscape with large fields and lower hedges. Most hedge types represented. Relative hedge height may be gauged by examining shadow lengths. Scrubby block top left.

1. Elongated stubble field.

2. Low type F hedge of Gorse, Bramble and Hawthorn.

3. Looking toward Baldongan Castle from the east. Very open landscape. Sparse type A and B hedges visible. No trees.

4. Gap in low type F hedge. Overgrown ditch.

5. Variable height hedge with tree.

6. Open landscape looking toward Baldongan Castle from the west.

Plate 6. Mixed stratum. Site Ballymaguire. Transects, top – "Farm", bottom – "Nick". Transects sample 6 farms. Arable-Pastoral mosaic clear – top left and bottom right pastoral farms. Different boundary management approaches between farming types apparent (note shadow lengths); taller hedges, trees and tree lines associated with pastoral areas, management more severe generally in arable areas.

1. Stubble fields and varying hedge management. Type B and type F hedge with trees; tall and short hedges beyond.

2. Variable type F hedge with gaps.

3. Farm house and yard.

4. Tall narrow hedge.

5. Tall type F hedge. Pasture fields in background.

6. Shorter "overgrown" type B hedge.

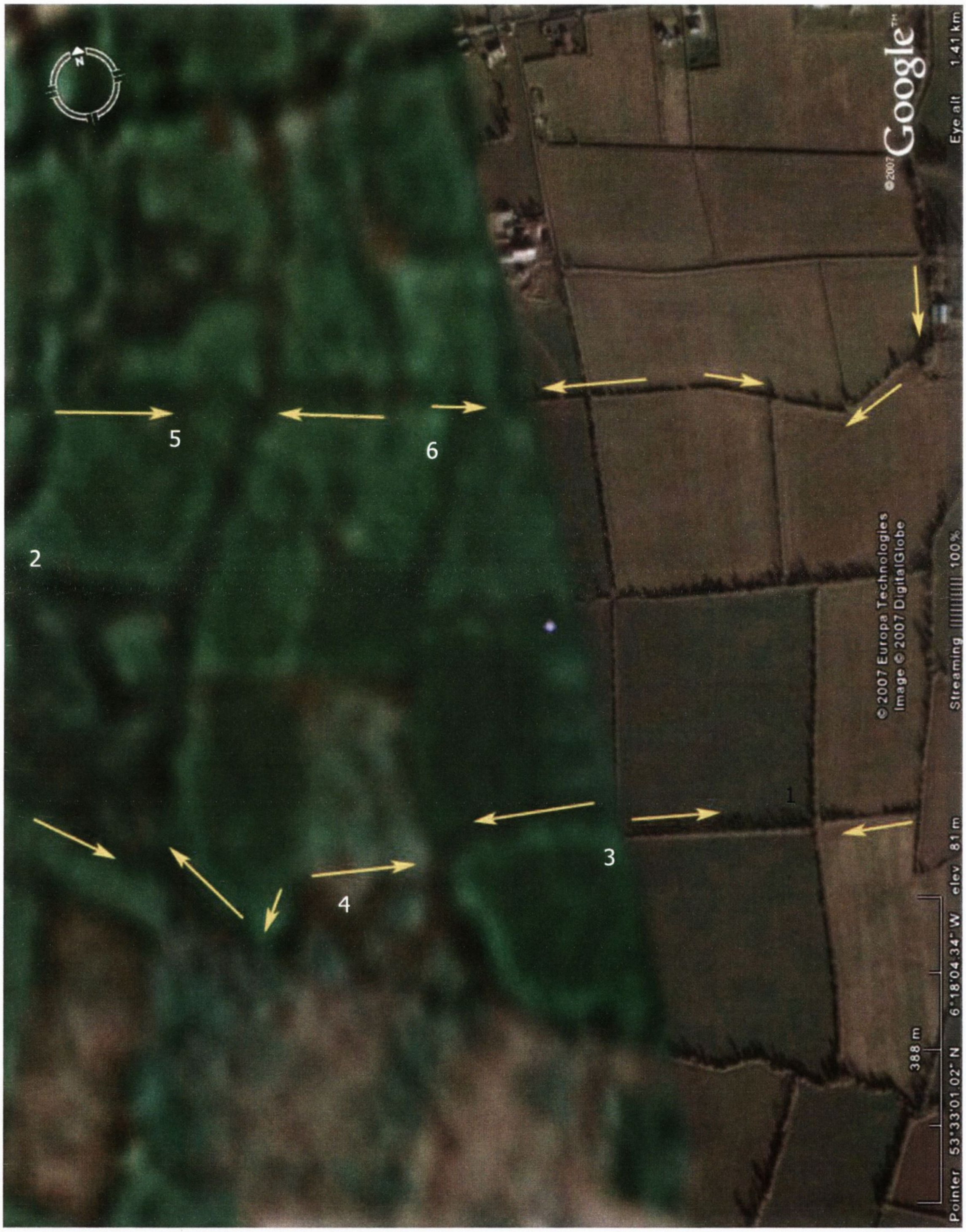


Plate 7. Pastoral stratum. Site Damastown. Transects, top – "Farm", bottom – "River". Transects sample 5 farms. Contrasting hedgerow management between two farms (note shadow length), one at top and the other, middle to bottom, in right hand side of plate. Left hand side, low resolution image.

1. Looking north, cereal and pasture mosaic.

2. Looking north, pasture fields.

3. Low, untidy type B hedge, recent management and regrowth.

4. Looking south, cereal and pasture mosaic.

5. "Gappy" type D hedge, early spring.

6. Low untidy hedge with Gorse and trees.

Plate 8. Pastoral stratum. Site Rowlestown. Transects, top – "Maguire", bottom – "Rooney". Overwhelmingly pastoral landscape. Arable fields top centre, bottom left. Transects sample 4 farms including intensive beef (top left) and REPS sheep farm (1 to 4). Trees are a dominating feature of field boundaries. D, E and F type hedges typical.

1. REPS sheep farm; bare patches are nettle stalks.

2. Type E hedge showing heavy "management by sheep".

3. Former ditch?

4. Undergrowth removed by grazing pressure.

5. Very sparse type D hedges.

6. "Gappy" type D hedge.

Plate 9. Pastoral stratum. Site Baldwinstown. Transects, left – “Reynolds”, right – “Horses”. Transects sample 5 farms. Low resolution image. Arable grassland mosaic and substantial tree lines apparent. F type hedges predominate.

1. Lush pasture or silage with large unmanaged type F hedges.

2. Large open field with grass grown for silage. Distant tree line.

3. Variable and diverse hedge with trees.

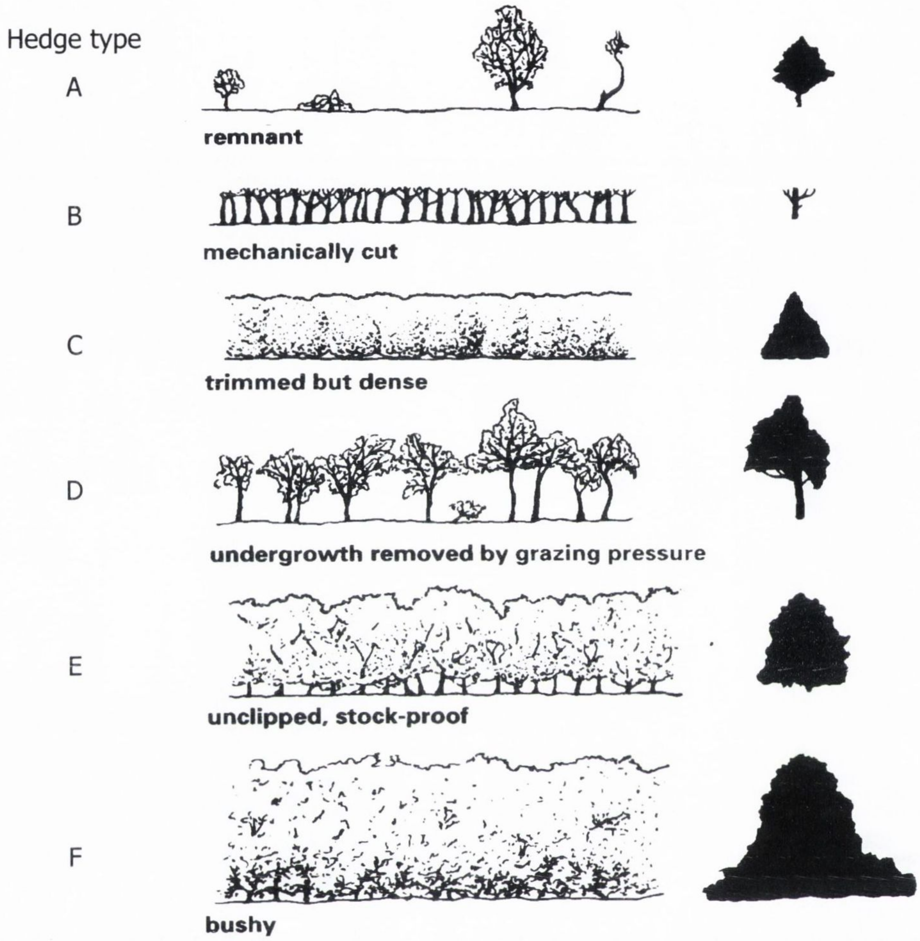
4. June. Bushy type F hedge intersection showing management difficulties with uncut silage grass.

5. Type F hedge with trees.

6. Cereal stubble, with wide field margin. Hedge shows signs of management.

Appendix 2

Hedgerow typology (after Pollard et al. 1974)



Criteria for scoring management and tightness (after Doogue 1994).

Hedge management scores

1 = no evidence of trimming
2 = slight evidence, usually lopped tree branches
3 = no recent evidence, but indications visible
4 = trimmed and shaped in recent past
5 = neatly shaped squared off hedges

Hedge tightness scores

1 = thin with many gaps, > 10% of hedge missing
2 = "gappy" but robust, < 10% of hedge open
3 = cattle could break through
4 = human could break through
5 = impenetrable

Appendix 3

List of all species seen from transects during surveys

Study species

Chaffinch	*Fringilla coelebs*	Linnet	*Carduelis cannabina*
Greenfinch	*Carduelis chloris*	Goldfinch	*Carduelis carduelis*
Bullfinch	*Pyrrhula pyrrhula*	Skylark	*Alauda arvensis*
Yellowhammer	*Emberiza citrinella*	Tree Sparrow	*Passer montanus*
Reed Bunting	*Emberiza schoeniclus*	House Sparrow	*Passer domesticus*

All other species

Grey Heron	*Ardea cinerea*	Pied Wagtail	*Motacilla alba yarrellii*
Greylag Goose	*Anser anser*	Dunnock	*Prunella modularis*
Shelduck	*Tadorna tadorna*	Robin	*Erithacus rubecula*
Teal	*Anas crecca*	Whinchat	*Saxicola rubetra*
Mallard	*Anas platyrhynchos*	Stonechat	*Saxicola torquata*
Hen Harrier	*Circus cyaneus*	Wheatear	*Oenanthe oenanthe*
Buzzard	*Buteo buteo*	Blackbird	*Turdus merula*
Sparrowhawk	*Accipiter nisus*	Fieldfare	*Turdus pilaris*
Kestrel	*Falco tinnunculus*	Song Thrush	*Turdus philomelos*
Merlin	*Falco columbarius*	Mistle Thrush	*Turdus viscivorus*
Peregrine Falcon	*Falco peregrinus*	Redwing	*Turdus iliacus*
Pheasant	*Phasianus colchicus*	Wren	*Troglodytes troglodytes*
Red-legged Partridge	*Alectoris rufa**	Blackcap	*Sylvia atricapilla*
Moorhen	*Gallinula chloropus*	Whitethroat	*Sylvia communis*
Lapwing	*Vanellus vanellus*	Sedge Warbler	*Acrocephalus schoenobaenus*
Golden Plover	*Pluvialis apricaria*	Willow Warbler	*Phylloscopus trochilus*
Curlew	*Numenius arquata*	Chiffchaff	*Phylloscopus collybita*
Redshank	*Tringa totanus*	Goldcrest	*Regulus regulus*
Snipe	*Galinago galinago*	Spotted Flycatcher	*Muscicapa striatus*
Black-headed Gull	*Larus ridibundus*	Coal Tit	*Parus ater*
Feral Pigeon	*Columba livia*	Blue Tit	*Parus caeruleus*
Woodpigeon	*Columba palumbus*	Great Tit	*Parus major*
Collared Dove	*Streptopelia decaocto*	Long-tailed Tit	*Aegithalos caudatus*
Cuckoo	*Cuculus canorus*	Rook	*Corvus frugilegus*
Short-eared Owl	*Asio flammeus*	Hooded Crow	*Corvus corone*
Swallow	*Hirundo rustica*	Raven	*Corvus corax*
House Martin	*Delichon urbica*	Jackdaw	*Corvus monedula*
Swift	*Apus apus*	Magpie	*Pica pica*
Meadow Pipit	*Anthus pratensis*	Starling	*Sturnus vulgaris*
Grey Wagtail	*Motacilla cinerea*	Redpoll	*Carduelis flammea*

Rare observations

Seventy species were recorded on or from transects (excluding species seen on the shore at Loughshinny) over the course of the four surveys. The more notable observations were single sightings of Hen Harrier, Redpoll, Cuckoo and Red-legged Partridge. All were seen "using" the farmland habitat. The Cuckoo was recorded on Loughshinny "Coast" during the second spring. The Harrier was observed hunting over a cereal stubble field during the second winter. A flock of 7 Redpoll was observed foraging from upright stems of ditch vegetation during the first winter. A pair of Red-legged Partridges, almost certainly "game-releases", was observed foraging along the edge of a brassica fallow during the second spring. Other interesting observations were: infrequent but regular observations of Ravens, a Whinchat that appeared to have established a breeding territory in a scrubby sedge field, and two records of Spotted Flycatcher.