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YELLOWHAMMER (*Emberiza citrinella*) ECOLOGY IN AN INTENSIVE PASTORAL DOMINATED FARMING LANDSCAPE

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Abstract

Farmland birds in Europe have declined as agriculture has intensified, with granivorous specialists disproportionately affected. Despite grassland based farming being widespread, farmland bird research to date has focussed on mixed and arable farms. Yellowhammers are a red-listed species in the UK. This study investigated year round habitat requirements, diet, and movements of yellowhammers at four grassland dominated farms in Ayrshire, Scotland. Data were obtained via field surveys and trials, radio-tracking and faecal analysis. Fine scale breeding season foraging habitat requirements were studied by comparing invertebrate and vegetation communities at foraging sites with paired controls across all four farms. A small scale winter supplementary feeding trial was conducted on one farm. Breeding yellowhammers avoided farmyards, but bred throughout the rest of the sites; average density was low at 0.08 pairs per hectare (range 0.06 to 0.15), lower than densities reported in arable and mixed regions. During the breeding season, yellowhammers preferentially foraged within 10m of field margins. There was no evidence that yellowhammers avoided foraging on pastoral habitat, contrary to results from studies in mixed and arable farming regions. Faecal analysis revealed that adults diet contained significantly more cereal than the diet of nestlings, with both including more invertebrate material than observed in previous studies. Diptera, Coleoptera and Araneae were key orders, with Lepidopteran larvae additionally important for nestlings. A low proportion of cereal was found in nestling diet, suggesting that the invertebrate dominated diet provided was of high quality. In contrast to summer diet, and despite grassland being the dominant habitat, cereal dominated winter diet; grass seeds and invertebrates accounted for <1% of diet in winter. Winter yellowhammer density at each farm was positively correlated with stubble availability. Radio-tracking found yellowhammers significantly selected stubble in early winter and game managed habitat in late winter. Supplementary feeding attracted an estimated 247 to 332 yellowhammers at a site where the previous year's winter surveys recorded only 5 birds despite holding a good breeding population. Survival rates of 1st years at the supplementary fed site appeared higher than elsewhere in the landscape, and a small increase in breeding density was observed post feeding, although it is unknown if this was a result of the feeding. As winter progressed, the use of the grain provided increased, suggesting that the late winter period was the most crucial time for the birds regarding food supply. Providing supplementary food represents a cheap and easy solution that could be utilised by agri-environment schemes to tackle late winter farmland bird food shortages. Alternatively, increasing winter stubble in grassland dominated regions should provide additional biodiversity benefits associated with increased landscape heterogeneity as well as increased winter food availability. This study highlights differences in breeding density, habitat selection, movements and diet of yellowhammers on grassland farms compared to arable and mixed farm populations. Restricted winter stubble habitat limits winter food availability, and hence the likely overall size of the population able to subsist in this habitat.

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Candidate’s Declaration

I declare that the work recorded in this thesis is entirely my own. The work described in this thesis is my own except where specifically acknowledged. No part of this thesis has been submitted for any other degree or qualification.

Signature of candidate ....

Date ....

Chapter 1 – Introduction

1.1 Farming in Britain

> Farming (noun) “the activity or business of growing crops and raising livestock” - Oxford Dictionary (online)

Farming is an important industry contributing, amongst other things, to Britain’s economy and food security. British farming provides full and part time employment to ½ million people whilst producing 58% of the country’s food requirements. It is the dominant land use in Britain with 70% of land utilised for agriculture (Wilson *et al.* 2009). The way in which Britain’s farmland has changed rapidly over the last century with advances in technology and knowledge.

1.1.1 Changes in the Farming landscape since the Second World War

Lowland farming in early 20th century Britain was characterised by low input, mixed farming systems utilising traditional, labour intensive techniques. Farming relied heavily on crop rotations to help maintain soil fertility and reduce the impact of pests. As different crops require work to be carried out on them at different times of the year, the mixed farming systems necessitated by crop rotations helped spread the workload evenly throughout the year. With advances in technology, farming became more mechanised leading to landscape level changes. For example, replacing scythes by mechanised mowers reduced harvest time and labour demands, and allowed previously time consuming harvesting to be completed in a short time period. The reduced need to spread jobs for a large workforce evenly throughout a year thanks to the smaller workforce required, combined with the large capital cost associated with purchasing specialised machinery, lead to individual farms becoming specialised (Shrubb 2003). In Britain, climate considerations determined a region’s specialisation; the dryer East focused on arable and the wetter West specialised in dairy and meat production, creating a polarised farming landscape across the country (Shrubb 2003). Another result of the capital cost of machinery was increased sizes of farm holding.

Post Second World War, tractor use took off, with the number on farms in England and Wales increasing over 2,000%, from 20,000 in 1930 to 416,725 by 1960 (O'Conner & Shrubb 1986). Tractors led to a further decline in both labour and the number of horses working on farms, which fell from 683,000 in 1930 to 21,000 by 1965 (O'Conner & Shrubb 1986). Horses required grazing paddocks, ponds to drink from, and oats to be grown as feeding, these habitats were lost with the horses, further increasing farmland habitat homogeneity.

Field sizes increased as larger field sizes are easier and more efficient for machinery to work in. For example, the doubling of field size from 6 to 12 Hectares saves an estimated 17% working time, and therefore money, whilst reducing hedgerow and field margin habitat on farmland. The characteristics of the remaining hedgerows have changed; the dense stock proof hedges resulting from traditional management practices such as coppicing and laying (which are both time and labour intensive) have been replaced with flail trimmed hedges which are characteristically low, tightly trimmed, with gaps at the hedge base. Fencing on farms has increased as fences are not only cheap and easy to install whilst being easier and more cost effective and easier to maintain than hedgerows, their capital costs are also often met by government grants. Many of these new fences were put alongside existing hedgerows, leading to the neglect of previously stock proof hedges. Hedges left unmanaged over a long period of time become a line of trees. A 1998 survey of hedges in England reported that 89% of the hedges surveyed had become remnant, relict or lines of trees/shrubs (Haines-Young *et al*. 2000).

This intensification of farming brought about by increased mechanisation was encouraged and speeded up by the 1947 Agriculture Act. This act guaranteed farmers set prices for crops and livestock (Shrubb 2003), with the government providing grants for capital investment in farms, funding operations such as land drainage, ploughing old grasslands, fencing, and constructing new buildings. Herbicide and pesticide use increased, leading to increased yields.

1.1.2 Changes in Grassland Farm Management

Today, pastoral farming accounts for over half of the farmland in Britain (Perkins *et al*. 2000), with the land falling into two broad habitat categories – rough grazing and permanent grass or ley. Rough grazing refers to areas of agriculturally unimproved or semi-natural grassland, which in Britain is predominantly hill grazing. Permanent grass or ley is improved or enclosed grassland. When grasslands are under five years old, they are classed as ley, older grasslands being classed as permanent. Since the Second World War, as agriculture has intensified, rough grazing habitat has been lost, usually because it has been drained, ploughed then reseeded, creating more permanent grassland. This loss of old grassland is one of the most significant changes in agriculture, declining by 92% in England and Wales since the 1930s (Shrubb 2003). Grassland management has intensified - fields have been reseeded with competitive fast growing high yielding grass species. Herbicides are now sprayed to remove perennial broadleaved weeds, and pesticides sprayed, targeting, for example Tipulidae larvae, which if left uncontrolled can cause bare patches in grassland and economic loss. Lime has been used, where appropriate, neutralising acid soils otherwise unsuitable for intensive pastoral farming. Organic (dung or slurry) and inorganic fertilisers are used, providing additional nutrients to grass crops, reducing diversity and increasing yield. Increase in cutting frequency and grazing pressure has led to a rise in sward density in both pasture and silage fields, as defoliation allows light to enter the base of the plants, promoting the growth of tillers.

Pastoral fields are utilised in two main ways; as pasture for grazing livestock for dairy or meat production, or to grow grass as a forage crop to be cut and stored as livestock feed.

1.1.3 Changes in Management of Forage Grass

The traditional method of preserving and storing grass long term to be used as animal feed was hay making. In the 1940s, almost all grass was preserved this way. It involves species-rich hay meadows being cut, dried and baled annually towards the end of the summer. Fields in the south were cut typically in June, with fields in the north cut later as the higher latitude slowed grass maturation, with Yorkshire typically cutting hay in July, and more upland areas harvesting into August. The hay harvests of the late 19th century were labour intensive processes. With increasing mechanisation post Second World War, labour demands decreased. Increasing use of fertilisers resulted in better growth rates and earlier hay harvests.

Hay is a difficult crop to grow; to ensure preservation the moisture content must be less than 20% when bailed (Devereux *et al.* 2006a). As a result, haymaking requires a period of good weather lasting several days to allow the crop to be cut and dried before bailing. In comparison to hay, silage - ryegrass monocultures - is more attractive for the farmers to grow as silage is less reliant on good weather for successful harvest as it can contain 40% to 80% moisture (Devereux *et al.* 2006a). Additionally, unlike hay meadows which are cut annually, silage fields are cut two or three times a year, producing larger annual yields per unit area. Fertilisers are extensively used, further increasing yields. With the recent development of technology and techniques to allow silage to be grown efficiently and economically, since 1960 there has been a rapid change in how grasslands are managed, moving away from hay production to silage production. In 1962, 10% of forage grass was grown for silage, increasing to over 75% by the mid 1990s (Shrubb 2003). Today, dairy herds are almost exclusively fed on silage, so hay is grown in very few areas. In 2006, only 15% of forage grass cut was hay (Devereux *et al.* 2006a), chiefly to supply the demands of Britain's recreational horse population. Livestock is increasingly being wintered indoors, increasing demands for silage, so more grassland is managed as forage grass at the expense of pasture. This trend looks to increase in the future as modern intensive dairy herds are in some cases beginning to be kept inside all year.

1.1.4 Changes in Management of Pasture

Pasture management has changed; the million horses kept in Britain for agricultural work in the early nineteenth century have been lost, resulting in the loss of their small species-rich grazing paddocks. At the same time, the 1947 Agriculture Act paid farmers per animal, leading to increased stocking densities of sheep and cattle. Stocking densities post-war were increased in many instances to an unsustainable level for the land resulting in overgrazing. Pastures became more uniform, characterised by short swards producing few seeds with the higher grazing and trampling pressure. Increased applications of both organic and inorganic fertilisers have improved grassland productivity, further increasing stocking density.

All the above changes in management have resulted in modern grasslands becoming dense, highly productive, species poor, ryegrass dominated swards.

1.1.5 Changes in Arable Management

With the increased mechanisation of arable farming, hand sowing has been replaced by seed drills. This provides better opportunity for efficient weed control, as planting in drills allows easy access for hoeing, first by hand later being replaced with machinery. The development of combine harvesters which are able to cut corn and separate the grain simultaneously have replaced scythes, self binders and threshing drums allowing for quicker and more efficient grain harvests with less spilt, and the disappearance of chaff heaps and corn ricks from the landscape (O'Conner & Shrubb 1986). This mechanisation has allowed arable farming to shift from spring to autumn sowing of crops in many areas, previously impossible with the time scales required for harvest and sowing. Autumn sowing, whilst increasing yields, has removed overwinter stubble from the landscape. The percentage of tilled land in England and Wales planted in spring has decreased from 78% in 1962 to 36% in 1982 (O'Conner & Shrubb 1986). Cropping patterns have changed, for example, land under oil seed rape cultivation in England has grown from 40,000 hectares in 1970 to over 462,000 hectares in 2005 (Wilson *et al*. 2009).

At the time of the Second World War, arable farming generally formed part of a three year ley system. Cereal was grown for three years, followed by three years of grass, with the management planned around the requirements of a dairy herd. The regular ploughing of the land, resulting from the ley management, helped control weeds. The development and widespread use of chemical herbicides in the 1960s removed the need for the use of rotations to control weeds, further increasing the specialisation of farming begun by mechanisation. At the same time as herbicide use increased, the use of insecticides and fungicides rose. The introduction of fungicides as seed dressing helped prevent diseases in crops such as mildew and rust, allowing autumn sowing of crops to spread. The percentage of cereals treated with insecticides went up from less than 10% in the early 1970s to over 80% by the late 1990s (Shrubb 2003). The chemical control of weeds, disease and pests contributed to increased crop yields.

1.1.6 Organic Farming

Organic farming has been around since the 1940s and is characterised by environmentally sustainable farming methods, using virtually no artificial pesticides or herbicides for controlling weeds and pests. Instead, for example, non-crop habitat is managed to allow natural predators of crop pests to flourish, helping control crop pests. In a similar way to traditional farming, organic farming exploits crop rotations to help maintain land fertility in addition to the use of natural fertilisers such as manure and compost, additionally these crop rotations help control weeds. The combination of the lack of chemical pesticides and fertilisers, the mixed farming that arises as a result of the use of rotation and the sympathetic management of non cropped habitats has been found in a recent review to increase the abundance and species richness of a variety of farmland taxa compared with conventional modern agriculture (Hole *et al*. 2005).

In recent years, as the demand from environmentally and ethically conscious consumers has risen, the area of farmland managed as organic farms has increased from 0.3 million hectares in 1990 to 7 million hectares in 2006 in Europe (Wilson *et al*. 2009). Therefore, in areas where land has been converted to organic farming, agriculture has become less intensive for the first time in generations.

1.1.7 Farming and Game Management

Sport shooting on farmland for game birds including partridge and pheasant is an important rural industry in Britain. Before the First World War, grey partridge *Perdix perdix* populations on farmland were high, with an estimated million pairs breeding in Britain (based on an analysis of shooting bags – Potts 1986). Driven shoots were common on estates throughout the country. Game keepers were employed to control mammalian and avian predators, and against a background of low-intensity farming, produced large bags. However, with the changes in agriculture described above, grey partridge numbers have gone into decline since the 1950s, as did the shooting bags (Potts 1986). With the decline in grey partridge shooting, there has been an increase in the release of reared birds on farmland for sport, mainly pheasants and red-legged partridge. Where such birds are released, the land is managed to provide them with cover and food (through sympathetic hedgerow management, growing of game crops) or supplementary grain is provided, benefiting other wildlife (e.g. Parish & Sotherton 2004).

1.2 Effects of Intensification of Farming on Wildlife

70% of Britain is covered by farmland (Wilson *et al.* 2009); therefore it is the dominant terrestrial habitat. The way in which this land is managed can either have a positive or negative impact on wildlife abundance and diversity. The traditional aim of a farm - to produce food - has driven the intensification of agriculture over the last 60 years. This aim is often in conflict with the needs of wildlife: as agriculture has intensified as outlined above, farming ecosystems have simplified. As more diverse ecosystems are more stable (e.g. Tilman & Downing 1994), the loss of ecosystem complexity has reduced the resilience of the system. Simple ecosystems are characterised by lower biodiversity, modern farmlands are no exception. Biodiversity losses have occurred across a wide variety of taxa, with the reasons for the declines being complex, often species specific a result of an accumulation of factors.

1.2.1 Flora

Plant diversity has declined as a result of changes in agricultural practise, in both pastoral and arable farms. As the use of fertilisers has increased, floral biodiversity has declined; plant species richness has been shown to have a negative correlation with nitrogen input in cereal and pastoral farming systems throughout Europe (Kleijn *et al.* 2009). Herbicides have also contributed to the loss of floral biodiversity, reducing the numbers of weeds present in both pastoral and arable fields (Wilson *et al.* 2009).

Lowland grasslands, as a result of the switch from hay to silage, increased reseeding, high fertiliser inputs, herbicide applications, alongside intensive cutting and grazing pressure, have become dominated by nitrogen responsive, competitive grass species such as Italian rye *Lolium multiflorum*, perennial rye *Lolium perenne* and meadow fescue *Festuca pratensis*. The dominance of ryegrass has caused a decrease in the diversity of native grass species in pastoral farmland, including bent species *Agrotis sp* and red fescue *Festuca rubra* (Shrubb 2003).

1.2.2 Invertebrates

The loss of plant diversity, in both arable and pastoral farms, caused by agricultural intensification has impacted organisms at higher trophic levels. Invertebrate assemblages have changed with the changing vegetation on farmland, with many invertebrate species declining as food plants decline and important habitats are lost (Wilson *et al.* 1999). Invertebrates play an important role in maintaining healthy agricultural ecosystems. Some are important pollinators, whilst others maintain soil quality, recycle nutrients in the environment or regulate crop pests (reviewed in New 2005). The main threats to farmland invertebrates are habitat loss and use of agri chemicals – both the direct loss caused through pesticide use, and the indirect loss through herbicide use through the loss of host plants (New 2005).

Agricultural intensification has reduced habitat diversity in farming landscapes, and simplified the ecosystem. In simple ecosystems, high densities of invertebrates may be present, but diversity is generally low. In modern farmland, a number of nematode species have increased, as their abundance is often positively correlated with the primary production of vegetation. Some species of beetles and earthworms have also become more abundant, whilst some species of sawflies, spiders, rove beetles, carabid beetles, parasitic wasps and cereal aphids have declined (New 2005).

Invertebrate abundance and diversity has been limited by the simple ryegrass-dominated sward of intensively managed grasslands. Here there has been a loss of conspicuous invertebrates including grasshoppers, ants, spiders and Lepidoptera larvae (Wilson *et al.* 1999). Where high levels of organic fertilisers have been applied, Tipulidae larvae (leatherjackets) have increased (Wilson *et al.* 1999). This increase has often been counteracted by the use of pesticides, as leatherjackets are an important pastoral pest causing damage and economic loss in grasslands. The increased proportion of land under silage production and corresponding decrease in pasture has decreased invertebrate numbers on farmland, as aerial invertebrates are two to four times more abundant over cattle grazed pasture than in arable and silage fields (Evans *et al*. 2007). The frequent and early cutting of silage has reduced the abundance of invertebrate species in groups such as the Heteroptera. The loss of broadleaved weeds in both arable and pastoral systems has removed invertebrate food plants, leading to a decrease in phytophagous insect diversity, and also in their invertebrate predators. Hedgerows support more invertebrates, in terms of both biomass and diversity, than adjacent fields (e.g. Bowden & Dean 1977, Trnka *et al*. 1990, Peng *et al*.1993). Thus, the loss of hedgerows has reduced the total invertebrate abundance on farmland, including local losses of species such as carabid beetle species that are restricted to hedges (Asteraki *et al*. 1995). The removal of farmland ponds has further reduced the species diversity on farms, with many pond invertebrates now red-listed as a result of habitat loss and fragmentation.

Bumblebees are perhaps the best studied farmland invertebrates of conservation concern, as their loss has serious implications for plant pollination throughout the countryside (Meffe 1998). Bee populations have declined in part because the decline in hedgerows has removed suitable nesting habitat (Goulson *et al*. 2008). Bee populations have also been directly affected by the increased use of chemical pesticides, for example neonicotinoids (Whitehorn *et al*. 2012), and indirectly affected by herbicides reducing nectar rich food plants such as vetches *Vicia spp.* and red clover *Trifolium pratense* (reviewed in Goulson *et al*. 2008).

Butterflies have also been well studied, with population declines and range contractions recorded for many UK species (Warren *et al*. 2001), such as the common blue *Polyommatus icarus* and small copper *Lycaena phlaeas* (Leon-Cortes *et al*. 2000), and in Europe (Van Dyck *et al*. 2009). These declines have been attributed to habitat loss, fragmentation and degradation, pesticide use and the loss of host plants essential for butterfly larvae (e.g. New 2005, Rands & Sotherton 1986). Moths have also declined (e.g. Conrad *et al*. 2004, Conrad *et al*. 2006) on farmland as agriculture has intensified. A long term study in Hertfordshire has found the number of moths caught in light traps on farmland since 1960 has declined in species diversity and abundance by two thirds compared to the numbers caught in the 1950s, whereas the diversity and abundance of moths caught in woodland remained unchanged (Woiwod & Harrington 1994).

1.2.3 Amphibians and Mammals

The impact of the intensification of farming on habitat diversity, vegetation communities and invertebrate communities has affected vertebrate populations, with declines recorded in many farmland species across amphibians, reptiles, mammals and birds. However, there have been relatively few long term studies of the distribution and density of British amphibian, reptile and mammal populations, as their populations are often difficult to study directly. Nonetheless, it is known that habitat loss through land drainage and farm pond removal has caused populations of amphibians on farmland to decline. For example, the decline of the great crested newt *Triturus cristatus* across Britain has been attributed to loss and pollution of ponds (Wood *et al*. 2003). Like amphibians, water voles *Arvicola terrestris* in Britain have declined as a result of drainage and agricultural intensification reducing wet habitat on farmland (Battersby *et al*. 2005). Remaining suitable habitat for water voles is often in the form of fragmented, linear strips. This degraded habitat has increased their vulnerability to predation by the introduced and increasing American Mink *Mustela vison*, whereas in extensive wetlands, mink have less impact on water vole populations.

Bats forage on aerial nocturnal invertebrates, and as more of these can be found on organic farms than conventional farms, as a result, bat declines have been less steep on organic farms than on conventional farms (Wickramasinghe *et al*. 2003). The decline of hedgerows brought about by agricultural intensification has reduced the suitability of farmland as bat foraging habitat, as bats rely on these linear features (Walsh & Harris 1996) to connect habitats and as they contain higher numbers of invertebrates than infield habitats.

Hedgehogs *Erinaceus europaeus* have undergone recent population declines in Great Britain (Hof 2009), with this decline correlating with the loss of hedges and the increased use of pesticides decreasing their invertebrate prey. Harvest mice *Micromys minutus* which are also thought to have declined (Battersby *et al*. 2005), prefer tall dense vegetation and hedgerows so like the hedgehog, they may have been affected by the loss and degradation of hedgerow and field margins. Annual flail trimming of hedges has reduced berry availability, an important winter food source for harvest mice. In addition to nesting in hedgerows, harvest mice nest in arable fields. With the change from spring to autumn sowing bringing forward harvest dates, crops are now harvested before the end of the harvest mouse breeding season. Another small farmland mammal suffering a long term decline in numbers is the field vole *Microtus agrestis* and the common dormouse *Muscardinus avellanarius* (Battersby *et al.* 2005). Field vole decline correlates with the loss of their preferred habitat, traditional pasture, rough grazing and field margins (Battersby *et al.* 2005), whilst hedgerows are important for dormice (Wolton 2009).

Not only have field voles declined as a result of the loss of field margin habitat, so have brown hares *Lepus europaeus*. The homogenisation of farming landscapes brought about by farming intensification has reduced the variety of foraging habitats available including field margins, leading to their population declining steeply (Edwards *et al.* 2000). The frequent mowing of silage fields has also caused high level of mortality, especially of leverets, alongside an increase of predation pressure as foxes *Vulpes vulpes* have increased (Edwards *et al.* 2000).

1.2.4 Birds

Birds are generally more visible than mammals, therefore, easier to study. This has allowed the population trends of farmland birds to be extensively studied and documented over the last century. This research has found that farmland birds across Europe are of major conservation concern, as during the last fifty years populations across a wide range of species have undergone rapid declines (reviewed in Newton 2004) with 14 of the 52 bird species currently on the U.K.'s red list of species of conservation concern primarily associated with farmland. The decline in bird populations has occurred at the same time as the intensification of farming (Shrubb 2003).

Figure 1.1 highlights the extent of farmland bird declines in Britain since the 1970s. From the late 1970s, populations rapidly declined until the early 1990s, where the rate levelled off. Generalist species, which occur on farmland but not exclusively, including woodpigeon *Columba palumbus*, rook *Corvus frugilegus* and greenfinch *Carduelis chloris* have remained relatively stable. Farmland specialist species, including grey partridge, skylark *Alauda arvensis*, corn bunting *Emberiza calandra* and yellowhammer *Emberiza citrinella*, have not fared so well, undergoing population declines by over 50% compared with their numbers in 1970. This is a result of these specialists' specific habitat requirements no longer being met as a result of the extensive changes that have occurred in agricultural practice throughout Britain in the last fifty years.

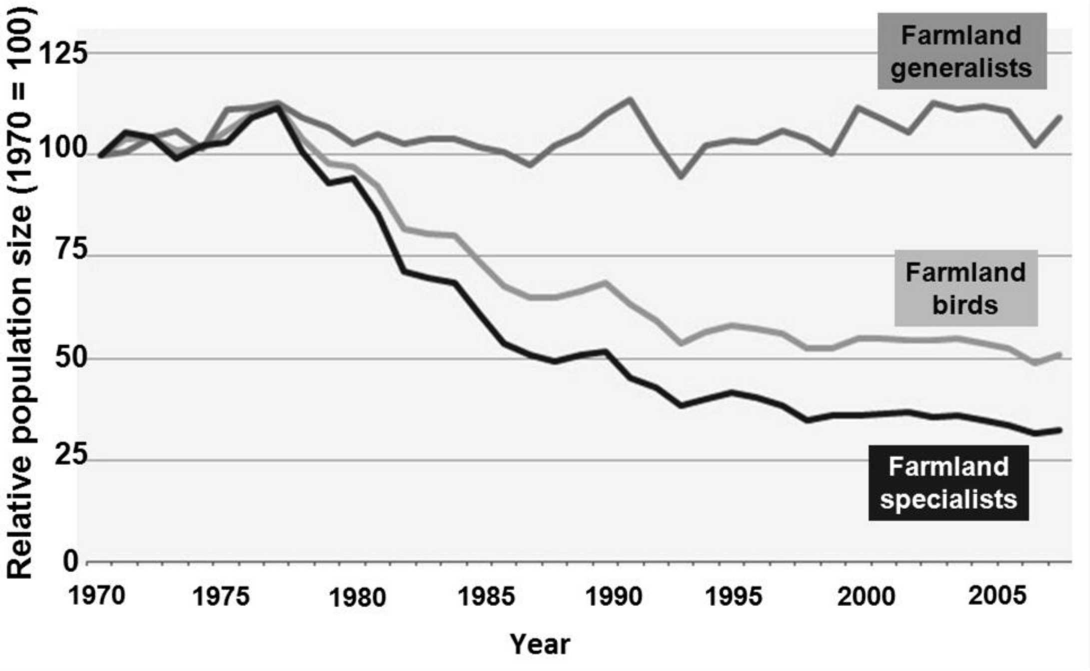


Figure 1.1 Farmland bird populations in Britain (adapted from www.bto.org.uk)

The specific mechanisms behind each decline vary across species, and also potentially within species across farming landscapes. The following sections will attempt to summarise the impacts of some of the most important recent changes in agricultural practice on bird populations.

1.2.4.1 Changes in farmyard habitat

Old farm buildings with wooden frames and roof space have been replaced with modern buildings constructed using concrete and steel, in part funded through government grants. These new buildings are unsuitable for nesting birds such as swallows *Hirundo rustica*, starlings *Sturnus vulgaris* and house sparrows *Passer domesticus* (Wilson *et al*. 2009). Areas around farm buildings have become cleaner, with less grain spilt reducing feeding opportunities for granivorous birds. Hygiene regulations now require grain to be stored in bird-proof silos, further reducing feeding opportunities (Shrubb 2003).

1.2.4.2 Drainage of land and loss of ponds

Breeding waders associated with wet agricultural grassland including snipe *Gallinago gallinago* and curlews *Numenius arquata* have declined (Wilson *et al*. 2005) at the same time as grasslands have been drained. The wet soil is essential for the birds to be able to probe for invertebrates (Wilson *et al*. 2009). Drainage has also affected the foraging ability of some passerines including the yellow wagtail *Motacilla flava*, which preferentially selects fields with shallow edged pools or ditches to breed in (Bradbury & Bradter 2004). The song thrush *Turdus philomelos*, a red-listed species of conservation concern, also selects wet areas for foraging, and has declined more severely in areas where more extensive drainage has occurred (Peach *et al*. 2004).

Ponds, and their associated banks and vegetation, provide nesting habitat and foraging habitat for a variety of birds. The removal of farmland ponds has reduced suitable breeding habitat for birds moorhen *Gallinula chloropus*, water rail *Rallus aquaticus*, little grebe *Tachybaptus ruficollis* and grasshopper warbler *Locustella naevi*, and in the case of larger ponds, swans, geese and gadwall *Anas strepera* on farmland (Wilson *et al*. 2009). Birds such as meadow pipits *Anthus pratensis*, pied wagtails *Montcilla alba*, grey wagtails *Montacilla cinerea* and yellow wagtails frequently forage alongside ponds, with their loss impacting populations (Wilson *et al*. 2009).

1.2.4.3 Effects of changes in hedgerow management

The reduction in hedgerows has impacted farmland bird populations. For example, the grey partridge and yellowhammer declines have in part been attributed to the loss and degradation of remaining hedges, reducing suitable nesting habitat (e.g. Kyrkos 1997, Potts 1980). But the importance of hedges extends beyond a nesting habitat, since yellowhammers and grey partridge also utilise hedges and the areas around them for foraging. This is also true also for aerial foragers: hedges support larger invertebrate population than surrounding farmland, so foraging swallows preferentially forage alongside hedges and field margins instead of field centres, especially in bad weather and when the crop alongside the hedge is arable, generally a poor habitat for invertebrates (Evans *et al*. 2010). Swallows have declined most severely in arable regions, where field sizes have been increased and invertebrate availability in the crop has declined (Evans *et al*. 2007). Hedges are not only used by foraging passerines, they are also exploited by sparrowhawks *Accipiter nisus* hunting passerines (Newton 1986).

1.2.4.4 Switch from hay to silage

The switch from hay to silage production in pastoral farming regions has affected bird populations in three main ways – by reducing the suitability of nesting habitat, food availability and food accessibility.

As silage is harvested earlier than hay, more eggs and nestlings of ground nesting birds are lost as a result of mechanical damage, as the change in timing to late May means harvest now coincides with the time when many species' first broods are close to fledging. For example, the corncrake *Crex crex*, a bird of hay crops once widespread has declined in part as a result of the loss of late cut hay meadows to nest in. Not only is silage cut too early to be suitable for nesting corncrakes, the crop additionally is too dense for nesting (Stowe *et al*. 1993). As a result, corncrakes are now restricted to the West coast of Scotland and Outer Hebrides where traditional farming practices such as hay making are still widespread, allowing the birds the longer nesting period they require. Other species affected by the switch from hay to silage changing the suitability of the nesting habitat in grasslands either through changes in the vegetation structure or the shorter defoliation period which doesn't allow breeding pairs sufficient time to complete breeding attempts include corn buntings, meadow pipit, skylark and yellow wagtails (Wilson *et al*. 2009).

Hay meadows are cut in late summer after the crop has set seed. These meadows are therefore an important foraging habitat for granivorous birds in winter, especially for buntings which eat grass seeds. Silage on the other hand is harvested before it sets seed, so as a result is a poor foraging habitat in winter, for graniverous birds (Shrubb 2003). The loss of this seed resource has correlated with a decline in granivorous birds from pastoral areas in winter. Research has shown the impact of this loss of winter seed could be mitigated - trials have shown unharvested areas of silage attracted large numbers of foraging buntings in winter (Buckingham & Peach 2006).

Silage crops have a denser sward than hay meadows, providing poor accessibility for birds to the invertebrate and mammal prey items that are present. For example, barn owls *Tyto alba* are thought to be less able to catch mammals in silage fields (Barn Owl Trust 2012), and lapwings *Vanellus vanellus* prefer short vegetation from which to glean invertebrates (Devereux *et al*. 2004). Not all birds are affected by the sward density - a trial of captured wild starlings foraging on experimentally created dense and sparse turfs cut to 3cm (densities of tillers representative of intensive and extensive agriculture, respectively) found no significant difference in the birds’ ability to forage (Devereux *et al*. 2006a). However, silage fields only provide suitable habitat shortly after cutting, as a similar experiment found starling foraging success declined with increasing vegetation height (Devereux *et al*. 2006b). The increase in silage fields at the expense of pasture has reduced the quality of foraging habitat for barn swallows in pastoral regions, as swallows preferentially forage over pasture fields where the presence of livestock positively influences aerial invertebrate populations.

1.2.4.5 Intensification of pasture management

Increasing stock density on farms has led to a shorter, more uniform sward in many pasture fields. The resultant short sward provides less nest cover for ground nesting species including the skylark, and the increase in stocking density increases the risk of nest trampling of species including the red-listed lapwing (Shrubb 1990). The increase in grazing pressure has also resulted in fewer seeds produced, decreasing the suitability of pasture as a foraging habitat, especially for granivorous birds in winter (Shrubb 2003).

This resultant shorter sward from the increased grazing pressure has decreased the suitability of grasslands for foraging birds including the meadow pipit, which prefer areas with longer more heterogeneous swards in winter (Whittingham & Devereux 2008). Other species, including starlings, have benefited from the shorter sward which provides easier access to food. However, starling populations have suffered through other changes in pasture management – the annual spraying of fields for leatherjackets, a pastoral pest, has removed an important food resource for them, perhaps contributing to the observed decline in starling numbers across Britain (Robinson *et al*. 2005).

1.2.4.6 Intensification of arable production

In Europe, there is a contrast between the trends of farmland birds between Western Europe where agriculture is more intensive where populations are declining and the more extensive agricultural farming areas in Eastern Europe where farmland bird populations are more favourable. In the West, the increase in the autumn tillage, pesticide and herbicides use has lead to increased cereal yields but at the expense of farmland bird populations.

The move towards autumn rather than spring tilled crops has had an enormous impact on farmland birds. The resultant loss of winter stubble from the landscape with autumn tilage has removed an important food supply for granivorous birds including yellowhammers, corn buntings and skylarks, contributing to their population declines (Wilson *et al*. 2009). The remaining stubble fields contain less food than they did prior to mechanisation as the advent and improvement of the combine harvester has resulted in more efficient harvest with less spilt grain, and has removed the winter chaff heaps which granivorous birds used to exploit as a food resource in winter plus the use of herbicides removes weed seeds (Shrubb 2003). The spread of autumn-tilled crops has also impacted birds in the breeding season, for example, skylarks which are able to have two breeding attempts each breeding season in spring sown crops, are only able to fit in one nesting attempt in autumn sown crops before the plants become too tall, dense and well developed. Skylarks have reduced breeding success in autumn sown cereals compared to spring sown (Donald 1999), contributing to skylark population declines. Both the direct impacts of pesticide use and the indirect impacts of herbicides have reduced invertebrate food for nestlings in the breeding season. For example, arthropod abundance remains lower 20 days after pesticide applications (Hart *et al*. 2006), which suppresses yellowhammer breeding success, as chick condition and fledging rate is correlated with arthropod availability (Hart *et al*. 2006).

1.2.4.7 Impacts of organic farming on birds

The recent trend of increasing organic farming may be beneficial to birds, with some studies reporting bird diversity and abundance up to 50% higher (McKenzie & Whittingham 2009) than on conventional farms, as organic farming supports higher diversity of both plants and invertebrates, providing better foraging habitat for birds. A study comparing organic and conventional farms found that organic farms had significantly higher numbers of six out of sixteen bird species in winter, including linnet *Carduelis cannabina*, jackdaw *Corvus monedula*, starling and greenfinch, whilst the total abundance for all species combined was greater (Chamberlain *et al.* 2010). In the same study, no significant difference for the other ten species was reported for species including yellowhammer, corn bunting, reed bunting *Emberiza schoeniclus*, skylark and tree sparrow *Passer montanus*, suggesting that current organic farming techniques do not significantly benefit the species of greatest conservation concern – declining granivores - in winter.

1.2.4.8 Impact of game management on farmland birds

Game cover crops may have a positive impact on farmland birds. For example, in winter, game crops in Eastern Scotland were found to contain up to 100 times as many birds per hectare as conventional crops (Parish & Sotherton 2004). Breeding passerines also use game crops as a foraging habitat in the summer (pers. obs), and there is some evidence that breeding birds additionally may benefit from reduced predator (both mammalian and corvid) abundance in areas managed by game keepers (Stoate & Szczur 2001).

The changes in farming brought about by agricultural intensification appear to have disproportionately affected granivorous farmland specialists (e.g. Wilson *et al.* 1999), with their populations suffering steeper declines than other farmland birds and range contractions (see Balmer *et al.* 2013). Research has been carried out to help quantify the birds' requirement so effective conservation measures can be developed. The yellowhammer, a granivorous farmland specialist well studied on mixed and arable farms, is a good model organism. Its requirements are typical of granivorous species – seeds throughout the year, suitable nesting habitat and invertebrates during the breeding season to feed their young.

Knowledge of how they utilise pastoral farming landscapes should be more widely applicable to a wider suite of declining granivorous farmland passerines.

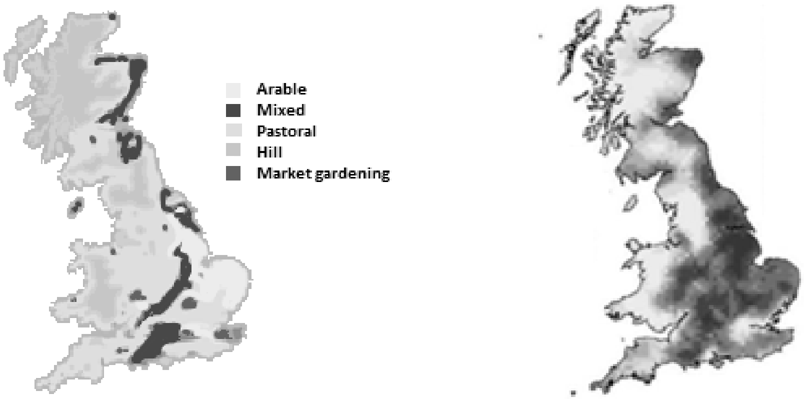
1.3 Yellowhammers

1.3.1 Yellowhammer identification and distribution

There are four breeding species in the *Emberizidae* (bunting) family, a seed eating family, associated with farmland in Britain: the corn bunting, cirl bunting *Emberiza cirlus*, reed bunting and the yellowhammer. Male and female yellowhammers are sexually dimorphic, with males brighter in colour than duller, brown streaked females. Yellowhammers are easily identified in the field by their yellow plumage, rich chestnut rump, and the male's distinctive call, often interpreted as "a-little-bit-of-bread-and-no-cheese" delivered repeatedly from a prominent song post in their territory throughout the breeding season (Cramp & Perrins 1994).

Yellowhammers are distributed throughout Europe. Across their range, three subspecies of yellowhammer have been identified (Svensson 1992). The nominate species, *Emberiza citrinella citrinella* occurs in south-East England and continental Europe to Western Russia. *E. c. erythrogenys* is found from the Baltic across to Siberia, and the third subspecies, *E. c. caliginosa* occurs in Scotland and Northern England (Cramp & Perrins 1994). Differences between the races are clinal, with the Scottish race having a brighter yellow plumage compared to the nominate race. On the continent, yellowhammers are partial migrants (Cramp and Perrins 1994), unlike British yellowhammers, which are resident throughout the year. Here they are sedentary in nature, with 95% of recoveries of ringed yellowhammer within 25km of the initial site of ringing, with the median distance travelled 1km (Forrester & Andrews 2007).

Yellowhammers are a species primarily associated with farmland, but small numbers can be found in woodland and heath land (Cramp & Perrins 1994). Yellowhammers are most abundant breeding in mixed and arable farming regions, but are still widespread in areas of pastoral farming, albeit at lower densities (Forrester & Andrews 2007) as highlighted in figure 1.2.



(a) (b)

Figure 1.2 (a) Farming Distribution in Britain (adapted from www.bbc.co.uk) and (b) Relative Abundance of Breeding Yellowhammers in Britain, from Breeding Birds Survey data in 2003 (adapted from www.bto.org.uk) with darker colours indicating higher abundance. The darkest colours on the right, indicating the highest relative abundance of yellowhammers, mostly corresponding with the areas of mixed and arable farming shown on the map on the left.

1.3.2 Yellowhammer Ecology

Yellowhammers can be found breeding in lowland farmland throughout Britain. Socially monogamous pairs are formed in early spring, with the male establishing and defending a breeding territory by singing and fighting with other males from February (Andrew 1955). Linear features such as hedges of ditches are more strongly defended than the corresponding area in the field, with the size of yellowhammer territory decreasing with increasing population density (Andrew 1955). Territories require nesting habitat, song posts, and foraging habitat nearby, such as field margins which adults preferentially forage in during the breeding season (Perkins *et al.* 2002, Stoate *et al.* 1998). Most foraging trips are within 100m of the nest (Morris *et al.* 2001). Female yellowhammers build their small, neat, cup shaped nest from grass, occasionally assisted by the male (Cramp & Perrins 1994), on or close to the ground, concealing it in thick vegetation, hedges or ditches. Once the nest is complete, the female lays her clutch of 3 to 6 eggs at the rate of one egg per day, with an average clutch size of 3.5 eggs (Peakall 1960). After clutch completion, she commences incubation lasting 13 days, resulting in young hatching synchronously (Peakall 1960). Once the eggs hatch, the male does most of the provisioning for the first few days whilst the female broods the chicks (Cramp & Perrins 1994, personal observation). Once the chicks are large enough to thermo regulate, both the male and female provision the young. Fledging occurs after an average of 12.4

days (Peakall 1960), with the parents continuing to feed the young for a short period after fledging.

Two, occasionally three breeding attempts may be made by yellowhammers in a breeding season, with yellowhammers nesting season lasting as late as September (Cramp & Perrins 1994, personal observation). Many yellowhammer nesting attempts are unsuccessful; a study of BTO nest record cards since the 1970‘s found that 69% of yellowhammer nests failed, usually at the nestling stage (Crick *et al.* 1994), with predation accounting for 50% of failed attempts – predation was mainly by mustelids, corvids and rodents. Just under 20% of nest failure was attributed to damage caused by agricultural activities, with the remaining 30% lost due to natural causes (e.g. weather, predation of adults) (Crick *et al.* 1994).

After breeding territories dissolve in late summer, yellowhammers form flocks, often with other farmland finches and buntings, including chaffinch, greenfinch, linnet and reed bunting. Flocking behaviour allows scattered but concentrated food supplies to be found efficiently, whilst reducing an individual’s predation risk through the dilution effect. Additionally, post breeding season, adult yellowhammers undergo full body moult beginning from early July to late August and lasting on average 55 days (Ginn & Melville 1983). Juveniles undergo a partial moult between July and October, moulting body feathers and occasionally greater coverts, tertials, and central tail feathers (Ginn & Melville 1983). The difference in moult strategy between first year and adult birds allows birds in the hand to be aged to these categories; adult tails are fresher and more rounded than the abraded, sharp angled tail feathers that the first year birds have grown quickly in the nest (Svensson 1992), but these differences can be difficult to detect (Jenni & Winkler 1994).

1.3.3 Yellowhammer diet

Yellowhammers are considered to be exclusively granivorous in winter, feeding primarily on *Graminae* seeds including cereals (Cramp & Perrins 1994). However, like most granivorous species, yellowhammers feed invertebrates to their nestlings; invertebrates are a good source of both fat and proteins essential for growth (Capinera 2010). A study of yellowhammer nestling diet in a mixed farming area of Leicestershire found nestling diet to be dominated by large Araneae (>5mm), Lepidoptera larvae, Coleoptera and Diptera (Stoate *et al.* 1998). This study was based on faecal analysis and also reported that 85% of nestling faecal sacs contained unripe cereal in addition to invertebrates, but did not quantify the importance of cereal in the diet (Stoate *et al.* 1998). Other studies have implied that cereal is less important than invertebrates for nestling yellowhammer diet, as cereal has been shown to be fed more in poor weather when foraging for invertebrates becomes more difficult cold, wet weather reduces their activity (Bradbury *et al.* 2003). Additionally, nestling fledging condition is positively correlated with the amount of invertebrate material in their diet (Douglas *et al.* 2012) suggesting that they are a better quality food source for yellowhammer nestlings. Yellowhammer nestling condition on day 6 has been shown to positively correlate with higher arthropod content in diet, and broods with chicks in good condition at this stage have a lower probability of brood reduction (Hart *et al.* 2006). Five adults studied during the breeding season were, unlike the nestlings, found to be feeding exclusively on cereal (Stoate *et al.* 1998). This contrasts with a study of adult yellowhammer diet carried out in Slovakia which found adult yellowhammers during the breeding season primarily feeding on invertebrates (77% of diet) with only 23% of diet from plant sources (Holland *et al.* 2006). Another study of yellowhammer nestling diet, this time using samples obtained from neck collars in addition to faecal samples, found that the nestling diet consisted of 38% Diptera, 23% Coleoptera, Lepidoptera 22% and 12% spiders (Moreby & Stoate 2000), and found no significant difference in yellowhammer diet as determined by faecal sample analysis and neck ligature. However, the lack of differences reported may be a result of the techniques sharing similar biases; faecal analysis often underestimate small soft bodied prey items (Moreby 1988) as few identifiable remains are detected in the faecal samples compared to hard bodied prey items such as Coleoptera. Similarly, neck can also underestimate small prey item but for different reasons; they sometimes can pass straight through the ligature (Johnson *et al.* 1980). Additionally, neck collars left in place for too long may result in food disgorgement or adults removing food from nestling gapes (Johnson *et al.* 1980).

1.3.4 Yellowhammer population trends

Like all the farmland buntings, as a result of agricultural intensification, the yellowhammer has undergone population declines throughout their range in Europe (Cramp & Perrins 1994). Corn buntings, yellowhammers and cirl buntings are currently all red-listed species of conservation concern after declines of over 50%, with the previously red-listed reed bunting being downgraded in 2009 to the amber list as a result of recent improvement in its numbers (Eaton *et al.* 2009).

In 1990, the Yellowhammer population in Britain was described as having "long-term overall stability" by the landmark text published by the BTO 'Population Trends in British Breeding Birds' (Marchant *et al.* 1990). This book brought together for the first time population data for all British breeding birds, highlighting declines in many. The stability in 1990 of the yellowhammer population contrasted with other populations of granivorous species including corn bunting, linnet, skylark and tree sparrow which had been declining since the 1970s. However, since the 1990's, the yellowhammer population has gone into decline, and declining by 2009 by 53% compared with numbers 25 years ago (Eaton *et al.* 2009). Population figures in Britain take no account of the different subspecies of yellowhammers and their relative numbers. This is an important consideration as conservation should retain as much genetic diversity in populations as possible, so relative numbers of each should be determined. However, in reality this will be difficult to do as differences between the two races are clinal.

There has been a contraction of the yellowhammer's range (figure 1.3). Greatest losses have occurred in Ireland, North West Scotland, and over upland areas in Northern England and Wales. Losses have occurred mainly in areas of hill and pastoral farming. These pastoral regions may be more marginal habitats for yellowhammers, making them more sensitive and susceptible to changes in management.

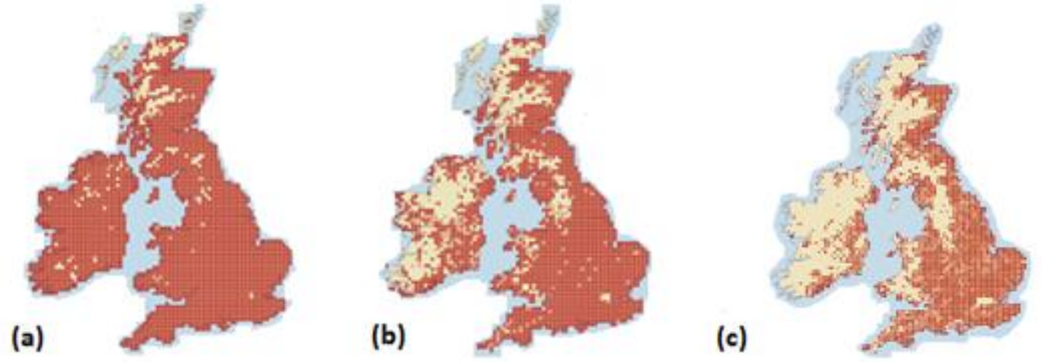


Figure 1.3 **Yellowhammer Breeding Distribution (a) 1968 – 72 Breeding Atlas (b) 1988 – 91 Breeding Atlas (c) 2008 – 2011 Breeding Atlas with red dots representing areas where yellowhammers were present during the breeding season (adapted from www.bto.org.uk)**

Yellowhammer declines do not appear to be a result of factors occurring during the breeding season; productivity per yellowhammer breeding attempt was higher between 1988-91 and 1992-95 when the population was declining than during periods of population stability (1982-87 and 1966-77), and expansion (1962-65 and 1978-81) (Siriwardena *et al.* 2000b). This increase in productivity may be a result of density dependent factors, e.g. the reduced population benefiting from reduced competition in the breeding season and not having to using marginal breeding habitat, leading to an apparent increase in productivity. It is however, unknown if the number of breeding attempts made by yellowhammers during a breeding season has changed. Assuming there has been no change in the number of breeding attempts made per season, the cause of the decline will be a result of factors operating outwith the breeding season. In New Zealand, where yellowhammers are a successful alien species, yellowhammer breeding success is lower than in Britain. This lends support to the hypothesis that decreased winter food supply has reduced winter survival of British yellowhammer populations (MacLeod *et al.* 2005a), but the observed differences in population trends between New Zealand and Britain may be a result of less pressure from predation and parasites in their introduced range. The current hypothesis for yellowhammer declines is that a problem with late winter food supply, creating a “hungry gap” before spring invertebrates and seeds become available, is reducing overwinter survival, and accounting for the observed population declines. The declines of yellowhammers, and other farmland biodiversity, in Britain are currently being addressed through farming policy and agri-environment schemes. However, for these schemes to be successful, they must be informed by research, and their effectiveness monitored.

1.3.5 Yellowhammer habitat choice

One of the most pertinent questions when considering best how to implement suitable conservation measure for a species is ‘what habitat does it require?’. Generally, in ecology this question is answered by looking at what habitat, the place where an organism normally lives or dwells, an organism is utilising more frequently, as the most profitable habitat in terms of survival and breeding success are predicted to be occupied first (Newton 2013), thus ‘good’ quality habitat is used more than ‘poor’ quality habitat.

Habitat choice can be studied in a variety of ways; most methods compare the amount observations of habitat choice to the availability of habitat. More frequent use of a habitat relative to its availability indicates that the animal (either through passive or active selecting the habitat) has higher fitness in such habitat as a consequence of the selected habitat offering higher survival and or fitness benefits to the organism. Resource selection functions model the probability of habitats being selected relative to their availability (Boyce 2002), and utilise a variety of statistical techniques, including GLMs (proportion habitat selection versus availability) or logistic regression (to analyse presence/absence data) to predict what habitats are selected. Habitat is selected at different levels (Manly *et al.* 1993), it can be studied over large geographical areas such as the range of a species, at a finer scale such as home range (which can vary throughout the year) and within the home range (e.g. selection of certain features as foraging habitat within home range). When considering foraging habitat choice of birds, a host of factors can play an important role. During the breeding season, as birds are tied to a nest site, only the habitat within a certain distance that is economical for the bird to travel can be considered whilst outwith the breeding season, flocking behaviour means data points (observations of foraging birds) are not independent.

Habitat quality and food availability is able to influence both the reproductive success and survival of organisms (e.g. Newton 2013, Fuller 2012, Hole *et al.* 2002). Suitable year round habitat must be available over an appropriate spatial scale to allow an organism’s requirements throughout its life cycle to be met for successful survival and reproduction. Thus habitat availability and quality both play an important role in maintaining population levels, and thus must be considered when managing a species.

The suitability of habitat varies both spatially and temporally, as do an organism’s habitat requirements. Due to the mobile nature of birds, they are able to make rapid adjustments to their habitat selection, and move between habitats that best meet their needs throughout the year. Year round habitat choice has to be considered and made available over an appropriate spatial scale in order to successfully conserve a species. During the breeding season, yellowhammers require foraging habitat close to breeding habitat (vegetated ditches and hedges), as most foraging trips are within 100m of the nest (90% reported in Biber 1993 and 60% in Morris *et al*. 2001). Field boundary structures (hedges and ditches) as well as providing nesting habitat; they additionally represent an important foraging habitat with yellowhammers feeding nestlings during the breeding season selecting this habitat relative to availability (Morris *et al*. 2002, Perkins *et al*. 2002). Arable habitat (especially barley) is selected (Morris *et al*. 2002, Stoate *et al*. 1998) while pastoral habitat is avoided (Morris *et al*. 2002). As yellowhammers in pastoral farming landscapes have undergone larger range declines and range contractions than in arable and mixed farming regions (Balmer *et al*. 2013), with pasture and silage leys avoided by breeding yellowhammers (Bradbury *et al*. 2000), pastoral landscapes may be considered a poorer quality habitat for yellowhammers.

Yellowhammer winter habitat use depends not only on the distribution and concentration of food resources but also on ability to avoid predators and shelter from adverse weather conditions (Robinson & Sutherland 1999). Wintering yellowhammers preferentially forage in winter on stubble fields to grassland habitat (e.g. Wilson *et al*. 1996, Moorcroft *et al*. 2002), whilst grassland is selected significantly more than autumn sown wheat habitat (McMahon *et al*. 2013). Yellowhammers are ground feeders, gleaning spilt grain and weed seeds from the ground (Cramp & Perrins 1994), opportunistically exploiting feed intended for cattle (Calladine *et al*. 2006) and game birds (Parish 2009). Their occurrence in gardens has increased at the same time as populations have declines (Chamberlain *et al*. 2005), however, they avoid using garden feeders in all but the most extreme weather conditions. Yellowhammers require both summer and winter habitat over a relatively small spatial scale as in Britain they are local residents (Cramp & Perrins 1994). Radio tracking found yellowhammers moving a mean distance of 1.3 km in early winter compared to 0.6km in late winter (Calladine *et al.* 2006) with 70% of nestlings ringed found within 5km of natal site (Lack 1986). Therefore, for conservation of yellowhammers to be successful, summer and winter habitat must be made available together throughout the yellowhammers range as they do not appear to be able to move large distances between suitable breeding and wintering habitat.

1.4 Conservation of Farmland Biodiversity

The conservation of biodiversity is important to maintain healthy ecosystems, genetic diversity, whilst retaining aesthetic and cultural assets. Healthy environments are important for ecosystem service provision including clean air and water quality and an attractive landscape, providing space for leisure activities and contributing to people’s well-being. As farmland accounts for most of the UK’s terrestrial habitat, it is important that the biodiversity within this habitat is preserved. However, although the changes in arable and pastoral farming techniques introduced by British farmers to address food shortages experienced during the Second World War have led to increased food production, this has been at the expense of farmland biodiversity. When Britain became a member of the European Economic Union in 1973, guaranteed prices for agricultural products led to a further increased production as farmers were paid for what they produced, regardless of market demands. These policies were so successful that by the 1980s, there were ‘mountains’ and ‘lakes’ of surplus food (first milk, followed by wheat then meat). To tackle this overproduction, ‘set aside’ was introduced in 1988 under EU Common Agricultural Policy (CAP). Thus by 1992, cereal farmers would only received subsidies if 18% of their land was put out of production. The notion that farmers were being paid to do nothing was not popular with the public, but as a side effect, biodiversity benefited from the land left as fallow. Set aside was abolished in 2008, partly in response to increasing grain prices. This decision to remove set aside may result in further declines of farmland bird populations in arable regions, as wintering yellowhammer, linnet, grey partridge, skylark and cirl bunting all used set aside land significantly more than other available habitat, presumably because it provided a good foraging habitat (Buckingham *et al.* 1999).

Increasing political awareness of the impact of current farming methods on wildlife led to the Ministry of Agriculture, Fisheries and Food creating the Environmentally Sensitive Area (ESA) scheme in 1987, the first modern agri-environment scheme where the primary aim was to benefit wildlife. Farmers were paid grants for adopting wildlife sensitive agricultural practices. Since then, agri-environment schemes have evolved into the systems present today, with devolved powers controlling the different schemes that are in place across Scotland, England, Wales and Ireland. In November 2012, 68% agricultural land in England was under some sort of agri-environment scheme (Natural England), however, the proportion of this land that will directly be of benefit to biodiversity will be lower, as agri-environment schemes also provide payments for managing historic land and providing soil and water protection. Payments are made for a variety of measures that promote biodiversity, such as planting new hedgerows and sympathetic management of existing hedgerows, planting of wild bird cover crops, leaving stubble overwinter, creation of beetle banks and planting wild flower pollen mixes targeting bees and butterflies.

Agri-environment schemes are developed based on the results from research into farmland bird populations, this research has to date focussed on arable and mixed farming regions as opposed to pastoral regions despite pastoral farming accounting for a large proportion of Britain’s farming landscape. For agri-environment schemes to be a success, they need to be implemented in the right areas and at the right scale to benefit the target species. The level of payment for each conservation measure must accurately reflect the loss of land and the labour costs associated with its implementation. Otherwise, farmers will choose the easiest and most economically beneficial options rather than the best options to promote biodiversity on their farm. To date, agri-environment schemes have only been successful in tackling biodiversity declines when the schemes been tailored to meet the requirements individual rare and localized species. For example stone curlew, corncrake and cirl bunting population declines have been successfully reversed through habitat management prescriptions within agri-environment schemes tailored to each species (Newton 2004). These successes are contrasted with our inability to do the same for our more widespread declining farmland species. This may be a result of policy for the widespread species being inappropriate, or being implemented at an inappropriate scale.

1.5 Study Rationale

A reduction in mixed agriculture has resulted in Britain's rural landscape becoming polarised; the wetter west has specialised in pastoral agriculture and the drier east focused on arable production. This reduction in landscape heterogeneity has corresponded with a reduction of the diversity of birds at a landscape level with UK pastoral regions in the UK only containing half the number of bird species contained in arable and mixed farming regions (Aitkinson *et al.* 2002). Pastoral populations of farmland birds have shown marked declines, and have experienced more local extinctions than birds in arable and mixed farming landscapes (Chamberlain & Fuller 2000). Granivorous species of farmland birds have been particularly affected by population declines (Robinson *et al.* 2001). These declines are currently being addressed by expensive agri-environment schemes, but there is little evidence to date of their effectiveness except for when targeting rare local species such as the cirl bunting (Vickery *et al.* 2004). In order for these schemes to be effective and provide value for money, a good understanding of the ecology of the target species is required. Species requirements vary between spatial areas (Whittingham *et al.* 2007); therefore, solutions should be tailored to the landscape. Much of the work to date on granivorous bird ecology, including yellowhammers, has been carried out in arable and mixed farming regions (Atkinson *et al.* 2002). This study aims to re-dress that balance by studying the ecology of granivorous birds in a pastoral-dominated farming landscape, focusing on the red-listed yellowhammer as it breeds at sufficient densities in the study region to allow a viable study. Yellowhammers are considered a typical granivorous species, and have been used as a model organism for large buntings (e.g. Butler *et al.* 2010) therefore findings from this study should be applicable to other granivorous farmland passerines. An understanding of the scale at which to implement agri-environment measures is important, scales required vary between seed eating species, related to how far individuals move between seasons (Robinson *et al.* 2004), and may vary between landscapes.

1.6 Aims

This thesis will examine and describe the ecology of the red-listed yellowhammer in lowland pastoral dominated farms in Ayrshire, South West Scotland. It aims are to test the following hypotheses and answer the questions set out below:

- Pastoral regions have been disproportionately affected by yellowhammer population declines and range contractions. Therefore, I predict that breeding density will be lower in the pastoral study population than reported for arable and mixed studies. Age ratios of birds caught in mist nets will be compared at the end of the breeding season to look for evidence of low breeding productivity in the pastoral landscape. As yellowhammer population declines and range contractions have been more pronounced in pastoral regions, low breeding productivity is one hypothesis that would explain this observation. Yellowhammers have previously been shown to avoid pastoral habitat during the breeding season whilst selecting arable habitat studies carried out in mixed and arable farming regions, this study will test if yellowhammers breeding in the pastoral landscape avoid the dominant pastoral habitat (Chapter 2)

- Margin habitat (habitat alongside field boundary features) has been previously highlighted as important for foraging yellowhammers in arable study regions; I aim to test whether this preference is demonstrated by yellowhammers in pastoral landscapes. Yellowhammers in mixed and arable studies have been shown to avoid grassland habitat for foraging during the breeding season (MacLeod 2001, Bradbury *et al.* 2000, Kyrkos *et al.* 1998), this study aims to test the hypothesis that yellowhammers breeding on pastoral dominated farms also avoid foraging on pastoral habitat. Finally, by comparing vegetation and invertebrate communities and structure between sites known to have been used by foraging yellowhammers and control sites, I aim to test the hypothesis that not all habitat within a broad category is equally suitable for foraging yellowhammers, and describe the characteristics foraging sites selected by yellowhammers (Chapter 3).

- Yellowhammers in mixed and arable studies have been found to select stubble habitat in winter (e.g. Wilson *et al*. 1996, Moorcroft *et al*. 2002, Robinson 1997, Evans & Smith 1994). I aim to test the hypothesis that yellowhammers in the pastoral dominated study landscape will also exhibit this same habitat preference. Additionally, I will test what other habitats available to wintering yellowhammers in the pastoral study region are selected or avoided. Yellowhammer population declines are thought to be the result of low winter survival (Baillie *et al*. 2001). Juvenile birds may suffer higher mortality rates than adults; inexperience means they are less efficient foragers (e.g. Goss-Custard & Le V. Dit Durrel 1987, Greig *et al*. 1983) and thus less able to meet their energy requirements for survival. Yellowhammers will be captured in mist nets throughout the winter to study population age structure to look for evidence that winter survival may be contributing to the observed decline of yellowhammers in the pastoral region (Chapter 4).

- Winter food has been hypothesised as a major factor leading to the observed farmland bird population declines (e.g. Siriwardena 2008) with the lowest food availability in the late winter period corresponding with a peak in mortality of granivorous passerines (Crick *et al*. 1991). I hypothesise that the provision of supplementary food will increase the number of yellowhammers seen on a site in winter, with the use of the supplemented grain increasing in late winter as the natural food resources are at their lowest. Reductions in survival (as opposed to breeding parameters) have been observed in declining farmland bird populations (e.g. Siriwardena *et al*. 1999, Peach *et al*. 1999, Newton 2004), this study will look for evidence that winter food supplementation is able to increase survival rates of first year yellowhammers relative to elsewhere in the pastoral study region (Chapter 5)

- Habitat availability, and thus food resources available to foraging yellowhammers will differ between the pastoral study landscape and previous studies of yellowhammer diet. Therefore, I aim to test the hypothesis that yellowhammer diet in pastoral farming landscapes is different from mixed and arable farming landscapes throughout the year.

As yellowhammer fledgling condition is correlated with the proportion of grain provisioned, dietary investigation will give some indication of the suitability of pastoral farming landscapes as yellowhammer breeding habitat (Chapter 6).

The year round study of yellowhammer ecology in a pastoral dominated farming landscape should help answer one of the most pertinent questions in species conservation, “what habitat does it require”, whilst additionally highlighting at which life history stage conservation measures such as agri environment schemes for yellowhammers and other graniverous farmland birds in pastoral farming landscapes would be best focussed.

1.7 Study Sites

The study sites are located in Ayrshire, South West Scotland, representing some of the most northerly pastoral farming in Britain. Farmland bird populations at four farms were studied; three farms; Milton (Grid ref – NS4737), Killoch (Grid ref – NS5131) and Fail Mains (Grid ref NS4228) were studied throughout the duration of the project, May 2009 to August 2011. Carnell Home Farm (Grid ref – NS4732) was studied from May 2009 to July 2010, work was discontinued here as a result of access restrictions. Previous work was carried out (by G. Cook, unpublished) in winters 2006/7 and 2007/8 and during the 2007 breeding season at the four sites, so baseline breeding population data were available.

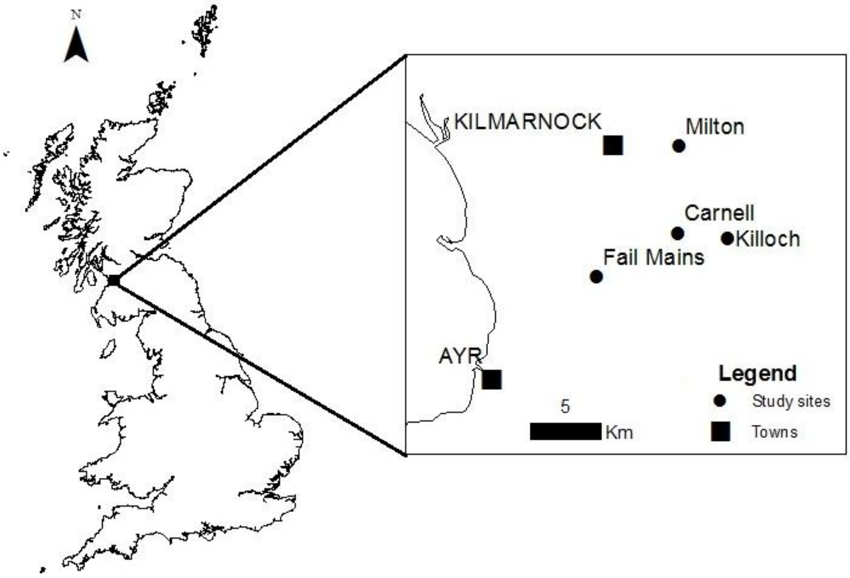


Figure 1.4 Location of Study Sites, © Crown Copyright/database right 2009. An Ordnance Survey Mastermap supplied service

As figure 1.4 highlights, the sites were in the same geographical region, but were not contiguous. Distance between neighbouring sites ranged from 2.7 to 5.5km. All sites being in the same geographical region helped control for factors such as weather and latitude. The study farms varied in size, with only part of the area of each farm being included in the study. The areas studied ranged in size from 69 to 89 hectares, and contained a variety of habitats (management summarised in table 1.1, detailed farm maps in appendix 1 and areas of habitat availability in appendices 7 - 10).

Three farms at the beginning of the study (Killoch, Carnell and Fail Mains) had both dairy herds and young stock, whilst Milton specialised in rearing young stock. By the last summer (2011), Fail Mains had sold its dairy herd, in part as a result of the economics of milk production. Sheep were grazed at these four sites in winter, except for during winter 2009/10 at Killoch. Grass fields at each farm were split between grazing and fodder crop, in all cases the fodder crop was harvested as silage.

Although each of the four farms were pastoral dominated, other crops were grown at a small scale, mainly barley for feeding stock. Throughout the study period, two fields at Milton, and one at Carnell was used to grow spring barley, these fields left as stubble over winter. At Killoch, during the first breeding season, all fields were under pastoral management, in the second summer, one silage field replaced with a maize crop, which was harvested as whole crop silage to feed to the dairy herd in winter, and the field left as stubble overwinter. In the third year, two fields at the farm were grown as maize, at the expense of silage. At Fail, the land use changed each year. The first year, the farm was pastoral dominated, with one spring sown barley field, left as stubble overwinter. In the second year, this field was re-seeded to grass. The sale of the dairy herd in spring 2011 decreased the farm’s demand for pastoral habitat (though the numbers of beef stock remained similar). The surplus pastoral fields were converted to arable production, with both spring wheat and spring barley being grown.

Carnell was intensively managed for game, employing a full-time gamekeeper. Game cover crops are grown, feeding provided throughout autumn and winter, pests controlled and thousands of pheasants and red legged partridge released annually, allowing regular driven shoots by paying clients. At Killoch, game is also released, but on a much smaller scale, the shooting is part of a syndicate, and is shot by walking through the land rather than having the birds driven towards the guns approximately once a week during the shooting season. The management is less intensive, with no full-time keeper, and food is only provided through feed hoppers. Although Fail itself was not managed for game, some of the adjoining land was managed for a small scale pheasant shoot.

Table 1.1 Summary of study site management characteristics

Farm	Livestock	Fodder crops	Arable	Miscellaneous
Carnell	Dairy herd (wintered indoors). Sheep grazed in winter.	Silage Generally two cuts, some fields grazed after first cut.	Spring barley	Stocked pheasant shoot, full time keeper, game crop and grain provided
Fail Mains	Dairy herd (2009 – spring 2011) and beef cattle. Wintered indoors. Sheep grazed in winter.	Silage	Spring barley in 2009 Spring wheat and barley in 2011	
Killoch	Dairy herd and beef cattle (wintered indoors). Sheep grazed in winter.	Silage Maize (2010 and 2011)	None	Small rough pheasant shoot
Milton	Beef cattle (wintered indoors). Sheep grazed in winter.	Silage Generally two cuts, some fields grazed after first. One field three cuts.	Spring barley	

Chapter 2 - Yellowhammer breeding densities and habitat choice

Farmland bird populations have undergone widespread population declines and range contractions over the last 50 years as agriculture has intensified. In the case of the yellowhammer *Emberiza citrinella*, these declines being more pronounced in pastoral farming regions suggesting pastoral habitat may be a sub-optimal breeding habitat. As expected, breeding density in a pastoral landscape in Ayrshire, SW-Scotland was lower than reported in studies carried out in mixed and arable regions. Yellowhammer breeding density varied across the study sites, however, no relationship was found between broad habitat availability and breeding density. This suggests factors operating outwith the breeding season, or at a different spatial scale are responsible for yellowhammer breeding density. Yellowhammers bred successfully at the pastoral-dominated farms with a high rate of double brooding. Productivity and post fledging survival appeared high (3.9 juveniles for every adult caught at the end of the breeding season), suggesting breeding habitat was adequate. Selection of habitat at the territory level showed yellowhammers avoided farmyards, whilst there was no evidence that yellowhammers were avoiding the (dominant) pastoral habitat for breeding territories, contrary to results from arable and mixed farming studies.

2.1 Introduction

Reproduction is a crucial part of an organism’s life history, where an individual’s genes get passed on to the next generation. Breeding success can be limited by the availability and quality of breeding and foraging habitat (e.g. Newton 2013, Fuller 2012). For successful breeding, the habitat must provide sufficient food, protection from predation, and allow the organism to display its normal behavioural repertoire. Breeding habitat has to be within reach of non-breeding (for convenience termed ‘wintering’) habitat and this wintering habitat has to be of sufficient quality to ensure both survival and sufficient maintenance of body condition for reproduction. Without suitable breeding and wintering habitats both being available over an appropriate spatial scale (which will depend on the movement or migratory capabilities of the species), populations of organisms will decline, perhaps in the long term leading to local extinction where habitat has become unsuitable.

The community of species present in an ecosystem can indicate its health, with the presence of specialists and species at higher trophic levels and ‘keystone’ species indicating good condition (Paine 1969). Throughout Europe, including in Britain, agricultural ecosystems have become degraded, as indicated by widespread declines of biodiversity across a variety of taxa, including plants (Marshall *et al*. 2003), invertebrates (New 2005), and mammals (Wilson *et al*. 2009). Most visibly, farmland bird populations have declined (reviewed in Newton 2004), with the most extensive declines occurring within farmland specialist granivorous species (Robinson *et al*. 2001). The degradation of farmland habitat from a biodiversity perspective has occurred at the same time as yields have increased as a result of intensification and changes in farming practices; population declines have been highest in Western Europe where agricultural intensification has been most widespread (Robinson *et al*. 2001). Pesticide and herbicide applications have increased (Shrubb 2003), spring sown crops have been replaced by autumn sown varieties and hay production replaced by silage have all contributed to changes in both plant and invertebrate communities in farmland. Such changes at these lower trophic levels impact further up the food chain. For example, the reduction in weeds in crops with the increased use of pesticides, and the reduction of floral biodiversity with the switch from hay to silage production have removed weed seeds important for granivorous birds throughout the year, as well as host plants important for invertebrates that these birds require to feed their nestlings (Newton 2004, Holland *et al*. 2006). Changes in farm buildings, crop types, the removal of hedges and ditches and changes in the management of existing ones have all contributed to a reduction in available nesting habitat for farmland birds (Wilson *et al*. 2009). The removal of hedges and ditches has the additional effect of reducing the availability of high quality foraging habitat – hedges and ditches hold higher invertebrate diversity and abundance than adjacent farmland (Bowden & Dean 1977, Trnka *et al*. 1990, Peng *et al*.1993).

The reduction in mixed farming has led to polarisation in Britain’s rural landscape; the wetter west has specialised in pastoral agriculture and the drier east focused on arable production. This reduction in landscape heterogeneity has reduced the diversity of birds at a landscape level; pastoral regions in the UK have been shown to hold half the number of bird species as arable and mixed farming regions (Atkinson *et al*. 2002). Pastoral populations of farmland birds have shown marked declines, and have experienced more local extinctions than birds in arable and mixed farming landscapes (Chamberlain & Fuller 2000). However, most farmland bird research to date in the UK has been carried out in mixed and arable farming regions, with the results of such research used to inform the agri-environment schemes designed to halt and reverse farmland bird declines. For these schemes to be both cost-effective and successful, they must be based on good quality and relevant research, but to date, pastoral dominated landscapes have been understudied despite pastoral populations of farmland birds being worst affected by population declines (Chamberlain & Fuller 2000) and pastoral farming accounting for ~67% of British agriculture (McCracken & Tallowin 2004). This study aims to address this imbalance by studying the ecology of granivorous passerines in the pastoral dominated farming landscape of Ayrshire, South-West Scotland, focussing on the yellowhammer *Emberiza citrinella*, which is still common enough in the region for a viable study. Yellowhammers are one of the farmland specialists that have declined alongside the rise in agricultural intensification; declining by over 50% in 25 years resulted in them being placed on the UK's red list of species of conservation concern. Yellowhammers are widely distributed throughout farmland in Britain, and like many declining granivorous passerines, they require hedges or ditches as nesting habitat, invertebrates to feed nestlings, and seeds throughout the year, hence they are a good model organism. This study aims to test the hypothesis that yellowhammer breeding density is lower on the pastoral study farms than found in mixed and arable farming regions. I will then look at variation in yellowhammer breeding density at the four study sites and test to see if these can be accounted for by differences in habitat available at each farm. Territory habitat selection will be investigated to test the hypothesis that, as found in other studies, pastoral habitat will be avoided by breeding yellowhammers whilst investigating what habitat is selected. Lastly, breeding productivity will be assessed to infer the suitability of pastoral-dominated farming landscapes as a breeding habitat for yellowhammers. Information gathered can be used to inform future agri-environment policies targeting yellowhammers and similar declining farmland birds in pastoral landscapes.

2.2 Methods

2.2.1 Boundary surveys

The breeding ecology of yellowhammers was studied at four grassland-dominated farms in Ayrshire, South-west Scotland. Data on densities and habitat use were collected using boundary transects (as nests are generally associated with boundary features such as hedges and ditches) carried out during the yellowhammer breeding season (late April – late August). Fixed routes (appendix 1) were walked along all suitable boundary features at a 10m distance from the features (where crops permitted). Routes ranged in length between 7.3 km and 11.5 km (see appendix 1) and covered all potential boundary features (hedges and ditches) that may potentially be utilised as nesting habitat by yellowhammers. At each farm 12 transect surveys were carried out in 2009, 13 surveys in 2010 (only 10 at one site - Carnell - due to access restrictions) and 5 surveys in 2011 (surveys were only conducted in the first half of the breeding season in this year, with Carnell excluded due to access restrictions) (for dates see appendix 2). Transects took 3 ½ to 4 ½ hours to complete and commenced within one hour of dawn, with the direction of travel being reversed in successive surveys to minimise the effect of time of day on bird locations. Binoculars were used to aid bird identification, and transects only took place on days when visibility and weather were good. The locations and behaviour of all observed yellowhammers were recorded on maps during the survey. Locations where breeding behaviour was observed (e.g. birds carrying nesting material, food and/or faecal sacs) were later revisited in order to try and locate the nest. Where nest sites could not be found, the approximate location of the nest site was estimated based on the behaviour observed. The identity of any colour-ringed yellowhammer seen was recorded, in order to help distinguish separate breeding territories.

2.2.2 Bird ringing

Ad hoc mist netting was carried out throughout the breeding seasons in order to catch and colour ring as many yellowhammers as possible to allow the identification of individuals in the field. At the end of the breeding season in 2009 and 2010, an additional ten ringing sessions were carried out in September and October (for dates see appendix 3) to assess breeding productivity, as yellowhammers caught can be reliably identified as adult of first calendar year individuals on the basis of tail feather shape (see Norman 1992 which reported 97% of individuals can be aged correctly). Yellowhammers were mist netted at sites on the farms where flocks had been observed during earlier surveys. Tape lures with Reed Bunting *Emberiza schoeniclus* or Chaffinch *Fringilla coelebs* calls were played in attempt to attract more birds to the netting areas on days when few birds were present (these appeared to be more effective than yellowhammer tape lures – pers. obs.). Standard North Ronaldsay mist nets were erected parallel to hedges on dry still days, commencing before dawn since early morning catching sessions tend to be most productive. The number of nets erected varied between sessions depending on the number of birds thought to be in the area (the aim being to maximise the numbers of birds that could be caught and ringed safely, rather than to standardise mist netting effort to look at variations in bird numbers present). All birds caught were identified, aged (using the shape of tail feathers as the main criterion in the case of yellowhammers), and sexed where possible using Svensson (1992) as a guide and fitted with a standard BTO metal ring.

2.2.3 Habitat and hedge surveys

The distribution and extent of broad habitat types were assessed for each farm during each breeding season, using fine-scale maps that indicated field boundaries and other geographical features. Land was assigned to one of the 12 mutually exclusive broad categories (for list of categories and definitions, see appendix 6). Hedges at all four study sites were mapped in ArcGIS (ESRI 2010) using a combination of aerial photography and fieldwork to confirm locations.

2.2.4 Data storage and calculation of habitat availability

The data on habitat types on each farm and in the immediately surrounding area were mapped in ArcGIS 10 (ESRI 2010) over OS Mastermap files for Ayrshire (downloaded from www.edina.ac.uk/maps). The locations of birds seen (alongside data on behaviour, time, date), and the locations of nest sites were stored in ArcGIS by creating a new polygon file for each purpose then the locations were added using the editor toolbar. The locations of hedges were added to the Arc database by drawing new features as part of a polyline file for the hedges, using aerial photography in combination with ground truthing during visits to the sites. The length of each hedge was calculated within ArcGIS. Study site was defined as the boundary feature next to the extent of the boundary transects, plus a 100m buffer. The 100m buffer was necessary as habitat just outwith the survey boundary would have had a strong effect on the birds' use of the study site and allowed nest sites just outwith the boundary transect extent to be considered. 100m was chosen since this was the maximum lateral distance around the transect I was confident I knew the locations of breeding yellowhammers for. The study site boundary was used to cut the edited OS Mastermap habitat files for the region. As some of the habitat polygons will have changed in size during the process of cutting, field geometry was recalculated in ArcGIS. For the summary of habitat areas available for each year at the study sites, see appendix 9 and for proportion, appendix 10.

2.2.5 Data analysis

As the farms were all different sizes, and the territories not always entirely contained within the study site, breeding density was calculated to allow comparison of the number of yellowhammers breeding at each farm and between years. Each yellowhammer territory was defined as the nest site plus a 100m buffer (calculated in ArcGIS (ESRI 2011)). 100m was selected for the buffer as previous work found most yellowhammer foraging trips during the breeding season were within 100m of nest sites. For example 90% of foraging trips were within 100m in Biber (1993) whilst Morris *et al.* (2001) found 60% of foraging trips within 100m. Personal observation of territorial yellowhammers during this study found most foraging excursions were within this distance of the nest site, with occasional longer flights (for example to collect nesting material or to visit farmyards to glean grain intended for cattle). To account for territories falling only partially within the study area, the proportion of each territory contained within the study site was calculated. Breeding density was the sum of the proportion of each territory falling within the study site, divided by the study site area.

One-way ANOVAs were carried out to compare mean breeding density between sites, between years (2009 – 2011) and between first and second broods (2009 &

2010). Second broods were defined as breeding territories occupied after mid June (most successful first brood breeding attempts fledged late May), though some of the breeding attempts termed ‘second broods’ would have in fact been replacement clutches for the first failed breeding attempt. Correlation analyses were carried out to look for relationships between mean yellowhammer breeding density at a farm and the mean proportion of pastoral, unmanaged or arable habitat available, and the mean hedge availability per ha at each farm (total hedge length within each study site was calculated in ArcGIS, then divided by the area of the respective study site). Means were used for each site to avoid pseudo replication as breeding density varied by site but the sample size was too small to include farm as a random factor. The length of hedge habitat available in each territory was summarised in and exported from ArcGIS. To determine if hedge length in yellowhammer breeding territories differed between study farms, an ANOVA with Fisher’s post-hoc comparisons was carried out to identify significantly different means.

To test for differences in territory habitat selection relative to availability, logistic regressions were used. For this, random territories had to be created ensuring the centre point contained suitable yellowhammer nesting habitat (ditch or a hedge). These locations were generated using ArcGIS (ESRI 2011) by first creating as many random points as possible (with the stipulation that points created are at least 1m apart) along each hedge and ditch habitat polygon. From these points, for each year surveyed at each farm, the same number of points were selected as the number of breeding territories observed using ‘subset features’ in Geostatistical Analyst Tools. Each subset was then checked that each point generated was separated by a minimum of 90m, and thus could have been used by a breeding yellowhammer. 90m was chosen as this was the closest distance between two yellowhammer territories recorded during the study. If this criterion wasn’t met, the previous step was repeated until satisfied, before the 100m buffer for the breeding territory was placed round the resulting set of random territory centres. Random territories (0) and occupied first brood territories (1) were merged with the habitat layer, with the proportion of each habitat in each territory calculated, allowing a logistic regression analysis was carried out using R (version 2.15.1) to test what habitats were associated with territory occupancy.

As the location of second breeding attempts often differed from the first breeding attempt, yet the broad farm scale habitat remained unchanged, differences in habitat composition of territories between breeding attempts was investigated to see if habitat requirements changed as the breeding season progressed. As the data on proportion of each habitat variable within individual territories was not normally distributed (assessed using Anderson-Darling tests), even after log10 or arcsin transformation, non parametric statistics (Kolmogrov-Smirnov tests) were used to test for differences in the proportion of each habitat in first and second brood territories.

I was unable to assess accurately breeding productivity through monitoring yellowhammer nests through to fledgling due to the difficulty of finding nests. Therefore, productivity was estimated by calculating the ratio of first year to adults caught in mist nets in September and October in 2009 and 2010. To test for differences in productivity between years, a χ^2 test was used, calculated in Excel. Unless otherwise stated, all statistics were carried out in Minitab 16 (2010).

2.3 Results

2.3.1 Yellowhammer breeding density in a pastoral landscape

Yellowhammers were found breeding throughout each of the study farms, the locations of the territories are summarised in figure 2.1. Nest sites within the study farms were, as expected for this species, associated with field boundary features, with both ditches and hedges being used. The earliest observed yellowhammer clutch initiation was 4th May in both 2009 and 2010, and 29th April in 2011, with clutch size between 2 and 5.

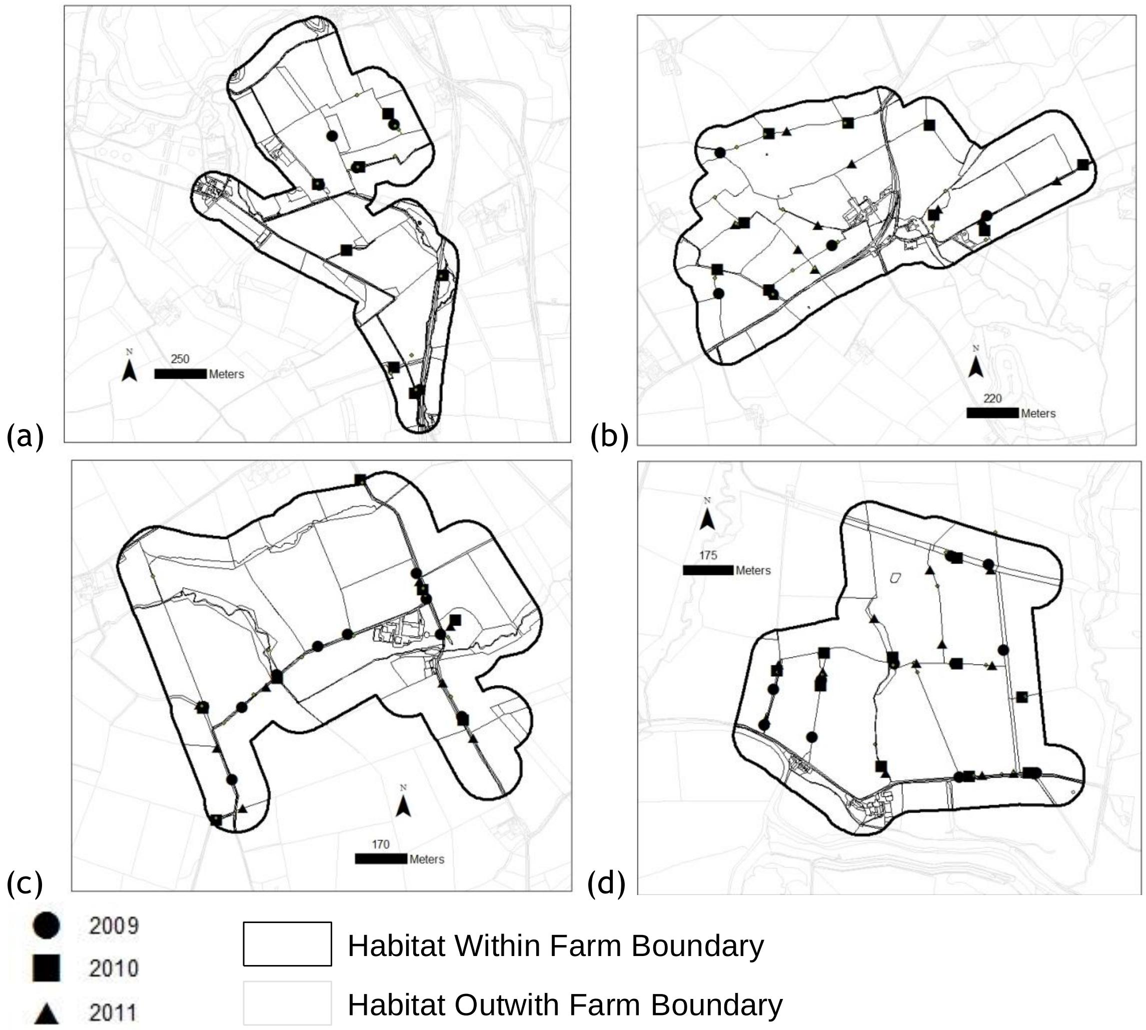


Figure 2.1 Yellowhammer 1st brood nest locations at each of the four study sites between 2009 - 2011 at (a) Carnell (no data collected 2011) (b) Fail Mains (c) Killoch and (d) Milton

The mean breeding density for first broods over all the years at all the study sites was 0.081 ± 0.009 pairs per ha. However, there was a significant difference in breeding density between sites (Figure 2.2 (a), One-way ANOVA, $F_{3,7} = 6.54$, $p = 0.007$) with Milton having a significantly higher first brood breeding density than the other study sites (Fisher's post-hoc comparison, $p < 0.05$). No significant difference was found in first brood breeding densities across years (Figure 2.2 (b) one way ANOVA, $F_{2,8} = 0.71$, $p = 0.52$). Most pairs of yellowhammers had two breeding attempts; there was no significant difference between first and second brood density in the years in which both broods were monitored (2009 and 2010) (Figure 2.2 (c), Paired t-test comparing within sites, $t = 0.18$, $p = 0.861$, 7 d.f.). Since the breeding density of yellowhammers varied more between the sites than between years, characteristics of individual sites were investigated to see if they could account for the observed spatial variation in yellowhammer breeding densities.

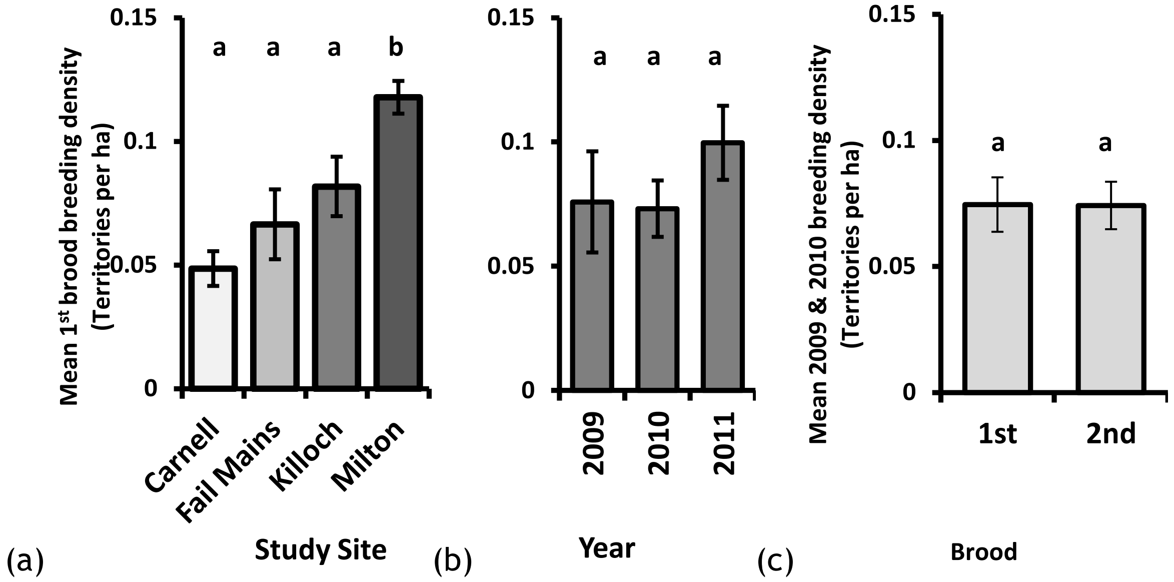


Figure 2.2 Breeding density ± 1 S.E. for (a) individual farms (2009 – 2011) (b) breeding seasons and (c) 1st and 2nd broods (2009 and 2010 only, since surveys were not done in the latter half of the breeding season in 2011). Means which do not share a letter are significantly different.

2.3.2 Can field type and hedge availability be used as a predictor of yellowhammer breeding density in the pastoral study landscape?

No significant relationships were found between the mean breeding density of yellowhammers and the mean availability of pastoral (Figure 2.3 (a), r = -0.387, p = 0.613, n = 4), unmanaged (Figure 2.3 (b), r = -0.094, p = 0.906, n = 4) or cereal (Figure 2.3 (c), r = 0.534, p = 0.466, n = 4) habitats at each farm, nor the mean hedge availability per ha at each farm (Figure 2.4, r = -0.520, p > 0.05, n = 4). However, as only four farms were studied, the power of the analysis is low. To confirm or deny any relationship, a larger number of farms should be studied.

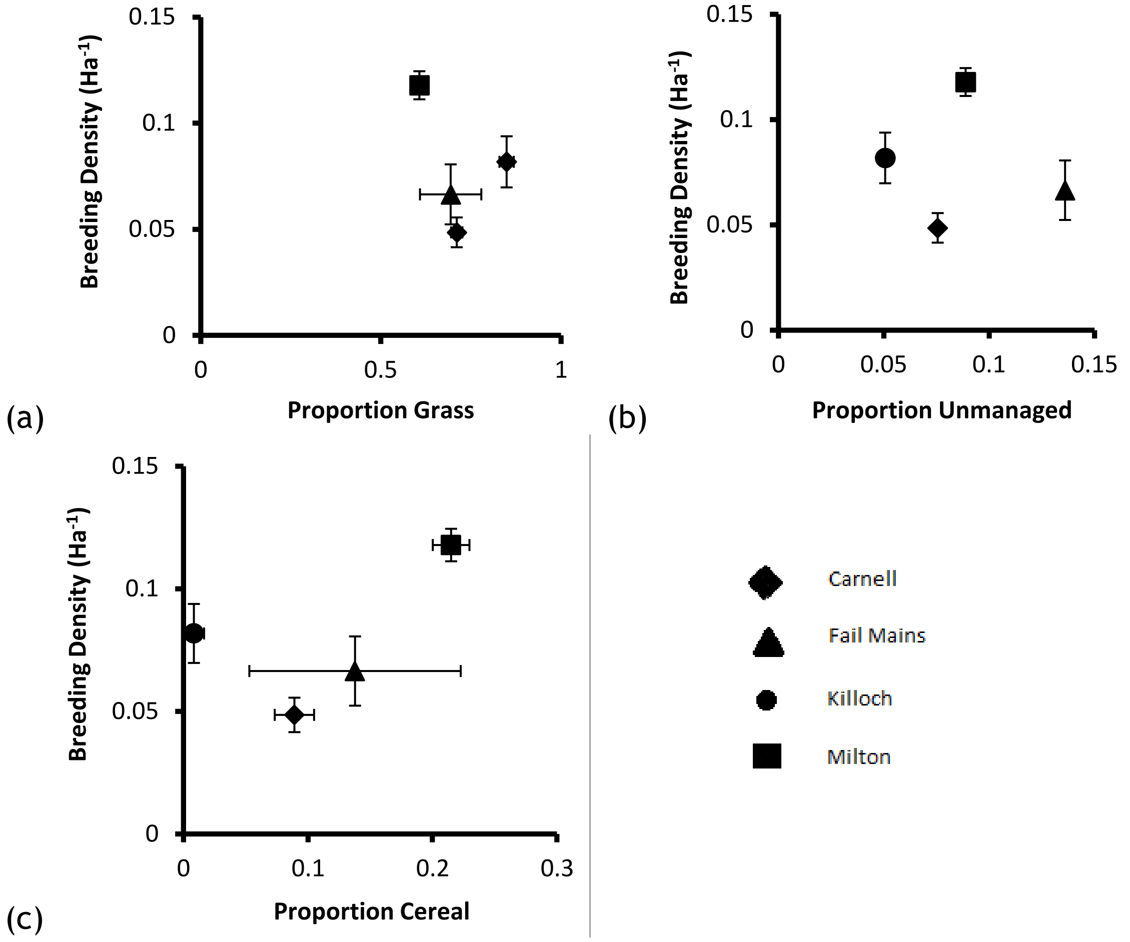


Figure 2.3 Relationship between mean breeding density ± 1 S.E. and mean proportion of habitat available at each farm ± 1 S.E. for (a) intensive pastoral habitat (b) unmanaged habitats and (c) arable habitat

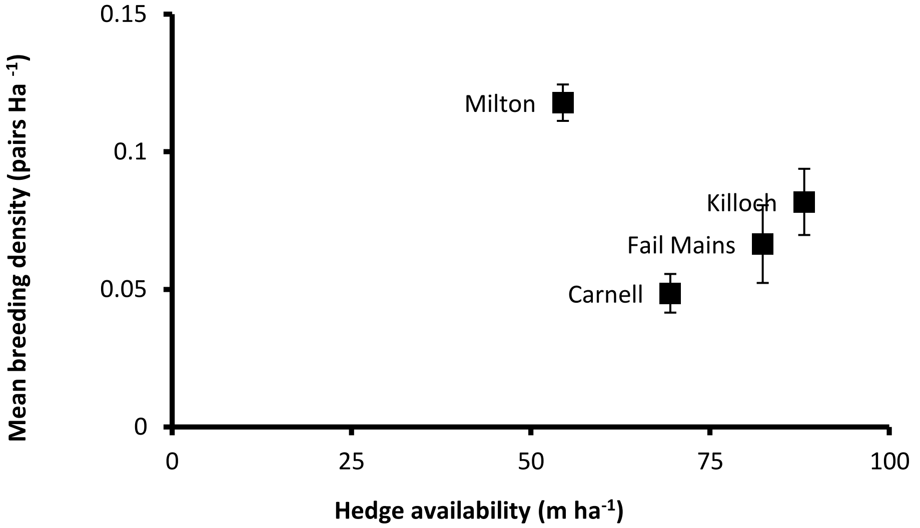


Figure 2.4 Relationship between mean breeding density in 2009 - 2011 ± 1 S.E. and mean hedge availability per hectare at a study site

2.3.3 Do the characteristics of yellowhammer breeding territories selected vary across study sites?

Mean amount of cereal habitat in yellowhammer territories significantly differed by farm (Figure 2.5(b), One way ANOVA, $F_{3,91} = 6.79$, $p < 0.001$), with yellowhammer territories at Fail Mains and Milton containing significantly more cereal habitat than territories at Killoch and Carnell. However, these differences can be attributed to differences in habitat availability at the different sites; there was no cereal habitat available at Killoch and a smaller amount at Carnell than at the other two sites. No significant differences was found in the amount of grass (Figure 2.5(a), One way ANOVA, $F_{3,91} = 0.64$, $p = 0.592$) but there was an indication that there may be differences in unmanaged (Figure 2.5(c), One way ANOVA, $F_{3,91} = 2.70$, $p = 0.0502$) habitat in yellowhammer territories. Hedge length per 1st brood territory differed significantly by farm (Figure 2.5(d), One way ANOVA, $F_{3,91} = 32.48$, $p < 0.001$). Carnell had significantly lower hedge length per territory than Killoch (Fisher's post-hoc comparison, $p<0.05$) whilst the hedge length per territory at Fail Mains and Milton did not differ significantly from either Killoch or Carnell. However, some of these differences may be attributed to differences in hedge availability at the different sites; Killoch had more hedgerow habitat per ha than at Carnell (88.1 m of hedge per ha compared to 69.4 m of hedge per ha, see figure 2.4).

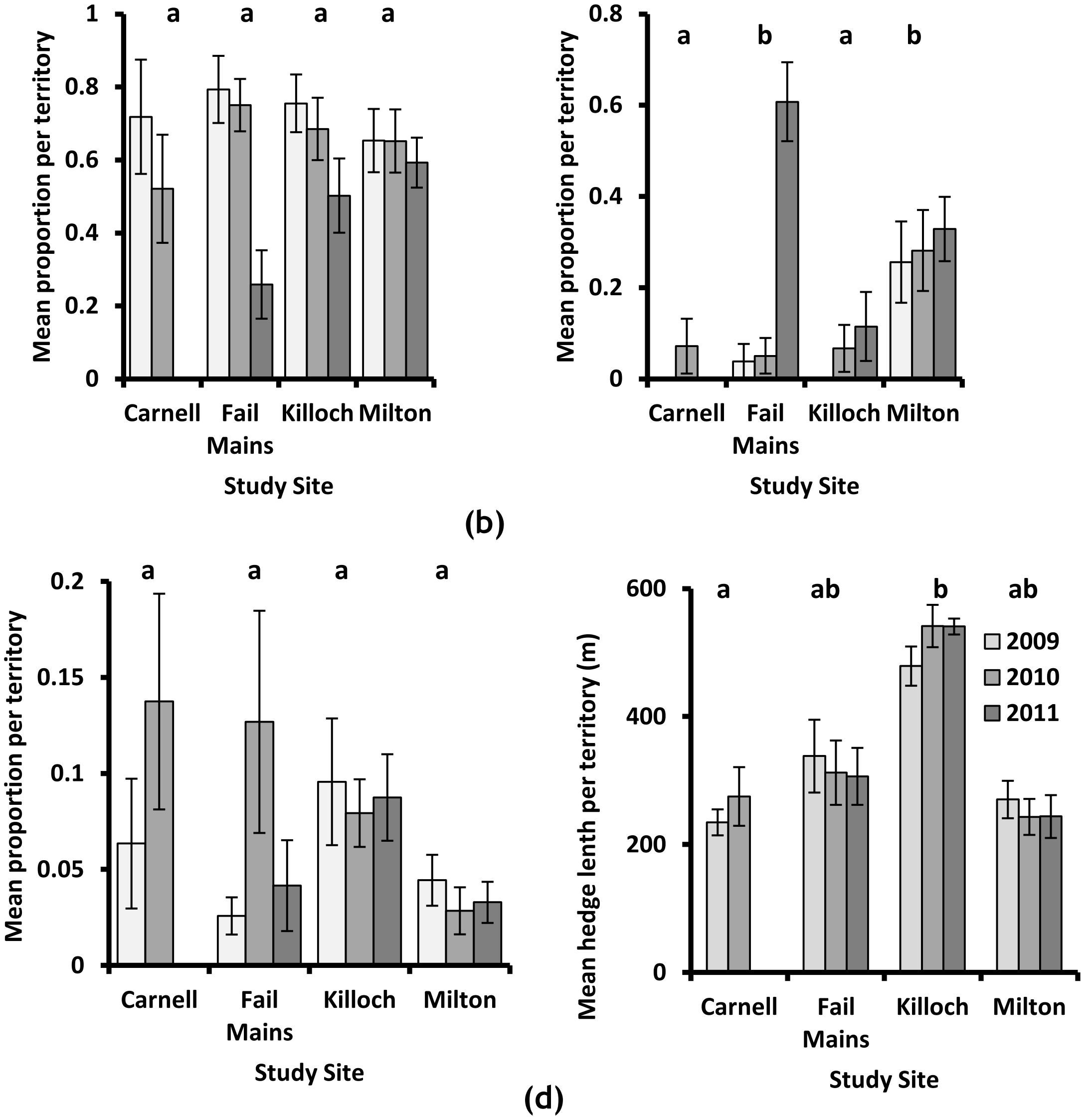


Figure 2.5 Mean proportion (a) grassland (b) cereal (c) unmanaged habitat and (d) mean hedge length ± 1 S.E. in 1st brood yellowhammer breeding territories at each farm during breeding seasons 2009 – 2011, means which do not share a letter are significantly different between farms

2.3.4 Do breeding yellowhammers select or avoid certain habitats and is habitat selection consistent between first and second broods?

There was a significantly lower probability of an area being selected by a yellowhammer for a breeding territory with an increased proportion of garden habitat (Table 2.1, p = 0.011, 189 d.f.). No significant difference was found in habitat availability for all other habitats between breeding and random territory locations (Table 2.1).

Table 2.1 Results from logistic regressions comparing habitats found in breeding territories of yellowhammers with random territories, significant results in bold

Habitat	Z value	p value	Mean habitat proportion	
			Occupied	Random
Cereal	z = 1.127	p = 0.2597	0.179	0.145
Game managed	z = -0.044	p = 0.9650	0.004	0.005
Garden	**z = -2.530**	**p = 0.0114**	**0.001**	**0.007**
Grazed	z = 0.415	p = 0.6785	0.255	0.274
Maize	z = 1.599	p = 0.1098	0.019	0.005
Manmade	z = 0.760	p = 0.4476	0.019	0.030
Re-sown pasture	z = 1.384	p = 0.1664	0.018	0.006
Silage	z = 0.497	p = 0.6189	0.337	0.325
Unmanaged	z = 1.686	p = 0.0917	0.062	0.070
Woodland	z = -0.806	p = 0.4205	0.027	0.031

No significant difference was found in the selection of different habitats in yellowhammer breeding territories between first and second broods (Figure 2.6, Table 2.2).

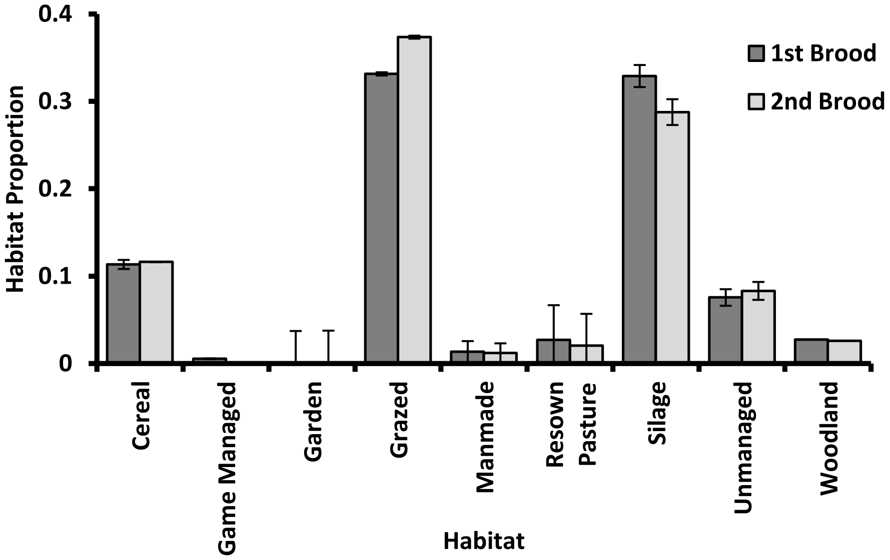


Figure 2.6 Mean proportion of habitat in yellowhammer territories in 1st brood (n = 95) and 2nd brood (n = 65)

Table 2.2 Results from Kruskal-Wallis tests comparing habitats selected in breeding territories of yellowhammers between first and second brood territories

Habitat	H value	DF	P value
Cereal	H = 65.83	d.f. = 69	p = 0.586
Game managed	H = 4.20	d.f. = 5	p = 0.521
Garden	H = 8.52	d.f. = 10	p = 0.579
Grazed	H = 135.13	d.f. = 131	p = 0.384
Manmade	H = 87.68	d.f. = 90	p = 0.550
Resown pasture	H = 10.69	d.f. = 10	p = 0.383
Silage	H = 100.01	d.f. = 97	p = 0.397
Unmanaged	H = 118.73	d.f. = 120	p = 0.516
Woodland	H = 46.7	d.f. = 48	p = 0.526

2.3.5 Yellowhammer breeding season productivity

During the mist netting sessions carried out in September and October 2009 and 2010 to act as an index of yellowhammer breeding season productivity, 327 birds were captured in mist nets, of these, 39 individuals were yellowhammers. Of these 39, 8 were adults and 31 were first year individuals, giving the mean ratio of first years to adults post breeding season for the study site of 3.875:1. No significant difference was found (Figure 2.7, χ^2 = 1.08, 1 d.f., p = 0.298) between the ratio of adults to juveniles caught in mist nets in September and October, post breeding season, in 2009 and 2010, suggesting there was no difference between the breeding productivity and fledgling survival between the two years, however, the sample size this was calculated from was small.

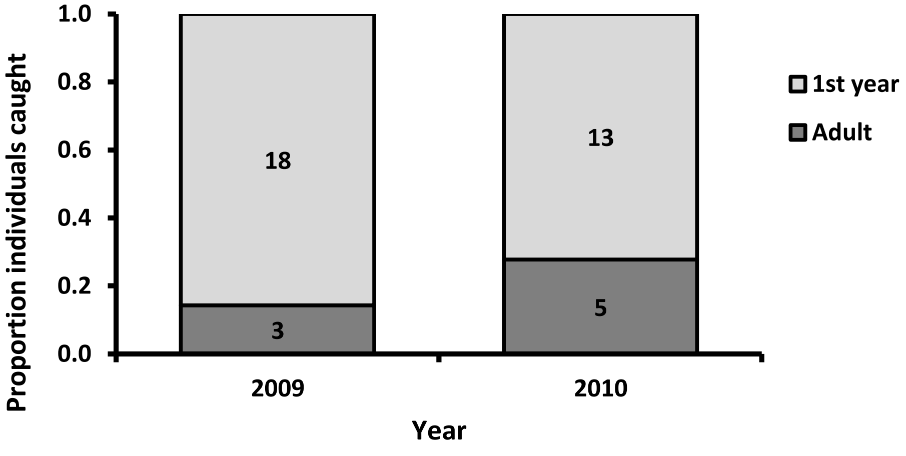


Figure 2.7 Ratio of 1^{st} years to adults caught in mist nets post breeding season (September and October) in 2009 and 2010

2.4 Discussion

2.4.1 Breeding Density

Mean breeding density across the four pastoral dominated study sites was 0.081 pairs per hectare. This is lower than found in previous studies of yellowhammer breeding density across the U.K. at both mixed and arable farms. For example, in a mixed farm in Leicestershire in 1995 the breeding density was 0.188 breeding pairs per hectare (Stoate *et al*. 1998). At another study carried out at nine mixed lowland farms in England, breeding densities ranged between 0.07 to 0.29 pairs per hectare (Bradbury *et al* 2000). The lowest density in this English study was comparable to the average density in the current study, with the lowest breeding density recorded in Ayrshire 60% of the lowest breeding density in the English study. The observed Ayrshire breeding densities were lower than figures from studies carried out elsewhere in Scotland; at two breeding sites in arable dominated farmland on the east coast of Scotland, the mean breeding density between 1998 – 2000 was 0.12 pairs per hectare with breeding densities at individual sites 0.094 and 0.146 respectively (MacLeod 2001). Results from Common Bird Census plots reported mean yellowhammer breeding density was 0.134 yellowhammer pairs per hectare in 1988, and 0.105 pairs per hectare by 1993 (Kyrkos *et al*. 1998). The low yellowhammer breeding density may be a result of the higher proportion of pastoral habitats in Ayrshire than in the other studies.

Yellowhammer breeding densities differed significantly by site with Milton holding the highest breeding densities. Breeding densities varied considerably across the four Ayrshire study farms, ranging from 0.042 pairs per hectare at Carnell in 2009 to 0.129 pairs per hectare at Milton in 2011. However, there was some level of pseudo-replication; surveys were carried out over three years thus weren’t independent, but with the small sample size it was not possible to control for the effect of year. However, no relationship could be found between hedge or broad habitat availability at the farm and yellowhammer breeding density. However, the chance of detecting such a relationship in the current study is very small as a result of the small number of farms (n = 4) considered. To detect a relationship or correctly conclude that no relationship exists, a larger number of farms should have been studied. As yellowhammer breeding density on a landscape level scale is higher in both mixed and arable farming regions than in pastoral regions, a relationship between breeding density and land management on the individual farm scale may exist. Thus future studies investigating the relationships between habitat availability at the level of the farm and breeding density should consider a much greater number of sites in order to detect or reject habitat availability at a farm as a predictor of breeding density. Assuming that the no relationship detected in this study is a true reflection of reality, this suggests that yellowhammer breeding density at a site is determined by factors from out-with the breeding season. Previous work supports this contention, having demonstrated that increasing amount of winter stubble, which is an important winter foraging habitat, is positively correlated with yellowhammer breeding density (Gillings *et al*. 2005). In reality, it is probable that both local habitat availability during the breeding season and outwith the breeding season are driving yellowhammer breeding densities in any area, with the relative importance of each difficult to tease apart.

Despite the lower breeding densities observed at the pastoral dominated study sites, pastoral habitats contain a significant proportion of Britain's breeding yellowhammers as pastoral farming accounts for a large proportion (67%) of agricultural habitat in Britain (McCracken & Tallowin 2004). This is why it is important to study pastoral habitats, even though the yellowhammer breeding density is lower, especially considering yellowhammer declines and range contractions have been more extensive in pastoral regions.

2.4.2 Breeding productivity

Yellowhammers in the study area generally undertook two breeding attempts, with no significant difference between the number of first and second broods each year for each site. In the nests found, the range of clutch sizes were within normal parameters expected for this species, however, the sample size of nests found was too small to allow more meaningful comparisons with other studies. The earliest observed yellowhammer clutch initiation was 4th May in both 2009 and 2010, and 29th April in 2011. This is later than the onset of egg laying reported in previous studies that found egg laying began in early April (for review see Cramp & Perrins 1994), and the earliest date was the 7th April from analysis of 1025 nest record cards (Yom-Tov 1992). However, the later clutch initiation date may be a result of the difficulty in finding nests resulting in early attempts being missed or the more Northerly location of the study population. Northerly latitudes are characterised by lower temperatures, which lead to later vegetation development and peak invertebrate availability, thus resulting in a later date of most efficient reproduction for birds and other organisms present (e.g. Sanz 1998, Newton 2013). Onset of laying has been found to be earlier on organic farms than intensively managed ‘conventional’ farms (Bradbury *et al.* 2000), suggesting that modern intensive agricultural practice of pesticide and herbicide use may impact negatively on breeding in yellowhammers. A delay in the onset of laying may limit the number of breeding attempts by yellowhammers in a season, therefore, conservation measures for breeding yellowhammers should ensure food availability is high as early as possible during a breeding season in order to maximise the number of potential reproduction attempts.

As only a small number of yellowhammer nests were found, reproductive success in the conventional sense (by following the progress of individual nests through to fledging or failure) could not be calculated. Instead, productivity was estimated by catching and ageing birds caught at the end of the breeding season, which indicated that yellowhammers’ breeding productivity and post fledgling survival was high in the pastoral study region, with 3.9 young birds caught for every adult. This suggests the pastoral study region has a higher reproductive success than the estimated mean of 3.27 ± 0.07 nestlings fledged per breeding pair (Bradbury *et al.* 2000) in England. As most first year mortality in a variety of avian species is known to occur in the initial few weeks post fledging (e.g. Anders *et al.* 1997, Nisbet & Dury 1972, Yackel Adams *et al.* 2006), this estimate could be an underestimate of Ayrshire yellowhammer breeding productivity. However, mist netting has a tendency to overestimate the numbers of young birds relative to adults as first year individuals are easier to catch (Peach *et al.* 1996). Therefore, the estimated figure of 3.875 young produced by the end of the breeding season per adult should be treated with caution, and care should be taken when comparing this index of productivity with estimates of numbers of nestlings fledged per pair quoted in the literature. Another potential explanation for the high numbers of first year yellowhammers caught at the end of the breeding season is that the adults are less likely to be caught due to restrictions on mobility placed on them by their annual complete moult, or adult mortality post breeding season is high.

2.4.3 Yellowhammer habitat choice during the breeding season

As found in previous work (Morris *et al.* 2001, Biber 1993), during the breeding season, yellowhammers spent the majority of their time within 100m of the nest sites (pers. obs.). Therefore it is important that good quality habitat is close to nesting habitat, to reduce the energetic costs of foraging excursions to parents and reducing the time nests are left unattended. Bradbury *et al.* 2000 found no relationship between adjacent land use and breeding success, suggesting that yellowhammers may be able to offset the costs of poor quality foraging habitat on breeding territories, but this would come at the expense of their own survival.

Birds were observed undertaking occasional larger movements (over 700m observed from territory centres) for example to collect cattle hair to line their nests, or to glean grain from either the buildings where it was stored (at Killoch) or directly from the troughs where the cattle were being fed (at Milton). This is in line with previous studies which have recorded movements of up to 600m from breeding territories (Dale & Manceu 2003). The large distances travelled to find grain, a poor quality food source for yellowhammer nestlings (Douglas *et al.* 2012) with lower protein content than invertebrates (Capinera 2010) suggests that occasionally, yellowhammers found the grain to be the most profitable food source. This was generally in periods of poor weather (cold, wet – pers. obs.) when invertebrate activity would be lowest, making them more difficult to detect by foraging birds.

Contrary to other studies which report yellowhammers avoid breeding in areas of silage and pasture ley (e.g. MacLeod 2001, Bradbury *et al.* 2000, Kyrkos *et al.* 1998) there was no evidence that yellowhammers in the study population avoided grassland habitat when selecting breeding territories. Grassland habitat (a combination of silage, pasture and re-sown pasture) was both the dominant habitat within the study sites (71.1%) and within occupied yellowhammer breeding territories (mean of 71.4% ± 2.1%). Perhaps the dominance of this habitat and widespread nature throughout the study sites made it impractical for breeding yellowhammers to avoid. However, this seems unlikely, as there was no evidence of other habitat being selected relative to availability. If pastoral habitat really was poor quality breeding habitat for yellowhammers compared to for example the cereal fields, clusters of yellowhammer territories around the cereal fields could have been expected, and a relationship between cereal habitat and breeding density (no evidence for which was found). Woodland habitat was not found to be selected by breeding yellowhammers, unlike in Poland where yellowhammers actively selected woodland habitat (Golawski & Dombrowski 2002).

Garden habitat was avoided by breeding yellowhammers, preferring to locate their nests in hedges and ditches further away from human habitation than expected if territories were distributed at random throughout apparently suitable hedge and ditch nesting habitat. Studies of garden feeder use have reported that yellowhammers are rare garden visitors, confining their visits to rural gardens to periods of harsh weather conditions in winter (Chamberlain *et al*. 2005). This avoidance of garden habitat (and thus human habitation) during the breeding season suggests future expansion of development and increased urbanisation of rural areas will negatively impact breeding yellowhammers.

2.4.4 Improving pastoral landscapes for breeding yellowhammers

Yellowhammers during this study preferred to nest in vegetated ditches and margin features (pers. obs.). As yellowhammer nestlings leave the nest at a very young age, long before they can fly, it is important that there is sufficient cover to protect them from predation during this vulnerable stage. Yellowhammers have been shown to significantly benefit from management of margins and boundaries under entry level stewardship agri-environment schemes (Davey *et al*. 2010). However, yellowhammer nests in hedgerows are more vulnerable to predation than those in ditches (Bradbury *et al*. 2000). Reducing stocking densities will allow an increase in herbaceous vegetation in ditches and along the hedges increasing cover for breeding birds. Reduced stocking densities will have the additional benefit that the habitat heterogeneity within a field will increase as the field should no longer be a uniformly cropped habitat. Shorter defoliation periods are important to allow plants to set seed (thus providing seed-rich foraging habitat for granivorous birds in winter).

Chapter 3 – Yellowhammer summer foraging habitat choice

Farmland birds, especially graniverous specialists including the yellowhammer *Emberiza citrinella*, have undergone population declines at the same time as increasing agricultural intensification and changes in management practices. Such declines are being addressed by agri-environment schemes where farmers are paid to manage habitat in wildlife friendly ways, however, for these schemes to be successful, they must be based on high quality research. The most important question that needs answered in order to design appropriate conservation measures for any species is “what habitat does the target organisms require?” During the breeding season, yellowhammers nesting in ditches and hedges require suitable foraging habitat within an accessible distance from their nests. The availability and quality of this foraging habitat is important as not only does it impact on adult survival, it additionally impacts the number and quality of young fledged whilst having lifelong impacts on the survival and subsequent fecundity of young fledged. Therefore the provision of suitable breeding season foraging habitat is of the utmost importance. Foraging yellowhammers were found to prefer habitat within 10m of field boundary features, as found in previous studies. The preference of margin habitat suggests that breeding yellowhammers would benefit from an increase in both hedge and ditch habitat on farms, as this would result in an increase in margin habitat available. Contrary to results from studies in mixed and arable farming regions, no evidence was found that yellowhammers during the breeding season avoided foraging on pastoral habitat. No significant difference was found in microhabitat structure between sites selected by foraging yellowhammers and sites not known to have been used, highlighting the high levels of homogeneity within fields on the pastoral study sites. Therefore, this study is unable to make specific recommendations about what habitat structure within fields is preferred by foraging yellowhammers.

3.1 Introduction

In order to survive and reproduce successfully organisms require access to good quality foraging habitat throughout the year. For many species, food availability and foraging habitat quality is the largest constraint on population size, limiting both winter survival and reproduction success. For example in the case of birds, food availability during the breeding season has been demonstrated to limit the reproductive success of a diverse range of species including Meadow Pipits *Anthus pratensis* (Vandenberghe *et al*. 2009), Capercaillie *Tetrao urogallus* (Baines *et al*. 2004) and Grey Partridge *Perdix perdix* (Rands 1985). The effect of low food availability during the breeding season may be masked as adults may trade off their own survival against an increased investment in the current reproductive event (Stearns 1992).

Farmland birds have declined as a result of habitat loss and change brought about by agricultural intensification; with granivorous species being disproportionately affected (Wilson *et al*. 2009). Agricultural intensification has resulted in a change in the availability of foraging habitats, the structure of vegetation within foraging habitats (and hence food accessibility) and the types and amounts of both invertebrate and seed foods available (reviewed in Newton 2004). Farms have become more specialised, resulting in habitat mosaics being replaced with more homogenous landscapes (Shrubb 2003). The drier east coast of Britain is now dominated by arable production with the West coast specialising in pastoral agriculture (Shrubb 2003). In pastoral regions, hay fields have been replaced with silage fields, whilst in arable regions, autumn sown cereals have replaced spring sown varieties (Wilson *et al*. 2009). Hedges and ditches have declined to facilitate increased field sizes, more efficient for mechanised agriculture. Remaining hedgerows have become neglected, moving towards becoming a line of trees, as they are now no longer required to be stock proof after widespread introduction of fencing.

In pastoral regions, silage production has resulted in thicker, more homogenous sward containing lower floral diversity than traditional hay fields. Silage fields set fewer seeds than hay fields due to multiple cuts taken each year. Increased stocking densities have resulted in pasture becoming uniform short swards, with the increased defoliation rate preventing development of seed heads, thus resulting in fewer seeds set in intensively grazed pasture. The reduction of floristic diversity on modern pastoral farms has reduced invertebrate diversity through the loss of host plants. Additionally, increased defoliation frequency in both silage and pasture fields prevents larger invertebrates from completing their life cycle.

So, to summarise, modern farmland presents to birds a more homogenous foraging habitat both at the field scale and the landscape scale, with a reduction in both invertebrate and seed food resources. However, providing habitat rich in an organism's preferred dietary items is not sufficient – the foraging habitat provided must be an appropriate distance from suitable breeding habitat, and the food items within the habitat must be accessible. A bird's choice of foraging habitat, and thus the food that is available to it, is affected by factors including the proximity of each habitat from nest site, the associated predation risk with the habitat (e.g. Cresswell 1993), age of individual (e.g. Cresswell 1994) and food accessibility (e.g. foraging in long v short swards) within the habitat. Therefore, detailed knowledge about how an organism forages within its environment is important. The ease with which different prey items can be detected is difficult to assess, therefore few studies have attempted to do so (Butler & Gillings 2004). Instead, studies of avian foraging behaviour have focussed on foraging patch selection and total food abundance.

This chapter aims to describe foraging habitat selection from what is available within territories selected by breeding yellowhammers *Emberiza citrinella* in a pastoral-dominated farming landscape, where little previous work has been carried out. Yellowhammers studied in mixed and arable farming regions have been shown to preferentially forage close to field boundary features, and avoid pastoral habitat, it is predicted that yellowhammers in the study landscape will demonstrate similar habitat preferences. Microhabitat selection will be studied by comparing invertebrate and plant community and structure at known yellowhammer foraging sites with paired control sites. It is predicted that control sites will differ from foraging sites as yellowhammers actively target the most profitable habitat available with regards to structure (influencing prey accessibility) and invertebrate and plant communities present, and these comparisons allowing such characteristics to be described and quantified. Detailed knowledge of foraging habitat choice during the breeding season is important to help design effective and appropriate future agri-environment schemes to provide not only food rich but accessible foraging habitat for breeding yellowhammers and similar graniverous species in pastoral farming landscapes. Provision of good quality foraging habitat during the breeding season has the potential to increase both breeding productivity and subsequent survival of both the adults and young, and thus ultimately influence population trends within populations.

3.2 Methods

Yellowhammer summer foraging habitat choice was studied at four pastoral-dominated study farms in Ayrshire, South West Scotland. Three of the study farms, Fail Mains, Killoch and Milton were studied from 2009 to 2011, the fourth, Carnell was only studied in 2009 and 2010. The farms were typically managed pastoral dominated farms, with both pasture (grazed by cattle) and silage fields. Additionally, a small amount of cereal was grown at some farms, with the exact amount varying by farm and across years. For full details of habitat availability see appendixes 9 & 10.

3.2.1 Broad scale foraging habitat choice

Boundary transects were carried out circa weekly at each farm during the yellowhammers' breeding season between May and August in 2009 and 2010 and in May and June in 2011 when only the first breeding attempt was studied (for transect dates see appendix 2). Boundary transects were fixed routes, walked 10m from boundary features (where crops etc permitted) and ranged in length between 7.3 km and 11.5 km (see appendix 1 for routes and lengths). Transects took 3 ½ to 4 ½ hours to complete and commenced within one hour of dawn, with the direction of travel being reversed in successive surveys to minimise the effect of time of day on bird locations. Binoculars were used to aid bird identification, and transects only took place on days when visibility and weather were good. Locations of breeding territories and foraging yellowhammers were recorded on maps, and later entered and stored in ArcGIS (ESRI 2011) alongside the habitat availability at each farm. This allowed yellowhammer foraging habitat choice to be compared with habitat availability, to identify habitats yellowhammers select relative to their availability in the landscape.

3.2.2 Fine scale foraging surveys

Locations where birds were observed foraging during breeding surveys were revisited later the same day and surveyed in detail. For each observation, a control site was sampled in similar habitat 75m away where birds were not observed foraging during the boundary transects (i.e. it is unknown if this habitat was being used by foraging yellowhammers). This control location was always taken from the same field, so the habitat would be under the same management regime, and thus represent a similar potential foraging habitat for the yellowhammer. If a suitable location 75m away was not possible (i.e. the size of the habitat parcel was very small), the control sample was taken from as close to 75m as possible. Surveys were only carried out if the vegetation was dry (invertebrate sweep sampling is ineffective in wet vegetation). A 2m^2 quadrat was placed over the observed foraging or control site (location recorded on map or handheld GPS). Invertebrates and above-ground seeds were collected using a sweep net; ten sweeps were made working forward across the quadrat. The contents of the sweep net were transferred (via a pooter) to 70% alcohol for preservation until identification. Invertebrates were identified to Order using a binocular microscope and reference key (Chinery 1993). Larvae and adults were recorded in separate categories as they represent a different type of food with differing accessibility to birds. Body length of each item was recorded to the nearest 1mm. The dry mass of each foraging and control invertebrate sample was determined. Samples were air dried for one hour then transferred to a drying oven preheated at 40^{o}C for three hours. The dried invertebrates were then weighed using a calibrated electronic balance to the nearest 0.0001g. Dry mass was used instead of mass as this better reflect the nutritional value to birds since invertebrate moisture content varies between 55% to 80% (Capinera 2010). Three hours was deemed sufficient time to dry all samples as returning the largest samples to the oven for an extra hour and re-weighing found no further decline in mass. Soil penetrability was measured in three locations in the quadrat using a soil penetromoeter (see Figure 3.1 for sampling locations). Within the 2m^2 quadrat, % cover of each vegetation species present was estimated (grass was treated as one species due to the time required for identification and difficulties in identification when no seed heads were visible). Three measurements of vegetation height were recorded at each of five locations within the quadrat (see Figure 3.1). The first was the maximum height of the vegetation, the second measurement the height of a 11g 30cm diameter plastic disc slid down a meter stick, and the last measurement was the height of a 6cm diameter 45g disc slid down the same meter stick on top of the first larger disc. The heights of the discs aim to capture the heterogeneity of the vegetation (Holmes 1974).

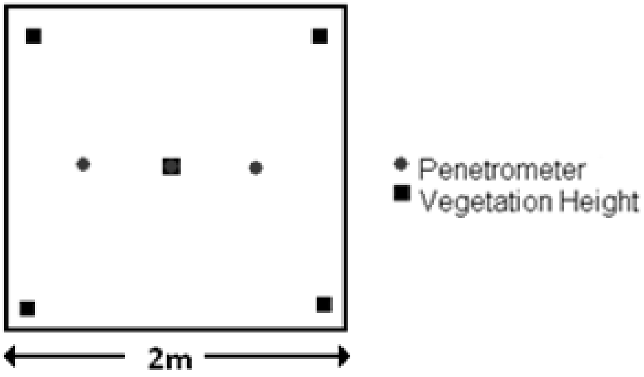


Figure 3.1 sampling locations within the 2m^2 quadrat for each foraging and paired control site surveyed

3.2.3 Data storage and analysis

Observations of foraging yellowhammers and information on habitat availability each year across the study sites was stored using ArcGIS 10 (ESRI 2010). Habitats were assigned to mutually exclusive categories (outlined in appendix 6), and mapped in ArcGIS over OS Mastermap files for Ayrshire (downloaded from EDINA), alongside information on the locations of birds seen and their behaviour, time and date. A 50m buffer was placed around the transect route walked as 50m was the distance that a foraging yellowhammers could be reliably detect in. During the breeding season, yellowhammers are known to forage predominantly close to their nests, with Biber 1993 reporting 90% of foraging trips within 100m and Morris *et al.* 2001 finding 60% of foraging trips within 100m. Therefore, not all habitat at each farm is accessible to foraging yellowhammers. To account for this, only the foraging observations from the transect surveys falling within 50m of the boundary transect (to ensure individuals present could be detected) and within 100m of a territory centre were considered in the analysis. As territory locations differed each year, this had to be done separately for each year. The constraints when considering what habitat was available to breeding yellowhammers resulted in the initial 361 observations of yellowhammers foraging recorded during the boundary transects being reduced to 258 being recorded within 50m of the boundary route and on occupied yellowhammer territories. To test for differences in habitat selection by foraging yellowhammers relative to availability, resource selection functions were used (see Boyce *et al.* 2002). The 258 random foraging locations required (within 50m of transect route walked and within known yellowhammer breeding territories) for this analysis were created in ArcGIS (ESRI 2011) by first creating as many random points as possible within the target habitat polygons whilst stipulating that points created were minimum 1m apart. From these points, for each year surveyed, the same number of points was selected as the number of foraging observations using ‘subset features’ (Geostatistical Analyst Tools). Random locations (0) and foraging locations (1) were merged with the habitat layer in ArcGIS, then a logistic regression analysis was carried out in R (version 2.15.1) to test what habitats foraging yellowhammers were associated with. Both the effect of infield and margin habitat as well as broad habitat type was tested to determine what habitats foraging yellowhammers were associated with.

De-trended Correspondence Analysis’s (DCA) (carried out in R 2.15.1 using the Vegan extension (Oksanen *et al.* 2007)) were used to look for differences in invertebrate communities between yellowhammer foraging sites, necessitating any samples with zero invertebrates to be removed from the analysis. To prevent rare invertebrate orders having a disproportionate affect on the DCA analysis (could cause samples with rare invertebrates present to be located further from the origin), invertebrate groups with less than 10 recorded individuals across all sites were removed from the dataset prior to analysis. Envfit models with 1,000,000 permutations were run to test for differences in invertebrate communities between broad habitats and infield and margin habitat.

To look at the impact of broad habitat type and pastoral management on the number of invertebrate orders (as a proxy for diversity), the total number of invertebrates, invertebrate greater than 2mm, larvae, the mass of invertebrates, mean weight of individual invertebrates in a sample, number of broad leafed species, % bare ground, maximum, disc 1 and disc 2 height and variation and soil penetrability at sampled sites, ANOVA or Kruskal-Wallis (non-parametric) tests were used as appropriate (after testing for normality using Anderson-Darling tests). Paired foraging and control sites were compared for these traits using paired t tests or Wilcoxons signed rank tests (after Anderson-Darling tests were used to determine normality). Invertebrate characteristics including diversity were investigated as yellowhammers utilise a wide variety when provisioning nestlings (Cramp & Perrins 1994), with vegetation characteristics additionally investigated as these influence the accessibility of prey items to foraging yellowhammers.

Differences in invertebrate communities at paired foraging and control sites were investigated by carrying out a CCA in CANOCO Version 4.56 (2009) using a split plot. The split plot design allowed pairs of foraging and control sites to be blocked, allowing the differences between paired sites to be tested.

Unless otherwise stated, all statistics were carried out in Minitab 16 (2010).

3.3 Results

3.3.1 Breeding season foraging habitat choice

Yellowhammers were observed to forage in margin habitat (within 10m of boundary features such as hedges or ditches) significantly more than expected (logistic regression, margin, $z = 10.318$, $p < 0.0001$, 515 d.f.). However, no significant difference was found between the broad types of fields as selected by observed foraging yellowhammers and randomly generated locations within breeding territories (Table 3.1).

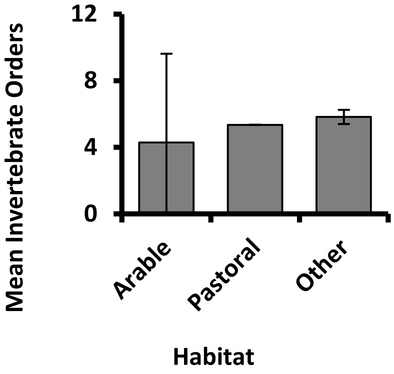
Table 3.1 Results from logistic regression comparing habitats at foraging locations yellowhammers observed using and random locations, 515 d.f.

Habitat	Z value	p value
Maize	Z = -0.719	p = 0.472
Manmade	Z = 0.042	p = 0.967
Pastoral	Z = -0.978	p = 0.328
Re-sown	Z = 0.359	p = 0.719
Unmanaged	Z = 0.487	p = 0.626
Water	Z = -0.030	p = 0.976
Woodland	Z = -0.341	p = 0.733

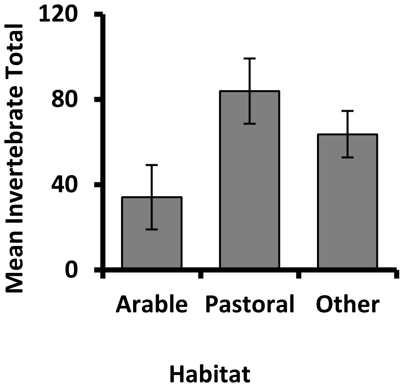
3.3.2 Foraging sites selected by yellowhammers and how they vary between habitats

94 of the 357 locations where yellowhammers were observed foraging during the breeding season were surveyed in more detail with regards to the vegetation and invertebrates communities present. The 94 yellowhammer foraging sites sampled were from a variety of habitats; 3 sites where no invertebrates were present in the sweep net samples collected were removed from the analysis (as the DCA's require that invertebrates were present). Of the remaining 91 samples, 49 were collected in pastoral habitat, 14 in arable habitat and 28 in 'other' habitat. 'Other' habitat was predominantly unmanaged habitat, with 15 of these samples collected in road margins and 11 in unmanaged grassland. The remaining 2 samples were collected in game crop habitat.

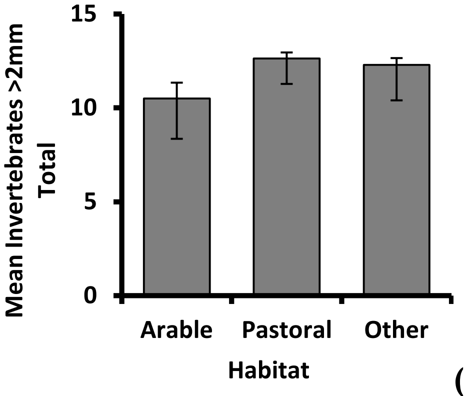
There were significantly higher number of invertebrate orders at foraging sites selected by yellowhammers in other habitat than in arable, but not when the sequential Bonferroni correction was applied (Figure 3.2 (a), Table 3.2), and significantly higher numbers of invertebrates in other and pastoral habitat than in cereal (Figure 3.2 (b), Table 3.2). Despite the higher number of invertebrate orders and numbers of all invertebrates, no significant differences was found in either the number of invertebrate greater than 2mm or the total number of larvae in each sample across the broad habitat categories (Figure 3.2 (c) and (d), Table 3.2). There was no significant difference in the total dry weight of invertebrates per sample (Figure 3.2 (e), Table 3.2), but when the number of individuals in the sample were taken into account, found that the mean weight of items in the samples was significantly higher in arable habitat than in pastoral and other (Figure 3.2 (f), Table 3.2). As well as differences between the invertebrates collected in sweep samples at the foraging sites selected by yellowhammers in the different habitats, differences in vegetation communities and structure were also found. Significantly higher numbers of broad leafed species were present in foraging sites selected by yellowhammers located in pastoral and other habitat than in arable (Figure 3.2 (g), Table 3.2), with significantly more bare ground and tarmac in 'other' habitat than in pastoral (Figure 3.2 (h), Table 3.2). Vegetation heights at foraging sites selected by yellowhammers were also significantly different according to the broad habitat that they were in, with arable sites having significantly higher vegetation than in pastoral and other habitat for both maximum vegetation height and height of disc 1, but not when the sequential Bonferroni correction was applied (Figure 3.2 (i) and (k), Table 3.2). The highest variation in vegetation heights present around yellowhammer foraging sites was found in other habitat, with significantly higher vegetation height heterogeneity than present in pastoral and arable habitat but not after sequential Bonferroni correction was applied (Figure 3.2 (j), Table 3.2). No significant differences were found between the variation in disc 1 and disc 2 vegetation height, or the soil penetrability or its variation across the broad habitat categories (Figure 3.2 (l), (n), (o) and (p), Table 3.2).


Mean Invertebrate Orders
12
8
4
0
Arable
Pastoral
Other
Habitat

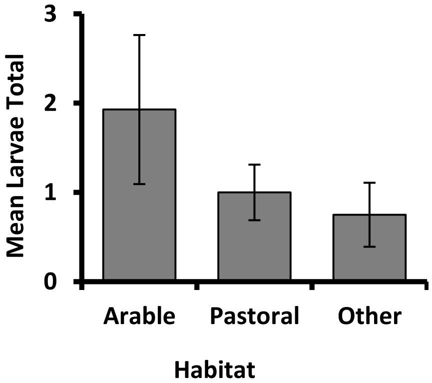
(a)


Mean Invertebrate Total
120
80
40
0
Arable
Pastoral
Other
Habitat

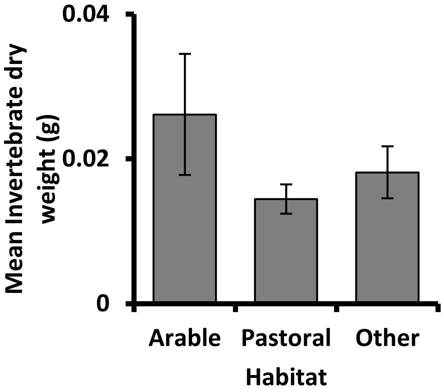
(b)


Mean Invertebrates >2mm Total
15
10
5
0
Arable
Pastoral
Other
Habitat

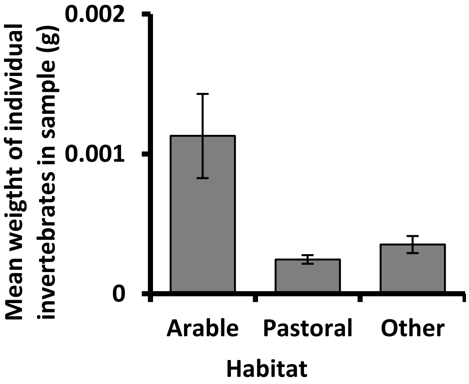
(c)


Mean Larvae Total
3
2
1
0
Arable
Pastoral
Other
Habitat

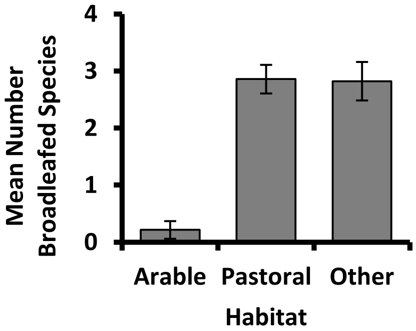
(d)


Mean Invertebrate dry weight (g)
0.04
0.02
0
Arable
Pastoral
Other
Habitat

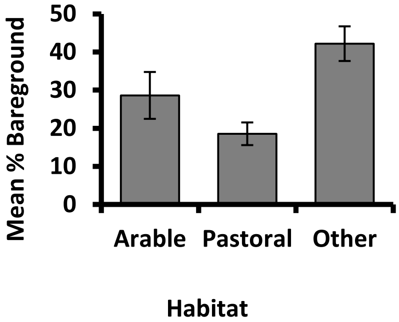
(e)


Mean weight of individual invertebrates in sample (g)
0.002
0.001
0
Arable
Pastoral
Other
Habitat

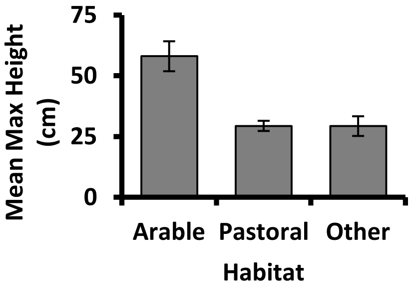
(f)


Mean Number Broadleafed Species
4
3
2
1
0
Arable
Pastoral
Other
Habitat

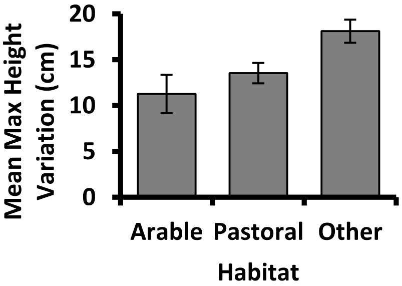
(g)


Mean % Bareground
50
40
30
20
10
0
Arable
Pastoral
Other
Habitat

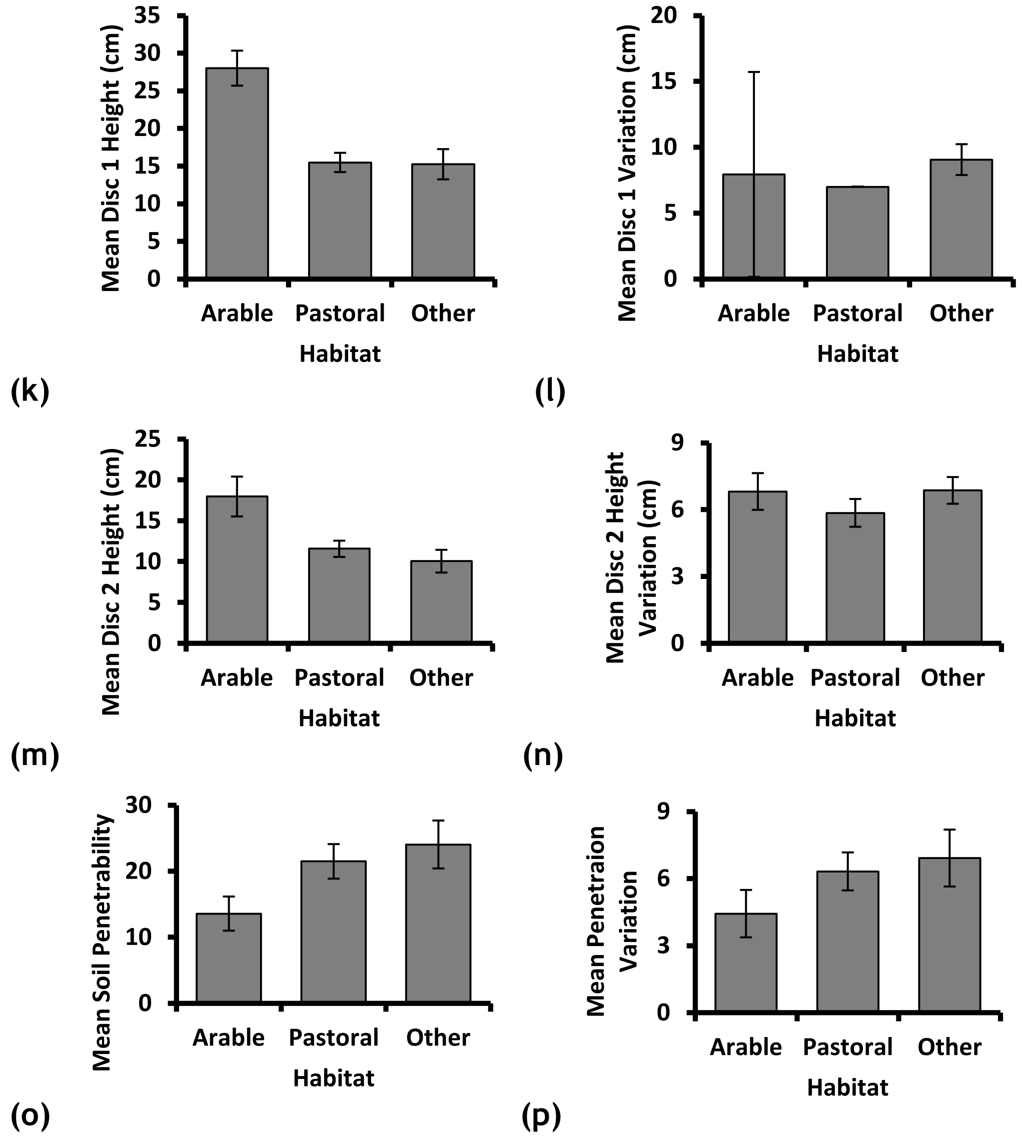
(h)


Mean Max Height (cm)
75
50
25
0
Arable
Pastoral
Other
Habitat

(i)


Mean Max Height Variation (cm)
20
15
10
5
0
Arable
Pastoral
Other
Habitat

(j)



(k) (l)

(m) (n)

(o) (p)

Figure 3.2 Comparing the mean number of (a) Invertebrate orders (b) Invertebrate total, (c) Invertebrates >2mm, (d) Larvae total, (e) Total invertebrate dry weight (grams), (f) Mean dry weight of individual invertebrates in a sample (grams), (g) Number broad-leafed species, (h) % Bare ground (including tarmac), (i) Maximum vegetation height (cm), (j) Maximum vegetation height variation (cm), (k) Disc 1 Height (cm), (l) Disc 1 height variation (cm), (m) Disc 2 height (cm), (n) Disc 2 height variation (cm), (o) Soil penetrability and (p) Soil penetrability variation in foraging sites selected by yellowhammers in arable, pastoral and other habitat

Table 3.2 Results from either ANOVA or Kruskal-Wallis (depending on normality of data being tested) comparing yellowhammer foraging sites between grassland, cereal and other habitat. Significant results are shown in bold

	Results from Anderson-Darling test for normality		Results from appropriate parametric (ANOVA) /non parametric test (Kruskal-Wallis)		Significance level required under sequential Bonferroni
	AD value	p value	H value/F value	p value	
(a) Invertebrate orders	AD = 1.586	p < 0.005	H = 7.57, 2 d.f.	p = 0.023	p = 0.005
(b) Invertebrate total	AD = 7.380	p < 0.005	H = 7.82, 2 d.f.	p = 0.020	p = 0.005
(c) Invertebrates >2mm	AD = 2.736	p < 0.005	H = 0.64, 2 d.f.	p = 0.725	p = 0.025
(d) Larvae total	AD = 15.641	p < 0.005	H = 2.90, 2 d.f.	p = 0.234	p = 0.01
(e) Total invertebrate dry weight (g)	AD = 5.961	p < 0.005	H = 1.39, 2 d.f.	p = 0.499	p = 0.013
(f) Mean dry weight of invertebrates in a sample	AD = 12.482	p < 0.005	**H = 18.25, 2 d.f.**	**p < 0.001**	**p = 0.003**
(g) No. broad-leafed species	AD = 2.308	p < 0.005	**H = 25.76, 2 d.f.**	**p < 0.001**	**p = 0.003**
(h) % Bare ground (& tarmac)	AD = 2.577	p < 0.005	**H = 15.58, 2 d.f.**	**p < 0.001**	**p = 0.004**
(i) Max. vegetation height (cm)	AD = 3.068	p < 0.005	**H = 16.84, 2 d.f.**	**p < 0.001**	**p = 0.004**
(j) Max. vegetation height variation (cm)	AD = 0.388	p = 0.379	$F_{2,88}$ = 3.93	p = 0.024	p = 0.006
(k) Disc 1 Height (cm)	AD = 1.979	p < 0.005	H = 9.08, 2 d.f.	p = 0.011	p = 0.004
(l) Disc 1 height variation (cm)	AD = 0.656	p = 0.084	$F_{2,88}$ = 1.77	p =0.177	p = 0.05
(m) Disc 2 height (cm)	AD = 3.069	p < 0.005	H = 5.11, 2 d.f.	p = 0.078	p = 0.006
(n) Disc 2 height variation (cm)	AD = 1.130	p = 0.006	H = 3.76, 2 d.f.	p = 0.152	p = 0.008
(o) Soil penetrability	AD = 2.990	p < 0.005	H = 4.03, 2 d.f.	p = 0.133	p = 0.007
(p) Soil penetrability variation	AD = 4.545	p < 0.005	H = 0.88, 2 d.f.	p = 0.645	p = 0.017

Despite significant differences being found in vegetation characteristics between the broad habitat categories, no significant difference was found in the invertebrate communities present in the different broad habitat types grass (pastoral), cereal (arable) and other (Figure 3.3 (a), envfit, R^2 = 0.08, p = 0.141), or between infield and margin habitat (Figure 3.3 (b), envfit, R^2 = 0.01, p =

0.665). However, this was probably a result of the small sample sizes, if the control sites were included in the analysis, invertebrate communities present in cereal habitat is found to be significantly different from grass and other (road margin, unmanaged and game crop) habitats.

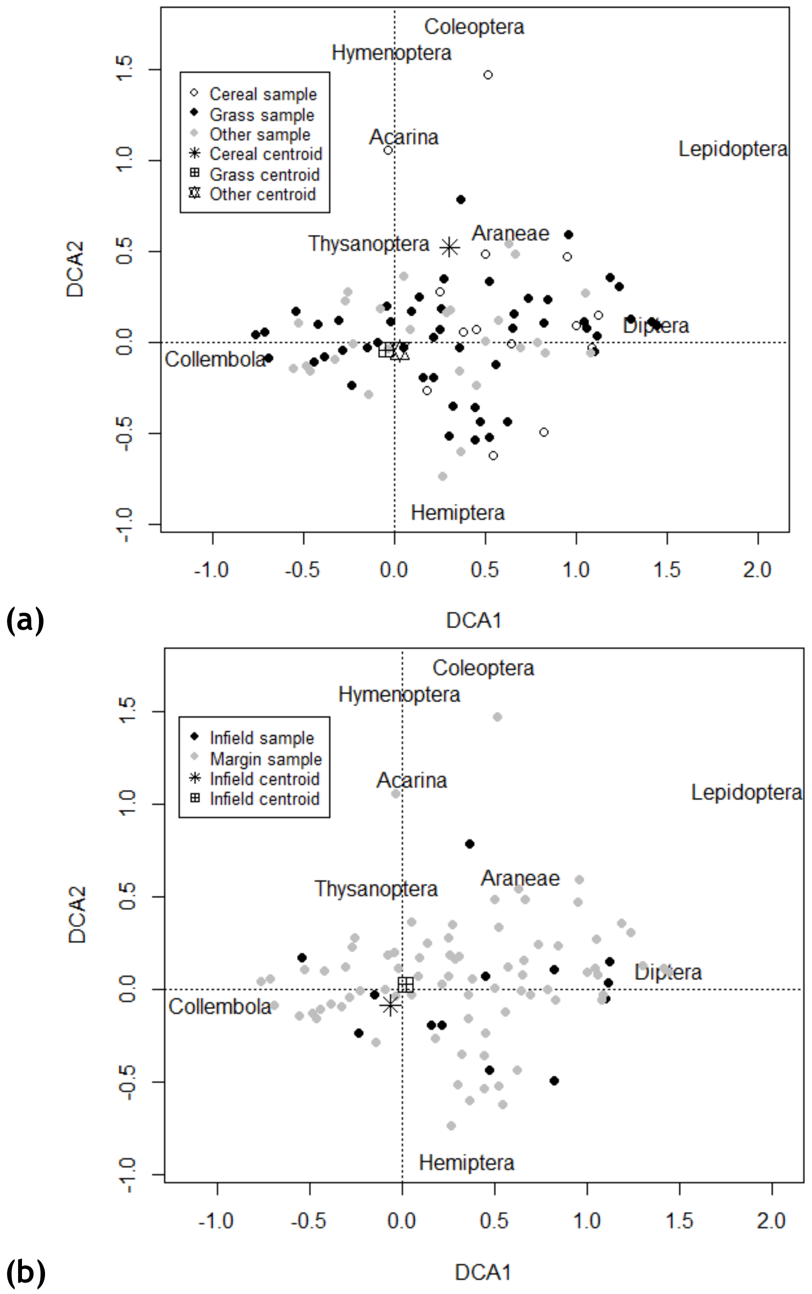
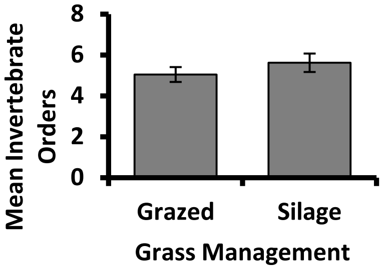


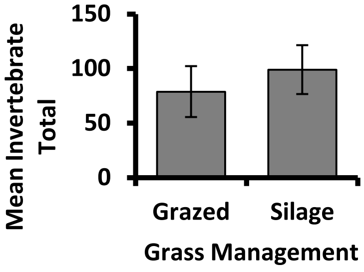
Figure 3.3 DCA looking at differences in invertebrate communities (identified to order) in foraging sites selected by yellowhammers with regards to (a) broad habitat categories (cereal (n = 14), grass (n = 49) and 'other' (n = 28)) and (b) infield (n = 13) and margin (n = 78) habitat

3.3.3 Silage versus grassland foraging sites selected by yellowhammers

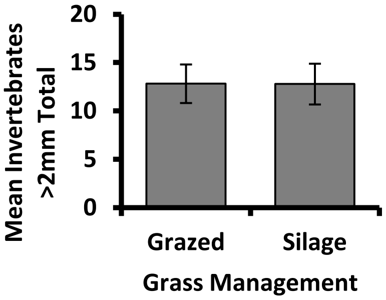
Within pastoral habitat, silage and pasture represents a visibly different foraging habitat, therefore, it is expected that foraging sites selected by yellowhammers will differ in characteristics between the two habitats. This was done by looking at the 49 foraging sites sampled in grassland in more detail. Of these 49 samples, only 4 were collected in recently re-sown fields and thus were removed from the following analysis due to the small sample size. Of the remaining 45 samples, 27 were collected in cattle grazed pasture and 18 in silage fields. Unlike between the broader habitat types, there was no significant difference between the number of invertebrate orders present in foraging sites selected by yellowhammers in grazed and silage grassland habitat, (Figure 3.4 (a), Table 3.3) despite there being significantly higher numbers of broad leafed plant species in pasture than silage fields at sites selected by foraging yellowhammers, but not when the sequential Bonferroni correction was applied (Figure 3.4 (g), Table 3.3), but with significantly higher numbers of larvae found in yellowhammers foraging sites in silage rather than grazed habitat, but not when the sequential Bonferroni correction was applied (Figure 3.4 (d), Table 3.3). No significant differences were found between invertebrate number and dry mass, vegetation height and structure and soil penetrability (Figure 3.4 (b), (c), (e), (f), (h), (i), (j), (k), (l), (m), (n), (o) and (p), Table 3.3) between silage and grazed pastoral foraging sites selected by yellowhammers.


Mean Invertebrate Orders
8
6
4
2
0
Grazed
Silage
Grass Management

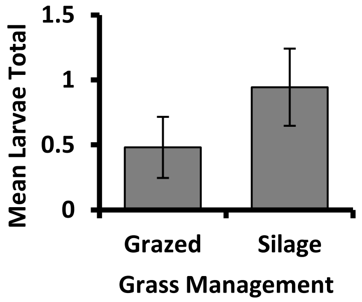
(a)


Mean Invertebrate Total
150
100
50
0
Grazed
Silage
Grass Management

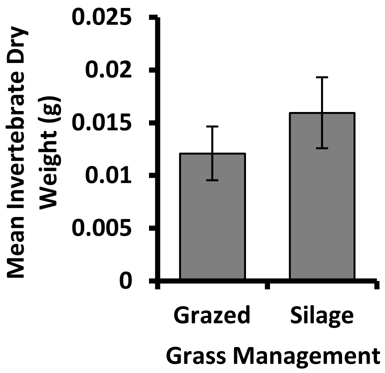
(b)


Mean Invertebrates >2mm Total
20
15
10
5
0
Grazed
Silage
Grass Management

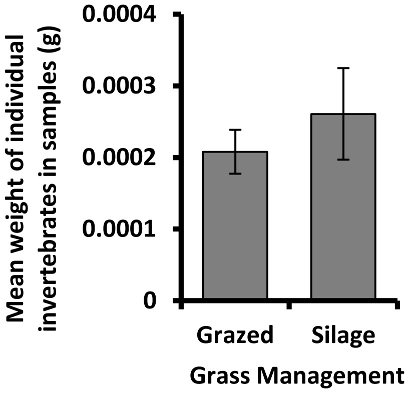
(c)


Mean Larvae Total
1.5
1
0.5
0
Grazed
Silage
Grass Management

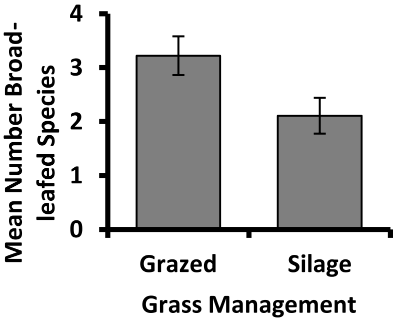
(d)


Mean Invertebrate Dry Weight (g)
0.025
0.02
0.015
0.01
0.005
0
Grazed
Silage
Grass Management

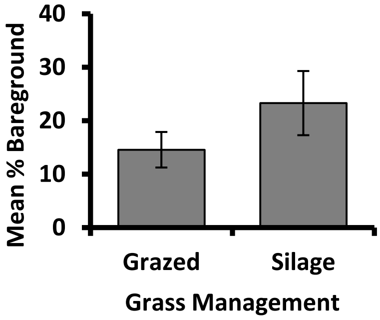
(e)


Mean weight of individual invertebrates in samples (g)
0.0004
0.0003
0.0002
0.0001
0
Grazed
Silage
Grass Management

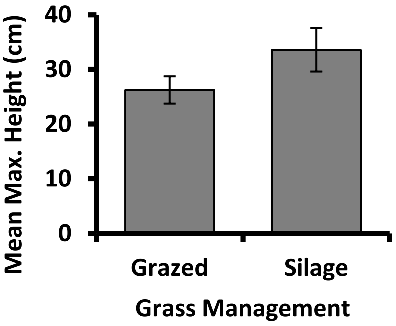
(f)


Mean Number Broad-leafed Species
4
3
2
1
0
Grazed
Silage
Grass Management

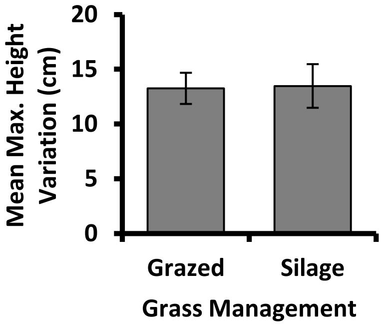
(g)


Mean % Bareground
40
30
20
10
0
Grazed
Silage
Grass Management

(h)


Mean Max. Height (cm)
40
30
20
10
0
Grazed
Silage
Grass Management

(i)


Mean Max. Height Variation (cm)
20
15
10
5
0
Grazed
Silage
Grass Management

(j)

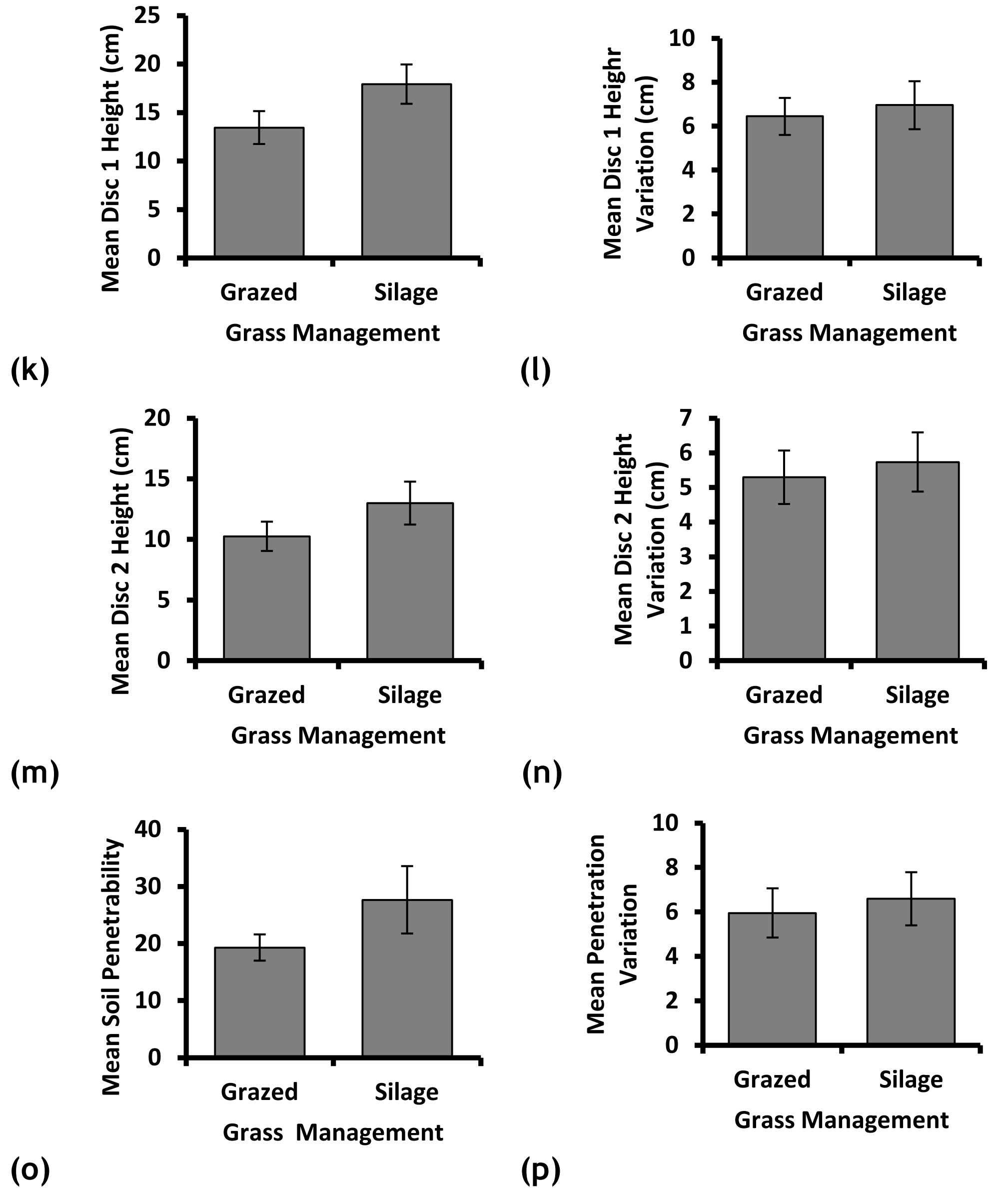


Figure 3.4 Comparing the mean number of (a) Invertebrate orders (b) Invertebrate total, (c) Invertebrates >2mm, (d) Larvae total, (e) Total invertebrate dry weight (grams), (f) Mean dry weight of individual invertebrates in a sample (grams), (g) Number broad-leafed species, (h) % Bare ground (including tarmac), (i) Maximum vegetation height (cm), (j) Maximum vegetation height variation (cm), (k) Disc 1 Height (cm), (l) Disc 1 height variation (cm), (m) Disc 2 height (cm), (n) Disc 2 height variation (cm), (o) Soil penetrability and (p) Soil penetrability variation in foraging sites selected by yellowhammers in grazed and silage managed pastoral fields

Table 3.3 Results from either ANOVA or Kruskal-Wallis (depending on normality of the data being tested) comparing yellowhammer foraging sites in pastoral habitat managed as pasture and silage

	Results from Anderson-Darling test for normality		Results from appropriate parametric (ANOVA) /non parametric test (Kruskal-Wallis)		Significance level required under sequential Bonferroni
	AD value	P value	H value/F value	P value	
(a) Invertebrate orders	AD = 1.163	p < 0.005	H = 0.77	p = 0.380	p = 0.006
(b) Invertebrate total	AD = 4.489	p < 0.005	H = 2.98	p = 0.084	p =0.004
(c) Invertebrates >2mm	AD = 1.476	p < 0.005	H = 0.01	p = 0.917	p =0.025
(d) Larvae total	AD = 7.044	p < 0.005	H = 4.82	p = 0.028	p = 0.003
(e) Total invertebrate dry weight (g)	AD = 2.830	p < 0.005	H = 1.42	p = 0.233	p = 0.005
(f) Mean dry weight of individual invertebrates in a sample (g)	AD = 4.352	p < 0.005	H < 0.01	p = 0.991	p = 0.05
(g) Number broad-leafed species	AD = 0.951	p = 0.015	H = 3.98	p = 0.046	p = 0.003
(h) % Bare ground (including tarmac)	AD = 3.129	p < 0.005	H = 0.29	p = 0.590	p = 0.01
(i) Maximum vegetation height (cm)	AD = 1.023	p = 0.010	H = 2.10	p = 0.148	p = 0.004
(j) Maximum vegetation height variation (cm)	AD = 0.567	p = 0.133	F = 0.05	p = 0.823	p = 0.013
(k) Disc 1 Height (cm)	AD = 0.947	p = 0.015	H = 3.31	p = 0.069	p = 0.004
(l) Disc 1 height variation (cm)	AD = 0.895	p = 0.020	H = 0.02	p = 0.901	p = 0.017
(m) Disc 2 height (cm)	AD = 1.515	p < 0.005	H = 1.63	p = 0.202	p = 0.005
(n) Disc 2 height variation (cm)	AD = 1.018	p = 0.010	H = 0.42	p = 0.518	p = 0.008
(o) Soil penetrability	AD = 2.901	p < 0.005	H = 1.13	p = 0.289	p = 0.006
(p) Soil penetrability variation	AD = 2.414	p < 0.005	H = 0.58	p = 0.447	p = 0.007

No significant difference in invertebrate communities between silage and grazed fields within the grassland habitat (Figure 3.5 (a), envfit, R^2 = 0.01, p = 0.771) or between orders in infield and margin habitat in grassland (Figure 3.5 (b), envfit, R^2 = 0.01, p = 0.735) was detected.

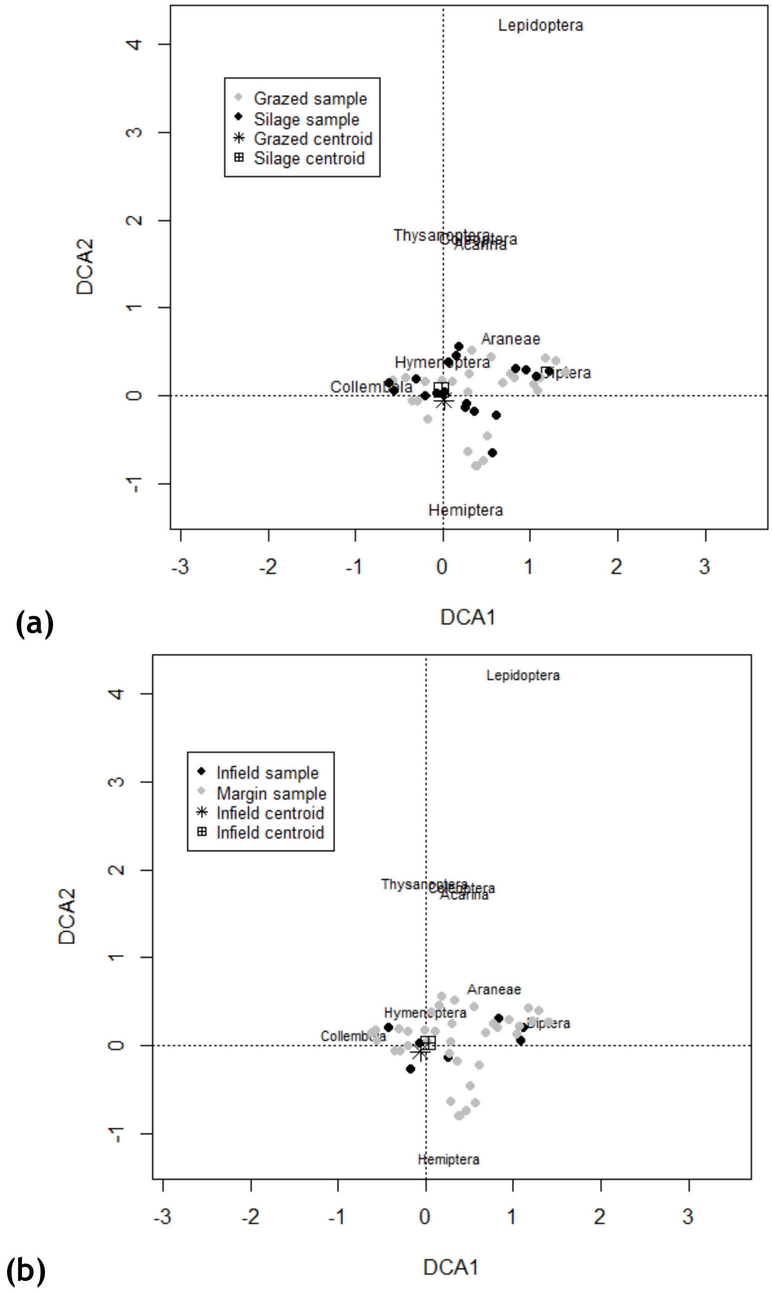


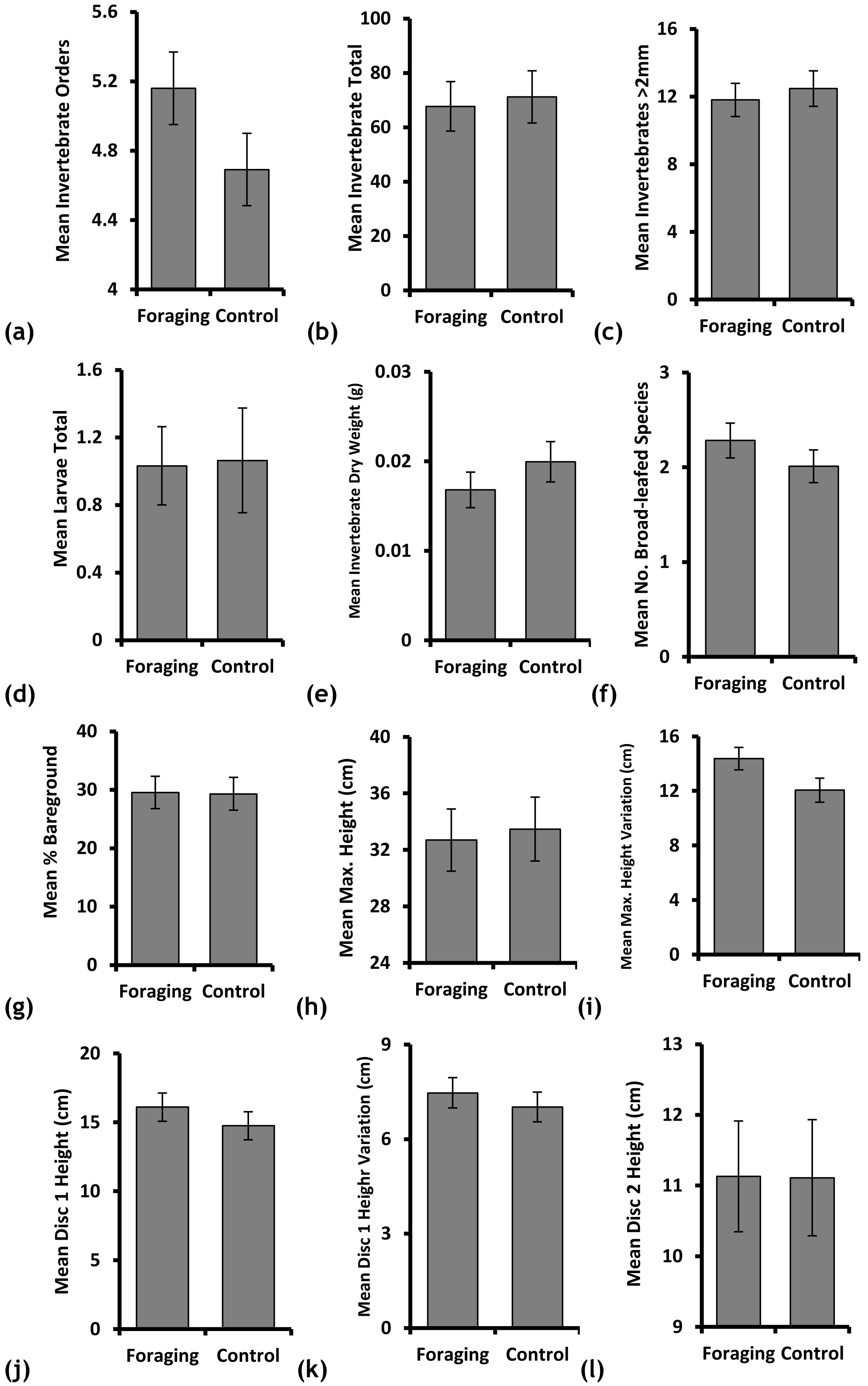
Figure 3.5 DCA's looking at the invertebrate communities at foraging sites selected by yellowhammers in grassland habitat and how they vary with (a) management - grazed (n = 27) versus silage (n = 18) and (b) location relative to boundary feature with margin habitat (n = 38) within 10m of boundary feature and infield (n = 7) all other habitat

3.3.4 Foraging sites selected by yellowhammers compared with paired control sites

For each of the 94 foraging sites sampled, each had a paired control sample collected to compare characteristics of sites yellowhammers selected for foraging with sites in the same habitat 75m away. Foraging sites were found to contain a significantly higher number of invertebrate orders in than at the paired control sites (Figure 3.6 (a), Table 3.4), with foraging sites on average containing 0.47 more invertebrate orders than in the paired control sites. However, when the sequential Bonferroni correction (to minimise the risk of a 'false' significant result) was applied, the difference was no longer significant. No significant differences were found in the total numbers of invertebrates or the mass of invertebrate material, the diversity of broad leafed species, amount of bare ground, the structure of the vegetation and the soil penetrability at foraging and control sites (Figure 3.6 (b), (c), (d), (e), (f), (g), (h), (i), (j), (k), (l), (m), (n) and (o), Table 3.4).

Table 3.4 Results from paired T - tests either paired t test or Wilcoxons test (depending on normality of the data being tested) comparing foraging sites selected by yellowhammers with their paired control sites, significant results in bold

	Results from Anderson-Darling test for normality		Results from appropriate parametric (ANOVA) /non parametric test (Kruskal-Wallis)		Significance level required under sequential Bonferroni
	AD value	P value	Wilcoxons value/T value	P value	
(a) Invertebrate orders	AD = 1.586	p < 0.005	1710.5	p = 0.013	p = 0.003
(b) Invertebrate total	AD = 7.380	p < 0.005	1844.0	p = 0.944	p =0.05
(c) Invertebrates >2mm	AD = 2.736	p < 0.005	1816.0	p = 0.892	p =0.025
(d) Larvae total	AD = 15.641	p < 0.005	440.0	p = 0.692	p = 0.01
(e) Total invertebrate weight (g)	AD = 5.961	p < 0.005	1854.5	p = 0.346	p = 0.004
(f) Number broad-leafed species	AD = 2.308	p < 0.005	1198.0	p = 0.070	p = 0.004
(g) % Bare ground (inc. tarmac)	AD = 2.577	p < 0.005	708.0	p = 0.677	p = 0.006
(h) Max. vegetation height (cm)	AD = 3.068	p < 0.005	2176.5	p = 0.605	p = 0.006
(i) Max. vegetation height variation (cm)	AD = 0.388	p = 0.379	t = 1.17	p = 0.244	p = 0.004
(j) Disc 1 Height (cm)	AD = 1.979	p < 0.005	1764.0	p = 0.491	p = 0.005
(k) Disc 1 height variation (cm)	AD = 0.656	p = 0.084	t = 0.42	p = 0.679	p = 0.007
(l) Disc 2 height (cm)	AD = 3.069	p < 0.005	1543.0	p = 0.714	p = 0.013
(m) Disc 2 height variation (cm)	AD = 1.130	p = 0.006	1422.0	p = 0.688	p = 0.008
(n) Soil penetrability	AD = 2.990	p < 0.005	1489.0	p = 0.799	p = 0.017
(0) Soil penetrability variation	AD = 4.545	p < 0.005	1641.5	p = 0.357	p = 0.005


Mean Invertebrate Orders
5.6
5.2
4.8
4.4
4
Foraging Control
(a)
Mean Invertebrate Total
100
80
60
40
20
0
Foraging Control
(b)
Mean Invertebrates >2mm
16
12
8
4
0
Foraging Control
(c)
Mean Larvae Total
1.6
1.2
0.8
0.4
0
Foraging Control
(d)
Mean Invertebrate Dry Weight (g)
0.03
0.02
0.01
0
Foraging Control
(e)
Mean No. Broad-leafed Species
3
2
1
0
Foraging Control
(f)
Mean % Bareground
40
30
20
10
0
Foraging Control
(g)
Mean Max. Height (cm)
40
36
32
28
24
Foraging Control
(h)
Mean Max. Height Variation (cm)
16
12
8
4
0
Foraging Control
(i)
Mean Disc 1 Height (cm)
20
15
10
5
0
Foraging Control
(j)
Mean Disc 1 Heighr Variation (cm)
9
6
3
0
Foraging Control
(k)
Mean Disc 2 Height (cm)
13
12
11
10
9
Foraging Control
(l)

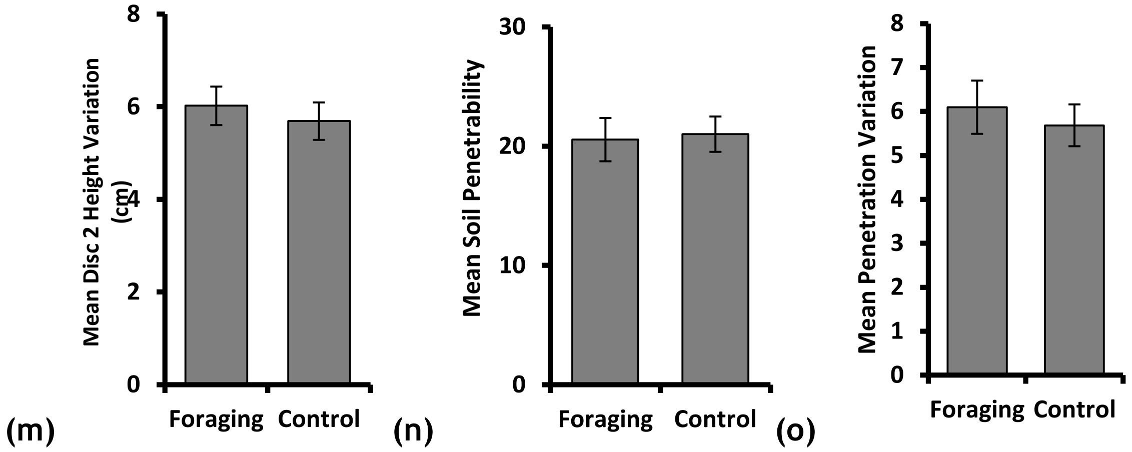


Figure 3.6 Comparing the mean number of (a) Invertebrate orders (b) Invertebrate total, (c) Invertebrates >2mm, (d) Larvae total, (e) Total invertebrate dry weight (grams), (f) Number broad-leafed species, (g) % Bare ground (including tarmac), (h) Maximum vegetation height (cm), (i) Maximum vegetation height variation (cm), (j) Disc 1 Height (cm), (k) Disc 1 height variation (cm), (l) Disc 2 height (cm), (m) Disc 2 height variation (cm), (n) Soil penetrability and (o) Soil penetrability variation between foraging sites selected by yellowhammers and control sites

There was no significant difference between foraging and control sites with respect to the invertebrate communities present (Figure 3.7, envfit, p = 0.858). However, this did not take into account the paired structure of the data. To do so, DCA axis 1 was compared between paired foraging and control sites, however, no significant difference was found (paired t test, T = 0.19, p = 0.850). However, this approach meant a lot of the variation in the dataset was excluded for the analysis. For a more robust analysis, differences between paired sets of foraging and control sites were investigated in CANOCO putting a block on site. No significant difference was found between the invertebrate communities present at pairs of foraging and control sites (F-ratio = 0.24, number of permutations = 499, p = 0.532).

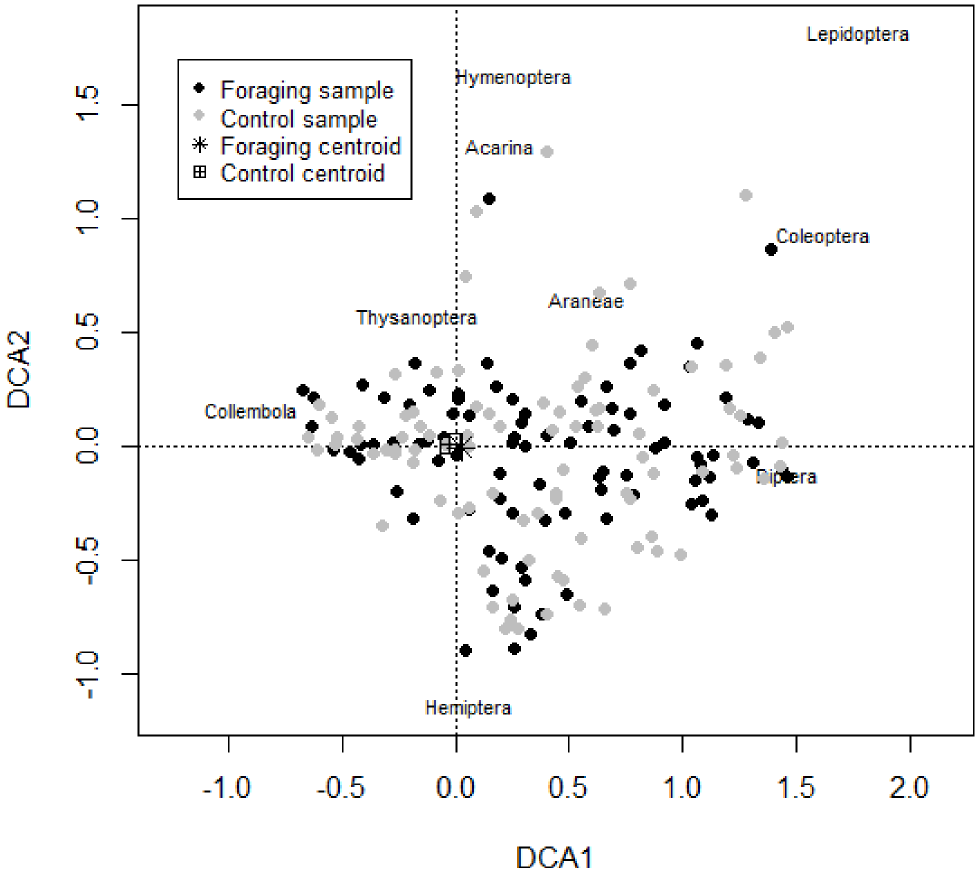


Figure 3.7 DCA's showing invertebrate communities at foraging sites selected by yellowhammers and their paired control sites showing how they vary between foraging and control sites

3.4 Discussion

3.4.1 Broad scale habitat choice

Yellowhammer foraging habitat choice during the breeding season in the pastoral dominated study landscape was not random. Margin habitat (within 10m of field boundary features) was selected more than expected based on availability. The observed preference of yellowhammers to forage in margin habitat has been found in other studies from mixed and arable farming regions (e.g. Perkins *et al*. 2002, Morris *et al*. 2001, Stoate *et al*. 1998) with the Handbook of the Birds of Europe the Middle East and North Africa describing the yellowhammer as "a ground feeder with strong attachment to bush and scrub cover" (Cramp & Perrins 1994).

As habitat choice is not random, it is likely to be being driven by food availability and accessibility within each habitat, the predation risk associated with each habitat, or a combination of these factors. Most margin habitat at the farms contained a hedge as the boundary feature; sometimes additionally the hedge was coupled with a ditch. Associated with hedgerows there is higher invertebrate biomass and biodiversity compared with in field habitat (Bowden & Dean 1977, Trnka *et al*. 1990, Peng *et al*.1993), with margins demonstrated as having a beneficial impact on Carabid beetles (Cole *et al*. 2008), Hemiptera, Opiliones and Symphyta larvae (Cole *et al*. 2012) and Arannae (Clough *et al*. 2005). Symphyta larvae previously shown to be an important dietary item for yellowhammer nestlings (Buckingham 2005) with beetles an important component of nestling diet (e.g. Cramp & Perrins 1994, Stoate *et al*. 1998, Moreby & Stoate 2000, Douglas *et al*. 2012 & MacLeod 2001). Therefore, higher food availability in margin habitat may account for the observed preference of field margins as foraging habitat in both the current and previous studies.

In addition to the increased availability of invertebrate material in margin habitat, seed availability may have been higher in both silage fields and cereal field margins. The extreme edges of silage fields alongside both ditches and hedges may be unable to be harvested as they are less accessible to machinery, thus seed heads were able to develop, whilst in cereal fields, less herbicides may have been sprayed round the edges of the crop. Both these mechanisms have the potential to increase the availability of seed food resources in margin habitat.

As well as higher food availability, food may have been more accessible to foraging yellowhammers in margin habitat. During this study, yellowhammers were frequently observed foraging along habitat interfaces such as where road margins met roads or where the grassy margin around cereal fields met the crop. Perhaps the differences in vegetation density increased prey detect ability; the yellowhammers were generally observed foraging from the less dense habitat (the road, the crop) gleaning prey items from the vegetation in the denser habitat (the grassy crop margin, the road margin). Livestock tended to congregate alongside hedges to avoid inclement weather conditions, thus, levels of poaching were higher in field margin habitat compared with infield (pers. obs.). This increase in bare ground may have led to an increase in accessibility of invertebrate prey items in margin habitat of pasture fields compared to infield habitat for the foliage gleaning yellowhammer. However, the preference of margin habitat by foraging yellowhammers may not only result from increased food availability and accessibility, the proximity of hedgerows may also offer protection from predation. Predation risk may have been an important driver of yellowhammer habitat choice at the study sites, as sparrowhawks *Accipiter nisus* were observed during the breeding season on occasion at all four study farms, and yellowhammers respond to the presence of predators by seeking cover (Whittingham & Evans 2004).

Despite the location within the field for foraging being found to be important, there was no evidence that yellowhammers were selecting different field types for foraging or avoiding others in the pastoral dominated study region. This was surprising, and contrary to findings from other studies (e.g. Perkins *et al.* 2002, Morris *et al.* 2001, Stoate *et al.* 1998) which find yellowhammers during the breeding season forage preferentially on cereal habitat or unmanaged habitat whilst avoiding pastoral habitat. Not finding a difference is unlikely to be a result of different detect ability rates across the different habitat types as only habitat within 50m within boundary transects was considered to allow comparable detect ability rates across all habitats. One explanation might be that cereal habitat was found to be selected in the other studies as autumn cereal was grown, thus during the breeding season, ripening grain would be available to foraging yellowhammers; ripening grain has been found to be included in nestling diet (Stoate *et al.* 1998). This contrasts with the spring sown cereal in the current study, which develops later in the season, therefore useable grain in this habitat was not available until the end of the yellowhammer breeding season, thus represents a different foraging habitat. Findings from this study suggest that in the pastoral study landscape, spring cereal and pastoral habitat were equally suitable for foraging yellowhammers during the breeding season.

No evidence was found to suggest that yellowhammers avoided foraging on the dominant intensively managed grassland habitat (which accounted for 71.2% of habitat available) during this study. This is contrary to results from previous work reporting the avoidance of grassland by yellowhammers during the breeding season (e.g. Macleod 2001, Bradbury *et al.* 2000, Kyrkos *et al.* 1998) and other bunting species (e.g. Brickle *et al.* 2000). However, the avoidance of grassland habitat in these recent studies may be a result of the intensive management of modern pastoral farms coupled with the availability of autumn sown cereal (unlike the spring sown cereal in this current study). In a 1960's study of yellowhammer ecology, yellowhammers were found to prefer traditional (i.e. mixed, lower intensity) agricultural landscapes to modern monocultures (Glutz von Blotzheim 1962) and to select pasture habitat pre agricultural intensification (Wild 1938, as reported in Morris *et al*. 2001) when hay was grown as opposed to silage. Hay is a more floristically diverse and heterogeneous crop than modern silage fields that are ryegrass dominated with dense swards. Dense swards can prevent access to food resources (Perkins *et al*. 2000), and may result in an increased need for vigilance on the generally taller and denser silage fields. Support for this comes from the observation that chaffinches, a similar species, spend more time on vigilance in taller vegetation (Whittingham & Evans 2004).

As a mixed model was not carried out taking into account territory as a random effect when investigating yellowhammer habitat choice, there will be some level of pseudo replication in the analysis. Territory was not included in the model as in a few instances, yellowhammer territories overlapped, thus it was unclear what territory to assign foraging observations. However, the effects of these repeated measures should be minimal; there were few instances of multiple foraging observations of individuals from the same territories.

3.4.2 Fine scale foraging habitat

No significant differences were found between the number of invertebrate orders (proxy for diversity) and the numbers of invertebrates found at yellowhammer foraging sites across the different habitats. This helps to account for the earlier observation that yellowhammers were not observed to select any one habitat type over another for foraging in during the breeding season. However, characteristics of foraging sites selected by yellowhammers differed significantly between habitats, with pastoral sites having significantly lower vegetation heights and increased diversity of broad leaved plants than arable habitat. The high mean maximum height of vegetation in arable habitat in foraging patches highlights that yellowhammers select this habitat only when the crop is well established. Although the temporal availability of invertebrate food resources in arable habitat wasn't studied, it is likely to have been higher later in the season as the crop became established, with additionally ripening grain becoming available at the very end of the breeding season.

When comparing yellowhammer foraging locations in silage and grazed pastoral fields, no significant differences were found in invertebrate or vegetation communities and structure. This is surprising as most studies find pasture to be more floristically diverse than silage (Wilson *et al*. 2009). Increased plant species richness is associated with increased invertebrate diversity (Vickery *et al*. 2001) and abundance (e.g. Asteraki *et al*. 2004, Koricheva *et al*. 2000). Previous work has shown the dense swards in silage fields can prevent birds accessing food resources (Perkins *et al*. 2000). Also, the longer swards in silage fields may present a riskier habitat to foraging in terms of predation risk. Chaffinches *Fringilla coelebs*, a similar granivorous species to the yellowhammer, reacted slower to model sparrowhawks when foraging in longer vegetation despite having an increased vigilance rate (Whittingham & Evans 2004). In addition to the increased risk of predation, the chaffinches in the longer vegetation decreased their peck rates (13% reduction in pecks in the long vegetation compared to the short), thus the long vegetation probably represents a less efficient habitat to forage in whilst being riskier in terms of predation. Improved grasslands tend to contain low biodiversity due to low temporal, spatial and structural heterogeneity and the intensity of the managements (Sheridan *et al*. 2008). Extensification of pastoral agriculture (reducing stocking density, hay production as opposed to silage) will be beneficial to foraging yellowhammers during the breeding season as they will result in increases in food availability and accessibility.

No significant difference was found between invertebrate communities present between paired foraging and control sites. This is despite invertebrates being important for provisioning nestlings, with yellowhammers previously been found to avoid arable fields where insecticides have been recently sprayed (Morris *et al*. 2005). One possible explanation for the lack of differences between foraging and control sites is that invertebrate communities were very homogenous across individual fields (where samples were collected). Further work perhaps should focus on why certain fields were selected over others, with the expectation that foraging yellowhammers would select fields with higher food availability; previous work has shown they avoid fields recently sprayed with herbicides (Morris *et al*. 2005) presumably as a result of lower invertebrate availability reducing their profitability as a foraging habitat.

The lack of differences between invertebrate and vegetation communities and structure between foraging and control sites found in this study suggests yellowhammers may be selecting foraging sites non-randomly within habitats. However, this lack of difference might be down to limitations of the experimental design, the control sites may also have both been suitable for and used by foraging yellowhammers; the weekly boundary surveys carried out only allowed a snapshot of micro habitat selection, thus the comparisons may have unknowingly been made between two foraging sites. Future studies should consider the temporal variation in invertebrate communities present in the different habitats that may come with temporal variation in vegetation influencing invertebrates' life cycles when considering factors driving yellowhammer foraging habitat choice. Instead of foraging sites being compared to similar sites (i.e. from the same field, and distance relative to the boundary feature as the foraging location), they should be compared to sites in fields under different management regimes, and different distances from boundary features within the field selected. Knowledge of the different characteristics of sites at different distances relative to boundary features would help determine of yellowhammers were preferentially foraging near boundary features as they represent higher food availability and/or accessibility relative to infield habitat (and thus food availability is limiting in infield habitat). If no difference is found, it would suggest that the yellowhammers preference of foraging close to margins is predominantly a result of anti predation behaviour.

3.4.3 How knowledge of yellowhammer foraging habitat choice in pastoral landscapes can be used to influence agri-environment policy

Good quality foraging habitat is important during the breeding season as food is an important factor predicting breeding success in birds (Martin 1987). If parents are not able to source enough food for rapidly growing chicks, nestling mortality will be high (e.g. Högsted 1981). Mortality may be a result of direct mortality through starvation or a result of the increased predation risk with hungry nestlings begging more (an honest signal of their nutritional state), attracting predators (e.g. Redondo & Castro1992, Haskell 1994), or the increased time the parents spend away from the nest foraging making the nestlings more vulnerable. Studies of foraging yellowhammers during the breeding season have previously shown that most foraging trips are within 100m of the nest (Morris *et al.* 2001), with the maximum distance travelled 300m from a visual study (Stoate *et al.* 1998) and 600m recorded in a radio tracking study (Dale & Manceau 2003). Therefore, it is important that good quality foraging habitat is available for yellowhammers near suitable nesting habitat (vegetated hedges and ditches). If the habitat is far away, the birds will incur a high energetic cost of provisioning nestlings. In addition to this, hungry less attended nestlings may be more vulnerable to predation as increased rates of begging may attract predators.

As yellowhammers were found to preferentially forage in margin habitat, breeding yellowhammers would benefit from the creation of new hedgerows and the reversal of the trend to increase field sizes, as this would increase the availably of their preferred foraging habitat. This addition of new hedgerows would also have the additional benefit of creating new nesting habitat, should these measures have the desired effect of increasing the numbers of breeding yellowhammers the landscapes were able to support. Yellowhammers are not the only species that would benefit from the increase in hedgerow availability, other species of declining farmland birds would benefit from an increase in important nesting habitat, including grey partridges (Rands 1987) whilst fieldfares *Turdus pilaris* and redwings *Turdus iliacus* which eat berries in hedges (Snow & Snow 1998) would benefit from increased autumn food availability. Benefits of additional hedges to biodiversity would not be limited to birds, hedges are important habitat for bats (Walsh & Harris 1996) which use them for foraging, commuting and roosting. Small mammals such as the hazel dormouse *Muscardinus avellanarius*, bank vole *Clethrionomys glareolus*, hedgehog *Erinaceus europaeus* and harvest mouse *Micromys minutus* (Battersby *et al.* 2005) have declined, with these declines being attributed at least in part to the removal of hedges. Invertebrates will benefit from additional hedgerow habitat, as it has been demonstrated that hedgerows support a greater biomass and diversity than in adjacent fields (e.g. Bowden & Dean 1977, Trnka *et al.* 1990, Peng *et al.*1993). Any increases in invertebrate availability should have positive impacts further up the food chain, both for insectivorous mammals and birds. Hedges are important foraging habitat for pollinators including butterflies (Dover & Sparks 2000) whilst bees would gain an increase in important nesting habitat (Goulson *et al.* 2008).

As hedgerows not only provide important habitat for wildlife, they additionally provide important ecosystem services including the reduction of soil erosion, capture of pollutants including fertilisers and pesticides whilst acting as a carbon store. Thus agri environment schemes increasing their availability represents good value for money with longer lasting benefits than many other schemes where payments are made to provide short term habitats that are non self-sustaining. However, the creation of new hedgerows may prove unpopular with farmers, who prefer larger field sizes as it is more efficient for mechanised farming (Shrubb 2003) and could have a negative impact on the suitability of the landscape for birds of open farmland such as lapwings *Vanellus vanellus* and skylarks *Alauda arvensis*.

Chapter 4 – Yellowhammer winter habitat choice and movements in a pastoral farming landscape

Agricultural intensification has resulted in a reduction in the availability and quality of winter foraging habitat for farmland birds, with winter food shortages one of the main hypotheses for the observed decline in graniverous farmland birds including yellowhammers *Emberiza citrinella*. Despite pastoral farming being widespread, little work has been carried out looking at habitat choice of graniverous birds in these landscapes; this knowledge is important to help inform future agri-environment schemes, this study aims to address this gap in knowledge. Re-sampling analysis found radio tagged birds selected stubble and unmanaged habitat in early winter, with this preference switching to game managed habitat by late winter. The switch in habitat preference from stubble where seed resources become depleted as winter progresses to game managed habitat where seeds are replenished and available at high levels throughout the winter is consistent with the hypothesis that late winter seed availability is affecting farmland birds. Field counts found that the dominant pastoral habitat was avoided in winter at the study farms, with garden habitat selected in early winter switching to unmanaged habitat in late winter. Ratios of young birds to adults caught in mist nets declined as winter progressed, suggesting that winter survival of first years is lower than adults. Low first year survival rates have the potential to negatively influence population trends, agri-environment schemes should aim to increase winter survival and thus recruitment into breeding populations. This could be done by increasing the availability of stubble or other seed-rich winter foraging habitat, which is currently limited in its availability in pastoral farming landscapes.

4.1 Introduction

The non-breeding season is an important period in life history, especially in altricial birds (Sæther *et al.* 1996). Organisms not only have to survive, but additionally must regain body condition lost during the previous reproductive attempt and maintain sufficient condition for the next reproductive event. If an individual is not in sufficiently good condition at the end of the non-breeding season, it may be forced to miss a breeding season, have fewer or poorer quality offspring, or have reduced longevity. All of these lower the individual’s life time reproductive success. Therefore, factors affecting organisms during the non-breeding season (such as changes in food availability) can lead to population declines if survival and breeding parameters are negatively affected. Agricultural intensification has reduced the amount of winter food availability for granivorous farmland birds. The switch from hay to silage production, spring sown to autumn sown crops and the resultant loss of stubble habitat, the increased use of herbicides, more efficient harvesting and the specialisation of farming landscapes have all contributed to a reduction in the availability of both weed seeds and spilt grain on farmland habitat in winter (Wilson *et al*. 1999). These changes coincided with reductions in annual survival rates and declines in abundance of many species of granivorous farmland specialist (Siriwardena *et al*. 1998). An increase in winter food availability has been experimentally demonstrated to result in increased survival rates in house sparrows *Passer domesticus* (Hole *et al*. 2002) therefore, low winter food availability could potentially account for the observed declines in house sparrow populations. The results from correlational studies on linnets suggest that winter agricultural intensification may affect breeding population size. Britain has undergone more extensive agricultural intensification than both Denmark and Sweden; the linnet *Carduelis cannabina* population in Sweden (which migrates to and winters in Britain) has declined more extensively than the population in Denmark, which is resident throughout the year (Wretenberg *et al*. 2006).

Birds are highly mobile organisms and thus are able to move between habitats, actively selecting those that may offer the least physiological stressors including food limitation, poor weather, competition and predation. In winter, granivorous farmland birds are often found in large mixed flocks which can be highly concentrated: one Scottish study reported that half of the seed-eating passerines that were counted occurred in 1.4% of the area surveyed (Hancock & Wilson 2003). Winter flock formation allows rare but concentrated sources of food to be found most efficiently whilst reducing individual predation risk through dilution and confusion (Clark & Mangel 1984). The winter foraging habitat choice of granivorous birds has been well studied in mixed and arable farming regions, with many studies reporting a preference for stubble habitat (e.g. Wilson *et al*. 1996, Moorcroft *et al*. 2002, Robinson 1997, Evans & Smith 1994). An increased prevalence of stubble habitat in winter has been shown to correlate with more stable yellowhammer population trends (Gillings *et al.* 2005). The availability of stubble habitat in Britain has declined with the move towards autumn sowing of cereal crops in arable landscapes and with the loss of arable production in pastoral regions with the increased specialisation of farms and landscapes. Remaining stubble fields are not as rich in seeds as they were in the past, herbicide use has decreased the amount of weeds within the crop, and hence the seeds, with the increase in harvest efficiency reducing spilt grain. Autumn sown cereal is a poor winter foraging habitat since it contains few seeds and is therefore unfavourable for, and thus avoided by seed eating birds (e.g. Firbank *et al.* 2003, McMahon *et al.* 2013). Within pastoral habitat, wintering granivorous birds prefer to forage in grassland fields managed with greatest number of seeding grasses (Perkins *et al.* 2000) such as those managed the previous summer for hay or under low intensity grazing regimes, whilst avoiding silage fields, where shorter defoliation periods prevent plants from setting seed.

The results of previous research in mixed and arable farm landscapes have informed the development of agri-environment prescriptions designed to help granivorous birds in winter – mainly by paying farmers to provide overwinter stubble or to plant wild bird seed crops to increase the birds' winter food supply. Although studies from mixed and arable farming regions have shown an avoidance of pastoral habitat by granivorous farmland birds (e.g. Morris *et al.* 2001), populations still persist in pastoral-dominated farming regions, which account for a large proportion of the farming landscape in many parts of the world including Britain. Therefore it is important to understand how granivorous birds utilise this landscape to develop appropriate agri-environment schemes appropriate for this landscape that can help to reduce (and ultimately reverse) the decline of granivorous farmland specialists here. Little work on graniverous passerine ecology has been previously conducted in winter in such pastoral landscapes (Atkinson *et al.* 2002).

This study aims to test the hypothesis that yellowhammers which have previously been shown to select stubble habitat in winter (e.g. Wilson *et al.* 1996, Moorcroft *et al.* 2002, Robinson 1997, Evans & Smith 1994) will exhibit this same habitat preference in pastoral dominated landscapes. If this is indeed the case, as stubble habitat is a rare resource in pastoral landscapes, I hypothesise that this may result in low winter survival of yellowhammers, and will test this by studying the ages of yellowhammers caught in mist nets throughout winter. The results will help inform future agri-environment schemes implement suitable winter habitat for granivorous birds in pastoral landscapes. The yellowhammer was chosen as the study species since it is considered representative of a suite of other granivorous species whilst remaining common enough in the study area (Ayrshire, S.W. Scotland) to allow a viable study.

4.2 Methods

4.2.1 Boundary surveys

Habitat preference and numbers of wintering yellowhammers was studied at four grassland-dominated farms in Ayrshire, south-west Scotland by walking boundary transects. Yellowhammers were focussed on as they were the only declining graniverous farmland species seen with any regularity on the study farms; corn buntings are extinct in the study area and linnets and skylarks *Alauda arvensis* very scarce. Six boundary transects of fixed routes (see appendix 1), 7.3 km to 11.5 km, were walked 10m from boundary features (e.g. hedge/ditch/fence) at each site in winter 2009/10. Boundary surveys were used as they were less time consuming than carrying out both boundary surveys and transects across each field, and have been demonstrated to record 89% of yellowhammers present than the more time consuming methodology (Atkinson *et al*. 2006). In winter 2010/2011 five surveys were carried out at Milton and Fail Mains 2010/11 (for dates see appendix 2). Carnell was not surveyed in this winter due to access restrictions, and although boundary transects were carried out at Killoch, the data have been excluded from this chapter as the numbers and distributions of the birds observed had been altered by provision of supplementary wheat throughout that winter (for details see chapter 5). Transects took 3 ½ to 4 ½ hours to complete and commenced within one hour of dawn, with the direction of travel reversed in successive surveys to minimise the effect of time of day. Binoculars were used to aid bird identification and transects only took place on days when visibility and weather were good. The locations and behaviour of all observed yellowhammers were recorded on maps during the survey, and later entered into an ArcGIS (ESRI 2011) database, alongside the habitats available at each study farm.

4.2.2 Mist netting and ringing

Throughout both winters, when weather permitted, standard North Ronaldsay mist nets were used to catch birds for ringing on sites where yellowhammers had been observed during winter surveys. Nets were placed alongside hedges at the edge of fields. The length of nets erected depended on the numbers of birds present in the area and therefore likely to be caught, with the aim of catching the largest number of birds that could be handled safely. Nets were erected before dawn and mist netting was carried out until either the numbers of birds caught tailed off or weather conditions deteriorated. Tape lures (reed bunting *Emberiza schoeniclus* or chaffinch *Fringilla coelebs*) were on occasion used to increase the amount of birds around the netting area. Both 2 and 4 shelf nets were used depending on the height of the hedges at each netting site. The nets were 6m, 12m and 18m long nets depending on what was best suited to each individual ringing site. All birds were fitted with a BTO metal ring, and aged and sexed where possible (using Svensson 1992). Wing length, weight and tarsus length were measured for all birds captured using standard methodology (see Redfern & Clark 2001). Yellowhammers were additionally fitted with Darvic coloured rings in unique combinations to allow individual identification in the field, removing the need of recapture to study movements and survival.

4.2.3 Radio tracking

A sample of the birds caught in mist nets for ringing at Fail Mains farm on 25th October 2010 (n=5) and 28th January 2011 (n=8) were fitted with 0.44g PIP tail-mounted radio tags (Figure 4.1) from Biotrack Ltd. As yellowhammers typically weigh ~26 grams, this tag weight is less than 2% of typical bodyweight. Light tags were selected in order to minimise the costs of carrying them to the birds in order that the behaviour and habitat selection observed during the tracking periods were representative. Tail-mounted tags were chosen as they would be lost by the birds naturally during annual moult. On the dates of tagging, two ringers were present (one to hold the bird and pass equipment, the other to mount the tag) to maximise the efficiency of the tag mounting process so as to minimise any stress experienced by the bird. Tags were activated by removing the magnets taped to their sides (which previously kept them switched off). The central two tail feathers were first de-greased using alcohol. Next, superglue was placed along the groove of the radio tag, and activator spray (reduces bonding time) was used on the bird's two central retrices (ensuring the preen gland was covered) then the tag placed close to the base of the feather shaft, with the feather shafts within the tag groove. Dental floss was used to tie the tag on to the tail as a backup in the event of the glue unbonding, and the antenna anchored along the bird's tail in several places using shirring elastic, with all knots being secured with superglue and activator spray. The bird was released after ensuring that the adhesive was dry.

During the tags' active period (14 day battery life) an attempt was made to locate each tagged bird at least once per day, using an Australis 26k scanning receiver (Tiley electronics, Australia) with a Yagi antennae (Biotrack, UK). When a bird was detected, its position was determined by triangulation. Since the tracking was all carried out by myself, there was an unavoidable delay (up to 10 minutes) between the taking of the two bearings required to calculated the bird's position, introducing potential inaccuracies to the locations recorded for each fix if the bird had moved between the collection of the two bearings. Therefore, all locations should only be considered accurate to within 50m. Locations where birds were recorded were marked on maps, and later entered into ArcGIS (ESRI 2011). Habitat surveys were carried out and also stored in ArcGIS to allow the habitat choice of yellowhammers to be quantified.

Figure 4.1 0.44g PIP radio tag from Biotrack Ltd tail-mounted on a yellowhammer

One of the birds tagged in October 2010 (L000387) was found dead on the day after tagging, but data on movements were obtained from the remaining 5 birds tagged then, plus the 8 birds tagged in January 2011. The mean weight of radio-tagged birds in early winter was 25.80 grams ±0.48, increasing to 26.98 grams

±0.46 in the late winter tracking period. The increase in weight between the two periods will be down to a variety of factors including age (increased number of adults in late sample), size of birds and probably also differences in the starvation and predation risks experienced by the yellowhammers at the different stages of the winter. Due to the difficulty involved in catching yellowhammers, birds were tagged as they were caught (for details of age, sex and weight of birds see table 4.1), thus it was not possible to balance the numbers tagged within specific age and sex categories. This resulted in 4 first years and one adult being followed in early winter (the second adult died shortly after tagging) compared to four adults and four first years during the late winter period.

Table 4.1 Age, sex and weights of yellowhammers radio-tagged

Bird ID	BTO ring number	Tracking period	Age	Sex	Weight (grams)
1	L000377	Early Winter	First Year	Male	24.9 g
2	L000379	Early Winter	First Year	Female	25.2 g
3	L000380	Early Winter	First Year	Male	25.9 g
4	L000383	Early Winter	Adult	Male	25.3 g
5	L000386	Early Winter	First Year	Female	25.4 g
6	L000387	Early Winter	Adult	Male	28.1 g
1	L001754	Late Winter	First Year	Male	27.8 g
2	L001755	Late Winter	First Year	Female	26.4 g
3	L001756	Late Winter	Adult	Male	28.7 g
4	L001757	Late Winter	First Year	Male	24.3 g
5	L001758	Late Winter	First Year	Female	27.5 g
6	L001768	Late Winter	Adult	Male	27.3 g
7	L001769	Late Winter	Adult	Male	26.7 g
8	L001770	Late Winter	Adult	Male	27.1 g

Table 4.2 summarises how long contact was made with each individual (i.e. the maximum known life span of the tag), the number and percentage of days on which each individual was located and how many contacts were made. Significant differences were found between the early- and late-winter tracking periods in terms of the number of days on which the birds were located and the number of fixes per bird, in each case with the values for the late season tracking period being significantly higher than those for the early season (Table 4.3). There was no significant difference between the two tracking periods with regards to the number of days from tagging each individual was followed for (Table 4.3).

Table 4.2 Summary of (a) early season and (b) late season radio tracking data collected

(a) **Early Season: (25th Oct – Nov 2010)**

5 individuals, 52 locations, 31 'bird days'

Bird ID	No. days tag active	No. days located on	No. locations	Mean no. locations/day	% days bird found during tag lifespan
1	11	7	12	1.09 ± 0.31	63.6
2	9	3	4	0.44 ± 0.24	33.3
3	8	7	11	1.38 ± 0.42	87.5
4	11	7	11	1.00 ± 0.30	63.6
5	12	7	14	1.17 ± 0.46	58.3
Mean (± 1 S.E.)	10.2 ± 0.7	6.2 ± 0.8	10.4 ± 1.69	1.02 ± 0.16	61.3 ± 8.6

(b) **Late Season: (28th Jan – Feb 2011)**

8 individuals, 189 locations, 106 'bird days'

Bird ID	No. days tag active	No. days located on	No. locations	Mean no. locations/day	% of days bird found during tag lifespan
1	14	14	39	2.79 ± 0.49	100
2	13	13	33	2.53 ± 0.33	100
3	14	11	30	2.14 ± 0.55	78.6
4	14	13	21	1.50 ± 0.25	92.9
5	13	9	22	1.69 ± 0.60	69.2
6	13	8	19	1.46 ± 0.54	61.5
7	13	6	13	1.00 ± 0.42	46.2
8	12	6	12	1.00 ± 0.43	50.0
Mean (± 1 S.E.)	13.3 ± 0.3	10.0 ± 1.1	23.6 ± 3.4	1.76 ± 0.24	74.8 ± 7.6

Table 4.3 Results from One-way ANOVAs testing for differences between early and late season tracking period

	F value	p value
Number of fixes per individual	$F_{1,11} = 7.99$	$p = 0.016$
Number of days each individual was found on	$F_{1,11} = 103.20$	$p < 0.001$
Number of days from tagging individuals successfully followed for	$F_{1,11} = 0.02$	$p = 0.901$

4.2.4 Habitat surveys

Habitat availability on each farm and in the surrounding region (as the radio tagged birds ranged much wider than at the study farm level) was surveyed in winter 2009/10 and 2010/11, with habitats seen recorded on fine scale maps of the areas showing boundary features. Winter habitat was assigned to one of 9 mutually exclusive categories (Appendix 6). Habitat data collected were stored in a spatial database (ArcGIS (ESRI 2011)) by editing OS Mastermap files for Ayrshire (downloaded from EDINA), allowing area of habitats available to be calculated.

4.2.5 Data analysis

4.2.5.1 Winter Density in relation to habitat availability

For analysis of data from boundary transects at the four study farms, each study site was defined as the boundary feature next to the extent of the boundary features, plus a 100m buffer. The 100m buffer was necessary as habitat outwith the survey boundary would have had a strong effect on the birds' use of the site. 100m was chosen since this was approximately the maximum lateral distance I was able to visually detect yellowhammers from the outer margin of transects. The study site boundary was used to cut the edited OS Mastermap habitat files for the region, with the areas recalculated to take into account their new geometry. For summary of area and proportion of habitats available at each site during the two winters, please refer to appendix 7 & 8.

To account for the different lengths of boundary transects carried out at each site, the numbers of yellowhammers seen during winter transects were expressed as the number observed per km walked, hereafter referred to as density. ANOVAs were carried out to test for differences in the numbers of yellowhammers seen in winter between farms, and also to test to see if the numbers seen on a particular farm varied between winters. Next, correlation analyses were carried out (in Excel) to examine the relationship between the number of yellowhammers observed in winter at each site and the number seen during the previous summer, as well as the relationship between winter yellowhammer numbers observed with the proportion of both grass and stubble habitat at each site.

4.2.5.1 Winter habitat choice at the farm level

Due to the flocking behaviour of yellowhammers in winter, individual observations cannot be treated as independent, with flocks of up to 28 individuals recorded during boundary transects. Instead, the total number of birds seen on a field during a survey was treated as independent datum, and re-sampling analysis used to determine if the number of yellowhammers recorded on each complete field surveyed at each of the four study sites differed from the value expected had yellowhammers been randomly distributed in the landscape. Each field was surveyed 6 times in winter 2009/10 (4 in the case of Carnell) for all sites and 5 times in winter 2010/11 for Fail Mains and Milton only. Rare, non 'field' habitats (game managed, garden, manmade surface, unmanaged and woodland) were treated as one field per farm and the yellowhammers seen on these habitats during each survey pooled. 14 fields were surveyed at Carnell, 18 in Fail Mains, 14 in Killoch and 9 in Milton, with field sizes ranging from 0.12 ha to 15.62 ha, mean 5.32 ha ± 0.46 ha. The multiple fields per farm and multiple surveys across the two winters resulted in a total of 437 yellowhammer counts (i.e. data points) being collected. On most surveys of individual fields, a count of zero yellowhammers was recorded (figure 4.2) with the 431 yellowhammers seen present in flocks of up to 27 individuals.

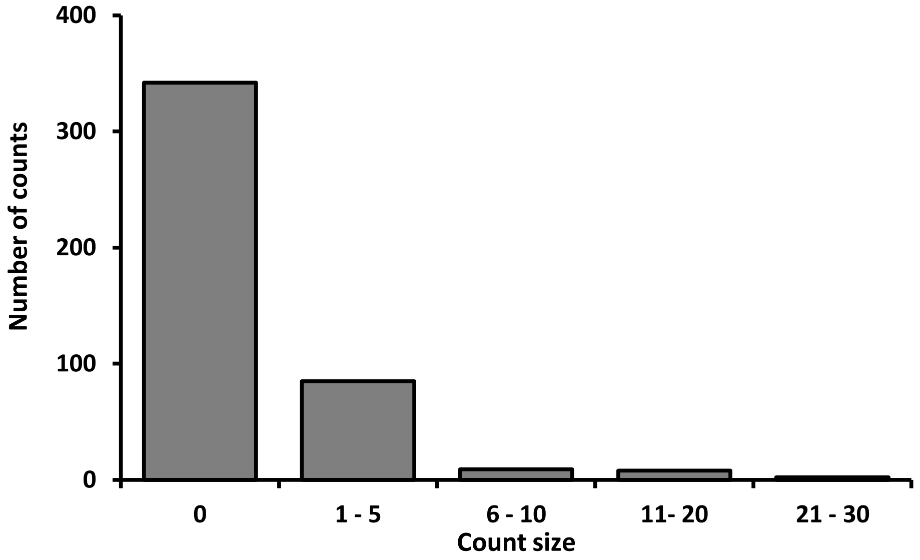


Figure 4.2 Numbers of counts of yellowhammers in different count size categories

Yellowhammer counts from both winter seasons were split up into those pre winter solstice (early winter) and post solstice (late winter) then re-allocated (10,000 times) to each habitat category (in excel) according to area of each habitat available. The distribution of the total numbers of yellowhammers predicted to be in each habitat as predicted by the re-sampling analysis was compared with the observed totals, and the proportion of these more extreme/less extreme than the observed value calculated. This is the p value, thus if the proportion more/less extreme than 0.025, the observed value of yellowhammers in a habitat is significantly different (at $p = 0.05$) from the expected value based on habitat availability.

4.5.2.2 Analysis of radio tracking data

As in the yellowhammer transect observations, each location or 'fix' of an individual yellowhammer generated from the radio tracking was stored in ArcGIS (ESRI 2011), alongside broad scale habitat information for the region over which they were ranging. Pseudo replication was removed from the radio tracking dataset by removing any point that was less than 500m from the last known location of an individual, unless 2 hours or greater had elapsed. This was done as birds were difficult to locate, but once the location of a bird was known, multiple points could easily be generated over a short time period, but these locations would not be independent. For both each individual, and each tracking period, minimum convex polygons (MCP's) were calculated in Arc Info, and the shape geometry of each polygon calculated. Maximum distances between known locations (furthest distance individual was known to have ranged over during tracking period) and between consecutive fixes, the areas of the MCP's was calculated for each individual in Arc, then the effect of tracking period (early and late) on the largest recorded movement for each individual, and the area of individual MCP were tested using Kruskal-Wallis tests carried out in R (as variances were unequal).

Kernel density plots were created in ArcGIS (ESRI 2011) to provide a visual summary of the areas the birds were more likely to be found during the two radio tracking periods.

As individuals during each tracking period were caught at the same farm and on the same date and were often found at the same locations, each location cannot be treated as independent data, so re-sampling analysis was carried out to compare the habitat the radio tagged birds were selecting relative to availability. Early and late winter were treated separately, with the counts of yellowhammers on each field (for most fields, the count was zero) within the respective MCP's were randomly distributed 10,000 times (using Excel) amongst the different habitat types according to availability. The totals observed on each habitat were then compared with the distribution of expected totals as calculated during re-sampling, and the proportion of these more extreme/less extreme than the observed value calculated to get the p value.

Unless otherwise stated, all other statistical analysis was carried out in Minitab 16 (2010).

4.3 Results

4.3.1 Winter transects

At the end of summer, breeding territories held since early May broke down; yellowhammers were now generally seen as part of small mobile flocks that consisted either solely of yellowhammers or additionally contained other graniverous passerines (usually chaffinches and/or reed buntings, and rarely tree sparrows). Figure 4.3 summarises the mean number of yellowhammers seen per km walked per survey at the four study sites in Winter 2009/10 and at two study sites during winter 2010/11. This is based on a total of 34 surveys, 24 carried out in the first winter and 10 in the second winter. There was no significant difference in the density of yellowhammers between winters (GLM, $F_{1,32} = 1.44$, $p = 0.240$) but within each winter there were significant differences in yellowhammer densities between farms (GLM, $F_{3,30}=6.75$, $p = 0.002$). Killoch had the lowest wintering density of yellowhammers. In winter 2009/10, Milton held a significantly higher density of yellowhammers than Carnell and Killoch (One-way ANOVA, $F_{3,20} = 4.47$, $p = 0.016$, Fishers test $p < 0.05$), with farm explaining 42.68% of the variation in yellowhammer densities each survey, whilst in 2010/11, Milton had a significantly higher density of yellowhammers than Fail

Mains (One-way ANOVA, $F_{1,8} = 6.22$, p – 0.037, Fishers test, $p<0.05$) with farm explaining 43.74% of the variation in yellowhammer densities seen each survey.

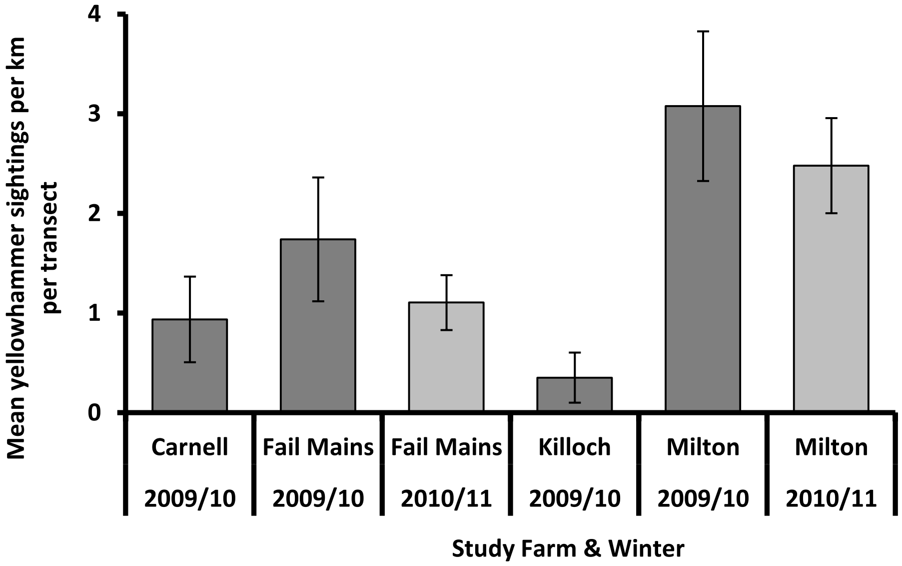


Figure 4.3 Mean number of yellowhammers ± 1 S.E. seen per survey expressed as yellowhammers km^{-1} to account for different survey lengths

The density of yellowhammers during the preceding breeding season at a site was not a predictor of the density during the winter (Figure 4.4). For example, Killoch, which held 10 breeding pairs in 2009, had a mean of over 4 yellowhammers per km during the breeding season compared to less than 0.5 per km in winter (i.e. much lower numbers seen in winter than expected based on breeding density), whereas at Milton (with a similar breeding density to Killoch) there was no difference between the mean number of yellowhammers seen per km in summer and winter (with just over 7 time the number per km seen than at Killoch). Winter habitat availability at each farm was related to the numbers of yellowhammers observed, with proportion of stubble habitat at a farm being positively associated with yellowhammer densities (Figure 4.5 (a), correlation, r = 0.932, $p < 0.05$, N = 4) accounting for 86.9% of the variation in winter density between farms, and grass negatively related to winter yellowhammer density, explaining 93.7% of the variation in density (Figure 4.5 (b), correlation, r = -0.968, $p < 0.05$, N = 4). However, area of pastoral habitat and area of stubble are highly correlated, higher areas of pastoral habitat is associated with lower areas of stubble habitat at a farm.

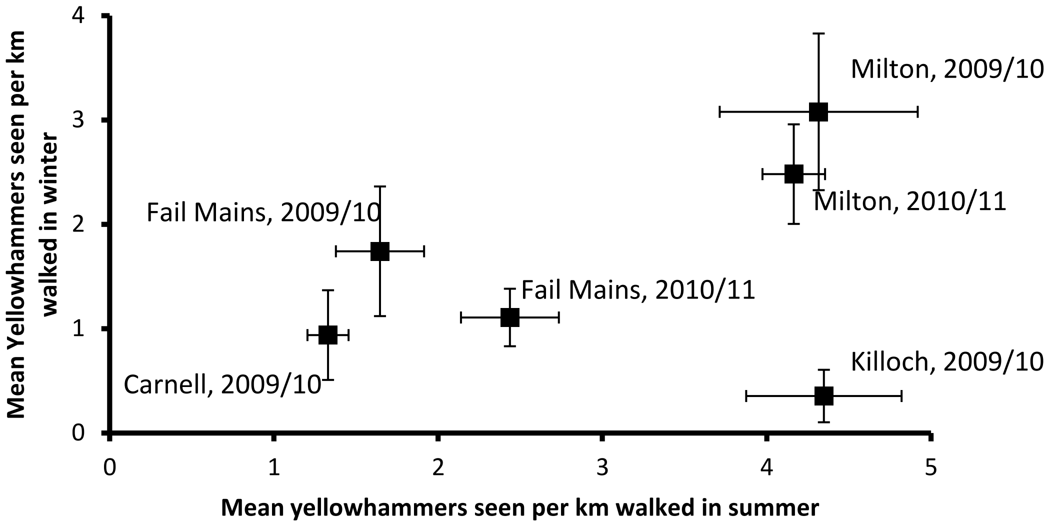
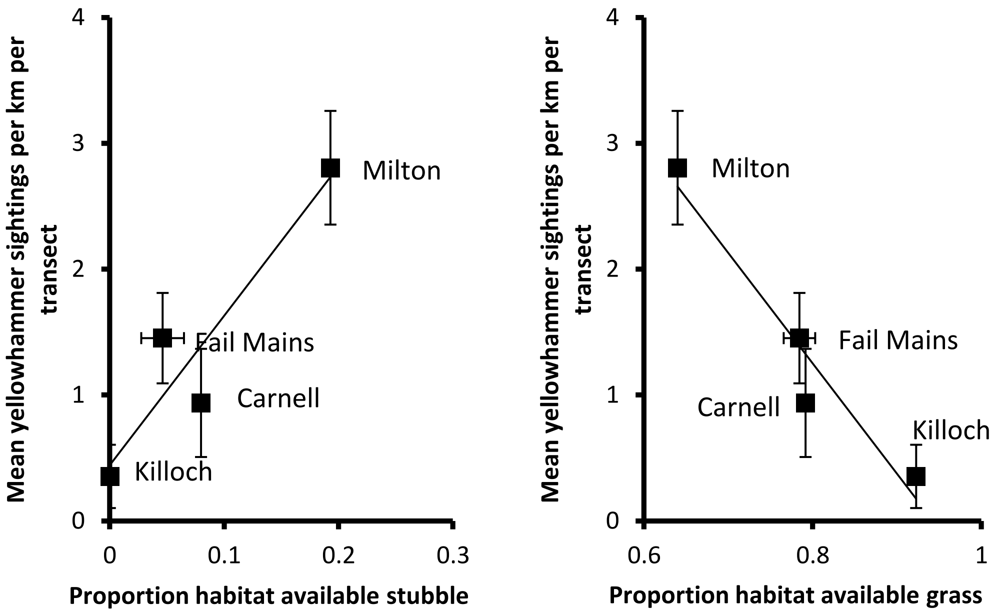


Figure 4.4 Relationship between the mean number of yellowhammers ±1 S.E. seen during breeding season transects with the numbers seen during winter transects ± 1 S.E. (No significant relationship, Correlation, r = 0.346, p = 0.51)



(a) Stubble (y = 0.441 + 11.87 x) **(b) Grass (y = 8.262 – 8.76 x)**

Figure 4.5 Relationships between the mean wintering density of yellowhammers ±1 S.E. at each farm and the proportion of that farm composed of (a) stubble and (b) grassland (all farms winter 2009/10, Milton and Fail Mains only winter 2010/11)

Similar trends were found when examining habitat preferences within farms. During the winter months yellowhammers were most commonly observed on improved grassland (39% of the observations), followed by rough grassland, stubble and roadside margin habitat (16.2%, 12.4% and 10.8%, respectively). However, this does not take into account the availability of each of these habitats, which is important to know when trying to understand what habitats the yellowhammers prefer. To address the issue of habitat availability, re-sampling analysis was used to test if winter habitat selection by yellowhammers was significantly different from what would be predicted based on habitat availability (Table 4.4, Appendix 11). This found that in the early winter, yellowhammers avoided the dominant pastoral fields whilst selecting garden habitat. By late winter, yellowhammers still avoided pastoral habitat relative to its availability in the landscape (Table 4.4, Appendix 11), instead selecting unmanaged habitat (including road margins, unimproved grassland and scrub habitats) significantly more than expected.

Table 4.4 Results from re-sampling analysis testing for differences in habitat (field) use by yellowhammers observed during winter surveys in both early (pre solstice) and late winter (post solstice), significant results in bold (p < 0.025). Avoid is the proportion of re-sampled totals smaller than the observed value for each habitat whilst select is the proportion of re-sampled totals greater than the observed value

	EARLY			LATE		
Habitat	Observed value	p value (AVOID)	p value (SELECT)	Observed value	p value (AVOID)	p value (SELECT)
Grassland	72	**p = 0.007**	p = 0.992	59	**p = 0.004**	p = 0.995
Stubble	42	p = 0.925	p = 0.066	16	p = 0.328	p = 0.644
Game	4	p = 0.863	p = 0.122	0	**p < 0.001**	p = 0.278
Garden	14	p = 0.997	**p = 0.003**	0	**p < 0.001**	p = 0.276
Manmade	6	p = 0.513	p = 0.429	11	p = 0.737	p = 0.236
Unmanaged	58	p = 0.934	p = 0.060	131	p = 0.999	**p < 0.001**
Woodland	12	p = 0.940	p = 0.225	6	p = 0.550	p = 0.386

4.3.2 Radio tracking

4.3.2.1 Yellowhammer movements

Figure 4.6 Locations of radio tagged birds were found in both the early season and ate season with minimum convex polygons (MCP) calculated for all individuals during a tracking period, plus individual MCP's for (b) early winter and (c) late winter. Note the difference in scale between (b) and (c)

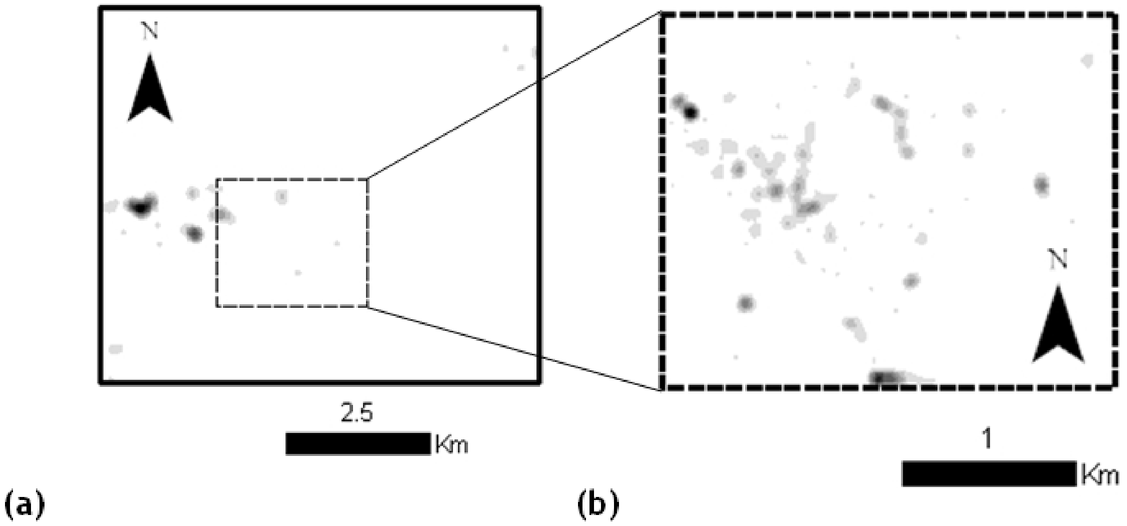


Figure 4.7 Kernel density plots for (a) early winter and (b) late winter radio tracking period. Darker shading represents areas radio tagged yellowhammers were detected more frequently. Note the difference in scale between (a) and (b) - the dashed line on (a) represents the spatial region occupied by diagram (b)

Figures 4.6, 4.7 & 4.8 (a) show that radio tagged yellowhammers in early winter (October – November) appeared to move further (largest distance between all known locations an individual) than in late winter, with a much larger variation in the distances travelled. However, this difference was not statistically significant (Table 4.5), probably as a result of the small sample size of birds tagged. There was no significant difference between the areas of the MCP's for individual birds between early and late winter (Table 4.5) but the variation in the areas of individual MCP's was much greater in early winter (Figure 4.8 (b)).

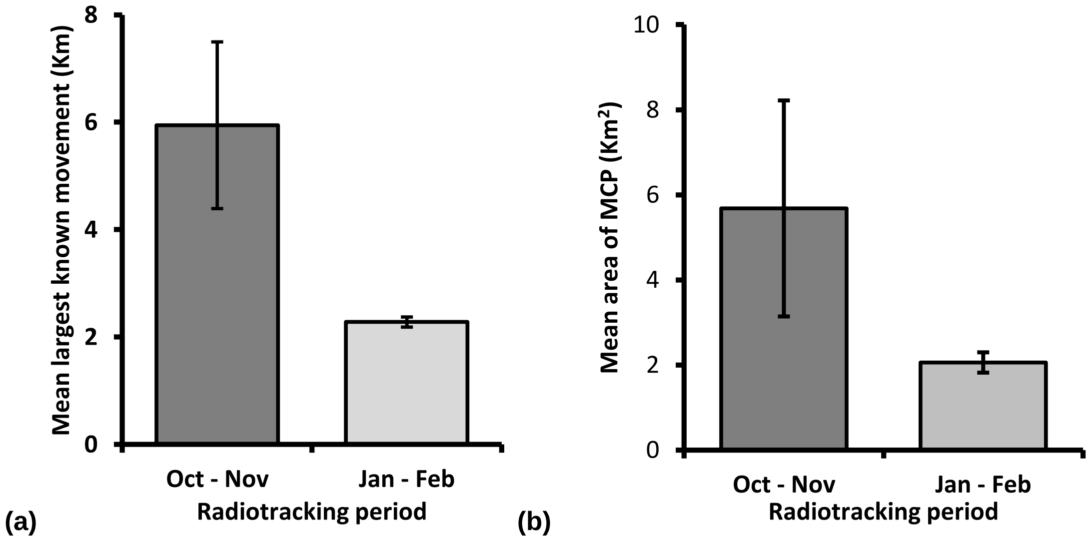


Figure 4.8 (a) Mean largest recorded individual movement (maximum distance between known locations of an individual) ±1 S.E. and (b) mean area of individual minimum convex polygons ±1 S.E. for early and late winter tracked yellowhammers

Table 4.5 Results from Kruskal-Wallis tests, testing for differences in movements between birds tracked in the early winter (Oct – Nov 2010) and late winter (Jan – Feb 2011)

	Kruskal-Wallis χ^2	**p value**
Maximum distance between an individual's known locations	χ^2 = 2.143, 1 d.f.	p = 0.1432
Area of individuals minimum convex polygons	χ^2 = 0.343, 1 d.f.	p = 0.5582

4.3.2.2 Habitat choice of radio tagged yellowhammers

Re-sampling analysis found that radio tagged yellowhammers in early winter selected stubble and manmade habitats (Table 4.6, Appendix 12) but by late winter, there was no evidence that they were selecting these habitats significantly more than expected based on availability. Instead, the yellowhammers were found to select game managed habitat (Table 4.6, Appendix 12). Contrary to the results from the winter field surveys at each of the four study farms, there was no evidence from the habitat choice of the radio tagged birds that they avoided grassland habitat (Table 4.6, Appendix 12), this might simply be a result of the small sample size.

Table 4.6 Results from re-sampling analysis looking at differences in the observed winter habitat selection of radio tagged yellowhammers in early and late winter, significant results (p < 0.025) in bold

	EARLY			LATE		
Habitat	Observed value	p value (AVOID)	p value (SELECT)	Observed value	p value (AVOID)	p value (SELECT)
Grassland	17	p = 0.0396	p = 0.9209	61	p = 0.5354	p = 0.449
Stubble	22	p = 0.9786	**p = 0.015**	20	p = 0.1188	p = 0.8621
Game	1	p = 0.8732	p = 0.0266	32	p = 0.9906	**p = 0.0078**
Garden	0	**p <0.0001**	p = 0.1067	6	p = 0.8175	p = 0.1461
Manmade	6	p = 0.9806	**p = 0.015**	4	p = 0.6046	p = 0.3233
Unmanaged	5	p = 0.6137	p = 0.291	60	p = 0.8626	p = 0.1285
Resown	0	**p <0.0001**	p = 0.6647	3	p = 0.0665	p = 0.8882
Woodland	1	p = 0.4166	p = 0.2853	1	p = 0.3121	p = 0.5205

4.3.3 Bird Ringing

A total of 316 captures of passerines were made in winter 2009/10, of which 32 were yellowhammers, whilst in 2010/11, 210 birds were caught in mist nets of which 27 were yellowhammers. There was a significant difference among yellowhammers in the ratio of first years to adults caught between early and late winter (Figure 4.9, $\chi^2 = 5.09$, 1 d.f., $p = 0.024$), with relatively more 1st years caught before the winter solstice.

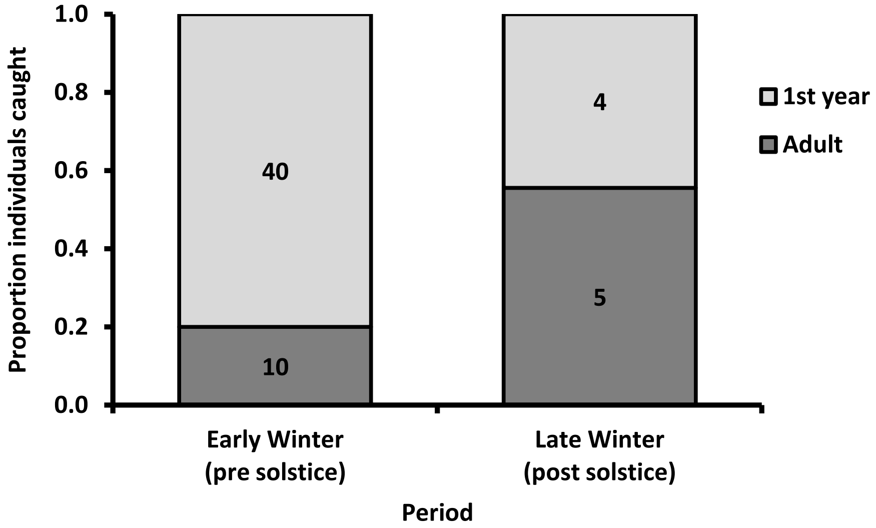


Figure 4.9 Ages of yellowhammers caught in mist nets in early (pre solstice) and late (post solstice) winter in 2009/10 and 2010/11 combined

4.4 Discussion

4.4.1 Winter density

Despite the same survey methodology being used during both the breeding season and winter transects, there was no correlation between the recorded yellowhammer density on each farm in summer and winter. Hence, I conclude that summer and winter habitat requirements of yellowhammers in the pastoral study region differ, or that there was a significant seasonal change in the suitability of certain habitats. In winter, there was a significant difference in yellowhammer densities between the study sites (but not between years), with site explaining 43% of winter density variation. As the study sites were contained within a restricted spatial scale, with the maximum distance between two sites being 12 km, climate and local weather conditions can be excluded as factors influencing the observed differences in yellowhammer densities. Therefore, differences were more likely due to variation between the habitats available and their quality between sites. Despite yellowhammers using the pastoral habitat during the breeding season (pastoral habitat accounted for a mean of 75.9% of the habitat in breeding territories selected by yellowhammers), there was a negative correlation between the extent of pastoral habitat on a farm and yellowhammer winter densities. Yellowhammer winter density within the study area was found to be correlated with stubble availability at each site, with proportion of stubble habitat on a farm explaining 86.9% of the variation. This finding is consistent with other work which has highlighted the importance of stubble habitat for yellowhammers and other granivorous passerine species in winter (e.g. Wilson *et al*. 1996, Moorcroft *et al*. 2002). However, stubble is a rare habitat within the pastoral-dominated Ayrshire landscape, and thus its availability is likely to be limiting yellowhammer numbers and distribution. Therefore, it is probable that the hypothesis that winter food availability is limiting granivorous farmland birds (Siriwardena *et al*. 2008) is relevant in the study region. The link between the winter yellowhammer density at a site and stubble habitat is purely correlational, a closer inspection of what habitat yellowhammers are selecting at the farm scale (from the boundary surveys) and at the landscape scale (from the radio tracked individuals) is required to ascertain the importance of stubble habitat to the study population of yellowhammers throughout the winter.

4.4.2 Winter habitat use and seasonal changes in habitat use

During winter boundary transects, both in early winter (pre-solstice) and late winter (post-solstice), yellowhammers avoided grassland, the dominant habitat, relative to its availability. The avoidance of pastoral habitat in preference for arable has previously been reported (e.g. Wilson *et al*. 1996, Moorcroft *et al*. 2002) and may be down to fewer seed resources being available in the pastoral habitat than in stubble (e.g. Robinson and Sutherland 1999 reported a higher density of seeds on stubble habitat than in grass leys). However, no data were collected to quantify the seed availability across the different habitats available in the study region so it is not know what was driving the observed winter habitat choice of the yellowhammers in this study.

Yellowhammer habitat choice changed as winter progressed, with the selection of stubble habitat at the landscape level (radio tracking) and gardens at the farm level (boundary surveys) in early winter being replaced with game managed habitat and unmanaged habitat selected relative to availability in late winter (post solstice), respectively. The selection of garden in early winter but not in late winter when the weather conditions would have been milder is consistent with findings from other studies that show yellowhammers only made use of gardens during harsh weather conditions in winter (Chamberlain *et al*. 2005).

The observed seasonal change in yellowhammer habitat selection may in part be driven by the changing age structure within the population; fewer first year birds were found as winter progressed. Age has been shown to affect habitat selection in a variety of other species (e.g. Cresswell 1994, Catry *et al*. 2004). In this study, the age of the yellowhammers observed was unknown in the case of the farm surveys and the radio tracking represents a small sample size and thus cannot be investigated statistically. However, as the move from stubble habitat to game managed habitat was more extreme than the change in the relative proportion of first year and adult yellowhammers tagged between the two periods or caught at the farms where the surveys were carried out in mist nets, age by itself (if indeed even it is a factor) is unable to account entirely for the shift in yellowhammer winter habitat preference. Therefore, other more important factors must be influencing yellowhammer winter habitat choice.

The move away from stubble habitat as the winter progressed cannot be attributed to a decline in stubble availability. The same area of stubble was available on both the farm level pre- and post-solstice, and between the two radio tracking periods (October - November and January – February) at the landscape level, as stubble habitat in Ayrshire generally is not ploughed in preparation for sowing next season’s crop until late on in the winter, being carried out at the study farms in April or early May. The observed late ploughing is at least in part due to the wet climate making the fields water-logged in winter, and thus unsuitable for getting machinery on. Therefore, the yellowhammers decision to move away from stubble was likely to be a result of declining food resources to a point where yellowhammers were no longer able to best meet their energy budgets in this habitat. Previous work has shown that seed availability declines in stubble habitat as winter progresses (Robinson and Sutherland 1999), and hence so does its profitability as a foraging habitat for granivorous birds. The declining profitability may account for the switch to game managed habitat in the late winter. This habitat was available during the earlier radio tracking period but not selected, suggesting that stubble habitat is the preferred foraging habitat for yellowhammers. Game managed habitat represents an unnatural source of grain (provided by man in large plastic hoppers targeting pheasants and other released game birds), and unlike the food supplies in stubble habitat, food here is replenished throughout the winter, thus yellowhammers selecting game managed in late winter that natural food resources are a limiting factor as they become depleted with progressing the winter season.

During the late winter boundary transects yellowhammers were observed significantly more on unmanaged habitats (e.g. scrub, rough grassland, road margins and farm tracks) both relative to its availability and compared with early winter. As previous work has shown the availability of cereal seeds was a better predictor of yellowhammer density than that of weed seeds (Robinson and Sutherland 1999), and yellowhammers were not observed to select this habitat significantly relative to availability in early winter suggests that the unmanaged habitat, like game managed habitat is poorer quality winter foraging habitat for yellowhammers, with the move away from the preferred habitat as seed resources will have become depleted suggesting stubble fields (or more specifically, winter food availability especially in late part of the season) may be a limiting factor to winter yellowhammer populations in the study landscape.

The different results from habitat choice from the two methods (radio tracking and surveys) highlights the influence of scale on results of habitat choice studies. The results from radio tracking possibly offer the more accurate insight into yellowhammer preference as it is able to consider habitats available over their entire winter range, whereas the farm surveys are only able to highlight what habitats are most preferred amongst the more limited habitats available on the individual farm scale (a fraction of the yellowhammers winter home range as found by radiotracking). The preference for unmanaged habitat as found during the farm surveys suggests this was the most important habitat out of those available at the study farms in late winter, whereas the results from the radio tracking highlight how little time birds caught and tagged on one of the study sites actually spend on the farm, with them showing a strong preference for game managed habitat in late winter (a habitat not available on the study site where the birds were caught for tagging).

Yellowhammers are not the only species of farmland bird to demonstrate a seasonal shift in habitat preference; wintering skylarks show seasonal a shift in habitat selection with less favourable habitat being used in late winter (Robinson & Sutherland 1999), suggesting that like in the case of pastoral study population of yellowhammers, changes in seed availability influence winter habitat preference.

4.4.3 Yellowhammer movements

As both sets of radio tagged birds were caught at the same farm during the same winter, the habitat available to both at the landscape level would be the same. Therefore differences in distances moved and habitat selected will reflect genuine differences in how yellowhammer ecology changes with season. The kernel density plots highlight both the different spatial scale the birds were moving over between the two tracking periods as well as the different areas selected by them.

Maximum distances moved by yellowhammers in the early winter appeared larger than in the late winter tracking period, although this difference was not statistically significant. The lack of difference is probably a result both the small sample sizes of birds tagged, and an underestimation of the distances ranged by yellowhammers in the early season due to the difficulty of finding birds with the limited range of the tags. As the birds moved distances of in some cases over 9 km, future radio tracking studies should consider employing tags with a greater detectability range in order to increase the likelihood of finding the birds again, however, this would come as a trade off against battery life of the tag. A previous radio tracking study in a mixed farming landscape reported yellowhammers moved significantly further in early winter compared with late, where the mean distance between sequential fixes was 1275 m pre-solstice compared with 660 m post-solstice (Calladine *et al*. 2006). Yellowhammers in the current study moved larger distances than expected for this species, with the maximum recorded distance being 9030 m. Ringing recovery data has shown a median distance travelled by yellowhammers of 1000 m from the initial ringing sites (Forrester and Andrews 2007). However, yellowhammers are capable of larger movements: ringing recovery data from the East coast of Scotland found 15 individuals moved 25.6 km between two study sites (Parish 2009). The observation that yellowhammers during the current study moved larger distances than mean ringing recovery data might be a result of the patchy and rare nature of the stubble habitat in the landscape forcing the birds to move large distances between preferred winter foraging habitat. This suggests that stubble is a limiting factor in the pastoral dominated study landscape. The yellowhammers preferred stubble despite the energetic costs of flight between patches of this relatively rare habitat, as opposed to exploiting the game-managed habitat that they had moved on to by late winter. Game-managed habitat is rarer but presumably richer in food than stubble habitats (and unlike stubble habitat the food supplies are both available at high levels and replenished throughout the winter, or at least until pheasant and partridge shooting season closes on 1st February), allowing the yellowhammers to range over a potentially smaller area in the late winter tracking period. The observed yellowhammer habitat choice suggests that the relative benefits (i.e. energy gain relative to predation risk) were greater in the stubble habitat than in game-managed habitat in early winter (despite the greater travel costs), but as seed resources in stubble declined as winter progressed, game managed habitat became more profitable. An alternative suggestion is that the birds moved further during the early winter period as they were exploring the landscape in order to identify and sample suitable winter foraging habitat. By late winter, the yellowhammers may not have had to move so far as earlier movements would have allowed them to identify the locations with the most profitable food resources, or previously lucrative food resources once worth travelling to may have declined in profitability.

4.4.4 Stubble as a winter foraging habitat in the pastoral dominated landscape

In line with other studies (e.g. Wilson *et al*. 1996, Moorcroft *et al*. 2002), this study found than in early winter, stubble habitat was selected by yellowhammers relative to availability. However, this study was not able to quantify what made the specific patches of stubble habitat selected by yellowhammers attractive as no data on seed densities in each habitat were collected. If these data were present, it would allow an assessment of what level of food availability was associated with the observed change in habitat preference from stubble to game managed habitat. This switch was presumably a result of game managed habitat in late winter offering a better balance between food availability and predation risk than stubble habitat as the seed resources in stubble became depleted. Previous research has shown that the density of cereal grain accounts for 91% of the variation in yellowhammer numbers between patches (Robinson & Sutherland 1999) with management playing an important role; under sown stubbles contain fewer seed resources than conventional stubbles (Robinson & Sutherland 1999).

In addition to the seed availability in stubble habitat, the height of the stubble has also previously been shown to influence predation risk associated with the foraging habitat. In a lab experiment carried out on artificial stubble habitat with a fixed seed density, chaffinches were found to react faster to a model sparrowhawk *Accipiter nisus* whilst foraging in short stubble (3cm) than in long (13 cm high) stubble (Whittingham & Evans 2004), despite a longer ‘head up’ vigilance period in the birds foraging in the longer stubble. Unfortunately no data were collected on either the heights of the stubbles or predator densities at each of the study sites to determine the influence of predation risk on the habitat choice of yellowhammers. There was no difference between farms regarding winter grazing regime of the stubble habitat – all fields were grazed by sheep over winter. Winter grazing of stubble has previously been shown to reduce the attractiveness of stubble habitat to foraging granivorous birds in winter (Robinson & Sutherland 1999), as plants and weeds that grow up amongst the crop lose their seeds heads through grazing.

4.4.5 Conservation implications of the observed habitat choices and movements of yellowhammers

Both radio tracking and the correlation between winter density at a farm and stubble habitat availability highlighted the importance of stubble habitat to yellowhammers in early winter. That yellowhammers moved away from this preferred habitat in the late winter period to use game managed habitat where seed supply is replenished throughout the winter, alongside the decline in the ratio of juveniles to adults caught, suggests that food availability in the pastoral study landscape may be a limiting factor impacting on winter survival especially in first years. Elsewhere, pastoral dominated landscapes have been found to contain fewer species of birds in the winter than during the breeding season (Atkinson *et al.* 2002), whilst in winter more species of birds are associated with mixed farming landscapes than in arable or pastoral (Atkinson *et al.* 2002). Therefore, in order to improve pastoral farming landscapes as a foraging habitat in winter not only for yellowhammers, but for other species of granivorous birds, habitat heterogeneity should be increased by encouraging farmers to grow arable crops and leave them as over winter stubble. Increasing both the quantity and quality of stubble habitat available within pastoral landscapes therefore should have a beneficial impact on yellowhammers and other granivorous species. There is evidence from other studies that this approach would be successful; a study found that having 15ha of stubble per km^2 (15% by area) available in a landscape correlated with stable yellowhammer populations (Gillings *et al.* 2005). The level of stubble habitat within the Minimum Convex Polygons calculated for all individuals combined for both the early and late winter radio tracking period exceeded this level (with 16.4% in the early winter and 20.8% of the habitat in late winter tracking period being stubble). Despite the apparently sufficient availability of stubble habitat over the areas the radio tagged birds ranged; at the individual farm level stubble habitat was below the 15% threshold (range 0.0% – 7.3%) in both winters, except for Milton where 18.5% stubble habitat was available. Perhaps the higher availability of winter stubble at Milton accounts for the observed higher breeding densities of yellowhammers than elsewhere in the study region (chapter 2) but despite having no stubble, Killoch still held the second highest breeding population (Chapter 2). If stubble habitat is to be provided, in order to maximise its benefit to birds, factors such as stubble height and how to maximise the seed density within it without negatively affecting the yield of the crop must be considered. Stubbles with lower herbicide inputs (resulting in higher weed seed densities) have been shown to be preferred by wintering yellowhammers, reed buntings and cirl buntings *Emberiza cirlus* (Bradbury *et al.* 2008) hence stubble management can have a large influence on its profitability as a foraging habitat.

Grassland has been shown to be selected by yellowhammers in preference to autumn sown cereal in a recent Irish study (McMahon *et al.* 2013). Therefore, in either pastoral landscapes, or arable dominated landscapes where autumn sown varieties are cultivated, other suitable winter foraging habitat must be provided. This could be done in more than one way, either by introducing seed rich habitats for birds (e.g. game crops or supplementary feeding) or by improving the pastoral land as a foraging habitat in winter. The avoidance of the dominant pastoral habitat at each of the study sites by the yellowhammers was probably a result of the intensive management. Very few seed heads were visible in winter as a result of the intensive summer grazing of pasture and multiple cuts of silage (pers. obs.), with the rapid defoliation in all fields resulting in a low level of seeds in the soil. If silage was replaced by hay production, foraging habitat quality would increase as the later harvesting of the crop allows it enough time to develop and set seed. Although the introduction of stock on stubble fields makes it less attractive as a foraging habitat to birds (Robinson & Sutherland 1999), grazing in autumn and winter increases the attractiveness of silage fields to wintering farmland birds (Buckingham & Peach 2005) presumably as a result of making the habitat less homogenous whilst increasing the accessibility of food resources and visibility for detecting predators. Autumn grazing by sheep of pastoral habitat, including silage fields, occurred throughout the study farms. A more dramatic way of improving that attractiveness of pastoral habitat for foraging granivorous birds in winter is to leave strips of 2nd cut silage unharvested. This has been shown to attract and hold large numbers of granivorous passerines including yellowhammers and reed buntings throughout winter (Buckingham & Peach 2006). Although this slightly reduces the 2nd cut silage yield, the first silage cut is more valued by farmers due to its higher nutritional content (Woolford 1984). However, the following year's silage yield is also impacted, and is negatively affected due to the rank vegetation, with yields down by a mean of 13% (Buckingham & Peach 2006). Therefore, the remuneration for such a potential agri-environment scheme must take the economic cost to the farmer through loss of future yield into consideration.

In conclusion, the study population in the pastoral dominated landscape appears to be limited by the availability of suitable seed-rich winter foraging habitat, namely stubble. This is resulting in yellowhammers moving large distances between seed rich habitats in early winter before concentrating on less natural food resources such as areas managed for game in the late winter period, with the scarcity of high quality foraging habitat perhaps accounting for the yellowhammers apparently lower first year survival rates than for adult in the pastoral study landscape. Conservation measures in pastoral regions for yellowhammers and similar granivorous species should therefore target this late winter period in the provision of seed rich foraging habitats such as stubble. While this study clearly shows that yellowhammers prefer stubble habitats during the early winter, to clearly identify the factors that influenced this decision further studies are needed. Such future work will help develop the most effective stubble management practices to benefit birds so that they are able to provide a seed-rich foraging habitat into the late winter period when food resources become scarce, or develop an alternative approach to this late winter food shortage such as the direct provision of grain.

Chapter 5 – Grain use and yellowhammer numbers at supplementary winter feeding

Farmland bird populations including the yellowhammer *Emberiza citrinella* have declined at the same time as agriculture has undergone intensification. The changes in farm management have resulted in a reduction of winter food availability leading to a late winter hungry gap; this is the current main hypotheses for the observed declines in graniverous farmland birds. To test this hypothesis supplementary wheat was provided in feeders and monitored for bird use and grain depletion rate and compared with baseline data collected the previous winter. Yellowhammer density increased by a factor of approximately 70 whilst habitat availability remained unchanged, suggesting previously food availability limited yellowhammer density at the site. Grain depletion rates increased as winter progressed supporting the late winter food limitation hypothesis. Data from bird ringing indicated food supplementation may have had a positive impact on first year survival rates compared to unfed sites. Further work looking at breeding densities and reproductive success over larger spatial and temporal scales should be carried out to confirm this and to quantify the longer term impact on survival and breeding densities. Provision of supplementary food is potentially a cheap and attractive option for farmers for future agri-environment schemes aiming to provide seed rich winter foraging habitat for declining graniverous farmland birds, but at present, further research need to be carried out to confirm its efficacy.

5.1 Introduction

Farmland birds have undergone extensive population declines that have occurred at the same time as the intensification of agriculture (Newton 2004). One of the main hypotheses regarding the decline in farmland birds is the lack of winter food, as a result of the intensification of farming (Siriwardena *et al*. 2008), with low winter survival thought to be the cause of the decline in yellowhammer populations (Baillie *et al*. 2001). Further evidence that late winter food availability is a constraining factor for graniverous farmland birds is that dead birds are most likely to be found in late winter (Crick *et al*. 1991) rather than in midwinter when day length is shortest reducing foraging time and weather conditions harshest increasing energy requirements. Similarly, yellowhammer and reed bunting *Emberiza schoeniclus* numbers on supplementary food were highest in late winter, suggesting that late winter food availability in the landscape is a constraining factor (Siriwardena *et al*. 2008).

The switch from spring to autumn sown crop varieties has reduced the amount of stubble habitat available in landscapes. The remaining stubble fields are a lower quality foraging habitat for birds than they were in the past as mechanisation (the advent of the combine harvester) has reduced grain spilled in the fields (Shrubb 2003) whilst the use of herbicides has reduced the amount of weeds within the crops and hence the amount of weed seeds (Wilson *et al*. 1999) with graniverous birds preferentially foraging on stubbles with low herbicide input (Bradbury *et al*. 2008).

The growing of hay as a crop for feeding livestock over winter has almost completely been replaced by silage production. Silage fields represent a poorer foraging habitat for farmland birds in winter as their more frequent harvesting results in the crop never getting the chance to set seed, unlike hay, a more floristically diverse crop, which is harvested at the end of summer and therefore gets the chance to set seed. Pastoral farming regions have been particularly affected by graniverous farmland bird declines and range contractions (see Balmer *et al*. 2013), with these declines correlating with the switch from hay to silage production and specialisation of agriculture.

Previous farmland bird research has shown in winter a preference of stubble habitat (e.g. Robinson & Sutherland 1999, Moorcroft *et al*. 2002, Perkins *et al*. 2002). The increase of stubble habitat availability under Countryside Stewardship Schemes in Devon correlated with an increase in numbers of breeding cirl buntings *Emberiza cirlus* (Peach *et al*. 2001). Stubble habitat is a limiting resource in pastoral regions, with stubble habitat availability within the study region being previously demonstrated to be positively correlated with winter yellowhammer density at the individual farm level (chapter 4). Although one of the options currently available under agri-environment schemes provides payment to farmers to retain winter stubble habitat in order to provide farmland bird winter foraging habitat, it is not appropriate in pastoral dominated farming regions as there is little habitat available that could potentially be managed under this scheme.

Bird winter seed crops are another option available under agri-environment schemes, but the uptake to date has been low as farmers see this option as both difficult and time consuming to implement necessitating land being removed from production. Farmland birds, including the red listed yellowhammer, have been observed utilising artificial food resources intended for both cattle and game birds in winter (Forrester & Andrews 2007). Therefore, a potential solution, with particular relevance to pastoral farming regions, would be to provide food directly to the birds (as trialled in Siriwardena *et al.* 2007 in Eastern England, an area dominated by mixed and arable agriculture) to help overcome the late winter food shortages that are thought to be restricting farmland bird populations.

This study aims to carry out food supplementation to test the hypothesis that winter food availability is limiting the number of wintering yellowhammers on a pastoral-dominated farm by comparing the numbers present with baseline data collected the previous winter. It is hypothesised that winter food availability like elsewhere will be limiting yellowhammers in the study populations. Bird numbers and grain depletion rate will be monitored to test the predictions that the provision of grain will lead to an increase in the number of yellowhammers seen on the farm. It is expected that peak use of provisioned grain will occur late winter, when natural food resources are at their most depleted. Age structure as a proxy for first year survival will be monitored and compared with control unfed sites nearby in the pastoral dominated farming landscape to quantify the impact of supplementary feeding on population structure and survival rates relative to unfed sites. Information gathered will help inform agri-environment schemes and allow them to better target crucial periods in graniverous bird’s life cycle that currently may be limiting populations in pastoral landscapes.

5.2 Methods

To test the hypothesis that food availability is a factor limiting the numbers of yellowhammers in pastoral landscapes in winter, a supplementary feeding trial was carried in winter 2010/11 at Killoch.

This site was chosen as previous work found it had the lowest number of yellowhammers seen per km (0.07 yellowhammers km^{-1}) when walked in winter

2009/10 (Chapter 4) despite holding the second highest breeding densities of the four study farms (0.10 pairs per hectare) in 2009 (Chapter 2). Additionally, the breeding density dropped in 2010 (0.06 pairs per hectare) after the complete loss of winter stubble habitat in winter 2009/10 (in winter 2008/9, a minimum of 7.7 ha of stubble habitat had been available). Thus providing anecdotal evidence that a change in winter habitat availability (loss of stubble, an important seed rich winter foraging habitat) lead to a decline in breeding density of yellowhammers.

Six locations were selected for the winter feeding stations (for locations see Figure 5.1) with the feeding stations all located on pastoral habitat. The feeders were placed 10m from the hedges as opposed to further in field, as previous research has found that yellowhammers prefer foraging close to boundary features (e.g. Morris *et al*. 2001, Perkins *et al*. 2002, chapter3). Characteristics of feeding sites in terms of hedgerow management, proximity to road and farmyard is summarised in table 5.1. Hedges at Killoch were dominated by hawthorn *Crataegus monogyna*, with small amounts of beech *Fagus sylvatica* present in places. The intensively managed hedges were 1m – 1.5m in height whilst the extensively managed hedges were taller than 2m, and less dense than the intensively managed hedges (and would soon become a line of small trees). In Ayrshire, roadside hedges tend to be cut approximately annually with flail trimmers in the late summer and autumn, with infield hedges cut less frequently. As a result, the three feeding stations next to intensively managed hedges had a road within 20m (with hedges present each side of the road). The roads were quiet single track country roads, which generally only had traffic associated with the farm and a nearby cottage. The three feeding stations by extensively managed hedges were located a minimum of 90 m (two over 150m) from the nearest road.

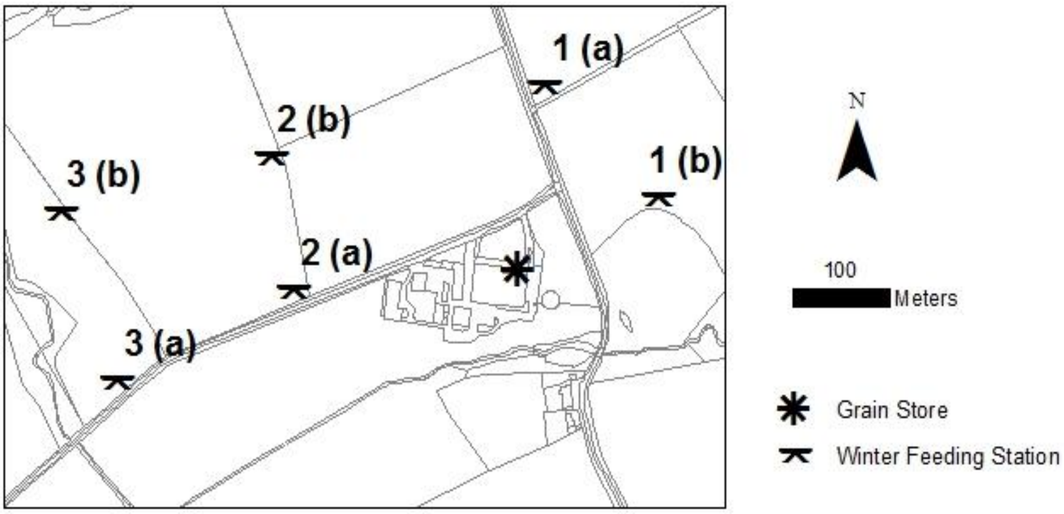


Figure 5.1 Locations of feeder stations providing supplementary wheat at Killoch, winter 2010/11 Feeders next to intensively and extensively managed hedges denoted (a) and (b) respectively

Table 5.1 Characteristics of feeding stations (* Farmyard defined as location of the grain store, the farmyard itself was extensive)

Feeding station	Intensively/extensively managed hedge	By road?	Distance from farmyard* (to nearest 10m)
1 (a)	Intensively	Yes	160m
1 (b)	Extensively	No	150m
2 (a)	Intensively	Yes	270m
2 (b)	Extensively	No	240m
3 (a)	Intensively	Yes	440m
3 (b)	Extensively	No	470m

Five out of the six feeding stations (all except 1(b)) were installed on the 23rd of October 2010. As there were still cattle out in the field in which feeder 1 (b) was to be positioned, it was not installed until 4th November 2010. Feeding stations consisted of plastic planting trays, dimensions 57 x 29 cm, depth 8cm, with drainage holes at the bottom which prevented build-up of rainwater. When full (level to top), each tray held 8 kg of wheat. Wheat was chosen for the trial as previous work has shown that yellowhammers and other granivorous species prefer this grain to barley and oats (Perkins *et al*. 2007). Additionally, wheat is cheap and readily available to purchase. Initially the trays were unprotected, which resulted in grain being depleted rapidly as a result of feeding by non-target species including corvids (*Corvus corone* and *Corvus frugilegus*) and pheasants *Phasianus colchicus*; as a result, the feeders ran out of food quicker than they could be replenished. To prevent non target large bird species from accessing the grain, and as sheep grazed on the farm for the winter from mid November, cages were installed over the trays on 4th November, allowing only small passerines direct access to the food resource (see Figure 5.2). The cages were constructed from strong metal mesh (size 8cm by 8cm), with a lid opening on the top to allow access to fill the trays. The aim was to have wheat available at all six feeding stations throughout the winter. However, on several occasions between installation and late December one or more feeders ran out due either to snow affecting access to the farm, or because of the initial uncertainty as to how often the feeders would need to be replenished. As a result the feeders were only constantly provisioned from late December 2010 until their removal on 29th March 2011, the period over which the data presented in this chapter was collected.

Figure 5.2 One of the six feeding stations (a shallow planting tray filled with 8Kg of wheat contained within a metal cage) at Killoch farm, being used by yellowhammers in March 2011. Cages were 85 x 47cm and 39 cm high

Regular visits to Killoch were conducted throughout the winter in 2010/11, with 20 visits between 23rd December and 29th March in order to both replenish the grain and record the amount used, to carry out point counts to monitor bird use of the feeders and to carry out bird ringing (for summary of dates and purpose of each visit please refer to appendix 4).

5.2.1 Monitoring grain depletion

The mass of wheat that could be contained by a full tray was known (8 kg). Therefore, it was possible to estimate to the nearest kg the amount remaining every time they were replenished by moving all the remaining grain to one side of the feeder until level with the top, and then estimating what proportion that made up of the total full volume. Moving the grain to one side also helped ensure grain remained fresh as it was being rotated circa weekly. If at any point the wheat appeared stale or had begun to germinate, it was removed and replaced with fresh wheat. The mass of wheat that was required to refill the tray was divided by the number of days elapsed since it was last replenished to give the mean daily grain depletion rate (kg day^{-1}) for each feeding station.

5.2.2 Point counts

Point counts of birds were carried out at each of the six feeding stations, commencing between late morning and early afternoon on 10 dates between 7/1/11 and 18/3/11 (see appendix 4). The total number of each species seen on or within 20m of each feeding station was recorded from a distance of circa 40m using binoculars. To minimise disturbance that might cause birds to be flushed away from the feeder both before and after the count (i.e. to prevent both artificially low counts at each station and double counting of individuals displaced to other feeding stations), feeding stations were approached cautiously, and the grain replenished only after point counts at all 6 feeding stations had been carried out.

Mist netting for the purposes of bird ringing was also conducted on five of the ten dates where point counts were carried out. In the case of one ringing session, the point count was carried out first (as the ringing unusually was conducted in the afternoon). On the other four occasions, point counts were only conducted after an hour had elapsed after the removal of the last mist net which appeared sufficient time to allow normal bird use of feeding stations to resume (pers. obs.).

In addition to the point counts, video recordings of up to 3 feeders lasting circa 1 hour each were made of the feeding stations on 5 dates between February and

March 2011. The aim of the filming was to identify individuals utilising the feeding stations, however, the videos were only of sufficient quality to detect that a bird was colour marked, but not high enough to read colour ring combinations.

5.2.3 Bird ringing

A total of 13 mist netting sessions (see appendix 4) were carried out between late December 2010 and late March 2011 at Killoch. The aim of the mist netting was to catch and colour-ring yellowhammers in order to help estimate the number utilising the winter feeding stations, to see if individuals remained throughout the winter or were more transient, and to see if individuals that used the supplementary winter food supply remained to breed. Bad weather in the early part of the winter, and the desire to not cause unnecessary disturbance to the feeders, resulted in the bulk of the ringing being carried out in March. Standard North Ronaldsay mist nets were erected parallel to hedges near feeding stations on dry still days, generally commencing before dawn since early morning catching sessions tend to be most productive. The number of nets erected varied between sessions depending on the number of birds thought to be in the area (the aim being to maximise the numbers of birds that could be caught and ringed safely, rather than to standardise mist netting effort to look at variations in bird numbers present). All birds caught were identified, aged and sexed where possible using the criteria outlined in Svensson (1992) and fitted with a standard BTO metal ring. Yellowhammers were additionally fitted with unique combinations of colour rings to allow individual identification in the field without the need of recapture. All birds handled were checked for visual signs of papillomavirus and trichomoniasis.

To provide a comparison between the age structures of yellowhammers present at the supplementary fed site with unfed control farms throughout the winter, six additional mist netting sessions were carried out at Milton and Fail Mains in winter 2010/11 (for dates see appendix 3).

5.2.4 Bird transects

To allow a comparison of the impact of the feeding trial with populations that are normally present at the farm, and to assess any impacts of winter feeding that carry over to the breeding population on the farm, breeding and wintering density of yellowhammers was studied at Killoch both before and after the winter feeding experiment. This was done by walking fixed route boundary transects (for details of routes see appendix 1) during the breeding season in 2009, 2010 and 2011 and in winter 2009/10 (for dates see appendix 2). Nest sites were identified during breeding transects, allowing breeding density at Killoch to be calculated (sum of the proportion of each yellowhammer breeding territory found within the study site boundary). During winter surveys in 2009/10, all encounters with yellowhammers were recorded, and winter density expressed as encounter rate per km walked.

To assess and compare the numbers of yellowhammers present post winter but before breeding territories are fully established in Ayrshire, an additional survey was carried out in 2010 and 2011. Dates were 7th April 2010 and 17th April 2011. This allowed the impact on the numbers of yellowhammers to be described shortly following the removal of the feeding stations relative to the baseline survey from the previous winter.

5.2.5 Data Analysis

Although the feeders were in place from late October, analysis of grain depletion and bird use was only carried out on data collected between late December and March. This was done in part to allow an ‘acclimatisation’ period where birds were able to both find and familiarise themselves with the experimental feeders, and also since on several occasions in the initial stages of the feeding experiment, the wheat intermittently ran out in one or more feeders due to both not knowing the required frequency of replenishment and snow in December affecting access to the study site.

To test the hypothesis that yellowhammer increased their use of the feeders increased as winter progressed (i.e. that food is a limiting factor, especially in late winter), linear regressions were carried out. This was done by looking at both how the mean number of yellowhammers seen on each of the six feeding stations varied by date in winter, and also how the grain depletion rate varied as winter progressed. To look at whether birds caught on the feeding stations were remaining throughout the winter, a χ^2 test was carried to see if the numbers of re-trapped and new birds changed throughout the season (split up into three periods; December to February, early March (before 16th), and late March (17th onwards)). A significant result would indicate that birds were remaining on the farm as opposed to a constant replacement of individuals passing through and using the feeding stations.

As the probability of catching first year yellowhammers elsewhere in the study region was shown to decline as winter progressed (Chapter 4), to test the hypothesis that this decline was a result of food limitation, a χ^2 test was carried out (using Excel) to see if there was a significant change in the ratio of first year to adult yellowhammers caught at the supplementary fed farm in winter. The same three periods were used as above, with this split allowing similar numbers of captures to be in each category. A further χ^2 test was carried to test if the ratio of adults to juveniles caught at the feeding trial between December 2010 and March 2011 differed significantly from those caught in mist nets at the two unsupplemented study sites during the same period.

To allow a comparison to be made between yellowhammer numbers recorded at the feeders and the winter density recorded the previous year's boundary transects, the total number of yellowhammers seen during the point counts at the six feeding stations on each date was divided by the length of the transect carried out during the previous winter. This assumes that yellowhammers at Killoch in winter 2010/11 were only present at the feeding stations, thus it should be considered an underestimate of yellowhammer density at Killoch during the winter feeding period.

The numbers of yellowhammers during the winter feeding experiment were estimated using a Lincoln index population analysis by comparing the total number of marked yellowhammers from winter with the proportion of colour ringed yellowhammers observed on territories at Killoch the following breeding season. This assumes that all the birds present breeding at Killoch were present in the preceding winter. An alternative estimate was calculated based on the number of birds ringed and re-trapped on the 13 mist netting occasions between 23rd December and 29th March using the Schnabel method which allows for multiple re-trapping dates.

Lincoln Index:

$$\text{Population estimate} = \frac{\text{Total number of marked individuals (initial sample)}}{\text{Number re-traps in 2}^{\text{nd}}\text{ sample/Total number sampled 2}^{\text{nd}}\text{ sample}}$$

Schnabel method:

$$\text{Population estimate} = \frac{\sum(CtMt)}{\sum Rt}$$

C_t = Number caught M_t = Number new individuals R_t = Number re-traps

Both the Lincoln index and Schnabel method assumes there were no births or deaths between the two periods. As this was done out with the breeding season, the first assumption held true. While it is unlikely that the second assumption (no deaths) was true, the number of deaths should have been low as there was only a short period of time (maximum of 154 days from the ringing of the first individual for the estimate based on re-sightings during the breeding season or a maximum of 90 days for the estimate based on winter recaptures) between the two sampling periods. Other assumptions include the survival of individuals remains unchanged by marking, and that the re-capture probability is the same for marked and unmarked individuals. Despite the limitations of the Lincoln index and Schnabel method, they were used in preference to a more complicated method of mark re-capture analysis due to the small numbers of re-captures during each sampling session.

The potential area of breeding habitat that would be required by the estimated number of yellowhammers present during the winter feeding experiment was assessed using the average breeding density over the four study farms for the duration of the study (chapter 2). Assuming this area was a circle round the feeding station site, the maximum theoretical distance individuals would be required to disperse to find suitable breeding habitat was calculated (using the formula A = π r^2).

ArcGIS 10 (ESRI 2011) was used to calculate the distance moved by one colour ringed bird that was originally ringed at Milton farm but then re-sighted at Killoch. IPMR was used to store all ringing data. Unless otherwise stated, all analyses were carried out in Minitab 16 (2010).

5.3 Results

5.3.1 Observations at feeding stations

Between late October and late March approximately ½ tonne of wheat was added in total across the six feeders, with 364 kg being provided between 29th December 2010 and 29th March 2011. A total of 624 passerine birds were recorded on the 10 dates where point counts were carried out at each feeder. Three species accounted for 97.8% of the individuals observed; yellowhammer (74.5%), chaffinch *Fringilla coelebs* (14.4%) and house sparrow *Passer domesticus* (8.8%), with other species (blackbird *Turdus merula*, dunnock *Prunella modularis*, crow and robin *Erithacus rubecula*) being recorded in small numbers (see Table 5.2).

Table 5.2 Total numbers of birds and percentage of each species across the six feeding stations over ten point counts conducted December 2010 to March 2011

Species	Total observed	Percentage of total
Yellowhammer	465	74.5%
Chaffinch	90	14.4%
House sparrow	55	8.8%
Blackbird	4	0.6%
Dunnock	4	0.6%
Crow	5	0.8%
Robin	1	0.2%

From the point counts it was difficult to get an accurate figure for the number of individual yellowhammers (and other species) using the supplementary feeding stations. This was because individuals were able to move between feeding stations and it was not possible to monitor all six stations simultaneously. No evidence was found for an increase in the number of yellowhammers counted per feeding station as winter progressed (Regression, Figure 5.3), with the largest numbers of birds being observed early February. The large S.E. bars for these means highlight the large variation in the number of birds seen at each feeder on a single day, reflecting the chance associated with observing a feeder when a flock happened to be present as well as any potential consistent variation in usage between feeders. Both personal observation and the video recordings of the feeding stations showed that yellowhammers did not use the feeders consistently throughout the day, but usually made brief visits, often in a flock as large as twenty or more individuals. On arrival, these flocks typically perched in the hedgerow in the vicinity of the feeder, and after a few minutes would filter onto the feeding tray and eat for a few minutes before flying away from the area as a group. Figure 5.4 shows that yellowhammers were the commonest species present at all the feeders, with the exception of feeder 1 (b) which was near a wooded area and was most used by chaffinches. House sparrows were found on feeding station 2 (a) (the one nearest the farmyard buildings) but not on the other stations.

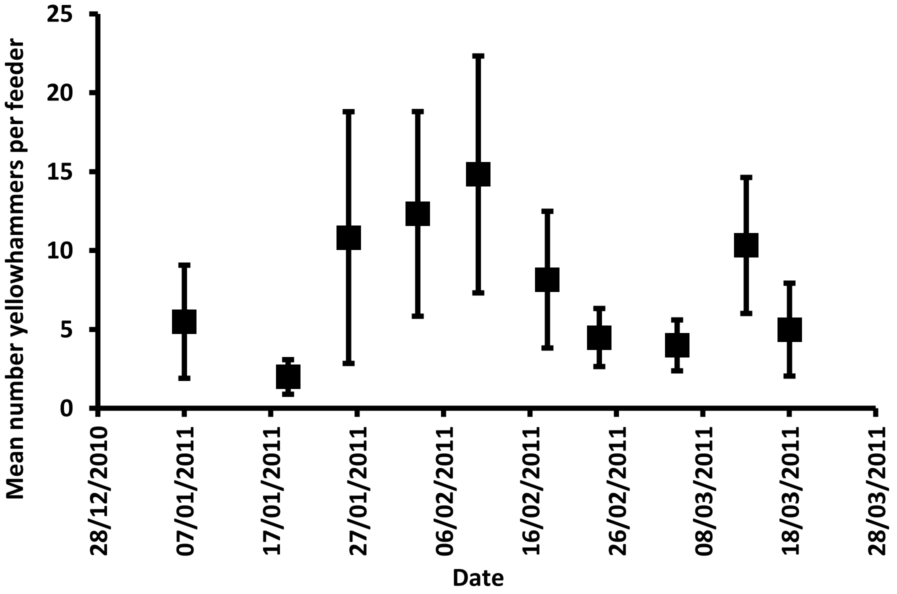


Figure 5.3 Mean number of yellowhammers ±1 S.E. per feeder seen over the ten point count dates throughout the winter (Regression, p = 0.943)

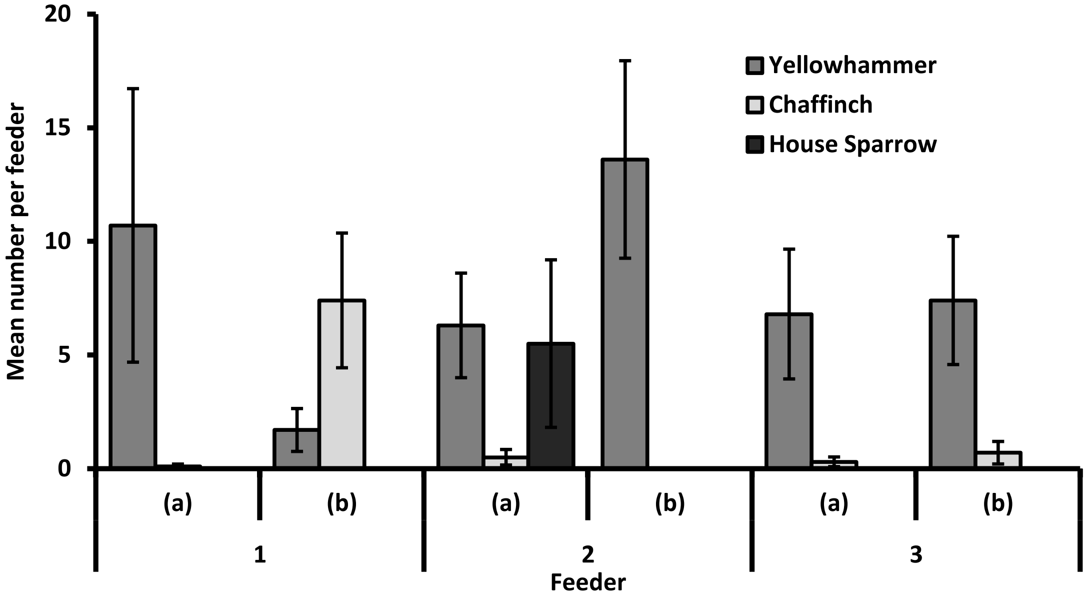


Figure 5.4 Mean number of yellowhammer, chaffinch and house sparrow per survey at each feeding station ±1 S.E.

Figure 5.5 shows that the rate of grain depletion significantly increased as the winter progressed (Regression, p = 0.004). The consumption rate varied significantly between feeding stations (Figure. 5.6, One-way ANOVA, $F_{5,60} = 2.60$, p = 0.034), however, feeder identity explained only 10.95% of the variation in the grain depletion rate.

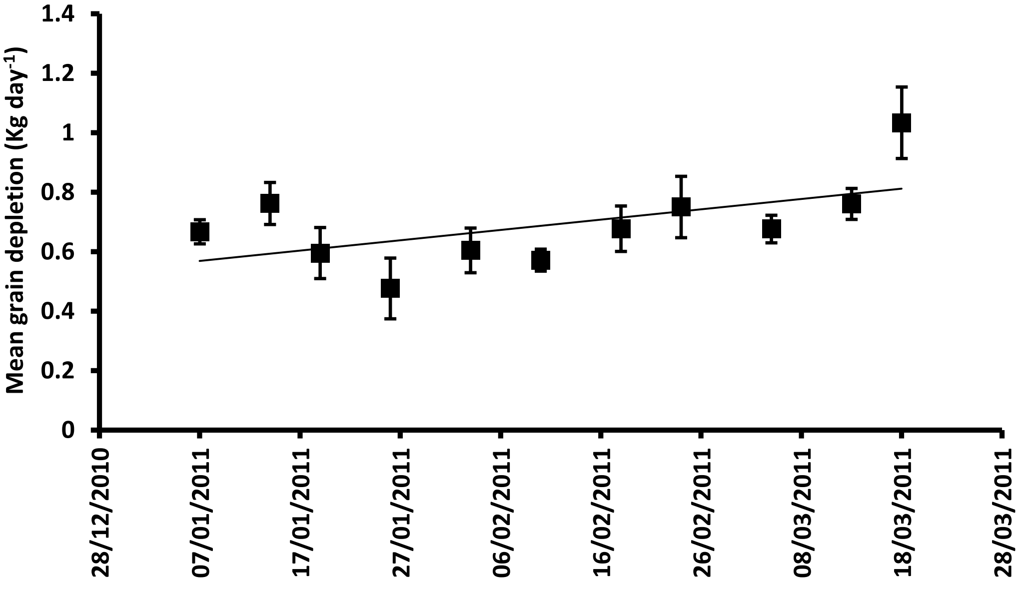


Figure 5.5 Mean daily grain depletion rate at each feeding station throughout the winter (Regression, p = 0.004, Mean daily grain depletion = 0.547 + 0.00347 * days from 1st January)

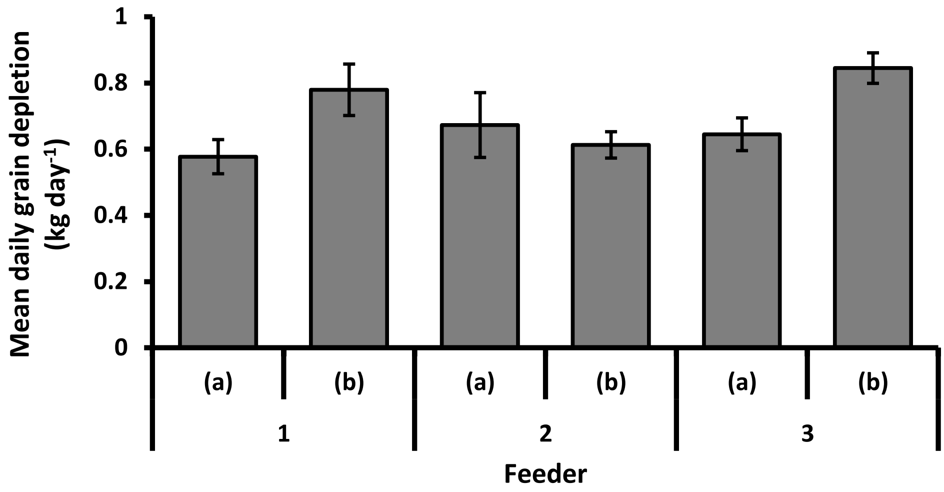


Figure 5.6 Mean daily grain depletion rate ±1 S.E. at the feeding stations between late December 2010 and March 2011

5.3.2 Ringing at feeding stations

A total of 231 captures were made over 13 mist-netting occasions, comprising 188 new birds ringed and 43 re-traps (Table 5.3). Of the 9 species caught, yellowhammers (55.0%), chaffinches (20.8%) and dunnocks (7.8%) were most numerous, accounting for 83.6% of captures (Table 5.3). Other species caught included song thrushes *Turdus philomelos*, great tits *Parsus major*, blue tits *Cyanistes caerulleus* and blackbirds. The diversity of birds captured was higher than that seen in the vicinity of the feeders during point observations, and the percentage of birds that were yellowhammers was correspondingly lower (55.0% of mist-netted birds compared to 74.5% of those seen in point counts). There were 127 captures of 108 individual yellowhammers (103 new birds plus 5 re-traps of individuals ringed prior to the feeding trial period - see appendix 5).

Table 5.3 Summary of ringing captures at the winter feeding trial at Killoch, winter 2010/11

Species	New Birds	Re-traps	Total	% captures
Blackbird	7	2	9	3.9
Blue tit	2	1	3	1.3
Chaffinch	40	8	48	20.8
Dunnock	13	5	18	7.8
Great tit	9	0	9	3.9
House Sparrow	5	1	6	2.6
Robin	8	2	10	4.3
Song thrush	1	0	1	0.4
Yellowhammer	108[#]	19	127	55.0

[#] 5 of these individuals were ringed prior to the feeding trial but counted as new birds when re-trapped for the first time during the feeding trial period (October 2010 to March 2011)

5 out of 11 yellowhammers previously colour ringed on Killoch prior to the feeding experiment (all ringed between mid June and early September in 2009 or 2010) were re-captured during the experiment. This suggests that a high percentage of the yellowhammers present on the farm during the breeding season utilised the feeding stations during winter. The number of re-traps increased throughout the observation period (Figure 5.7), suggesting that many of the same individual yellowhammers were remaining in the vicinity of the feeding stations during the winter.

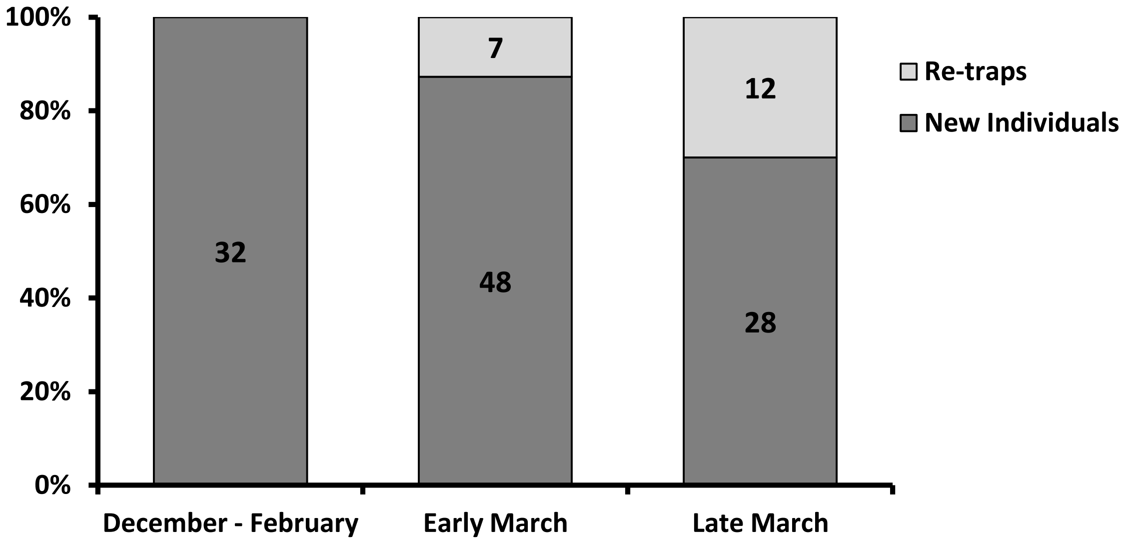


Figure 5.7 Ratio of re-trapped individuals to new individuals caught in mist nets during the feeding trial at Killoch winter 2010/11 (χ^2 = 12.96, p = 0.002, 2 d.f.)

Of the individual birds caught in mist nets, 82 were first year and 22 were adult (older than 1 calendar year) whilst age could not be determined for four individuals. This gives an age ratio of approximately 4:1 of first year individuals to adults. There was no significant difference in the ratio of first year birds to adults caught in mist nets over the three time periods (Figure 5.8, unknown aged birds excluded from the analysis, χ^2 = 3.55, 2 d.f., p = 0.17), but significantly more 1st years were caught at the supplementary feeding site than at the two unsupplemented study farms during the same period (Figure 5.9, χ^2 = 4.89, 1 d.f, p = 0.027).

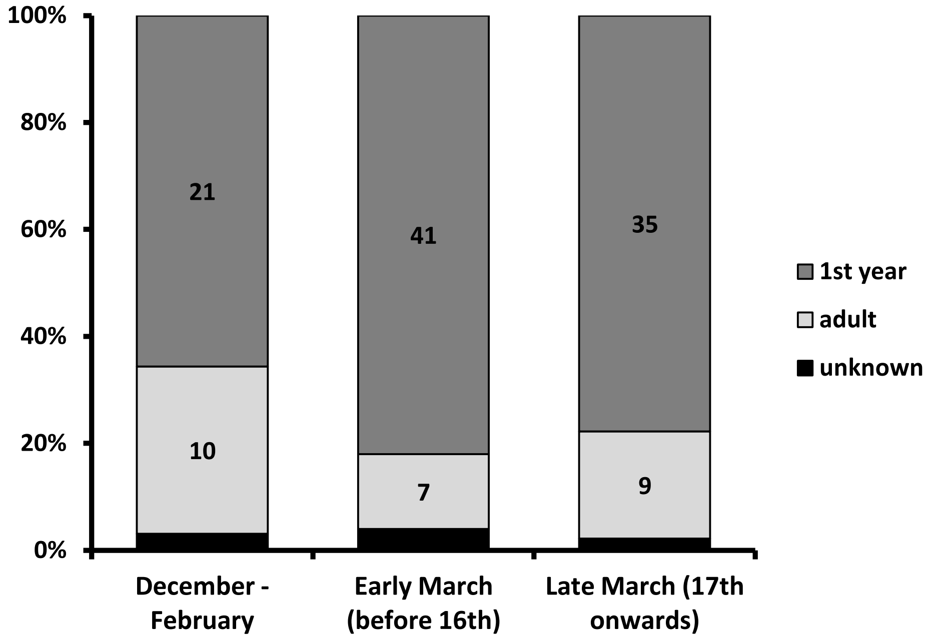


Figure 5.8 Ratios of adult to first year birds caught in mist nets over the winter feeding experiment

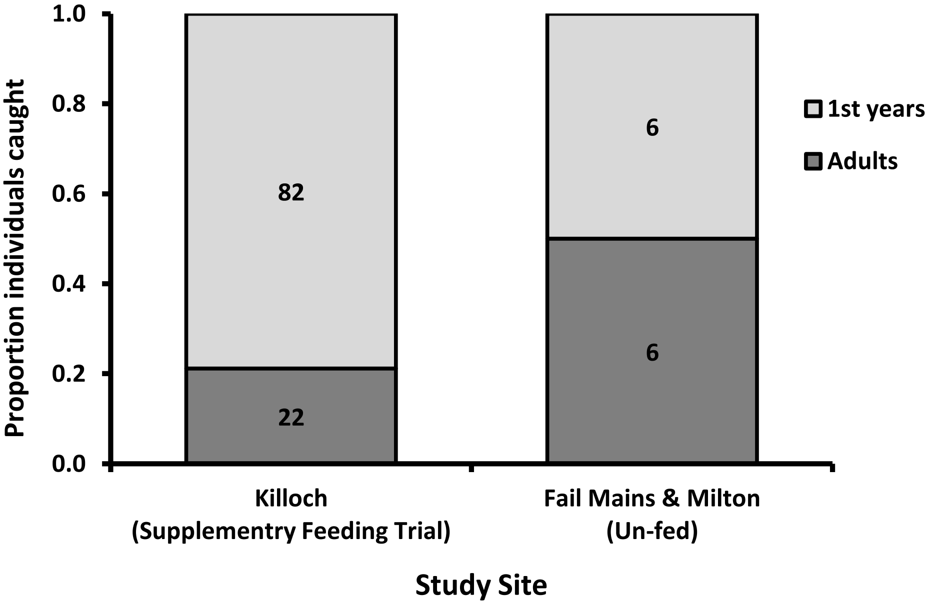


Figure 5.9 Numbers and ratios of adult and first year individuals caught at the supplementary feeding trial site and at the other study farms between December 2010 and March 2011

5.3.3 Yellowhammer numbers at Killoch after the feeding experiment

During the feeding experiment, the numbers of yellowhammers present at Killoch were an estimated seventy times higher than found during boundary transects carried out the previous winter, with an estimated minimum of 4.9

yellowhammers per km walked seen during the feeding experiment in winter 2010/11 compared with 0.07 in winter 2009/10 (Figure 5.10). This contrasts with a mean of 4.82 yellowhammers per km walked seen at Milton and Fail Mains in 2009/10 compared to only 3.58 yellowhammers per km walked in 2010/11, thus the increases cannot be attributed to there being higher numbers of yellowhammers everywhere during winter 2010/11. In April 2011, after the feeding stations had been removed, the numbers of yellowhammers seen at Killoch declined to a level comparable with the numbers seen in April 2010 (Figure 5.10) when no feeders were present. Presumably this was because the yellowhammers were forced to disperse to find alternative food resources. However, the yellowhammer breeding density in 2011 (i.e. after the winter feeding experiment) was slightly higher than in 2010 (Figure 5.11) but it is unknown if this was a direct result of the winter food supplementation.

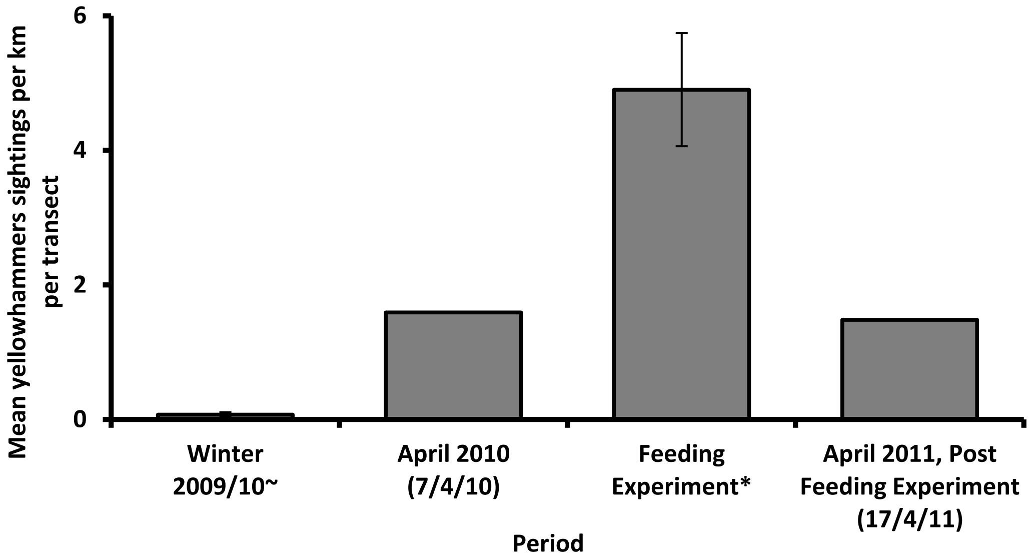


Figure 5.10 Mean yellowhammers density ± 1 S.E. at Killoch both during the feeding experiment and just after its removal compared with the numbers seen during the previous winter when the site was unsupplemented

* mean total number of yellowhammers seen during ten point counts carried out at each feeder between January and March 2011 divided by the distance of the transect survey. As the complete survey was not carried out (only the six feeding stations surveyed) the figure presented here will be an underestimate as yellowhammers potentially present elsewhere on the farm were not counted

~ mean yellowhammer density recorded during three boundary transects carried out between November 2009 and January 2010 (for dates see appendix 2)

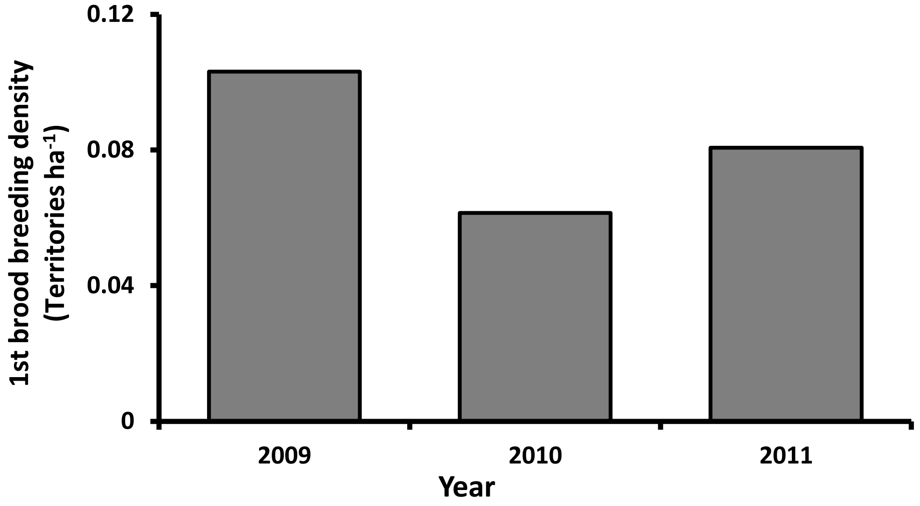


Figure 5.11 Yellowhammer breeding density at Killoch between 2009 and 2011

Eight colour ringed individuals were re-identified as breeding on Killoch farm in 2011, with an additional individual observed on a neighbouring farm (Figure 5.12). Of the eight individuals breeding at Killoch, seven were initially ringed at Killoch during the feeding experiment (two adults and five first year individuals). The eighth was initially ringed on Milton farm, 7.5 km away on the 9th September 2010 as a first year individual. Although this individual was not detected during the feeding trial period, it is possible that it still made use of feeders (note that during the feeder observations colour ringed combinations often proved impossible to read in full as, unlike during the breeding season, birds rarely remained in sight for long enough to read combinations before flying off).

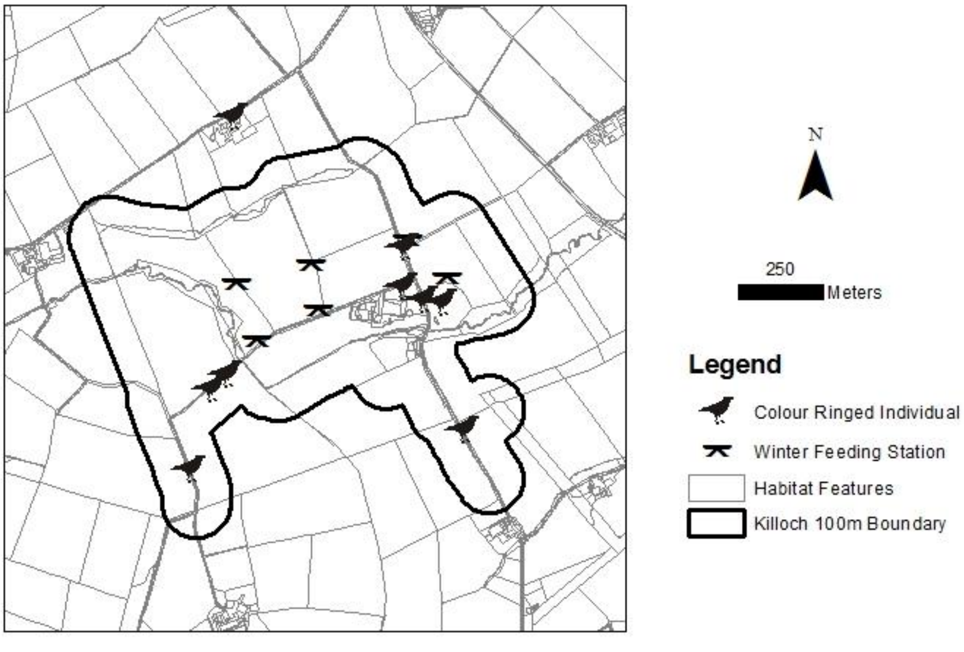


Figure 5.12 known breeding locations of colour ringed yellowhammers post feeding experiment

The population estimate (Lincoln Index) of the birds using the feeding stations, based on the total number of birds colour ringed at Killoch during the feeding experiment (108), the number of those that bred at Killoch (7) and the total number of birds breeding at Killoch (16) is given as:

Population estimate = 108 / (7/16)

= 246.86 individuals

This equates to a subsequent breeding population of 123.5 pairs using Killoch during the feeding experiment. Assuming a breeding density of 8.1 pairs per km^2 (average breeding density for the four Ayrshire study farms, see chapter 2) these birds would need 15.42km^2 of farmland habitat during the breeding season, i.e. all the habitat within a 2.20 km radius of the feeding stations.

An alternative population estimate using the Schnabel method based on the 13 mist netting sessions between 23rd December and 29th March:

$$\text{Population estimate} = \frac{\sum(CtMt)}{\sum Rt}$$

Ct = Number caught Mt = Number new individuals Rt = Number re-traps

= 331.7 individuals

This is a not dissimilar estimate to the estimate obtained using the colour ring resighting data.

5.4 Discussion

5.4.1 Numbers and species present at the feeding trial

The study population of yellowhammers demonstrated behavioural plasticity and a low level of neophobia, as highlighted by their ability to rapidly adapt to and exploit the feeding stations –a novel food resource. Organisms are predicted to be more behaviourally plastic in unpredictable or changing environments (Komers 1997), as may be typical of birds feeding on seed resources. Other winter supplementary feeding trials have successfully attracted yellowhammers (e.g. Siriwardena & Stevens 2004, Perkins *et al*. 2007).

The feeding stations attracted predominantly yellowhammers, which accounted for 55% of birds caught in mist nets and 74.5% of observations at the feeding stations. Other species recorded included chaffinches and house sparrows. Previous feeding trials have attracted a wider range of species, including corn buntings *Emberiza calandra* and tree sparrows *Passer montanus* (e.g. Siriwardena & Stevens 2004, Perkins *et al*. 2007). However, the species composition of birds using the feeding stations will be dependent on bird populations present in the landscape they are situated. For example, in Ayrshire, corn buntings are all but extinct (Forrester & Andrews 2007) and tree sparrow are a rare and localised bird, with neither species observed at Killoch prior to the feeding trial (pers. obs.), helping account for them not being recorded utilising the supplementary feeding. As reed buntings have previously been shown to utilise supplementary feeding (Siriwardena & Stevens 2004, Perkins *et al*. 2007), and as 1 – 2 pairs of reed buntings breed at Killoch each year (pers. obs.), it was surprising that they were never observed utilising the feeding stations. However, the grain provided (wheat) was larger in size than the reed buntings observed winter diet of annual weed seeds (Orlowski & Czarnecka 2007) and thus perhaps unsuitable.

A mean of 46.5 yellowhammers were observed in total per observation day between January and March at the six feeding stations, with flocks of up to 50 individual yellowhammers observed at a single feeding station. This contrasts with the low numbers of yellowhammers observed in 2009/10 at the same site during boundary transects (where a total of only two individuals were observed during three transects carried out between November and January). As there had been no change in habitat availability at the farm between the two winters (except for one silage field changing to maize, although yellowhammers were not observed using this field in either of the two winters), this suggests that it was indeed a lack of food in the winter that resulted in the low yellowhammer counts at Killoch during winter 2009/10.

Mean winter density increased from 0.07 yellowhammers per km in the winter pre feeding experiment the equivalent of an estimated minimum of 4.9 per km had the same surveys been carried out during the period when supplementary food resources were available. As yellowhammer density during the feeding experiment was calculated by dividing point count totals by the previous winter’s survey length, these densities will moreover tend to underestimate the true value since they assume that the only yellowhammers present on Killoch farm were at the feeding stations – an assumption that is unlikely to be correct. Although the period of the year over which the winter densities at Killoch were calculated were not identical (November to January during the winter prior to the feeding trial compared to January to March during the feeding trial itself), the increase in densities due to feeding should be robust. Large numbers of yellowhammers had been observed in November and December on the feeders prior to the standardised counts, and no yellowhammers observed during incidental visits to the site in February and March during the previous winter. The calculated mean winter density observed at the feeding site was greater than the highest mean winter density recorded elsewhere in the pastoral study landscape – 3.1 yellowhammers per km at Milton winter 2009/10 (chapter 4).

The fact that yellowhammer density on Killoch farm during the period of feeding increased from a previously very low level to one higher than the highest wintering densities recorded elsewhere in the study area suggests that winter food availability limited yellowhammer winter density not only at Killoch, but also elsewhere in the study landscape. Schnabel method calculations based on ringing recaptures in winter and Lincoln population index calculated using breeding season re-sighting data produced estimates of 332 and 247 yellowhammers, respectively, using the feeders. Both of these methods assumed that no births and death occurred. Although no births occurred during the period studies, the possibility that deaths occurred cannot be excluded. However, any potential overestimation in population size due to this assumption being violated is not likely to have been large as the periods between the initial sampling periods and the re-sampling periods were short. Another assumption that each population estimate makes is that the populations are closed, i.e. there is no immigration and emigration from other populations. Again, this assumptions is likely to have been violated on the local scale (birds entering and leaving the farm where the feeding stations were situated), but on a larger scale (over the ranges the yellowhammers were moving in winter) this assumption would have been better met. Yellowhammers are local residents and not undertaking partial or full migrations within the UK (Cramp & Perrins 1994) so the Ayrshire population would not have increased in winter with immigration from elsewhere. The mark recapture analyses assume that survival of marked birds (ringed and colour ringed yellowhammers) is the same as unmarked birds. No evidence can be found in the literature to suggest that this assumption is violated, and a study of redshanks found colour and metal ringing resulted in no change to predation rate or food intake rate (important components directly contributing to survival) between ringing and colour ringed and unmarked individuals (Cresswell *et al.* 2007), but it is unknown if this is the case for yellowhammers. For the estimates to be accurate from both the Schnabel method and the Lincoln population index, the likelihood of capturing marked and unmarked individuals must be the same. Trap shyness has been shown to occur in some passerines including the yellow wagtail *Motacilla flava* (Buckland & Hereward 1982) and across a range of American passerines (McArthur & McArthur 1974), thus it potentially could be occurring in yellowhammers. However, the positions of the nets constantly changed; moving nets has previously been shown to reduce the effect of avoidance and trap shyness in birds (Marques *et al.* 2013). However, the lower estimate from the re-sighting data might be the more accurate estimate (247 individuals) as the ringing estimate (332) might have been artificially inflated by trap shyness. Despite the differences in methodology of the two estimates, they are similar, giving more credibility to the estimations of numbers present.

5.4.2 Grain depletion at the feeding stations

Grain depletion significantly increased during the monitoring period between late December and March, with time of year accounting for 10.95% of the variation in grain depletion rate. This suggests that either the number of yellowhammers using the feeding stations increased as winter progressed, and/or that the individuals utilising the feeding stations were sourcing a larger proportion of their food requirements from the feeders. While there was no significant increase in the numbers of yellowhammers observed at the feeding stations as the winter progressed, the power of this analysis was limited due to the fact that the yellowhammer flocks were highly mobile and the number of yellowhammers seen at a feeder on a given date was subject to the chance that a count coincided with the arrival of a flock. Furthermore, increasing day length increasing foraging hours available as winter progressed might have influenced the ability of the point counts to accurately reflect the numbers of yellowhammers utilising the feeders throughout the winter. In late winter, foraging birds are less time pressured, thus fewer birds may have utilised the feeders at any one time and thus recorded as individuals would have been able to meet their energy requirements in a smaller proportion of the day. Additionally, the metabolic cost of maintaining body temperature is predicted to be higher earlier in the winter during colder weather. As the observed peak in grain depletion (late winter) doesn't match the predicted peak (mid winter), this suggests that temporal food availability rather than weather is influencing grain depletion. Therefore, the increase in the amount of grain consumed as winter progressed fits in well with the hypothesis that a late winter hunger gap is experienced by granivorous farmland birds (Siriwardena *et al.* 2008). Natural food resources in farmland landscapes such as the grain and weed seed availability in stubble fields decline as winter progresses (Robinson and Sutherland 1999). This also fits with the pattern seen in chapter 4, which showed a switch from yellowhammers using stubble fields in early winter to more unnatural food sources (farmyards, game feeders, gardens) in late winter at both the farm level (transects results) and at the level of individual birds moving around the landscape (radio tracking results).

5.4.3 Age structure of yellowhammers present at Killoch during and after the feeding experiment

A significantly higher proportion of the yellowhammers caught at the feeding stations were first year individuals compared to a sample of yellowhammers caught at Milton and Fail Mains (two unfed study sites) over the same period between December 2010 and March 2011. The ratio of first year individuals to adults caught at the feeding stations (approximately 4:1) is comparable to the ratio found at the other un-supplemented study sites between October and December, which then decreased in late winter suggesting that in these un-supplemented sites the survival rate of first year birds was lower than that of adults (Chapter 4). There are two possible explanations for the relatively high numbers of first year yellowhammers at the feeding stations; either the provision of supplementary feeding increased first year survival, or first year individuals were more attracted to the feeding stations than adults. Previous work carried out on house sparrows found that the provisioning of supplementary grain increased overwinter survival rates (Hole *et al.* 2002) but only in populations apparently limited by winter food. The provisioning of supplementary grain in the present study may have had a similar effect in yellowhammers. However, supplementary feeding may be more attractive to first year birds as they are of lower average quality and less experienced in foraging than older birds, so differing foraging strategies by different age classes cannot be excluded as an explanation for the high numbers of juveniles to adults. Even if supplementary feeding only benefited poorer quality individuals, the proportion of the colour ringed birds re-sighted at Killoch in the breeding season that were first years (6:2) was comparable to that which would be expected from the ratio of adults to first years ringed (4:1).

5.4.4 Potential temporal and spatial scale of the impacts of winter supplementary feeding

The feeding trial was successful in terms of targeting yellowhammers: these made up 55% of the birds caught and 74.5% of those observed at the feeding stations. The specificity of the feeding stations in attracting yellowhammers can be attributed to the large size of the grain provided; wheat has a larger grain size than some species are able to handle (Perkins *et al.* 2007). The ability to target the red listed yellowhammer so effectively potentially makes provision of feed cost effective.

The food provisioned was utilised both by yellowhammers that were present at the farm during previous breeding seasons (as seen by the high proportion of birds previously ringed at the site being re-trapped during the feeding trials) and by birds from out with the study site. The estimated 247 individuals present could not have come from the study farm alone, and would have require an estimated area of approximately 15.4 km^2 of breeding habitat (over fifteen times the area of the supplementary feeding trial site), assuming the mean yellowhammer density calculated in chapter 2 was representative of the wider Ayrshire landscape. Additionally, the re-sighting of an individual from 7.5 km away breeding after the winter feeding experiment suggests that the spatial scale over which supplementary feeding could potentially have an impact is even greater. However, it is unknown if that individuals presence was directly as a result of the winter feeding; its presence was not detected until after the feeders were removed.

Although the densities of yellowhammers present at Killoch after the removal of the supplementary feeding in March 2011 quickly returned to levels comparable to the same period during the previous year (1.59 yellowhammers observed per km in April 2010 compared with 1.48 in 2011), a slightly higher breeding density was recorded during the breeding season (0.08 pairs ha^{-1}) than during the previous breeding season (0.06 pairs ha^{-1}). However, it is unknown of this slight increase can be attributed to the presence of the winter supplementary feeding, especially considering that the breeding population in 2011 was not as high as in 2009 (0.10 pairs ha^{-1}), indicating that factors other than supplementary food play a large part in determining breeding densities. This supplementary feeding trial in a pastoral farming landscape requires repetition, ideally over both larger spatial and temporal scales to confirm the suggestion that supplementary feeding might have a positive impact on yellowhammer breeding density in pastoral dominated farming landscapes.

The anecdotal increase in breeding density following the winter food supplementation is contrary to findings from previous supplementary feeding which found no difference in yellowhammer breeding density between fed and unfed sites (Siriwardena *et al.* 2007) in arable landscapes. However, I feel that as pastoral dominated landscapes contain fewer potential seed rich-winter foraging habitats than arable landscapes for graniverous birds as their preferred winter stubble habitat is scarce, the potential benefits of providing winter supplementary feeding are greater.

The supplementary feeding was removed on the 29th March. This may have been too early for it to have had the maximum impact. In early April, it would have been too early for the new season's invertebrate and seed resources to have become available to foraging yellowhammers, resulting in the birds to disperse from the site in order to find sufficient food or else starve. Future trials should look at the impact of removing the feeding at different periods on subsequent breeding densities and reproductive success of granivorous farmland birds in terms of a cost benefit analysis so potential agri environment schemes can offer the best 'value for money' in terms of maximising the benefit whilst minimising the cost.

5.4.5 Theoretical grain requirements of the estimated population of yellowhammers using the feeders

Previous work has suggested that yellowhammers require 215 wheat grains per day (Robinson 1997), with the mean weight of grains being 38mg (Robinson 1997). Therefore, each yellowhammer would require approximately 8.2 g of wheat per day. If the 332 (ringing data) or 247 (breeding season re-sighting data) yellowhammers sourced 100% of their diet from the feeding stations, this would equate to between 162.0 kg and 211.8 kg grain required by the yellowhammer population during the 80 day period between 29th December and 18th March. Therefore, if entirely dependent on the feeders, grain consumption by yellowhammers would have accounted for 44.5% to 58.2% of the 364 kg of grain provided during this period. Yellowhammers accounted for 74.5% of the small passerines observed at the feeding stations, so if it is assumed that the food requirements for all of these species are the same as for yellowhammers, then the small passerines observed using the feeding stations would have accounted for 59.7% to 78.1% of the 364 kg of wheat provided during the monitoring period. This indicates that up to 40.3% of the grain was consumed by other (non-target) species or otherwise lost. This wastage could be reduced by improving feeding station design. Although large birds were unable to physically get inside the cages, pheasants, crows and rooks were occasionally observed putting their heads through the cage mesh in order to access the grain round the edge of the trays. A larger cage would increase the gap between the cage and seed tray, decreasing the probability that large non-target species of birds are able to access the grain. There was no evidence, wether from droppings or footprints in the mud surrounding feeders that rodents were using the feeding stations, however, rodents in other areas could potentially represent a major consumer of grain if it was to be provided in a similar way.

5.4.6 Suitability of winter supplementary feeding as a conservation measure for farmland birds

Farmland bird declines are being tackled by a range of agri environment schemes. The current main options available under current agri-environment schemes in Scotland and England for providing winter food for declining granivorous birds include paying farmers to leave harvested crops as overwinter stubble habitat or planting wild bird cover crops. These are areas of seed bearing crops including from cereals, kale *Brassica olerancea*, quinoa *Chenopodium quinoa*, sunflower *Helianthus annuus* and millet left unharvested to provide winter food, providing a seed-rich winter foraging habitat for granivorous birds. However, in pastoral landscapes such as the study area, a low proportion of farmland could potentially be managed to provide winter stubble, and there has been a low rate of planting wild bird cover crops since these are seen as being very time consuming and require land to be removed from normal agricultural use. Supplementary feeding has the advantage that it could be easily implemented in both arable and pastoral regions, requires no specialist machinery and does not require land to be set aside. Like the other agri-environment schemes targeting winter bird food shortages, supplementary feeding is not self-sustaining and would require farmers to the feed each year in order for it to continue to have a benefit to birds.

Since yellowhammers are a relatively sedentary species, with most ringing recoveries within 1 km (Forrester & Andrews 2007) and the maximum recorded movements in this study of over 9 km (Chapter 4), care should be taken to only implement such a potential measure if there is a known population of breeding yellowhammers nearby that could potentially benefit. This distance will probably be landscape-dependent since yellowhammers have been found to move further within the study pastoral landscape (Chapter 4) than in a mixed farming landscapes (Calladine *et al*. 2006). The cost of the raw materials for supplementary feeding was comparatively low to for example the £391 per hectare paid annually in Scotland to farmers implementing wild bird seed mix/cover crop option (www.scotland.gov.uk). The trays and cages were cheap, straightforward and simple to install and the estimated 500 kg of grain provided from October cost £130. This was the price of buying the grain in 25 kg bags, bulk buying would be cheaper yet. This low investment both in terms of finances and labour significantly increased the numbers of yellowhammers at the study site in winter, benefiting an estimated 247 to 332 yellowhammers during the feeding period.

Despite the apparent success of this experiment in attracting yellowhammers, supplementary feeding may not be the ideal solution for conserving yellowhammer populations. Radio tagged yellowhammers were seen to prefer stubble habitat over game feeders for foraging (chapter 4), even though this came at the cost of longer travel distances in early winter, despite the game feeders that they later used post solstice being available. The change in habitat preference of radio tagged yellowhammers suggests that the potential benefits of providing supplementary feeding increases as winter progresses. Further research should be carried out testing the optimal time of year to implement supplementary feeding stations, to minimise the cost of such schemes whilst maximising the benefits to birds. However, the optimal time to implement such a scheme will probably be landscape dependent, influenced by the availability and quality of stubble and other habitats actively selected by wintering yellowhammers.

Using supplementary food supplies may incur costs to an individual, such as an increase in predation risk around feeding stations. Birds may then decide to use foraging areas with lower food returns (Lima & Dill 1990). Furthermore, the large congregations of birds at feeding stations may increase the transmission of diseases. All captured birds were checked for visual signs of papillomavirus and trichomoniasis, and although these diseases were not detected in the yellowhammers caught at the feeding stations, some chaffinches were infected with papillomavirus and trichomoniasis. The potentially devastating impact of disease on populations should not be underestimated, for example, trichomoniasis was found to be responsible for a 35% decline in greenfinches *Carduelis chloris* (a species commonly found on garden bird feeders) in a year (Robinson *et al.* 2010). Moreover, in turtle doves *Streptopelia turtur* (another declining farmland bird), there was an increased incidence in the number of individuals carrying this parasite on farms where food had been provided for game birds (Lennon *et al*. 2013).

The impacts of supplementary feeding on future individual breeding success and survival was not quantified, but results from other passerines suggest there may be mixed effects of supplementary feeding. Blue tits provided with supplementary feeding in winter advanced their laying dates, and fledged more chicks per nest compared to unfed control birds despite having the same clutch and brood size (Robb *et al*. 2008) but a more recent study reported they fledged chicks in poorer condition (smaller, weighed less) that subsequently go on to have lower survival (Plummer *et al*. 2013). Therefore, it is important that the long term impact of supplementary feeding is fully understood.

Therefore, factors other than a reduced risk of starvation need to be taken into account when assessing the likely costs and benefits of providing additional food for farmland birds using feeders. As winter supplementary feeding has the potential to result in increased disease transmission or negatively impact on breeding parameters, until more research is carried out I feel supplementary feeding should only be considered as an option where other measures to increase late winter food availability are not available and winter food availability has been clearly demonstrated in that area to be causing a decline in breeding populations. However, if it can be demonstrated that positive benefits of winter supplementary feeding outweigh any potential negative impacts, it has the potential to deliver cost effectively as part of agri-environment schemes. Supplementary feeding has advantages over current agri-environment schemes such as provision of stubble or bird cover crops. Additionally, it is able to continue to provide seed-rich foraging for declining granivorous birds in the critical late winter period when seed levels are depleted in stubbles and bird cover crops, and could prove attractive to farmers as it does not require land to be removed from production.

Chapter 6 – Yellowhammer diet throughout the year and a comparison of adult and nestling breeding season diet

Farmland birds including yellowhammers *Emberiza citrinella* have undergone population declines at the same time as agriculture has intensified. Knowledge of the year round dietary requirements can help design conservation measures allowing the creation of food rich habitat. Faecal analysis was employed to study year round yellowhammer diet on pastoral farms. Diptera, Coleoptera, Aranae and Leptidoptera were the most common orders in nestling diet, comparable with previous studies. Nestling diet contained high levels of invertebrate material. As nestling condition has been shown to increase with invertebrate content in diet, pastoral farmland appears to provide good quality summer diet and thus represents adequate summer foraging habitat. Levels of invertebrates in adult summer diet were more similar to diet studies pre agricultural intensification than a recent arable study. As summer progressed, invertebrate material declined until winter diet was cereal dominated. This highlights the unsuitability of the dominant pastoral habitat as winter foraging habitat.

6.1 Introduction

What an organism eats helps shape its life history, with both the quantity and quality of available food affecting both survival and reproductive parameters. Most research to date has focussed on the effects of diet on breeding parameters affecting the young, which can have lifelong impacts on the young's subsequent survival and fecundity. Additionally, the parents' own nutritional state can impact not only their own survival probability but also their decisions about how much to invest in offspring (e.g. Navarro & González-Solís 2007, Christe *et al.* 1996). Food availability in the breeding season can influence the amount of investment the parent makes in both its offspring and self maintenance; these two competing demands can be traded off against one another. For example, an organism may choose to increase breeding success at the expense of its own self maintenance and hence survival, or vice versa (Stearns 1992).

An abundant, good quality diet is important for maintaining body condition, which in the case of female birds is important for producing large, high quality eggs (Galbraith 1988). Food availability also plays an important role during the chick rearing period, and can limit breeding success (e.g Furness and Tasker 2000, Davis *et al*. 2005, Siikamäki 1998). The timing of breeding attempts is critically important for many species of birds (Newton 2013), since there is temporal variation in food abundance and availability, and hence diet. Reductions in food availability during the breeding season as a result of habitat change may result in population declines (Thorup *et al*. 2010). Food availability outwith the breeding season can also influence reproductive success (Robb *et al*. 2008), as it can have a carryover effect via its influence on adult condition and thus resources available to invest in reproduction.

Not only does food availability have the ability to affect breeding success, the type of food available, and therefore the quality of the diet can also influence breeding success (Sydeman *et al*. 1991), fledging condition (e.g. Johnston 1993, Osterblom *et al*. 2006, Wilkin *et al*. 2009), growth rates (Birkhead *et al*. 1999, Johnston 1993), survival rates (Birkhead *et al*. 1999), adult body size reached by nestlings (Boag 1987) and nestling immune function (Birkhead *et al*. 1999). The effects of diet quality are not constrained to just the breeding season. Moult, one of the most energetically expensive periods of a bird's life cycle, increasing energetic demands by up to 100% (Lindström *et al*. 1993) is affected by food availability and quality (Pap *et al*. 2008) whilst winter food availability has the potential to limit populations (Hole *et al*. 2002, Siriwardena & Stevens 2004).

Farmland birds have undergone recent population declines at the same time as agricultural intensification (Newton 2004). Changes in land management have altered seed and invertebrate resources available to foraging birds. Winter stubble habitat availability has declined with the replacement of spring sown crops by higher yielding autumn varieties (Wilson *et al*. 1999). Remaining stubble fields are now a poorer seed following the advent of combine harvesters and the increased use of herbicides reducing weed seeds and spilt grain (Shrubb 2003). Hay has been replaced by silage as the fodder crop grown for feeding livestock wintered indoors (Shrubb 2003). Silage contains a lower diversity of plant species and is denser than hay, therefore contains lower invertebrate diversity, with those present less accessible. The more frequent and earlier harvesting of silage means that, unlike hay, it never gets the chance to set seed (Wilson *et al*. 1999) and large invertebrates are unable to complete their lifecycle (Shrubb 2003). As a result, modern grasslands are poorer foraging habitat for insectivorous and granivorous birds.

Herbicide use, in both pastoral and arable fields, has decreased invertebrate availability and diversity through the removal of host plants (Shrubb 2003). Further declines in invertebrate abundance and diversity have come with applications of pesticides, used by farmers to protect their crops from insect infestations which can cause economic loss through reduced yields. An unintended consequence of pesticide use is reduced avian breeding success as a result of the reduction of invertebrate food resources (e.g. Morris *et al.* 2005, Rands 1985, Boatman *et al.* 2004).

Agricultural intensification has changed the foraging habitat and food availability, and correlates with observed declines in many species of farmland birds. These declines may be a result of the habitat no longer providing a sufficiently high quality foraging habitat, and thus appropriate diet for birds. The Yellowhammer, a red listed species of conservation concern (Eaton *et al.* 2009), has been used as an indicator of farmland biodiversity since it is widespread and representative of a suite of granivorous farmland birds that eat seeds throughout the year but require invertebrates for their young. Yellowhammer diet has been well studied in the past in mixed and arable landscapes (e.g. Douglas *et al.* 2012, Macleod *et al.* 2005b, Moreby & Stoate 2000, Stoate *et al.* 1998), but few studies have been carried out in pastoral landscapes where declines and range contractions are more pronounced (Kyrkos *et al.* 1998). Since diets are affected by habitat, prey density and accessibility, travel time (for breeding birds) and habitat-specific predation risks, this study aims to test the hypothesis that pastoral yellowhammer diet of both adults and nestlings differs mixed and arable populations, and from historical pre agricultural intensification reports of diet. The dietary comparison may indicate if yellowhammers are limited by food in modern pastoral farming landscapes. Previous research has reported that yellowhammer fledgling condition is correlated with the proportion of grain provisioned (Douglas *et al.* 2012), dietary investigation will give an indication of the suitability of pastoral farming landscapes as yellowhammer breeding habitat. By understanding yellowhammer diet in pastoral landscapes, agri-environment schemes can be better informed when designing prescriptions providing high quality foraging habitat for yellowhammers and other graniverous passerines throughout the year.

6.2 Methods

6.2.1 Study sites

The diet study was carried out at four principal study farms located in Ayrshire, south west Scotland (Figure 6.1), and were typically managed pastoral dominated farms grazed by either dairy or beef herds in summer, sheep in winter and silage grown as a fodder crop. Additionally, a small amount of cereal (less than 30% of any site) was grown at some farms, with the exact amount varying by farm and across years. Dietary data were collected by means of faecal analysis from the four study farms (Killoch, Carnell, Milton and Fail Mains) throughout the duration of the study (May 2009 – August 2011) and at an additional site in winter 2009 only (Rowanmyle House).

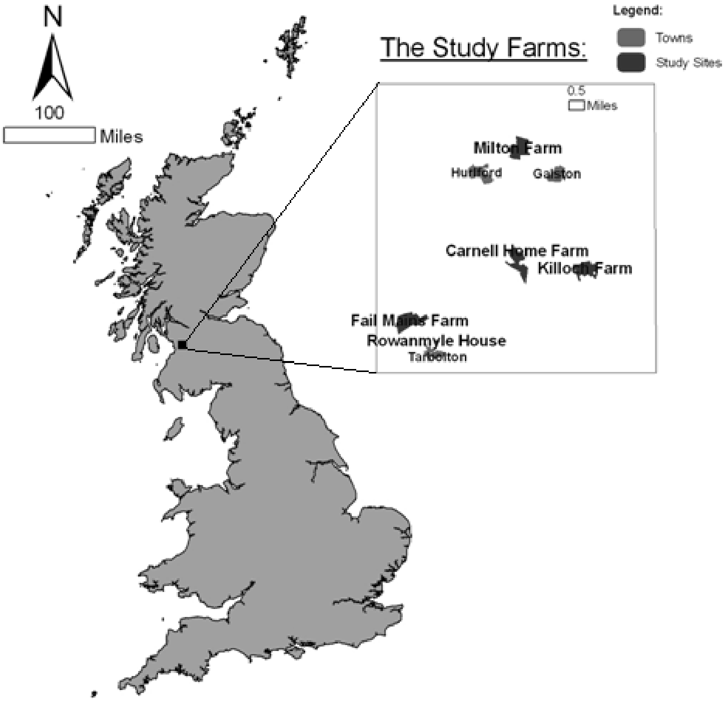


Figure 6.1 Location of study area and study farms

6.2.2 Faecal sample collection

During the breeding season, faeces were collected from full grown yellowhammers by capturing them in mist nets erected on the birds' territories (identified during breeding transects carried out each week throughout the breeding season). Birds were also mist-netted around farm buildings at sites where individuals occasionally visited to feed on grain intended for livestock (either where it was stored, as in the case of Killoch farm, or in the feed troughs in the cattle sheds as at Milton). In late summer and winter, yellowhammers were mist netted at sites on the farms where flocks had been observed during earlier surveys. Tape lures with Reed Bunting *Emberiza schoeniclus* or Chaffinch *Fringilla coelebs* calls were played on occasion to try and increase the number of birds in the catching area on days when few birds were present. Any yellowhammers caught in mist nets were placed upon extraction in clean, unused bird bags so as to ensure that faecal material produced by the bird whilst awaiting ringing could be collected with the certainty that it was not contaminated by faecal material from either another species or individual.

In order to collect faecal samples from nestlings, nests were located by watching adult birds enter and leave suspected nest sites that had earlier been recorded during the breeding season transects. Potential nest sites were watched from a distance (minimum 50 metres) using a telescope fitted with a 16–48x zoom lens. After observing a site for a minimum of 30 minutes, the nest was located by carefully examining the location at which the birds had been seen to enter or leave the vegetation. Chicks in the nest were ringed (if large enough), and any faecal material produced during handling was collected. All adult and nestling faecal samples were stored individually in labelled plastic vials in 70% alcohol until analysis.

6.2.3 Processing of faecal samples

In preparation for analysis, the faecal samples were drained of alcohol and soaked with water for 48 hours (as per Moreby 1988). At the end of the 48 hour period, each sample was washed under running water through a 210 micron sieve to remove uric acid and other small fragments which would otherwise 'cloud' the sample. Fragments from the sieve were transferred to a labelled plastic vial and stored in 100% Industrial Methylated Spirit until identification. Great care was taken to ensure the sieve was cleaned thoroughly between samples to ensure no cross contamination occurred. Each sample (only fragments greater than 210 microns) was then spread out on a petri dish etched with 100mm^2 grids on the underside, and the total sample area estimated to the nearest 5mm^2. Sample identification was carried out using a binocular microscope. Plant material was separated from that of invertebrate origin, and identified where possible as either grass, cereal or dicot seed with the area estimated as above to allow the proportion of seeds in the faecal sample to be calculated. Although this doesn't give an exact proportion of seeds to invertebrates in the diet due to different digestibility of different prey types, it does allow general trends to be described. Invertebrate material was identified as far as possible from identifiable hard fragments that are unchanged in appearance by the digestion process such as legs, mandibles and eggs (see Figure 6.2 for some examples found in the faecal samples studied) using Moreby 1988 and entomological id guides. The minimum number of individuals present of each invertebrate order/category was counted for each sample.

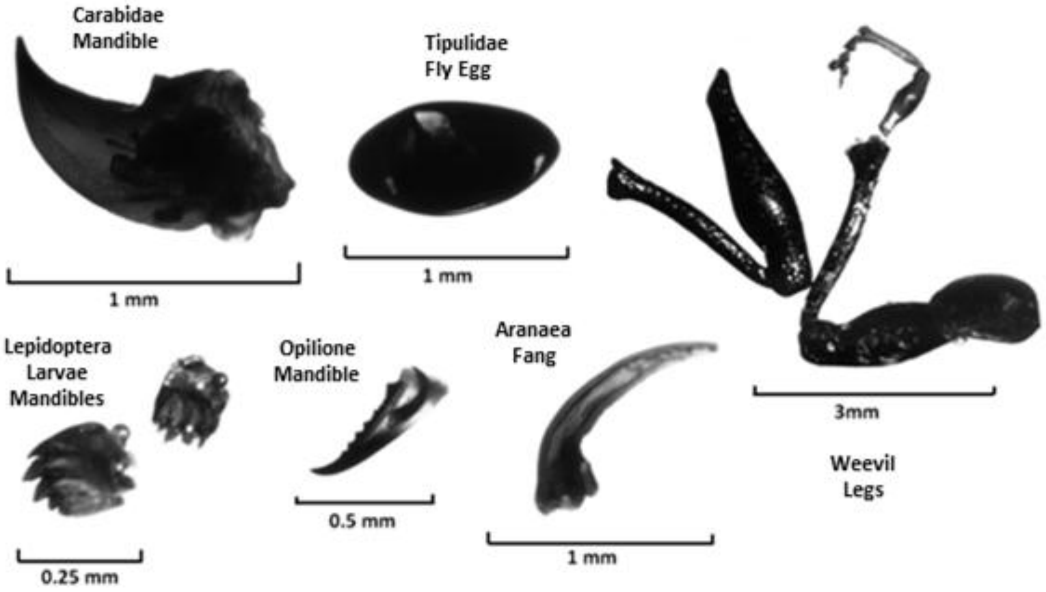


Figure 6.2 Examples of invertebrate fragments found in yellowhammer faecal samples

Arachnids were identified from chelicerae, or in the absence of these, from pedipalps, body or leg fragments. Lepidoptera larvae were identified from mandibles, (which could be distinguished from sawfly larvae by the orientation of the ‘teeth’ on the mandibles (Moreby 1988). Coleoptera larvae were identified by the presence of their prolegs, and the adults from intact legs, fragments of elytra, or mandibles. Wherever possible the family of beetles was noted, and were generally Carabidae (ground beetles), Chrysomelidae (leaf beetles) or Curculionidae (weevils). Adult Diptera, Heteroptera and Hymenoptera were all identified from their legs which pass through undigested, with additionally wing fragments used to identify both Heteroptera and Diptera. Additionally eye fragments were used to identify Diptera, or in the case of gravid female adult Tipulidae flies, from the presence of eggs. The number of tipulid eggs present in each sample was counted to determine the minimum potential number of individuals they came from, female tipulid fly in some larger species theoretically contain up to 1,000 eggs (Pritchard 1983). Dipteran larvae were identified from spiracles.

6.2.4 Invertebrate sampling of breeding season yellowhammer foraging locations

To study the invertebrate availability at sites chosen by foraging yellowhammers, invertebrates were collected using ten sweeps of a sweep net within a $2m^2$ quadrat placed around known yellowhammer foraging locations identified during surveys carried out to identify breeding territories and nest locations. Invertebrates were collected from the sweep net using a pooter, and transferred to an individually labelled pot and preserved in 70% alcohol until identification. Identification to order was carried out under a binocular microscope with the help of entomological field guides and the length of the carapace of each item measured to the nearest mm. For further methodology details please refer to chapter 3.

6.2.5 Data Analysis

Dietary items less than 1mm in maximum length were excluded from the dataset prior to analysis (e.g. springtails, thrips and mites) since it was considered unlikely that the yellowhammers were actively selecting prey items of this size, but were merely obtained incidentally as they foraged for and ate larger prey items (Morris *et al.* 2005). In order to examine seasonal variation in the number of invertebrate orders and the proportion of seeds present in the diet of yellowhammers, the year was split up into three distinct time periods; breeding season (1st May to July 31st), late summer, when yellowhammer adults undertake their annual complete moult (1st August to 30th September) and winter (1st October to 30th April). The effect of time period (breeding season, late summer and winter) on dietary composition was analysed using one way ANOVAs, with Fisher's post hoc least significant difference (LSD) test being used to determine significant differences between groups. Adult and nestling yellowhammer diet during the breeding season were compared, using Wilcoxon's signed rank tests with paired = False (thus a Mann-Whitney U test) was carried out in R, version 1.12.1 to determine whether the number of invertebrate orders present in the diet or the proportion of diet composed of seeds differed between adults and nestlings.

Diet composition data were further analysed after first estimating the relative importance of each invertebrate order in a given dietary sample. To account for the differing number of invertebrate individuals, and the different proportion of each sample that consisted of invertebrate material, for each sample, the total number of individuals for each order was divided by the total number of invertebrate individuals identified then multiplying this by the proportion of invertebrate material. These datasets were then subjected to Detrended Correspondence Analyses (DCA's), carried out using vegan in R (version 2.15.1) with the decorana function. The first DCA summarised differences between adult and nestling diet during the breeding season, and the second summarised the differences in adult yellowhammer diet between summer (breeding season and late summer date combined to allow sufficient sample size) and winter. The factors season (summer/winter) and age (adult/nestling) were fitted to each ordination plot (100,000 permutations), respectively, using envfit function in vegan for R, producing centroids for each category and so giving a visual representation of the typical diet for each category. Finally, the centroids were tested to see if they were significantly different from each other using the envfit function.

To test whether the invertebrates taken by foraging yellowhammers in summer (as identified from the faecal analysis) were a random selection of those available, a χ^2 test was carried out using R (version 2.15.1) to compare the number of individuals from each invertebrate order present in each faecal sample with the numbers greater than 2mm found in sweep samples collected at the 91 known yellowhammer foraging locations sampled. Items less than 2mm in length were excluded since the yellowhammers are unlikely to be actively selecting prey items that small (Morris *et al.* 2005). Each separate invertebrate order was then tested individually using χ^2 tests to determine which groups were significantly selected or avoided.

Unless otherwise specified, all analyses were carried out in Minitab 16 (2010).

6.3 Results

A total of 120 yellowhammer faecal samples were available for analysis, of these, 103 were from full grown birds, and the remaining 17 were collected from nestlings during the breeding season. Of the 103 samples from full-grown individuals, 76 were collected in winter (October – March), 15 in later summer (August and September) and 12 from the breeding season (May – July). Seasonal variation in the number of adult samples reflected the relative difficulty of catching yellowhammers in mist nets during each time period. No samples were obtained in April.

Yellowhammer faecal samples collected in winter were significantly more likely to contain grit (χ^2= 4.12, 1 d.f., p = 0.0425) than samples collected from full grown yellowhammers during the summer months (breeding season combined with late summer samples). Only 25.9 % of summer samples analysed contained grit compared to 46.8% of winter samples. As grit only accounted for 0.004% of all faecal material identified by volume, and its presence in diet is only to aid digestion and by itself it is of no nutritional value, it was excluded from subsequent analyses. These initially examined seasonal variation in diet by comparing samples of adult yellowhammers from the breeding season (May – July), late summer (August and September) and winter (October – March). Later comparisons are of adult and nestling diet during the breeding season.

6.3.1 Full grown yellowhammer diet throughout the year

Faecal samples from three full grown yellowhammers analysed in May contained on average 5.04% cereal remains, but cereals then increased rapidly in importance until nearly 100% of the faecal samples analysed by volume was made up of cereal remains by October. The cereal content of the diet remained at this high level throughout winter (Figure 6.3). No faecal samples were obtained between the beginning of March and mid May so it is not known when in the spring the study population of yellowhammers switched from a cereal-dominated to an invertebrate-dominated diet. The proportion of total seed material in yellowhammer faecal material varied significantly by period (One-way ANOVA, $F_{2,100}$ = 98.00, $p<0.001$, Figure 6.4), with season explaining 65.5% of the observed variation. The mean % seeds in the diet was lowest during the breeding season (28.6%) but with the highest variation, significantly increasing by late summer (88.5%) with a further significant increase in winter to 98.2% (Figure 6.5, Fisher's LSD test ($p<0.05$)).

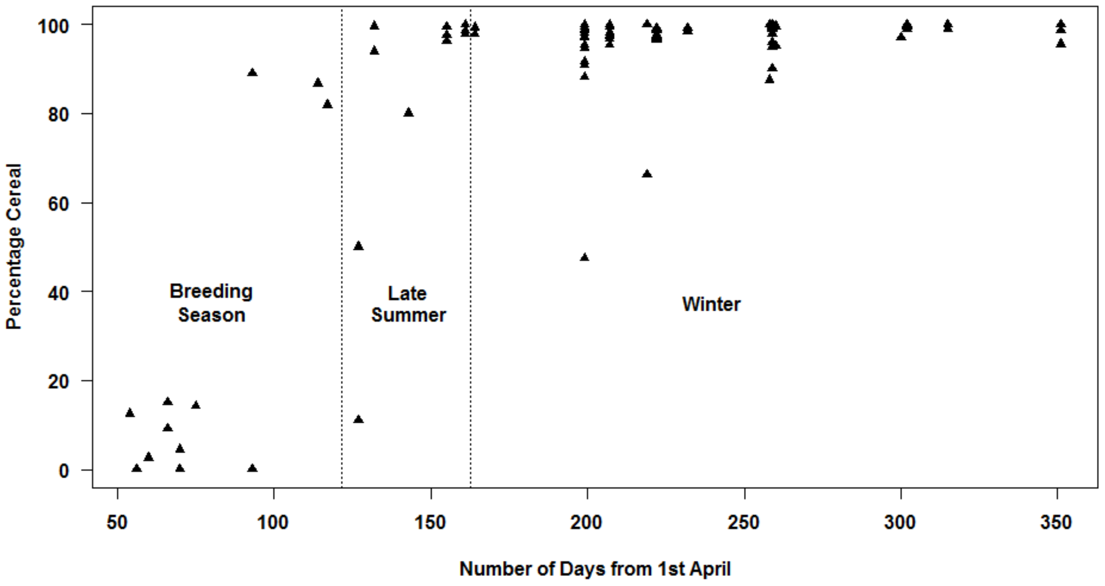


Figure 6.3 Cereal remains as a percentage of the diet in full grown yellowhammer faecal samples in relation to time of year

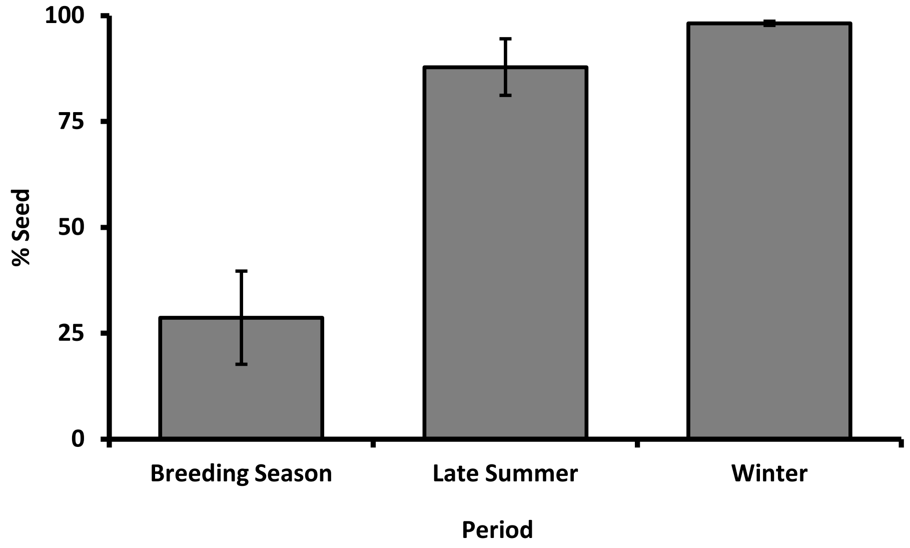


Figure 6.4 Percentage of the full grown yellowhammer faecal samples identified as seed material in relation to time of year (data presented as means ±S.E.)

At the same time as seed (predominantly cereal) use in adult yellowhammers increases from the breeding season through to winter, the richness of invertebrate orders included as part of the diet declines (Figure 6.5). Season explained 32.1% of the variation in the number of invertebrate orders identified in each faecal sample (Figure 6.6, One-way ANOVA, $F_{2,100} = 25.08$, $p < 0.001$), with a significant drop from the breeding season to late summer, and a further decrease in winter ($p < 0.05$, Fisher's LSD tests).

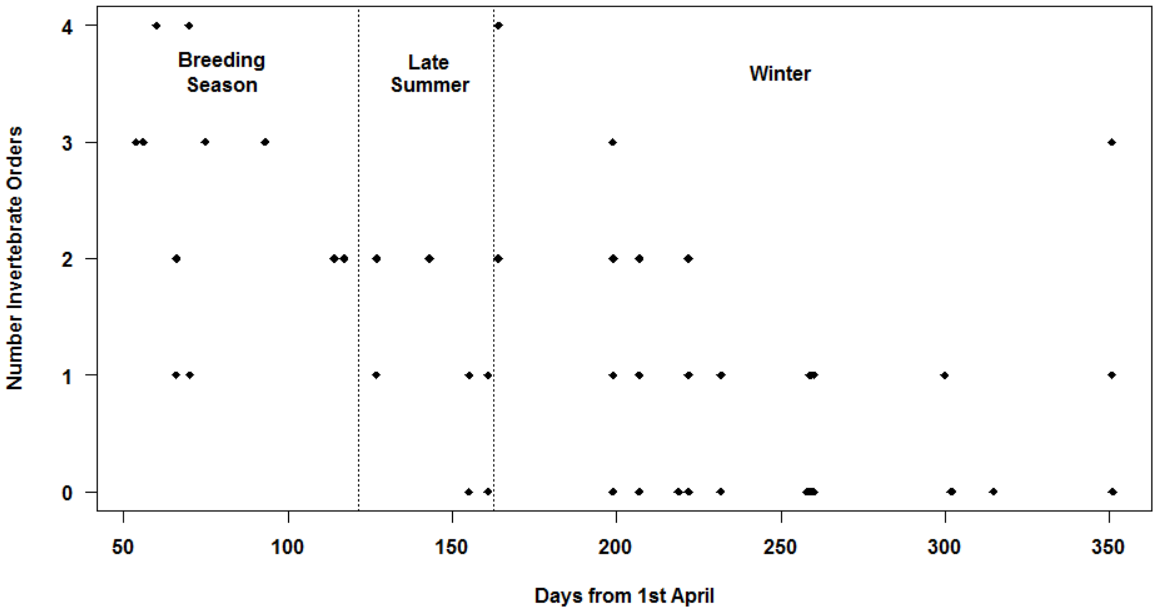


Figure 6.5 Number of invertebrate Orders found to be present in full grown yellowhammer faecal samples throughout the year

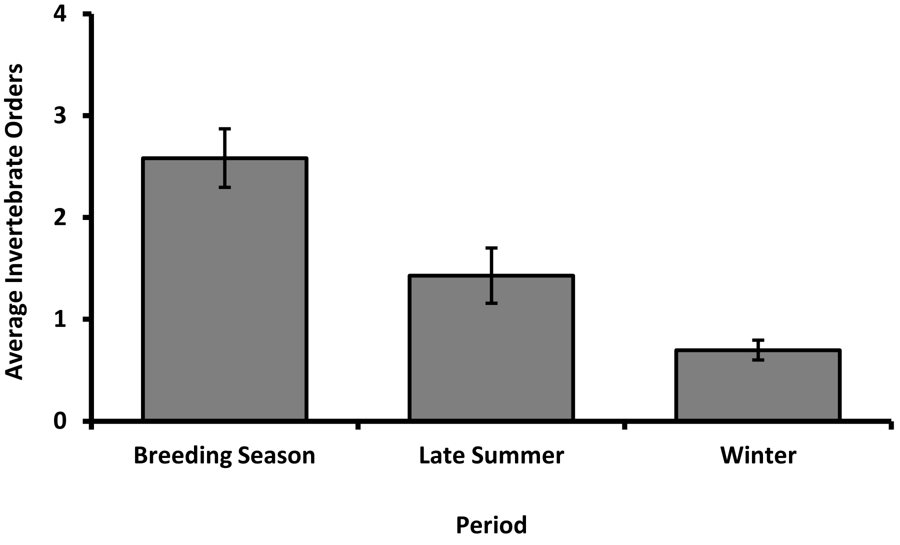


Figure 6.6 Mean number of invertebrate orders present in each adult yellowhammer faecal sample analysed by season ±1 S.E.

Figure 6.7 shows that season was clearly separated along axis 1, with samples from winter having low DCA1 scores (when the diet was dominated by seeds) and summer samples having higher DCA1 scores (summer diet had more invertebrates present than in winter). Summer and winter adult yellowhammer diet were significantly different (envfit, $p < 0.00001$), with season accounting for 32.8% of the observed variation in the diet. The short axis lengths of DCA1 and DCA2 shows there is not much variation between items selected by foraging yellowhammers throughout the year (i.e. there is no complete turn over in the items present in yellowhammer diet as axis shorter than 4 DCA units), however, there was more variation in the types of invertebrates taken in summer than in winter (as the summer samples are more spread out along DCA axis 2 in figure 6.7).

Table 6.1 DCA ordination plot (Figure 6.7) Eigen values and Inertia values for axes 1 – 4

	DCA Axis 1	DCA Axis 2	DCA Axis 3	DCA Axis 4
Eigen values	0.4798	0.2941	0.26184	0.23466
Inertia	48.97%	22.12%	8.16%	4.96%

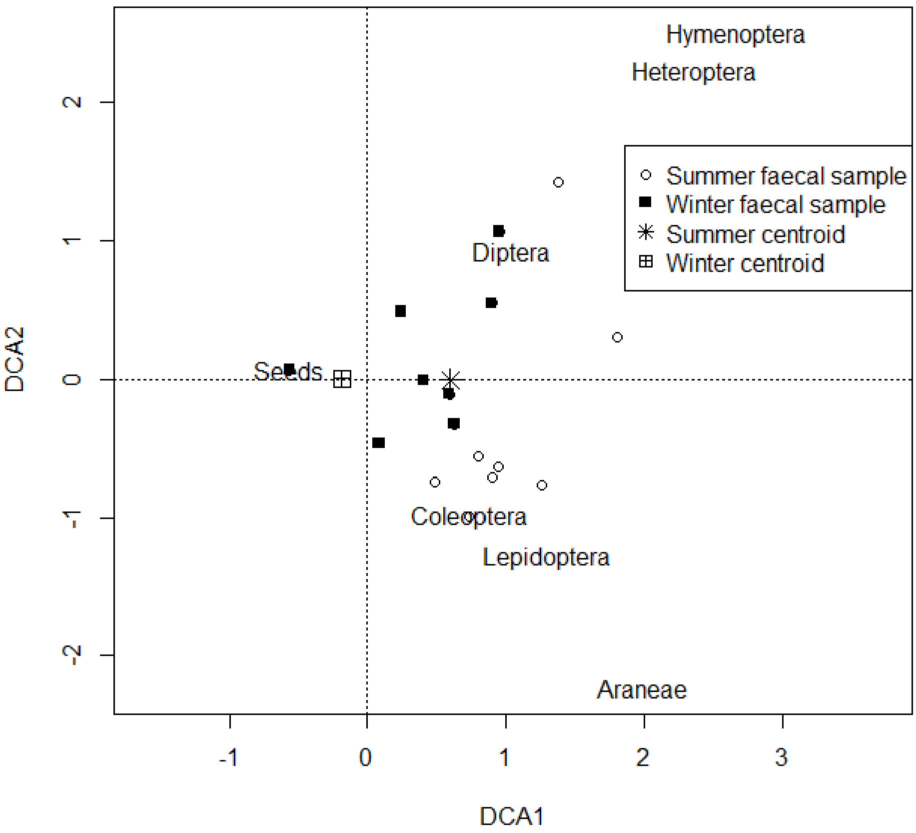


Figure 6.7 DCA ordination plot based on proportion of each dietary item present in full grown yellowhammer faecal samples collected during summer (May – September, n = 27) and winter (October – March, n = 76), with centroids shown for each season. Note that many of the winter points are overlapping

Diptera and Coleoptera were the two most important invertebrate orders taken throughout the year in adult yellowhammer diet in the pastoral study population (Table 6.2). Diptera taken were mostly adult (e.g. tipulid, bibionid) as opposed to larvae (e.g. syrphid), reflecting the relative accessibility of the different stages of the lifecycle of Dipterans to yellowhammers which forage by gleaning invertebrates from vegetation and bare ground. During the breeding season remains of gravid adult female tipulid flies were found in 16.7% of adult summer samples analysed, representing a large proportion, both in terms of numbers and biomass, of the flies taken by foraging yellowhammers. The relative importance of tipulids as a dipteran in summer yellowhammer diet has potentially been underestimated here as a result of only recording presence; tipulids are much larger than other flies identified in the faecal remains, so therefore are likely to have a higher nutritional value. Coleopteran found in faecal samples included weevils, Chrysomelidae and Carabid beetles. Other orders recorded in yellowhammer adult diet included Araneae, Hymenoptera and Heteroptera.

Table 6.2 Presence of dietary items in yellowhammer adult and nestling faecal samples by season. Values for % composition (% seeds etc) indicate the estimated percentage of the sample (by area when spread to a thin layer) that consisted of this category. Percentages in parentheses indicate the percentage of the total number of samples that contained that item. Data for some Orders are further broken down (e.g. into adults and larvae)

	Nestling Breeding Season (n = 17) (May – July)	Adult Breeding Season (n = 12) (May – July)	Adult Late Summer (n = 15) (August – September)	Adult Winter (n = 76) (October – March)
Number of samples containing seed material	7 (41.2%)	9 (75%)	12 (92.3%)	76 (100%)
Mean % seeds in faecal samples (± 1 S.E.)	3.9% (± 1.5%)	28.6 % (± 11.0%)	79.8% (± 9.8%)	98.1% (± 0.5%)
Mean % cereal in faecal samples (± 1 S.E.)	3.6% (± 1.5%)	26.3% (± 10.5%)	78.1% (± 19.7%)	96.7% (± 0.8%)
Mean % of seeds that were cereal seeds (± 1 S.E.)	85.7 % (± 14.2%)	91.6 (± 6.6%)	97.4% (± 1.4%)	98.7% (± 0.7%)
Number of samples containing invertebrates	17 (100%)	12 (100%)	10 (76.9%)	36 (47.4%)
Mean % invertebrate material in faecal samples (± 1 S.E.)	96.1% (± 1.5%)	71.4% (± 11.0%)	20.2% (± 9.8%)	1.9% (± 0.5%)
<u>Number of samples containing:</u> Diptera:	17 (100%)	10 (83.3%)	6 (46.1%)	26 (34.2%)
Adults – all Diptera	17 (100%)	9 (75.0%)	6 (46.1%)	26 (34.2%)
Adults – only Tipulids	4 (23.5%)	2 (16.7%)	1 (7.7%)	0 (0%)
Larvae – all Diptera	2 (11.8%)	1 (8.3%)	0 (0%)	0 (0%)
Coleoptera:	14 (82.4%)	10 (83.3%)	7 (53.8%)	24 (31.6%)
Adults	14 (82.4%)	10 (83.3%)	7 (53.8%)	22 (28.9%)
Larvae	0 (0%)	0 (0%)	0 (0%)	2 (2.6%)
Lepidoptera (larvae)	9 (52.9%)	2 (16.7%)	2 (15.4%)	2 (2.6%)
Araneae:	2 (11.8%)	5 (41.7%)	1 (7.7%)	0 (0%)
Spiders	1 (5.9%)	4 (33.3%)	0 (0%)	0 (0%)
Harvestmen	1 (5.9%)	1 (8.3%)	1 (7.7%)	0 (0%)
Heteroptera	2 (11.8%)	2 (16.7%)	0 (0%)	2 (2.6%)
Hymenoptera	2 (11.8%)	1 (8.3%)	0 (0%)	0 (0%)

The numbers of each invertebrate group in yellowhammer breeding season diet as found by faecal sample analysis of both adult and nestling samples were significantly different from the numbers expected based on numbers of invertebrates greater than 2mm found at 95 known yellowhammer foraging sites sampled during the same period (Figure 6.8, χ^2= 76.22, 6 d.f., p <0.00001). Therefore, adult yellowhammers appear to be actively selecting particular prey items during the breeding season whilst avoiding others. When considering each invertebrate orders individually, a significant difference was found between the numbers of Hemiptera and Coleoptera, (Table 6.3, p values < 0.001) present in the diet as determined from faecal sample analysis compared with the numbers found at known yellowhammer foraging sites, but no significant difference in the numbers of Hymenoptera or Diptera (Table 6.3, p values > 0.05). Figure 6.8 highlights that there were more Coleoptera in the diet than expected whilst there were less Hempitera.

Table 6.3 Results from χ^2 test comparing the number of each invertebrate group separately in breeding season faecal samples with the number of each invertebrate group greater than 2mm found at foraging sites (n = 95) selected by yellowhammers

Invertebrate group	Results from χ^2
Araneae	n/a (expected value < 5)
Hempitera	χ^2 = 40.18, 1 d.f., p < 0.001
Coleoptera	χ^2 = 12.92, 1 d.f., p < 0.001
Hymenoptera	χ^2= 2.46, 1 d.f., p = 0.121
Diptera	χ^2 = 0.22, 1 d.f., p = 0.637
Lepidoptera	n/a (expected value < 5)
'Others'	n/a (expected value < 5)

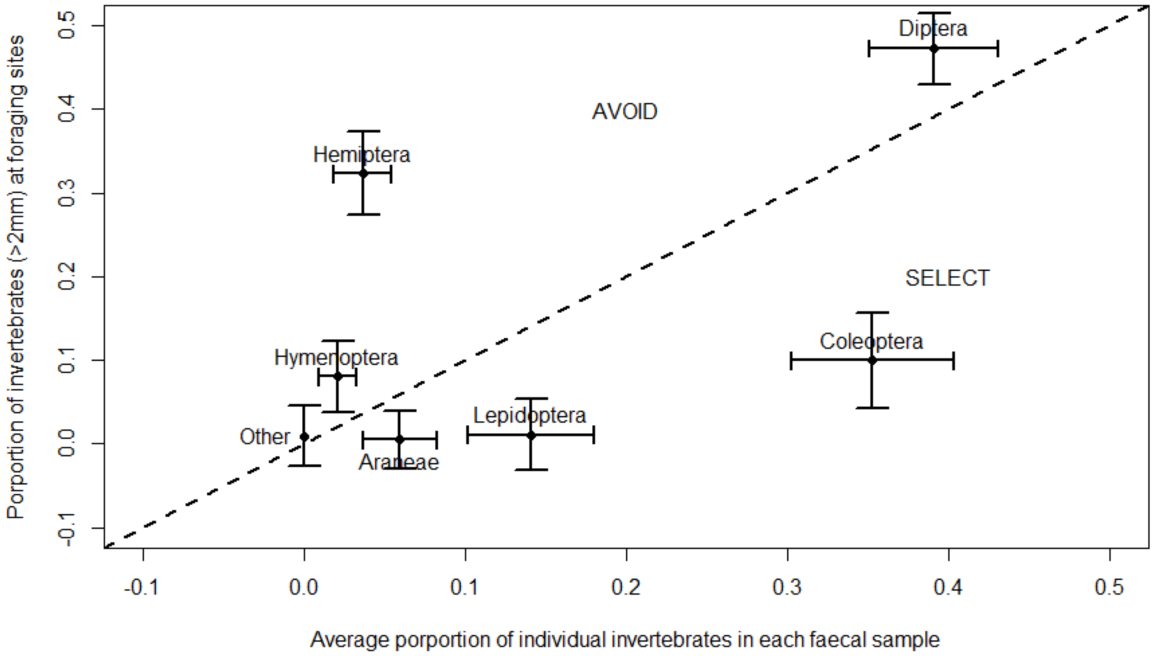


Figure 6.8 Mean proportion of each invertebrate group per summer yellowhammer faecal sample analysed ± 1 S.E. (adults and nestlings samples combined, n = 29) compared to mean proportion of invertebrates at known yellowhammer foraging locations ± 1 S.E. during the same time period (n = 95)

6.3.2 Comparison of adult and nestling yellowhammer diet during the breeding season

The diet of adult and nestling yellowhammer was compared in the breeding season (May to July), although sample sizes were small (17 nestling and 12 adult faecal samples). Significantly more seeds were found in the faecal samples obtained from full grown yellowhammer than in nestling yellowhammer (Figure 6.9 (a), Mann-Whitney U test, $W_{(27)} = 149.5$, $p = 0.029$). However, no significant difference between adults and nestling yellowhammer was found in the number of invertebrate orders per faecal sample (Figure 6.9 (b), Mann-Whitney U test, $W_{(27)} = 80.5$, $p = 0.329$).

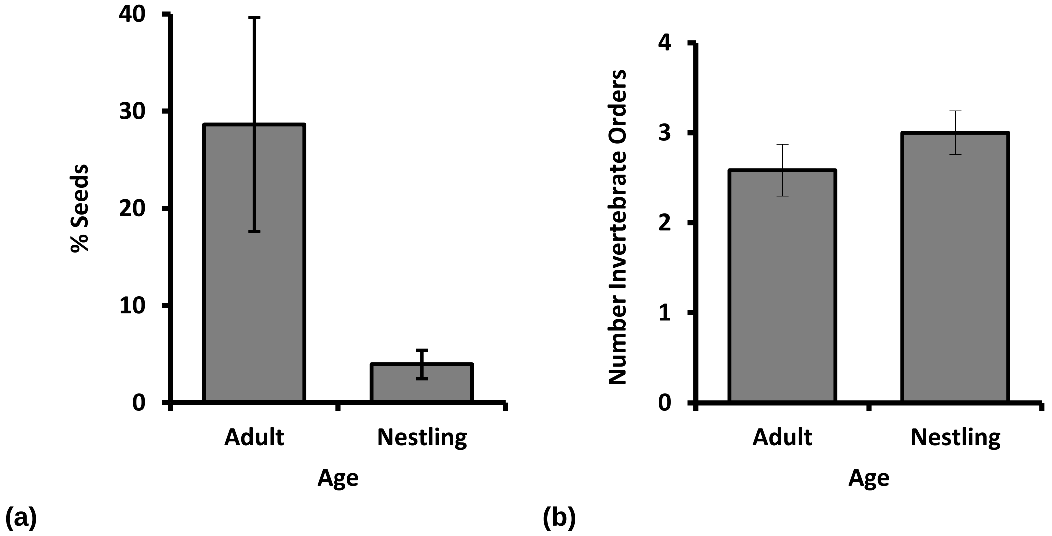


Figure 6.9 Comparison of adult and nestling yellowhammer faecal samples collected during the breeding season. (a) Mean percentage ± 1 S.E. of the sample (by area when spread to a thin layer) that consisted of seeds; (b) Mean number of invertebrate Orders ± 1 S.E. found per sample

No significant difference was found between the numbers of each category of invertebrate per faecal sample during the breeding season diet between adult ($n = 12$) and nestling ($n = 17$) faecal samples (table 6.4, Mann-Whitney U test, all $p > 0.05$).

Table 6.4 Mean number of each invertebrate group per faecal sample in adult and nestling yellowhammer, plus a comparison between number of each present by age category

	ADULT		NESTLING		Results from Mann-Whitney U test
Invertebrate Group	Mean	Standard Error	Mean	Standard Error	
Aranaea	0.33	0.14	0.18	0.18	p = 0.085
Opilone	0.08	0.08	0.06	0.06	p = 0.840
Coleoptera (adult)	1.42	0.34	1.06	0.16	p = 0.541
Diptera (adult)	1.17	0.27	1.65	0.19	p = 0.167
Diptera (larvae)	0.08	0.08	0.18	0.13	p = 0.769
Lepidoptera (larvae)	0.50	0.42	1.00	0.31	p = 0.083
Hymenoptera (adult)	0.08	0.08	0.12	0.08	p = 0.801
Heteroptera	0.25	0.18	0.12	0.08	p = 0.684

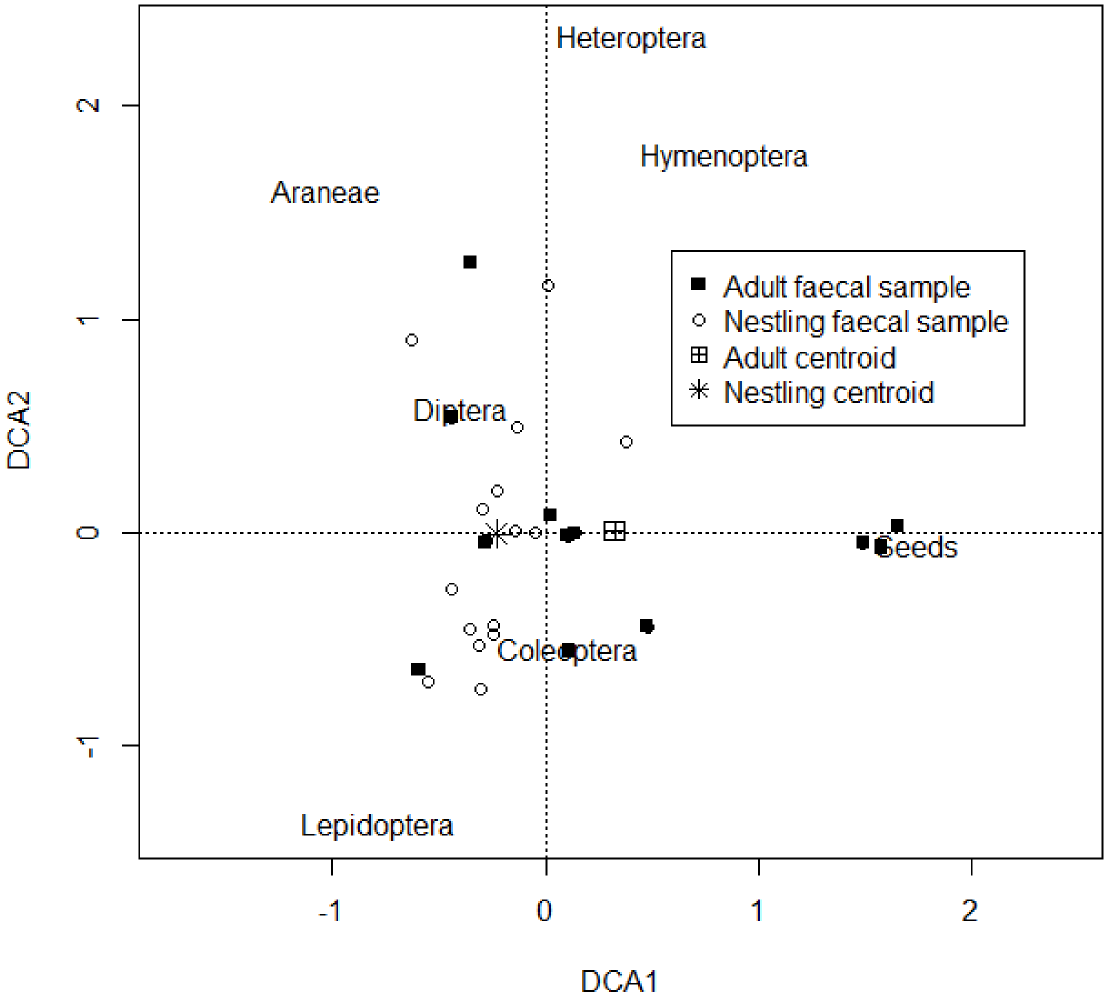


Figure 6.10 DCA ordination plot based on proportion of each dietary item present in yellowhammer adult (n = 12) and nestling (n = 17) faecal samples collected during the breeding season, with centroids shown for the two age categories

The DCA ordination plot (Figure 6.10) of adult and nestling yellowhammer diet during the breeding season yielded Eigenvalues of 0.5469, 0.3405, 0.3077 and 0.22791 for axes 1 – 4, respectively. Age was clearly separated along axis 1, with samples from nestlings having low scores (diet contains more invertebrates) and adult samples having higher scores (diet contains more seeds). The breeding season diet is significantly different for adults and nestlings (envfit, p=0.024), with age accounting for 12.3% of the observed variation in diet. As the DCA1 and DCA2 axes are short (less than 4 DCA units), there is never a total turnover of diet as found from the analysis of yellowhammer adult and nestling faecal samples (i.e. all faecal samples analysed must have a minimum of one item in common with other samples). Complete turnover in DCA analysis occurs at 4 DCA units (Legendre & Legendre 2012).

6.4 Discussion

The study of avian diet through faecal sample analysis is an improvement on the use of field observations to determine diet without being as intrusive or potentially harmful as neck collaring (which allows the removal of whole prey items from the gape of nestlings for identification) or use of chemicals (emetics) to induce regurgitation. However, it can often underestimate small soft bodied prey items (Moreby 1988). Despite potential biases associated with the technique, the results of the faecal analyses presented in this chapter should provide a good evaluation of the diet of yellowhammers since the method has been shown to produce results with this species that are not significantly different from those obtained by neck ligature (Moreby & Stoate 2000). However, the similarities in diet may be a result of both techniques having different limitations that result in similar biases. For example, neck collaring may also underestimate small prey items as they can pass straight through the ligature, and when left in place for too long, food may be disgorged or adults may remove the food from the nestlings gape (Johnson *et al.* 1980).

Most published information on adult yellowhammer diet throughout the year pre-dates agricultural intensification, and while both the analysis of stomach contents and observational studies list extensive use of both invertebrates and seeds (summarised in Cramp & Perrins 1994), this does not indicate whether yellowhammers have such a broad diet in intensively farmed landscapes. Very little recent work has been carried out on adult diet; one small study looked at five faecal samples collected during the breeding season in an arable-dominated region (Stoate *et al*. 1998). Nestling diet has been studied more extensively, perhaps as a result of the relative ease of obtaining samples. Historical diets in traditional low-intensity farming habitats are well summarised in Handbook of the Birds of Europe, the Middle East and North Africa; and there has been several recent studies of nestling diet (e.g. Douglas *et al*. 2012, Macleod *et al*. 2005b, Moreby & Stoate 2000, Stoate *et al*. 1998) all carried out in arable-dominated or mixed farming landscapes with the exception of one Southern English pastoral study (Buckingham 2005). Therefore the present study provides important information regarding current diet of both nestlings and full grown yellowhammers throughout the year in a modern intensive pastoral-dominated farming landscape.

Although this study presents results from a limited sample size, preventing dietary comparisons between narrow time frames and between years, the data are still sufficient to describe differences between broad time or age categories (breeding season/late summer/winter and adult/nestling), especially since elements of the diet varied so much both throughout the year and between age categories. Knowledge of diet variation throughout the year is important to inform future agri-environment schemes for yellowhammers and other granivorous birds, to ensure provision of foraging habitat that meets the birds' requirements throughout the year.

The small sample sizes of faecal samples analysed in this study reflect the difficulty of catching the adults from the low density study population in mist nets, especially during the breeding season when the birds are territorial as opposed to within loose mobile flocks with other granivorous species. Nestling samples were hard to obtain as nests were difficult and time-consuming to locate due to the three dimensional nature of the nest habitat in the study region: vegetated margins, ditches and hedges were often simultaneously found together, thus ensuring nests were well concealed. Additionally, as the anti-predation strategy of nestling yellowhammers results in them leaving the nest before they are fully grown (as early as having their wings still half in pin), a cautious approach was adopted when approaching potential nest sites, especially when hatch date was unknown. As a result, fewer samples were obtained than recent studies of yellowhammer nestling diet (e.g. 144, 97 and 85 faecal samples respectively were analysed in Stoate *et al.* 1998, Buckingham 2005 and Douglas *et al.* 2012, whilst samples from 51 broods were analysed in Macleod *et al.* 2005b).

6.4.1 Adult winter diet

Outwith the breeding season yellowhammers are considered almost exclusively granivorous, primarily eating graminae seeds including cereal, whilst only opportunistically eating invertebrates (Cramp & Perrins 1994, Hoyo *et al.* 2011). Results from the current study and previous work is summarised in Table 6.5.

Table 6.5 Summary of findings from studies of yellowhammer adult winter diet

Study	Location	Methodology	Diet summary
Current	Ayrshire, Scotland	Faecal analysis (n = 76)	98.1% seeds 98.7% of seeds cereal Invertebrate material in 47% of samples Mainly Diptera and Coleoptera Invertebrates - 1.9% of faecal material
Prys-Jones 1977#	Oxfordshire, England	Gullet analysis	Cereal - 60% of sample mass in January, 51% in February. The remainder of diet was grass seeds, especially Festuca and Lolium species
Eber 1956#	Schleswig-Holstein, Germany	Feeding observations (n = 4106)	Cereals - 73% of plant material consumed (September – April). Grass seeds important. 1% invertebrates in February

Results summarised in Cramp & Perrins 1994

As found in previous studies, yellowhammer winter diet in the study population was seed dominated. This was indeed the case with the winter diet: although invertebrates were found in 47% of the 76 winter samples analysed, invertebrate material only accounting for an average of 1.9% of faecal fragment volume, thus invertebrates did not contribute significantly to the winter diet of the Ayrshire yellowhammer study population. The remaining 98.1% of diet consisted of seeds.

Despite previous work showing that the diet of adult yellowhammers includes a diversity of seeds including cereals and other graminae seeds (especially from *Festuca*, L*olium* and P*oa* species), nettle *Urtica dioica*, dock *Rumex spp.*, chickweed *Stellaria media*, mouse-ear *Cerastium fontanum*, vetch *Vicia spp.*, clover *Trifolium spp.* and dandelion *Taraxacum officinale* (Cramp & Perrins 1994), over 96% of the winter diet (and 98.7% of seeds) was cereal within the study population. This is consistent with observations made during the winter surveys that yellowhammers selected the relatively small areas of stubble habitat and game managed habitat where grain is provided throughout the winter, whilst avoiding the dominant grassland habitat.

The observed low winter diet diversity reflects how modern grassland farm management is failing to provide diverse seed rich foraging habitats for yellowhammers (and presumably other granivorous species) in winter, especially considering that historical studies show significant proportions of grass seeds were eaten when grassland management was less intense (e.g. Prys-Jones 1977 & Eber 1956 as reported in Cramp & Perrins 1994). For example, prior to agricultural intensification in Oxfordshire, 60% of yellowhammer gullet and stomach content mass in January was cereal, declining to 51% in February. The remainder of the diet was dominated by grass seeds, especially Festuca and Lolium species (Prys-Jones 1977 as reported in Cramp & Perrins 1994). Between September and April in Schleswig-Holstein, Germany, 73% of plant material in yellowhammer stomach and gullet samples was cereal, especially oats (Eber 1956, as reported in Cramp & Perrins 1994). In the area covered by the present study, grassland accounted for an average of 74.5% of study farm area in winter 2009/10 and 77.7% in winter 2010/11, and was similarly dominant in the surrounding landscape (64.9% of 89.6 km^2 surveyed in winter 2009/10 and 67.1% of 98.4 km^2 in winter 2010/11). The <1% grass seeds found in the winter diet by the faecal sample analysis highlights how unsuitable this dominant habitat is for wintering yellowhammers. Like most modern pastoral landscapes, silage was grown as the fodder crop in the study area. Unlike hay which is harvested annually at the end of summer, silage crops are unable to set seed due to multiple cuts taken throughout the summer months. Pasture fields were intensively grazed throughout the year; by cattle in summer then sheep in winter, resulting in a short uniform sward containing few seed heads. Therefore, modern intensive management of pasture and silage fields has resulted in grasslands becoming a seed-poor foraging resource for birds, especially in winter.

As a result, yellowhammers were observed to avoid grassland (Chapter 4), instead relying on scarcer habitats such as stubble from which to obtain their diet. Winter yellowhammer numbers at each farm significantly correlated with stubble habitat availability (chapter4), suggesting that winter foraging habitat, and hence food availability may be a limiting resource. Modern stubble fields are a poorer seed resource than they were in the past, due to increased efficiency of mechanisation reducing spilt grain, and increased herbicide reducing weed seed availability (Wilson *et al.* 1999). Additionally, stubble fields in spring are often ploughed in and resown before invertebrates and weed seeds become available to foraging birds again. Other potential foraging habitats containing winter cereal available to yellowhammers in the study area include farm buildings where livestock were fed and feed materials were stored, gardens where food was provided for birds (especially in winter) and from areas where game birds such as pheasants and partridges were fed. Yellowhammers are known to utilise farm buildings (pers. obs.), game feeders (e.g. Brickle 1997, pers. obs.) and game crops (e.g. Parish & Sotherton 2004, pers. obs.). Despite yellowhammers showing a slight increase in their use of garden feeders, they were present on 2.3% of weeks of the year across gardens studied as part of the Garden Bird Feeding Study (Chamberlain *et al.* 2005), with yellowhammers generally avoiding gardens in all but the harshest weather. Therefore gardens are not a preferred foraging habitat of yellowhammers. Providing supplementary cereal food at first glance appears to be a suitable and easily implementable solution to the low natural winter food availability in both intensive modern pastoral and arable fields; yellowhammers and other granivorous species have been demonstrated to exploit supplementary food resources (e.g. Siriwardena *et al.* 2007). However, concentrating large numbers of birds round a small food resource such as a feeder or baited site can result in increased disease and parasite transmission; feeder use is associated with increased incidences of salmonellosis, trichomoniasis, aspergillosis and avian pox. These diseases typically lead to the mortality of infected individuals and can have impact on population demographics. For example, the decline of wintering greenfinches *Carduelis chloris* in 2009 in Finland correlates with the arrival of Trichomoniasis (Lehikoinen *et al.* 2013). Trichonomiasis has been demonstrated to be the primary factor causing recent declines in greenfinches across Britain (Robinson *et al.* 2010) whilst also affecting a range of species including doves, pigeons, birds of prey, house sparrows *Passer domesticus* and yellowhammers. Therefore, I suggest that when considering measures to increase winter food availability for wintering granivorous birds, landscape scale solutions where natural food resources are increased over larger areas (e.g. seed rich stubble, final cut silage left in place) should be preferred to the provision of concentrated food sources.

The restricted winter diet of the yellowhammers in the study area, with their heavy reliance on cereals, may leave them vulnerable to future changes occurring in the pastoral-dominated farming landscape. For example, if farmers either further reduce the area of arable crops available in the landscape or improve grain storage, then the already scarce habitats the birds rely on for foraging will decline along with the food resources they depend upon. Perhaps the best solution for the birds would be to encourage farmers to manage the dominant grassland habitat in such a way as to make it more attractive to foraging granivores in winter. For example, in selected areas management could be extensified by reducing grazing intensity, by reverting back to hay production or by leaving areas of silage grassland uncut at the end of the summer to increase seed resources for wintering birds.

6.4.2 Seeds in adult summer diet

In contrast to the birds' diet in winter which was predominantly cereal, seeds only accounted for an average of 28.6% of faecal sample remains during the breeding season, increasing to 79.8% by late summer, with cereal accounting for 91.6% and 97.4% of the seeds respectively. Other species of farmland birds including corn buntings *Emberiza calandra* show this seasonal shift in diet from seed-dominated in winter to including variable amounts of invertebrates in the breeding season (Cramp & Perrins 1994). As no adult yellowhammer samples were obtained between mid March and mid May, it is not known when the switch from a cereal- to an invertebrate-dominated diet occurred. Seed content of adult yellowhammer diet differed from results of some previous studies, summarised in table 6.6

Table 6.6 Summary of findings from studies of yellowhammer adult summer diet

Study	Location	Method	Diet summary
Current	Pastoral dominated, Ayrshire, Scotland	Faecal analysis (n = 27)	Seeds present in 75% samples 28.6% of diet May – Jul, 79.8% Aug - Sep 96.1% of seeds cereal Invertebrates present in 100% samples May – Jul, 76.9% Aug – Sept Important orders: Coleoptera, Diptera, Lepidoptera & Araneae.
Stoate *et al.* 1998	Arable dominated, Leicestershire, England	Faecal analysis (n = 5)	100% cereal
Holland *et al.* 2006	Slovakia	Literature review	77% invertebrate and 23% plant material
Eber 1956#	Schleswig-Holstein, Germany	Observation (n = 247)	Invertebrates - 53% of items June – Aug. Seeds – Lolium, Poa & dandelion.
Prys-Jones 1977#	Oxfordshire, England	Stomach analysis	Seeds – present in 80% of samples
Inozemtsev 1962#	Moscow, Russia	Stomach analysis (n =34)	56.5% of items seeds (of which 21.1% wheat and oats)

Results summarised in Cramp & Perrins 1994

The proportion of cereal eaten in summer by the study population is lower than that found in an analysis of the diet of five adult yellowhammers caught in June on breeding territories on intensive arable farmland in Leicestershire, England, in which faecal analysis found the diet to be 100% cereal (Stoate *et al.* 1998). Although sample sizes in both studies were small, there are clear differences in adult diet: all adult samples analysed in the current study contained invertebrate material whereas no samples did so in the Leicestershire study. However, not all previous work on the summer diet of adult yellowhammers has found them as reliant on cereal: a Slovenian study reported the diet to be composed of 77% invertebrate and 23% plant material (results summarised in the review by Holland *et al.* 2006), very similar to the 71.4% invertebrate material and 28.6% seed material in the current study.

Studies carried out prior to agricultural intensification also report invertebrates as an important component of the adult yellowhammer diet in summer. For example, between June and August invertebrates accounted for 53% of 247 observations of the prey taken by adult yellowhammers in northern Germany (Eber 1956, as reported in Cramp & Perrins 1994). Analysis of Yellowhammer stomach and gullet contents between April and June from England yielded 20%

by volume seeds, of which only half of which were cereal, with seeds absent from 20% of samples (Prys-Jones 1977, as reported in Cramp & Perrins 1994), whilst in Moscow, 56.5% of summer items were seeds, of which 21.1% were wheat and oats (Inozemtsev 1962, as reported in Cramp & Perrins 1994). As both invertebrate and seed food resources were more abundant prior to agricultural intensification (e.g. Wilson *et al.* 1999) when yellowhammer populations were not declining (Marchant *et al.* 1990), this suggests that the summer breeding season diet of the adult yellowhammers in the study area is of sufficiently high quality since it is more similar to historical diet studies and the Slovenian diet study (see Holland *et al.* 2006), (where yellowhammer populations are more stable, possibly as a result of the lower levels of agricultural intensification experienced in Eastern Europe compared to Western Europe) than the recent English study (Stoate *et al.* 1998) carried out in a landscape where yellowhammers are declining. Invertebrates are generally considered a more nutritious food resource than seeds, containing a higher calorific and protein (Capinera 2010) content per unit weight. The diverse diet of the Ayrshire adult yellowhammers compared to the recent British study suggests that the Ayrshire study population could be more resilient to future changes in summer food availability, as unlike in Leicestershire where adult diet was found to be 100% cereal (Stoate *et al.* 1998) they are not dependent upon a single food item.

6.4.3 Seeds in nestling diet

Seeds were present in fewer nestling than adult summer faecal samples analysed (41.2% compared with 75.0%) and accounted for a smaller proportion of breeding season diet (3.9% compared with 28.6%). Cereal accounted for the majority of seeds present in the diet of both age categories, but nestlings were fed a higher proportion of non-cereal seeds (85.7% of nestling seeds were cereal compared with 91.6% in adult samples). Not only did the nestling yellowhammer diet contain significantly lower levels of seeds and cereal than the diet eaten by the adults, the levels of cereal provisioned to the nestlings in the study population were lower than that found in other recent studies of yellowhammer nestling diet, results summarised in table 6.7 below.

Table 6.7 Seeds found in yellowhammer nestling diet, a summary of results from various studies

Study	Farming type and Location	Methodology	Seeds in diet
Current	Pastoral dominated, Ayrshire, Scotland	Faecal analysis (n = 17)	41.2% samples contained seeds, 3.9% of diet. 85.7% seed material cereal
Stoate *et al*. 1998	Arable dominated, Leicestershire, England	Faecal analysis (n = 144)	85% and 68% of samples contained cereal accounting for 42.1% and 33.7% of diet respectively
Buckingham 2005	Pastoral dominated, Devon & West Midlands, England	Faecal analysis (n = 97) and direct observation	Seeds: wide ranges of seed use, from 0% to nearly 100% 87% dietary seeds ripening cereal
Douglas *et al*. 2012	Arable, Aberdeenshire, Scotland	Faecal analysis (n = 85)	Seeds present 72% samples 34.6% of diet
Macleod *et al*. 2005b	Mixed, Angus, Scotland	Faecal analysis (n = 51 broods)	13.4% vegetation Predominantly cereal
Collinge 1924 – 7#	England	Stomach analysis (n = 17)	No plant material recorded
Eber 1965#	Schleswig-Holstein, Germany	Observation	No plant material recorded
Levin & Gubin 1985#	Ural Valley, Kazakhstan	Neck ligature (n = 10)	No plant material recorded
Bösenberg 1958#	Eastern Germany	Neck ligature (n = 124)	Wheat (6%), Barley (4.8), Sunflower (2%). Oats (1%)

Results summarised in Cramp & Perrins 1994

Levels of cereal provisioned to the nestlings in the study population were lower than that found in other recent. For example, samples collected in 1993 in an arable-dominated region in England 85% of nestling faecal samples contained cereal remains, accounting for 42.1% of diet, whilst in 1995 the corresponding values were 68% and 33.7% (Stoate *et al. 1998*). In Scotland, seeds were present in 72% of nestling faecal samples collected from an arable dominated area, accounting for an average of 34.6% of the diet (Douglas *et al*. 2012).

The lower proportion of cereal (and consequently higher proportion invertebrate material) provisioned to the nestlings in the present study population is probably advantageous, since not only are invertebrates more readily digestible, they have a higher nutritional value per unit weight, in terms of calories, protein and other nutrients (Capinera 2010), important for rapidly growing nestlings. Previous work has demonstrated that the proportion of arthropods in the diet is positively correlated with the body condition of nestling yellowhammers aged six days old (Hart *et al*. 2006) and at fledging (Douglas *et al*. 2012). Indirect evidence for the importance of invertebrates in the diet of nestlings comes from the finding that the breeding success of Yellowhammers is higher during dry, warm and sunny weather (a surrogate for invertebrate availability) (Bradbury *et al*. 2003) whilst nestling mortality is increased during cold weather (Stoate *et al*. 1998). Moreover, the extent of brood reductions in Yellowhammer nests increases with the amount of nearby foraging habitat recently sprayed with insecticides (Boatman *et al*. 2004), and nestlings of pairs breeding on land recently sprayed with pesticides have a lower body condition than those of pairs breeding on untreated territories (Morris *et al*. 2005). This is a direct result of the reduction in invertebrate availability (and hence nestling food) after pesticide applications.

As nestlings in the study population were fed a high proportion of invertebrates, this suggests pastoral farmland provides suitable foraging habitat for yellowhammers in the breeding season when compared to modern arable farmland. However, the level of cereal present in the nestling diet was perhaps still higher than ideal; historical studies report either no seed at all, or significantly lower levels than modern studies. For example, 13.8% of items from 124 collar samples from nestlings from Eastern Germany were seeds (Bösenberg 1958, as reported in Cramp & Perrins 1994), whilst no plant material was found in other studies (Collinge 1924-7, Levin & Gubin 1985 & Eber 1965, as reported in Cramp & Perrins 1994). These studies were conducted prior to agricultural intensification, when bird populations were stable and invertebrates and seeds were more abundant, suggesting that the preferred and more suitable diet is dominated by invertebrates. Therefore, it is probable that the nestling diet reported in modern studies (including the current one) contains more seed material (especially cereal) than is optimal for nestling yellowhammers, perhaps leading to a decrease in the fitness of the resultant fledglings. An alternative explanation is that the advances of cereal phenology (with the move from spring to autumn sowing) has allowed ripening cereal to become available as a food source for breeding yellowhammers where it was not available in the past. Nestling diet quality is important as a poor diet in the nest can have lifelong negative impacts. Despite appearing similar as adults, zebra finches *Taeniopygia guttata* fed a poor quality diet as nestlings (and thus experienced a reduced growth rate) have significantly greater mortality as adults (Birkhead *et al.* 1999) thus nestling diet quality has the ability to influence population demograhphy. Additionally, sex biases may occur; for example in zebra finches, have sex-baised (female) mortality of nestlings during periods of restricted food availability (Kilner 1998), with females on a low quality diet during egg laying had more male chicks (Bradbury & Blakey 1998). Clutch size may be reduced as seen in both wild great tits *Parsus major* and captive zebra finches (Haywood & Perrins 1992) and decreased levels of antioxidants regardless of quality of diet as adults (Blount *et al.* 2003).

6.4.4 Comparison of adult and nestling summer diet

Although no significant difference was found between the types of invertebrates present in adult and nestling yellowhammer faecal samples (possibly due to small sample sizes and insufficiently detailed identification), the diet of adults in the breeding season contained significantly more seed material than did that of the nestlings. This might indicate that invertebrates were a limiting resource within the study area, as not only was the amount of grain found in both adult and nestling diets higher than in studies carried out prior to agricultural intensification, but adults appear to be preferentially feeding invertebrate material to their young whilst supplementing their own diet with lower quality food items (seeds). A low quality adult diet during the breeding season and late summer may restrict the ability of yellowhammers to meet the energetic demands of expensive activities such as provisioning young, egg formation and moult, or may force them to trade off these demands against self maintenance and hence their own long term survival (Stearns 1992). Diptera, Coleoptera, Lepidoptera and Araneae were the orders most commonly present in the diet of both nestlings and adults in summer. Significantly more Coleoptera were found in yellowhammer summer diet than expected based on availability at known yellowhammer foraging locations. This may be a result of increased probability of detecting hard bodied coleopteran in faecal samples than the other invertebrate orders; faecal sample analysis found higher Coleoptera in dunnock *Prunella modularis* nestling diet in a comparative study with neck ligature (Moreby & Stoate 2000). The hard bodied nature means they are likely to pass through relatively undigested, perhaps this resulting in them being over represented in faecal samples compared to other taxa. Alternatively, yellowhammers were actively seeking in habitats not sampled. The importance of Diptera in yellowhammer diet may have been underestimated as a result limitations of faecal analysis; their soft bodied nature means few identifiable fragments remain undigested (Moreby & Stoate 2000).Invertebrates present in both yellowhammer adult and nestling diet during the breeding season was similar to results from previous studies, summarised in table 6.8.

Table 6.8 A summary of results of invertebrates in yellowhammer adult and nestling diet during the breeding season from dietary studies

Study, Farming type and Location	Method	Age	Summary of dietary invertebrates
Current, Pastoral dominated, Ayrshire, Scotland	Faecal analysis (n = 17)	Nestling	96.1% of identifiable material, present in 100% of samples. Most commonly consumed: Diptera (present in 100% samples), Coleoptera (82.4%) & Lepidoptera larvae (52.9%)
Stoate *et al.* 1998, Arable dominated, Leicestershire, England	Faecal analysis (n = 144)	Nestling	Coleoptera, Lepidoptera larvae, Araneae & Tipulidae most important
Buckingham 2005, Pastoral dominated, Devon & West Midlands, England	Faecal analysis (n = 97) & direct observation	Nestling	Coleoptera, Diptera, Orthoptera, Lepidoptera, & Symphyta larvae most important. Caterpillars & Orthoptera contributed greatest biomass
Douglas *et al.* 2012, Arable, Aberdeenshire, Scotland	Faecal analysis (n = 85)	Nestling	Present in 100% of samples. Diptera (38.2% of all invertebrate items), Coleoptera (30.9%), Lepidoptera (13.6%), Arachnida (10.1%), other invertebrates (2.4%).
Macleod *et al.* 2005b, Mixed, Angus, Scotland	Faecal analysis (n = 51 broods)	Nestling	Coleoptera (34.2%), Diptera (31.6%), Arachnida (11.6%) & Lepidoptera (8.0%) most important orders
Eber 1965[#], Schleswig-Holstein, Germany	Observations	Nestling	Orthoptera, Lepidoptera, Diptera & snails most important invertebrates
Levin & Gubin 1985[#], Ural Valley, Kazakhstan	Neck ligature (n = 10)	Nestling	Odonta, Lepidopterra (adult and larvae) & Coleoptera
Bösenberg 1958[#], Eastern Germany	Neck ligature (n = 124)	Nestling	Lepidoptera (29.3%), Coleoptera (22%), Diptera (10.8%), Earwigs (6%), Arachnida (5.2%), Orthoptera (3.6%), woodlice (2%), snails (1%)
Current, Pastoral dominated, Ayrshire, Scotland	Faecal analysis (n = 12)	Adult	Invertebrate present in 100% of samples, 71.4% material. Coleoptera, Diptera & Araneae most important orders.
Khokhlova 1960[#], Ukraine	Stomach analysis (n = 49)	Adult	Lepidoptera larvae & Coleoptera were most abundant
Tarashchuk 1953[#], Ukraine	Stomach analysis (n = 39)	Adult	Lepidoptera and Orthoptera most important

[#] Results summarised in Cramp & Perrins 1994

Despite the broad similarities to previous studies in the types of invertebrates eaten, some differences are apparent. For examples, Ayrshire yellowhammer nestlings were fed no Mollusca, previously reported as an important component of the diet (e.g. Macleod 2001, Stoate *et al.* 1998 and Buckingham 2005), nor were they fed adult Lepidoptera, which in Leicestershire accounted for a third of Lepidopteran prey items fed to nestlings (Moreby *et al*. 2001). However, those studies were carried out in predominantly arable landscapes, in which the invertebrate communities present would have differed, perhaps accounting for the observed differences in diet. A study of nestling diet in pastoral farmland in southern England found Orthoptera and Lepidoptera larvae to be the most important prey items in terms of biomass (Buckingham 2005), which contrasts with the present study where no Orthoptera remains were found in either nestling or adult faecal samples, despite the similarity in habitat. Climatic differences may account for the dietary disparity; Ayrshire is further north and hence cooler, resulting in lower densities of Orthoptera than in England (Marshall & Haes 1988). It is unlikely that Orthoptera were present in the study area but not chosen as no Orthoptera were found as part of the 13,060 invertebrates collected and identified from the 95 yellowhammer foraging locations studied or the 95 control sites (see chapter 3). Orthoptera have been found to be an important summer food item for similar granivorous farmland birds including cirl buntings *Emberiza cirlus* (Evans *et al*. 1997).

Tipulidae were a commonly found Dipteran Prey item in faecal samples collected in the present study from nestlings and adults in summer. Tipulidae are now less common in pastoral habitats than historically, due to an increase in the use of pesticides to control their numbers, limiting economic loss caused by their larvae feeding on roots and the base of stems (Blackshaw and Coll 1999). This reduction of Tipulidae has been implicated in the decline in the UK’s starling population (Robinson *et al*. 2005), as in summer Tipulidae larvae are their main prey item for provisioning nestlings (Rhymer *et al*. 2012). Despite the reduced availability of Tipulidae in modern grasslands, the summer diet of adult yellowhammers in the present study still contained proportionately more Tipulidae (and other Diptera) than has been recorded in their diet prior to agricultural intensification. For example, in Russia only 1% of dietary items were Diptera, all of which were Tipulidae (Inozemtsev 1962, as reported in Cramp & Perrins 1994) despite Diptera being important in nestling diet (e.g. Eber 1956 & Bösenberg 1958 as reported in Cramp & Perrins 1994).It is possible that Diptera are more important for nestling yellowhammers than for adults, since their soft bodied nature should make them readily digestible to chicks. The difference between modern and historical studies in the invertebrates present in the diet of yellowhammers suggests that they have adapted their diet in response to the changes in invertebrate abundance and community composition brought about by agricultural intensification. Lepidoptera and Coleoptera accounted for a mean of 14.1% and 35.2% of invertebrate items identified per summer faecal sample, respectively, whilst only accounting for a mean of 1.1% and 10.0% of each sweep sample at foraging sites (see Chapter 4). There is no evidence that Diptera were either selected or avoided relative to availability by foraging yellowhammers.

No Collembola were recorded in either the diet of adult or yellowhammer nestlings in this study, possibly as a result of limitations of faecal analysis as opposed to a genuine absence from diet; Collembola have previously been recorded in yellowhammer diet (Cramp & Perrins 1994) and were available in large numbers in the dominant pastoral habitat. Collembola, known to be eaten by grey partridge *Perdix perdix* (from crop samples) were not recorded in the diet through faecal sample analysis as their soft bodied nature reduced the likelihood of identifiable fragments passing through in faecal samples (Moreby 1998).

6.4.5 Pastoral dominated farming landscapes as a foraging habitat for granivorous birds

This analysis of yellowhammer faecal samples highlighted how reliant the birds were in winter on cereal as a seed resource, and therefore how unsuitable the dominant pastoral habitat was in its current state in winter. Winter food availability not only affects survival parameters (Newton 2013), it can additionally influence breeding success as animals arriving at the breeding season in poor condition are less able to invest in energetically expensive breeding activities such as egg production and parental care (e.g. Gunnarsson *et al*. 2005, Bogdanova *et al*. 2011). Results from the analysis of summer faecal samples indicated that the pastoral landscape provided a reasonable summer diet when compared to diets recorded on modern intensive arable farmland as they contained less cereal than other studies. Cereal has been demonstrated to have a negative impact on yellowhammer nestling fledgling condition (Douglas *et al*. 2012). However, this effect may have been a correlate with poor weather conditions (cold, wet) reducing invertebrate activity and thus their accessibility to foraging yellowhammers. However, the diet in the pastoral study population may be limiting with respect to the availability of large prey items important for nestlings such as Coleoptera, Lepidoptera larvae and Orthoptera. Future agri-environment schemes designed to provide food-rich foraging habitats throughout the year for yellowhammers and other granivorous species should aim to increase the availability of grass and other weed seeds in winter, for example by leaving areas of silage uncut at the end of summer, limiting the grazing intensity and encouraging farmers to grow hay over silage in some areas. The latter two options would have the additional advantage that they would tend to increase the availability of invertebrates during the breeding season. An alternative regime would be to increase the area of arable crops grown and then left as winter stubble within pastoral landscapes, which would provide additional winter foraging habitat for granivores whilst the increase in landscape heterogeneity would have further biodiversity benefits. Yellowhammers have already been demonstrated to have higher breeding densities in areas of mixed farming compared to pastoral-dominated farmland (chapter 2). The advantage of a mixed landscape is that it provides suitable invertebrate-rich foraging habitat for the summer and seed-rich foraging habitat for the winter in relatively close proximity to each other; bird ringing studies have shown that ~70% of Britain’s locally resident yellowhammer population winters within 5km of their breeding territories in Britain (Cramp & Perrins 1994).

In conclusion, the summer diet of the yellowhammers studied in the pastoral-dominated farming landscape of Ayrshire contained less seeds in summer than their arable and mixed farming counterparts, replaced the seeds with an increased proportion of invertebrates, whilst having a similar cereal-dominated diet in winter. In order to increase the suitability of pastoral farming landscapes to yellowhammers and other granivorous birds, this study suggests that in winter suitable seed-rich foraging habitat is a limiting resource, as may be a suitable abundance of large invertebrates in the breeding season, especially Coleoptera and Lepidoptera. Improving the availability of suitable foraging habitat for yellowhammers throughout the year would help reverse population declines of yellowhammers and other similar species of granivorous farmland birds.

Chapter 7 – General Discussion

7.1 Yellowhammer ecology in a pastoral dominated farming landscape

Results on yellowhammer *Emberiza citrinella* presented in this thesis supports Siriwardena *et al*. 2008 hypothesis that late winter food availability is limiting farmland birds. Stubble, previously shown to be important for graniverous farmland birds including yellowhammers (e.g. Robinson & Sutherland 1999, Moorcroft *et al*. 2002, Perkins *et al*. 2008), a rare habitat within the study region, was positively correlated with winter yellowhammer density. Habitat preference switched from stubble and unmanaged to game managed as winter progressed, presumably as a result of depleted seed resources in stubble. Grassland, the dominant habitat was avoided; winter diet was 98% cereal, highlighting the unsuitability of this habitat. Supplementary food attracted wintering yellowhammer increasing the numbers at a site compared with the previous winter. Grain use increased as winter progressed despite presumably highest energy requirements mid winter, suggesting natural food in late winter is limited. Yellowhammer population declines are thought to be the result of low winter survival (Baillie *et al*. 2001). Ratios of juveniles to adults declined as winter progressed, but not where supplementary feeding was provided suggesting this may positively influence first year survival rates. Lower first year survival may be a result of inexperience; young birds are less efficient foragers than adults (e.g. Goss-Custard & Le V. Dit Durrel 1987, Greig *et al*. 1983). Alternatively, age categories may demonstrate different habitat preferences or dispersal propensities. Previous work has found no significant difference in mortality rate between adults and first years (Siriwardena *et al*. 2000b), contrary to the results suggested by this study. Survival rates have the potential to influence population trends; yellowhammers experienced lower survival during a period of population decline compared with stable or increasing populations (Siriwardena *et al*. 2000a).

Breeding density was lower than in arable and mixed farming regions. However, pastoral- landscapes are important as they are widespread throughout the yellowhammer's range. There was no evidence that foraging yellowhammers avoided grassland during the breeding season. As in previous studies (e.g.

Perkins *et al*. 2002, Morris *et al*. 2001, Stoate *et al*. 1998), margin habitat close to boundary features was selected. A high ratio of first years to adults suggesting high breeding success and post fledgling survival, suggesting suitable breeding habitat was available. Further evidence for this came from the high invertebrate and low cereal diet provisioned to nestlings; previous work has found increased fledgling condition correlated with increased proportion of dietary invertebrates (Douglas *et al*. 2012). Breeding season diet contained more Lepidopteran larvae and Coleoptera than predicted based on prey availability at foraging sites.

7.2 Granivorous bird conservation in pastoral dominated farming landscapes

In light of the results presented in the thesis, I suggest agri-environment schemes in pastoral regions should aim to increase seed-rich winter foraging habitat availability, as opposed to the provision of breeding habitat, because winter foraging habitat appears limiting in the study landscape. Care must be taken to ensure that foraging habitat provided contains sufficient seed resources to last throughout the winter as the birds currently seem especially limited by natural food availability in late winter.

Agri-environment schemes will provide the main mechanism for implementing positive habitat management to benefit wintering granivorous birds in pastoral landscapes. As stubble habitat is rare within a pastoral agriculture landscape (chapter 4), with yellowhammers moving away from this preferred foraging habitat in late winter presumably as a result of declining profitability, I suggest that pastoral farmers should be encouraged through agri-environment schemes to increase production of spring sown crops and to leave winter stubble. Increased arable habitat availability in grassland landscapes has been found to be associated with higher breeding populations of not only yellowhammers but also grey partridge *Perdix perdix*, skylark *Alauda arvensis*, tree sparrow *Passer montanus*, corn bunting *Emberiza calandra* and reed bunting *Emberiza schoeniclus* (Robinson *et al*. 2001) so a number of species including yellowhammers would benefit. There is little evidence that the presence of stubble negatively influences populations of farmland birds, however, the rook *Corvus frugilegus*, not a species of conservation concern in the UK (Eaton *et al*. 2009), responds negatively to the presence of stubble (Gillings *et al*. 2005). It has been hypothesised that yellowhammers are unable to exist in landscapes where cereal production is below a certain threshold (Kyrkos *et al*. 1998), accounting for the recent range contractions experienced by yellowhammers in the pastoral dominated northern and western regions of Britain.

Where increasing the proportion of stubble habitat that is available within a pastoral-dominated landscape is impractical or unpopular, increasing the profitability of existing stubble habitat as a foraging resource should be considered. Stubble habitat can vary in attractiveness as a foraging habitat in two main ways, through food availability (seed density) and through stubble height. Both of these impact on food intake rates and hence the profitability of the habitat for foraging birds. Longer stubble results in an increased predation risk and reduced food intake rate for chaffinches *Fringilla coelebs* - a model organisms for small graniverous passerines - as a result of the increased need for vigilance (Whittingham & Evans 2004). Therefore, to increase profitability, short stubble lengths should be used. However, not all species will benefit from short stubble; grey partridge prefer longer stubbles (Butler *et al*. 2005) possibly as a result of their anti-predation strategy. Unlike small graniverous passrerines that flee to cover, grey partridge rely on crypsis to avoid predation (Butler *et al*. 2005) To increase seed availability, farmers could be paid to leave strips of cereal unharvested round the margins of arable fields as a seed resource for wintering granivores. Leaving the edges of fields unharvested would be ideal for granivorous species such as yellowhammers, chaffinches and reed buntings which forage preferentially in margin habitat as a result of their anti predation strategy, but would be less beneficial, although not detrimental, for skylarks which preferentially foraging in the centre of fields (Vickery *et al*. 2002). An alternative to leaving strips unharvested to increase the amount of winter food available would be to encourage weedier stubble by restricting the amounts of herbicides applied (e.g. Bradbury *et al*. 2008); many species that forage within stubble habitat in winter should benefit from this measure as a result of the increased food availability, no negative consequences are anticipated.

Wild bird seed mix/unharvested crop (which can include kale *Brassica olerancea*, cereals, linseed *Linium isitatissimum*, millet and sunflower *Helianthus annuus*) have also been introduced as an agri-environment option in Scotland and

England to provide a source of winter seeds for granivorous birds. Wild bird cover crops would benefit pastoral populations of yellowhammers, but to date they have proven unpopular with farmers for practical reasons, demonstrated by the low uptake rate.

Although grasslands were largely avoided by yellowhammers in winter throughout this study, they don't necessarily have to be a poor foraging habitat for yellowhammers. It is thought that the current management of modern grasslands with regular defoliation reduces food availability for graniverous birds (Buckingham *et al.* 2006). Extensification of grassland management (through reducing stocking density and/or reverting back to hay production) would increase the amount of seeds available in winter to granivorous birds as less frequent defoliation would allow seed heads to develop and set. It is not only yellowhammers that would benefit; all granivorous species should benefit from the increase in food availability (Buckingham *et al.* 2006) and extensive grasslands have been demonstrated to contain higher diversity and abundance of birds than intensively grazed and fertilised grasslands (Verhulst *et al.* 2011). However, species such as starlings *Sturnus vulgaris* that forage on invertebrates may not benefit from such extensification, as they preferentially select shorter swards for foraging (Buckingham *et al.* 2006). Extensification is unlikely to be a popular option with farmers; instead, strips of unharvested silage could be left over winter round the edges of fields. Trials have demonstrated that these attract large numbers of granivorous buntings including yellowhammers in winter (Buckingham & Peach 2006). However, skylarks would not benefit from such a measure due to their preference to forage in field centres. It has not yet been trialled if leaving similar patches of unharvested silage in the centre of fields would be of benefit to them (Buckingham & Peach 2006).

An alternative, cheap potential solution to the late winter hunger gap where increasing the provision of stubble or planting game crops is impractical would be to supply granivorous birds directly with supplementary grain in winter. Supplementary feeding attracted a large number of yellowhammers to a pastoral farm previously avoided in winter (Chapter 5), presumable as a result of a lack of profitable winter foraging habitat. The success of the feeding stations in attracting yellowhammers is probably in part due to their location near cover.

Previous studies have shown that yellowhammers are more likely to use supplementary feeding located near cover (Siriwardena & Stevens 2004) with yellowhammers preferentially foraging in margin habitat throughout the year (e.g. Perkins *et al*. 2002, Morris *et al*. 2001, Stoate *et al*. 1998, Cramp & Perrins 1994).

Given that yellowhammers in early winter were shown to prefer more natural foraging habitat (stubble) compared with their preference in late winter (game-managed habitat with feeders), and that grain consumption at the feeding stations increased throughout the winter, it may be possible to save on costs by implementing supplementary feeding stations only during the late winter period where natural food resources are at their most depleted. However, more research needs to be carried out to look at the impacts of timing of supplementary food provision. As yellowhammers appeared to range further in the early winter period (Chapter 4), it may be possible that for the scale over which the supplementary feeding benefits to be maximised. The supplementary food must be present in the early winter for the birds when the birds are ranging furthest, otherwise they might not be able to find and identify it as a possible food resource if it is only available during the late winter period when yellowhammer movements were shorter.

The supplementary feeding trial was only conducted over one winter at a single site, therefore it is essential that it is repeated over a larger temporal and spatial scale to assess the potential of winter supplementary feeding to positively impact populations of granivorous farmland birds in pastoral farming landscapes. Quantifying the impact of supplementary feeding stations on the transmission of disease was outwith the scope of this study, but this should be considered, since unnaturally large aggregations of birds around a concentrated food resource could lead to increased disease transmission. For example, a link has been demonstrated between the use of game feeders and trichomoniasis in the declining turtle dove *Streptopelia turtur* (Lennon *et al*. 2013). However, any risk in disease transmission must be considered in the context of the potential to increase survival rates and breeding populations.

Provision of winter feeding has previously been demonstrated to increase survival rates in house sparrow *Passer domesticus* populations limited by winter food availability (Hole *et al*. 2002). Positive impacts of supplementary feeding appear to have carried over to the breeding season, with a small increase in yellowhammer territory density observed at the winter supplementary feeding site during the following breeding season (chapter 5), with other studies demonstrating that winter feeding increases breeding productivity (e.g. in great spotted woodpeckers *Dendrocopos major* (Smith & Smith 2013). However, controversy exists in the literature regarding the benefits of supplementary feeding; for example, winter fed populations of blue tits *Cyanistes caerulleus* go on to fledge chicks in poorer condition (smaller, weighed less) that subsequently go on to have lower survival (Plummer *et al*. 2013). This may be a result of supplementary feeding allowing lower quality individuals to survive the winter period and go on to breed, so the net reproductive output at the population level might be higher, but not the mean productivity per pair. Therefore, further research needs to be carried out to assess the impact of the supplementary feeding on the breeding density and productivity of the study population of yellowhammers, as this was outwith the scope of the current study.

As yellowhammers seem to avoid such supplementary sites (e.g. farmyards and game feeders) until late on in the winter when natural food resources will be at their most depleted, there must be something fundamentally unattractive about these feeding sites. Combined with the unknown impacts on breeding success and disease transmission, I feel supplementary feeding should only be used in situations where increasing winter food availability through other means is impractical or not cost effective. Supplementary feeding is only able to benefit a few species of granivorous birds in winter, especially if only a restricted range of seed sizes are provided as in this study. In contrast, if habitat heterogeneity were to be increased in pastoral landscapes to increase winter food availability (through the increase in spring sown cereal and leaving winter stubble or the planting of wild bird cover crops), a wider suite of biodiversity (both plant, invertebrate and vertebrate) would derive benefits throughout the year. However, the option to increase habitat heterogeneity will likely be unpopular in pastoral dominated farming landscapes; therefore, supplementary feeding may have an important role to play if no negative impacts can be demonstrated with future research.

When implementing agri-environment schemes, the scale over which they will have an impact should be understood in order to put them into practice over an appropriate spatial and temporal scale. Although the scale of impacts of the supplementary feeding was not directly investigated by this study, the large numbers of yellowhammers which it attracted highlights the fact that such a scheme would potentially provide benefits over a wider spatial scale than just the farm it its implemented on. The estimated numbers of yellowhammers attracted to the feeders in this study would have required approximately 15 km^2 of breeding habitat, 15 times the area of the study farm. Elsewhere in the pastoral landscape, yellowhammers moved distances of up to 9 km in early winter, indicating that the potential ‘catchment’ area over which supplementary feeding is able to attract birds could be much larger. Future research on supplementary feeding should try to quantify the area over which birds are drawn in. In reality this will prove time consuming to do as it would require large numbers of individuals within the landscape to be individually marked, but such knowledge would help determine the best spatial scale at which such a policy should be implemented.

Within the UK, farming is heavily subsidised through Common Agricultural Policy. These payments to farmers, funded from the public purse, were designed to increase productivity and food security, to stabilise markets and provide affordable food for consumers whilst ensuring a fair standard of living within the agricultural community. It is these policies that provide the funding for agri-environment schemes. Therefore, in order for continued support from the public, they must be seen to be having a positive impact on conservation. Consumers demand cheap food, helping drive the intensification of farming practices, which have led to the reduction in winter food resources for farmland birds. If the public were made more aware of conservation issues faced by not only farmland birds but other associated taxa, they might be willing to pay a premium for food produced on farms where the farming practices were more sympathetic to the requirements of biodiversity to offset economic loss through the implementation of such wildlife friendly farming measures and subsequent reductions in yield. For consumers to have confidence in and thus be willing to pay for such a scheme, benefits to wildlife must be clearly demonstrable. There is evidence of how powerful consumer pressure is when it comes to food production; increasing concern over environmental and welfare issues has driven the increase in organic farming and free range eggs. Some consumers are willing to pay a premium for these products, offsetting higher production costs.

7.3 Future work

The response of yellowhammers and other granivorous passerines to winter supplementary food needs to be tested at more sites, both in Ayrshire and in other regions, to determine if the anecdotal beneficial impacts seen in this study are more widely applicable.

At present, there are gaps in our knowledge about the scales over which to implement agri-environment schemes in order to maximise their benefit to wildlife in a cost effective manner. More research needs to be carried out testing the responses of yellowhammers and other farmland birds, for example to winter supplementary feeding over different spatial and temporal scales.

Potential negative consequences of supplementary feeding have been reported in terms of increased disease transmission (Lennon *et al*. 2013) and on reproductive parameters (Plummer *et al*. 2013). Therefore, further work needs to be carried out to assess potential negative impacts on reproduction and disease transmission of supplementary feeding on granivorous farmland passerines, placing such findings in the context of potential increases in survival and breeding density.

The effects of location of supplementary feeding stations relative to boundary feature, as well as the effects of altering the composition of seeds provided should be studied in order to ensure the maximum number of both individuals and species are able to benefit from supplementary feeding stations. During this current study mainly yellowhammers were attracted by the feeders that were placed 10m from boundary features and provided with wheat, but linnet, skylark and reed buntings (present on the trial site in low numbers during the breeding season) were never observed to utilise the supplementary feeding, perhaps as a result of the specific grain provided or the proximity to boundary features.

Future work should investigate the potential of adapting the management of riparian buffer strips so that besides reducing diffuse pollution and improving water quality, these strips have additional benefits to wildlife, including birds as foraging habitats. Restricted grazing in autumn or winter should not compromise the diffuse pollution mitigation aims (as critical periods for the management of diffuse pollution are in spring and summer) whilst opening up the vegetation and increasing the heterogeneity of the habitat, potentially benefiting foraging birds both during the breeding season and in winter.

The potential of managing road margins as an invertebrate rich foraging habitat should be investigated during the breeding season for farmland birds and as a seed rich foraging habitat in the winter. Cutting times and regimes could be manipulated (i.e. only cut half the width of the margins) to test their impact on invertebrate and seed abundance, and foraging habitat choice by farmland birds including yellowhammers.

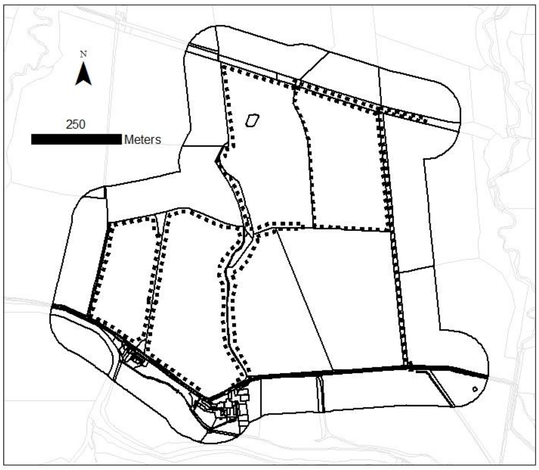
7.4 Conclusions

Yellowhammers are almost entirely reliant on farmland, and have similar needs to a suite of declining granivorous species. Therefore they are a good indicator species of farmland landscape quality. Their wide distribution, bright plumage, well-known ‘a-little-bit-of-bread-and-no-cheese’ song and confiding nature during the breeding season make yellowhammers an ideal flagship species for farmland birds. In order to prevent further range contractions occurring in pastoral-dominated regions, signifying further degradation of pastoral farming landscapes as habitats for wildlife, the availability of winter foraging habitat should be increased, increasing winter food availability. Ideally this should be done by preventing future loss of overwinter stubble from pastoral dominated farming landscapes, and increasing the seed availability in this habitat through sympathetic management. Where this is not practical, provision of alternative winter food such as unharvested silage, supplementary feeding stations or wild bird cover crops should have a beneficial impact on yellowhammer populations and other graniverous farmland birds.

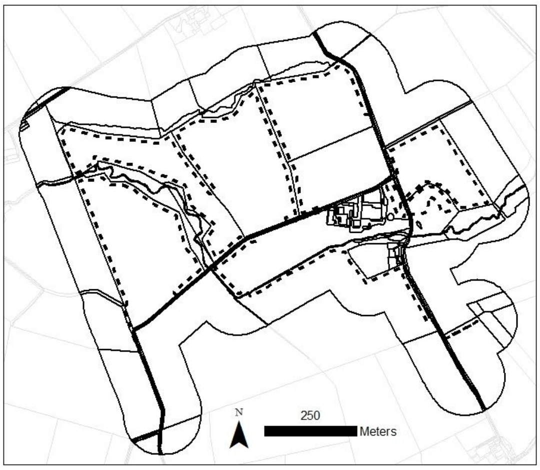
Appendices

Appendix 1 - Breeding and winter transect survey routes and farm outlines

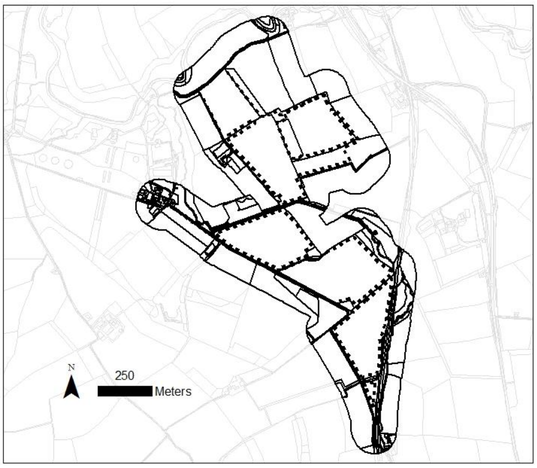
Milton



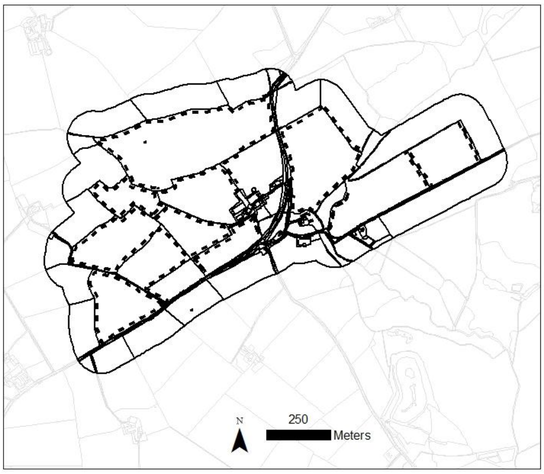
Killoch



Carnell



Fail Mains



Study site areas & survey route lengths

Farm	Transect Length	Area of study site
Carnell (Full route)	9.41 Km	120.46 Ha
Carnell (Restricted route)	7.74 Km	120.46 Ha
Fail Mains	11.40 Km	123.24 Ha
Killoch	9.45 Km	96.98 Ha
Milton	7.26 Km	93.00 Ha

Legend:

▭ **Habitat within study site**

□ **Habitat outwith study site**

▪▪▪▪ **Transect route**

Appendix 2 – Transect Dates

Breeding Season Transect Dates

2009

Round Number	Study Farm			
	Milton	Killoch	Fail Mains	Carnell
1	12/05/2009	13/05/2009	15/05/2009	14/05/2009
2	18/05/2009	19/05/2009	21/05/2009	20/05/2009
3	25/05/2009	26/05/2009	28/05/2009	27/05/2009
4	01/06/2009	03/06/2009	04/06/2009	02/06/2000
5	08/06/2009	09/06/2009	11/06/2009	10/06/2009
6	15/06/2009	16/06/2009	20/06/2009	17/06/2009
7	22/06/2009	23/06/2009	25/06/2009	24/06/2009
8	29/06/2009	30/06/2009	04/07/2009	01/07/2009
9	06/07/2009	07/07/2009	09/07/2009	08/07/2009
10	13/07/2009	14/07/2009	16/07/2009	15/07/2009
11	20/07/2009	21/07/2009	23/07/2009	22/07/2009
12	27/07/2009	28/07/2009	04/08/2009	29/07/2009

2010

Round Number	Study Farm			
	Milton	Killoch	Fail Mains	Carnell
1	20/04/2010	21/04/2010	22/04/2010	23/04/2010
2	05/05/2010	04/05/2010	06/05/2010	07/05/2010
3	10/05/2020	11/05/2010	12/05/2010	18/05/2010
4	19/05/2010	20/05/2010	21/05/2010	23/05/2010
5	24/05/2010	29/05/2010	02/06/2010	03/06/2010
6	04/06/2010	06/06/2010	07/06/2010	08/06/2010
7	14/06/2010	12/06/2010	16/06/2010	17/06/2010
8	21/06/2010	23/06/2010	24/06/2010	25/06/2010
9	28/06/2010	29/06/2010	06/07/2010	07/07/2010
10	12/07/2010	13/07/2010	15/07/2010	16/07/2010
11	23/07/2010	27/07/2010	28/07/2010	*
12	01/08/2010	05/08/2010	04/08/2010	*
13	06/08/2010	11/08/2010	24/08/2010	*

* - No survey carried out (access restrictions due to shooting)

2011

Round Number	Study Farm		
	Milton	Killoch	Fail Mains
1	02/05/2011	04/05/2011	03/05/2011
2	09/05/2011	13/05/2011	11/05/2011
3	15/05/2011	18/05/2011	17/05/2011
4	25/05/2011	27/05/2011	22/05/2011
5	03/06/2011	30/05/2011	31/05/2011

Winter Transect Dates:

Winter 2009 - 2010

Round Number	Study Farm			
	Milton	Killoch	Fail Mains	Carnell
1 (early)	24/08/2009	25/08/2009	02/09/2009	27/08/2009
2 (early)	15/09/2009	17/09/2009	23/09/2009	*
3 (early)	13/10/2009	21/10/2009	07/11/2009	*
4 (early)	08/11/2009	17/11/2009	01/12/2009	02/12/2009#
5 (late)	13/01/2010	14/01/2010	22/02/2010	20/02/2010#
6 (late)	23/02/2010	07/04/2010	08/04/2010	02/04/2010#

shorter survey route carried out avoiding the game crop areas of farm to conform to access permissions

* No survey carried out due to access restrictions

Winter 2010 - 2011

Round Number	Study Farm	
	Milton	Fail Mains
1 (early)	30/08/2010	02/09/2010
2 (early)	22/10/2010	24/10/2010
3 (early)	13/12/2010	15/12/2010
4 (late)	19/01/2011	21/01/2011
5 (late)	21/03/2011	08/04/2011

Additional transect to quantify impact of removing feeding stations

Killoch - 17/4/11

Appendix 3 Dates mist netting was carried out to assess yellowhammer demography, total number of captures plus number of yellowhammers caught on each date

Yellowhammer breeding season productivity

Date	Farm	Total Captures	Number Yellowhammers
11/09/2009	Carnell	13	0
11/09/2009	Killoch	12	0
12/09/2009	Fail Mains	7	3
17/10/2009	Milton	132	18
18/10/2009	Killoch	22	0
03/09/2010	Milton	29	4
08/09/2010	Killoch	3	1
09/09/2010	Milton	13	4
12/10/2010	Killoch	74	0
25/10/2010	Fail Mains	22	9

To compare early and late winter demography

Winter 2009/10

Date	Farm	Total Captures	Total Yellowhammers
17/10/2009	Milton	132	18
18/10/2009	Killoch	22	0
09/11/2009	Fail Mains	57	14
10/11/2009	Fail Mains	15	0
28/11/2009	Fail Mains	15	0
11/12/2009	Fail Mains	23	0
15/12/2009	Carnell	5	0
17/12/2009	Fail Mains	1	0
21/02/2010	Fail Mains	36	0
10/03/2010	Fail Mains	10	0

Winter 2010/11

Date	Farm	Total Captures	Total Yellowhammers
12/10/2010	Killoch	74	0
25/10/2010	Fail Mains	22	9
06/11/2010	Fail Mains	38	3
19/11/2010	Fail Mains	8	3
15/12/2010	Fail Mains	7	3
22/01/2011	Milton	17	1
28/01/2011	Fail Mains	44	8

Appendix 4 Winter feeding station replenishment dates, point count and ringing dates included in analysis

Date	Feeding stations replenished?	Point counts conducted?	Ringing conducted?
23/12/10	Yes (incomplete data)	(incomplete data)	Yes
29/12/2010	Yes	(incomplete data)	No
07/01/2011	Yes	Yes	Yes (before point count)
14/01/2011	Yes	No	No
19/01/2011	Yes	Yes	No
20/01/2011	No	No	Yes
23/01/2011	No	No	Yes
26/01/2011	Yes	Yes	Yes (before point count)
03/02/2011	Yes	Yes	No
10/02/2011	Yes	Yes	Yes (before point count)
18/02/2011	Yes	Yes	No
24/02/2011	Yes	Yes	No
05/03/2011	Yes	Yes	No
13/03/2011	Yes	Yes	Yes (after point count)
16/03/2011	No	No	Yes
18/03/2011	Yes	Yes	Yes (before point count)
23/03/11	No	No	Yes
24/03/11	No	No	Yes
28/03/11	No	No	Yes
29/03/2011	No (feeders removed)	n/a	Yes

Appendix 5 Summary of yellowhammers caught in the vicinity of feeders during the supplementary feeding trial

Ringing Session	Date	New captures	Total re-traps	Retrap initially ringed prior to feeding trial	Retrap initial ringed during feeding trial	Cumulative individuals (new + pre feeding trial)	Cumulative captures
1	23/12/10	12	1	1	0	13	13
2	07/01/11	3	1	1	0	17	17
3	20/01/11	5	0	0	0	22	22
4	23/01/11	4	0	0	0	26	26
5	26/01/11	3	0	0	0	29	29
6	10/02/11	3	0	0	0	32	32
7	13/03/11	8	1	0	1	40	41
8	16/03/11	36	5	1	4	77	82
9	18/03/11	3	2	0	2	80	87
10	23/03/11	7	2	0	2	87	96
11	24/03/11	11	6	1	5	99	113
12	28/03/11	6	6	1	5	106	125
13	29/03/11	2	0	0	0	108	127

Appendix 6

Habitat classifications used to describe the breeding habitat available to yellowhammers at each farm between 2009 and 2011

Habitat Category	Habitat Description
Pastoral habitats (improved grassland)	
Grazed	Improved grassland grazed either by cattle or horses
Silage	Improved grassland managed for silage production, cut a minimum of twice per year
One-cut silage then grazed	Improved grassland managed initially for silage production, the first cut taken late May/early June (so in effect, silage habitat for the first breeding attempt) but cattle added post harvest and grazed for the rest of the season (so grazed habitat for the second breeding attempt).
Re-sown	Re-sown pastoral habitat, sown in spring (pre breeding season) resulting in a less dense pastoral habitat during the breeding season
Other habitats	
Cereal	Spring and autumn sown cereal crops (barley and wheat)
Game crop	Maize grown as a cover crop for game birds, grain available in feeders and spread throughout the area by game keeping staff
Garden	Garden habitat, may contain bird feeders
Maize	Maize crop grown as a fodder crop for cattle
Manmade	Tarmac or unnatural surfaces including road, pavement, railway, farmyard plus buildings and other manmade structures.
Unmanaged	Unimproved grassland, scrub, marsh, roadside margin, farm track and railway embankment
Water	Water features including ponds, streams and rivers
Woodland	Coniferous, non-coniferous and mixed woodland

Habitat classifications used to describe the wintering habitat available to yellowhammers at each farm and in the surrounding landscape over which the radiotagged birds ranged in winter 2009/10 and 2010/11

Habitat Category	Habitat Description
Grassland	Improved grassland either grazed by sheep or ungrazed
Stubble	Barley, wheat or maize stubble
Game Managed	Habitat actively managed for game, either through provision of game crops, feeders or both
Garden	Garden habitat, may contain bird feeders
Manmade Surface	Tarmac or unnatural surfaces including road, pavement, railway, farmyard plus buildings and other manmade structures.
Resown/Ploughed	Fields either ploughed in or resown, could be either grass or autumn cereal
Unmanaged	Unimproved grassland, scrub, marsh, roadside margin, farm track and railway embankment
Water	Water features including ponds, streams and rivers
Woodland	Coniferous, non-coniferous and mixed woodland

Appendix 7 Winter habitat availability (Ha) within 100m buffer of the boundary of each study site in winter 2009/10 and 2010/11

Farm	Total Area	Winter	Game Managed	Garden	Grass	Manmade Surface	Re-sown	Stubble	Unknown	Unmanaged	Water	Woodland
Carnell	120.64	2009/10	2.42	0.63	87.53	3.14	0	8.83	0	7.74	0.98	9.39
Fail Mains	123.80	2009/10	0	0.79	93.11	3.44	2.03	8.02	0	15.86	0.29	0.27
		2010/11	0.18	0.79	99.77	3.44	0	3.37	0.01	15.68	0.29	0.27
Killoch	96.98	2009/10	0	0.12	85.65	2.09	0	0	0.77	4.26	0.46	3.62
		2010/11	0	0.12	81.69	2.06	0	4.65	0.21	4.16	0.46	3.62
Milton	106.45	2009/10	0	0.24	65.53	1.46	4.70	19.73	0	9.09	2.04	3.66
		2010/11	0	0.24	65.45	1.45	4.70	19.73	0.11	9.07	2.04	3.66

Appendix 8 Winter habitat proportion available within 100m buffer of the boundary of each study site in winter 2009/10 and 2010/11

Farm	Winter	Game Managed	Garden	Grass	Manmade Surface	Re-sown	Stubble	Unknown	Unmanaged	Water	Woodland
Carnell	2009/10	0.020	0.005	0.726	0.026	0	0.073	0	0.064	0.008	0.078
Fail Mains	2009/10	0	0.006	0.752	0.028	0.016	0.065	0	0.128	0.002	0.002
	2010/11	0.001	0.006	0.806	0.028	0	0.027	0	0.127	0.002	0.002
Killoch	2009/10	0	0.001	0.883	0.022	0	0	0.008	0.044	0.005	0.037
	2010/11	0	0.001	0.842	0.021	0	0.048	0.002	0.043	0.005	0.037
Milton	2009/10	0	0.002	0.616	0.014	0.044	0.185	0	0.085	0.019	0.034
	2010/11	0	0.002	0.615	0.014	0.044	0.185	0.001	0.085	0.019	0.034

Appendix 9 Breeding season habitat availability (Ha) within 100m buffer of the boundary of each study site (2009 - 2011)

			Habitat Area (Ha)															
Farm	Total Area	Year	Autumn Cereal	Game Managed	Garden	Grass (management unspecified)	Grazed (cattle)	Grazed (horse)	Maize	Manmade Surface	Unknown	Silage (one cut then cattle grazed)	Re-sown Grass	Silage	Spring Cereal	Unmanaged	Water	Woodland
Carnell	120.64	2009	0	2.42	0.63	21.62	26.90	0	0	3.14	0	7.60	0	27.60	12.64	7.74	0.98	9.39
		2010	0	2.42	0.63	18.21	44.20	0	0	3.14	0	0	0	25.12	8.83	7.74	0.98	9.39
Fail Mains	123.80	2009	0	0	0.79	17.72	31.57	0	0	3.20	0	0	0	43.82	10.05	16.11	0.29	0.27
		2010	0	0	0.79	14.34	33.54	0	0	3.20	0	0	8.02	43.59	3.37	16.39	0.29	0.27
		2011	0	0	0.79	23.92	30.54	0	0	3.44	0	0	0	10.69	37.71	16.15	0.29	0.27
Killoch	96.98	2009	0	0	0.12	10.37	30.17	0.77	0	2.09	0.35	24.14	8.57	12.06	0	4.26	0.46	3.62
		2010	0	0	0.12	5.79	38.74	0.77	2.27	2.09	0.35	8.10	0	28.02	2.39	4.26	0.46	3.62
		2011	0	0	0.12	18.05	37.43	0	6.45	2.09	0.35	13.74	0	10.40	0	4.26	0.46	3.62
Milton	106.45	2009	4.70	0	0.24	0.88	33.27	1.09	0	1.46	0	7.76	0	22.47	19.73	9.09	2.11	3.66
		2010	4.70	0	0.24	0.88	31.52	1.09	0	1.46	0	19.26	0	12.72	19.73	9.09	2.11	3.66
		2011	0	0	0.24	1.25	33.22	0.83	7.25	1.46	0	7.76	0	19.92	19.73	9.09	2.04	3.66

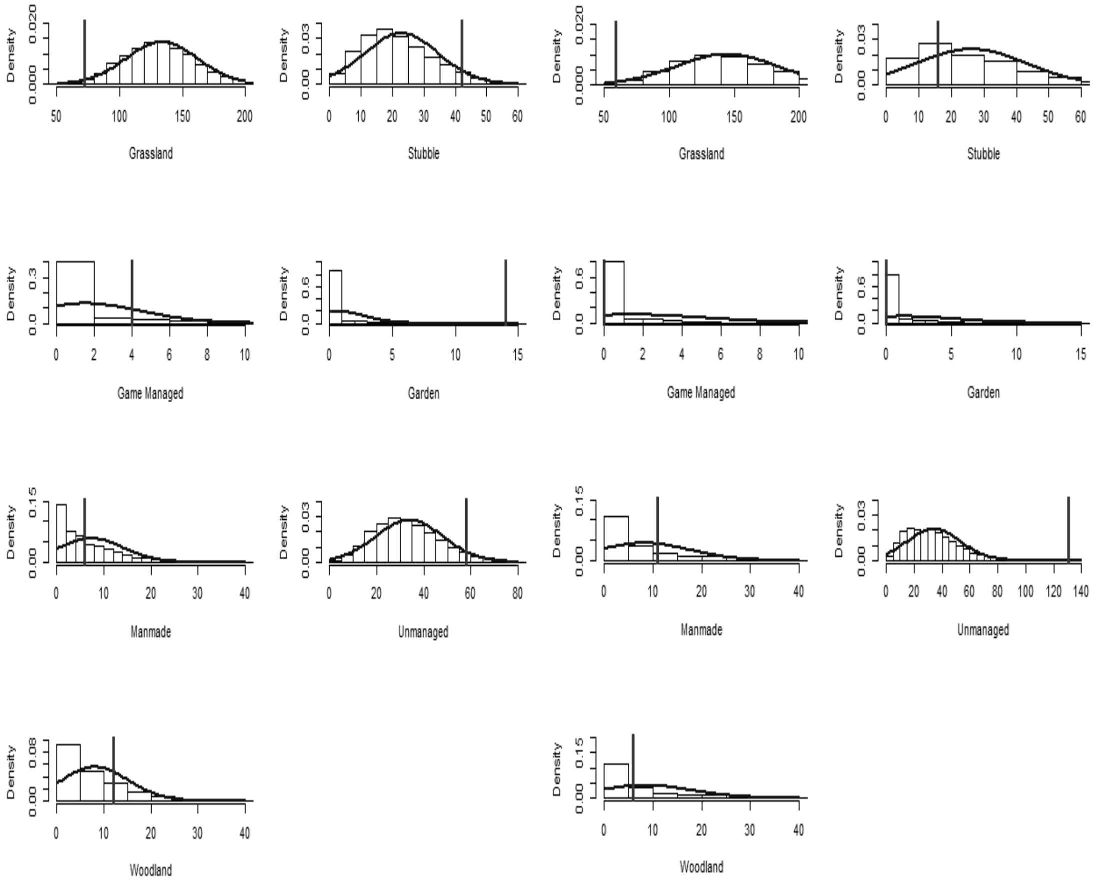
Appendix 10 Breeding season habitat proportion available within 100m buffer of the boundary of study sites (2009 – 2011)

		Habitat proportion															
Farm	Year	Autumn Cereal	Game Managed	Garden	Grass (management unspecified)	Grazed (cattle)	Grazed (horse)	Maize	Manmade Surface	Unknown	Silage (one cut then cattle grazed)	Re-sown Grass	Silage	Spring Cereal	Unmanaged	Water	Woodland
Carnell	2009	0	0.020	0.005	0.179	0.223	0	0	0.026	0	0.063	0	0.229	0.105	0.064	0.008	0.078
	2010	0	0.020	0.005	0.151	0.366	0	0	0.026	0	0	0	0.208	0.073	0.064	0.008	0.078
Fail Mains	2009	0	0	0.006	0.143	0.255	0	0	0.026	0	0	0	0.354	0.081	0.130	0.002	0.002
	2010	0	0	0.006	0.116	0.271	0	0	0.026	0	0	0.065	0.352	0.027	0.132	0.002	0.002
	2011	0	0	0.006	0.193	0.247	0	0	0.028	0	0	0	0.086	0.305	0.130	0.002	0.002
Killoch	2009	0	0	0.001	0.107	0.311	0.008	0	0.022	0.004	0.249	0.088	0.124	0	0.044	0.005	0.037
	2010	0	0	0.001	0.060	0.399	0.008	0.023	0.022	0.004	0.084	0	0.289	0.025	0.044	0.005	0.037
	2011	0	0	0.001	0.186	0.386	0	0.066	0.022	0.004	0.142	0	0.107	0	0.044	0.005	0.037
Milton	2009	0.044	0	0.002	0.008	0.313	0.010	0	0.014	0	0.073	0	0.211	0.185	0.085	0.020	0.034
	2010	0.044	0	0.002	0.008	0.296	0.010	0	0.014	0	0.181	0	0.119	0.185	0.085	0.020	0.034
	2011	0	0	0.002	0.012	0.312	0.008	0.068	0.014	0	0.073	0	0.187	0.185	0.085	0.019	0.034

Appendice 11

Predicted yellowhammer count distributions in each habitat type (from re-sampling analysis) with the observed value (vertical line) for yellowhammers observed during winter boundary transect survey

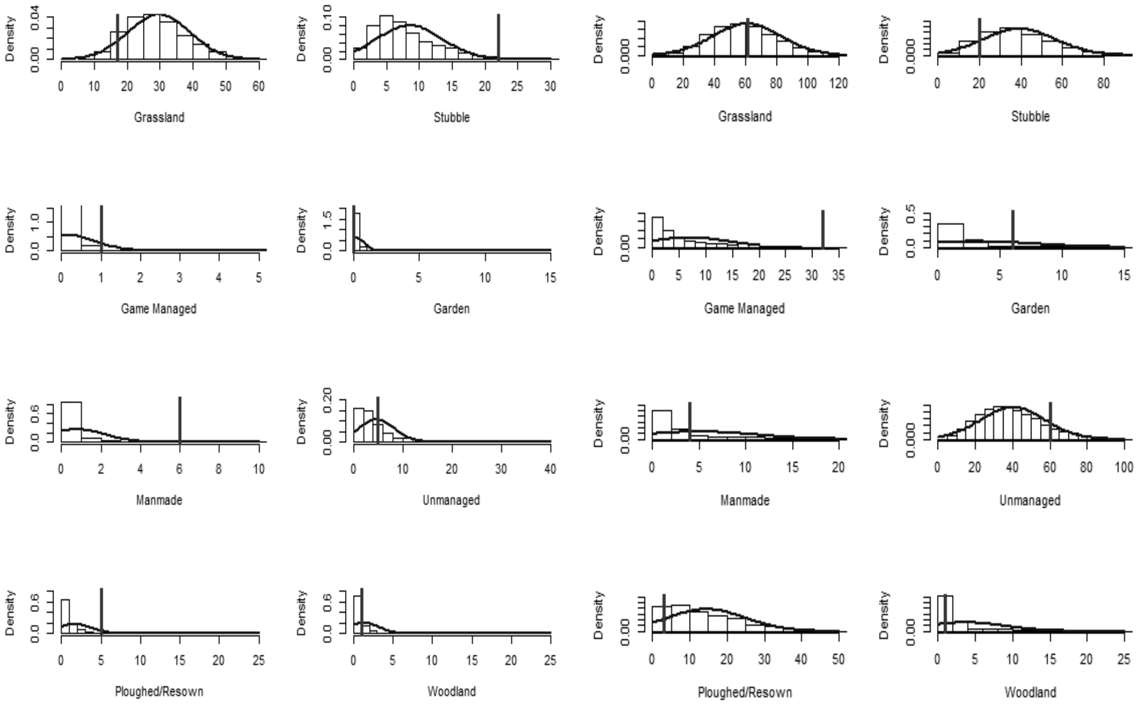
Early winter (pre-solstice) **Late winter (post- solstice)**



Appendice 12

Predicted yellowhammer count distributions in each habitat type (from re-sampling analysis) with the observed value (vertical line) for radio-tagged yellowhammers

Early winter (pre-solstice) **Late winter (post- solstice)**



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