Insect availability for breeding yellowhammers on lowland farmland

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

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Abstract

Granivorous farmland passerines have declined in Europe as a result of agricultural intensification. Many of these species' require insects during the breeding season, the availability of which has declined in recent decades, potentially impacting on demographic rates via reduced adult foraging efficiency.

Sympathetic management of foraging habitats may be crucial in promoting population recovery of farmland birds. This requires data on the underlying food availability and the way in which birds' exploit these resources. The foraging behaviour of a key granivorous passerine, the yellowhammer *Emberiza citrinella*, was investigated during the breeding season in relation to insect abundance and accessibility in key foraging habitats (cereal crops and field margins).

Insect abundance differed temporally between crop types under varying management, due in part to the timing of crop development. Insect distributions exhibited considerable spatial heterogeneity within cereal crops, with evidence of localised aggregations.

Field margins were used heavily by foraging yellowhammers in early summer. However, margin use declined in late summer, with a marked shift to cereal crops. This shift occurred despite margins supporting higher insect abundance than cereals, and was most likely due to seasonal vegetation growth within margins, restricting accessibility to insects. At a finer patch-scale, yellowhammers selected foraging sites with short, sparse vegetation and high insect abundance. These results suggest that accessibility to food, mediated by vegetation structure, is an important determinant of habitat selection at both the habitat and patch scale.

Field margins were experimentally cut to create open patches within the sward, and the response of foraging yellowhammers tested. The use of such patches increased between early and late summer, and patches were used more frequently as vegetation height increased in the adjacent margin. These results suggest that open patches within tall, dense swards may increase accessibility to food for foraging birds.

Nestling provisioning rates and body condition were significantly higher in the presence of experimental margin patches, possibly indicating that such patches may enable greater adult foraging efficiency. The positive response of yellowhammers to margin manipulations suggests that creating heterogeneity in vegetation structure within a habitat may be a means for enhancing food availability for farmland birds. Field margins managed within agri-environment schemes may require more frequent, targeted cutting to ensure accessibility to insects for foraging birds in late summer.

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Chapter 1: Introduction

Farmland bird populations have shown large declines and range contractions in the UK and elsewhere in Europe over recent decades (Krebs *et al.* 1999; Donald *et al.* 2001). In the UK these declines began mainly in the 1970s, and many formerly common and widespread bird species now exist on farmland at a small fraction of their former abundance (Fuller *et al.* 1995; Siriwardena *et al.* 1998a). Although the downward trends of some species have recently stabilised, others continue to decline and a considerable proportion of farmland species are currently listed as being of high conservation concern (Eaton *et al.* 2007).

A large volume of research has been conducted over recent years to identify the causes of these declines, and there is now a wealth of evidence implicating changes in farming practice (e.g. Chamberlain *et al.* 2000; Fuller *et al.* 2000). These changes have resulted from a general intensification of agricultural management. In arable landscapes this includes the loss of non-cropped habitat including hedgerows, the switch from spring to autumn sowing of cereals and increased use of pesticides and fertilizers to enhance crop yields (Chamberlain *et al.* 2000; Robinson & Sutherland 2002). The result of these changes has been an overall deterioration in the quality of farmland habitat for biodiversity.

One group of farmland birds that has shown particularly large declines are granivorous passerines such as skylark *Alauda arvensis*, yellowhammer *Emberiza citrinella* and corn bunting *Emberiza calandra* (Fuller *et al.* 1995). Although chiefly seed-eating these species require protein-rich insects during the breeding season, which are essential for nestling growth and development (Wilson *et al.* 1999). An exception being linnet *Carduelis cannabina* which provisions nestlings entirely on seeds (Bradbury *et al.* 2003). Insect abundances have declined on farmland over recent decades (Ewald & Aebischer 1999; Benton *et al.* 2002). For instance, Benton *et al.* (2002) showed that 15 arthropod orders had declined by an average of 48% from 1972-1997. These declines are thought to be due to aspects of agricultural intensification such as increased pesticide use and the loss of non-cropped habitat, which may act as a rich source of invertebrates on farmland (Benton *et al.* 2002).

A general link has been shown between invertebrate abundance during the breeding season, bird population size and measures of farm management (Benton *et al.* 2002). In addition, Wilson *et al.* (1999) showed that declining granivorous birds relied significantly more on insects than those not in decline. However, to date the grey partridge *Perdix perdix* remains the only species of farmland bird for which a mechanistic link has been identified between summer arthropod availability and population size, through reduced nestling survival (Southwood & Cross 1969). This is perhaps not surprising, as the grey partridge is precocial, and therefore the chicks will bear any costs of reduced insect availability directly.

For many altricial species such as granivorous passerines there is little evidence of a decline in measures of reproductive output per nesting attempt over the period of population decline (Siriwardena *et al.* 2000a). Indeed, for a number of species falls in survival rate rather than productivity are more often associated with population declines (Peach *et al.* 1999; Siriwardena *et al.* 1999, 2000b). However, for a number of granivorous passerines, including yellowhammer and tree sparrow *Passer montanus,* variation in annual survival and fledgling production per nesting attempt alone are insufficient to explain changes in abundance (Siriwardena *et al.* 2000a). This suggests that changes in post-fledging survival rates and/or the number of breeding attempts could be important.

A reduction in insect availability for altricial birds could impact on such demographic rates through changes to adult foraging efficiency, as this will affect the rate at which food is delivered to nestlings, and also the work rate required by the adults to deliver food. Insect availability for foraging birds has declined directly on farmland through the changes in abundance described above, but also indirectly through changes to sward structure, reducing accessibility to insects (McCracken & Tallowin 2004; Wilson *et al.* 2005). For example, in cereal crops, advances in crop breeding and increased fertilization have resulted in increased sward densities (Wilson *et al.* 2005). In addition, a general consequence of agricultural intensification has been the loss of habitat heterogeneity at multiple spatial scales (Benton *et al.* 2003), reducing the value for foraging birds both within and between habitats. Low insect abundance in habitats surrounding the nest has been shown to be correlated with low nestling growth rates and body condition in corn bunting, reed bunting *Emberiza schoeniclus* and yellowhammer (Brickle *et al.* 2000; Brickle & Peach 2004; Hart *et al.* 2006). This suggests that when insects are scarce and/or inaccessible for foraging birds, adults may struggle to collect sufficient insects to provision nestlings. This represents a potential mechanism by which post-fledging survival rates may be reduced, as studies on other passerine species have shown that nestling growth rates and body condition are known to have important effects on future survival and lifetime reproductive success (Magrath 1991; Wright *et al.* 1998; Lindstrom 1999; Blount *et al.* 2006). Therefore if parents maintain offspring quantity at a cost of offspring quality in poor environments, post-fledging survival rates may decline whilst measures of “per-nest” productivity remain unchanged.

Alternatively, for altricial breeders, any effects of reduced food availability may be ‘buffered’ by the adults through higher work rates when provisioning nestlings

(Tremblay *et al.* 2005). Indeed, in short-lived passerine species, where many individuals may have only one breeding season in their lifetime, this strategy is more likely than in longer-lived species where birds may simply not breed in poor conditions (Clutton-Brock 1988). Reproduction imposes costs on parents, and under conditions of increased food stress e.g. low food abundance in natural conditions or through experimentally increased brood sizes, parents increase their work rate (Drent & Daan 1980; Dijkstra *et al.* 1990; Tremblay *et al.* 2005). However adults must balance the energetic costs of collecting nestling food against the effect on their own body condition, and increased provisioning effort may reduce both future survival and reproductive output of adults (Nur 1984; Roskaft 1985; Daan *et al.* 1996).

Reductions in summer insect availability therefore have the potential to influence both current and future productivity and survival rates of both juvenile and adult granivorous passerines on farmland, via effects on adult foraging efficiency. Determining the importance of insect availability on foraging efficiency for breeding adults, and designing measures to improve foraging conditions, requires detailed knowledge of several aspects of foraging ecology: i) the underlying insect distribution within foraging habitats; ii) the foraging patterns of farmland birds in relation to food availability (abundance and accessibility); iii) whether habitats can be manipulated to improve food availability, and; iv) whether such management has tangible benefits for the productivity of breeding birds.

In the rest of this chapter each of these four factors are reviewed, summarising current knowledge and highlighting areas requiring further research. Although I focus on arable farmland, many of the issues regarding insect accessibility for granivorous passerines are equally likely to apply in pastoral landscapes (Vickery *et al.* 2001; McCracken & Tallowin 2004).

i) Insect distributions within foraging habitats

Comparisons of insect abundance in different foraging habitats of granivorous passerines reveal that uncropped areas such as field margins generally support higher insect abundance than cropped fields such as cereals (Thomas & Marshall 1999; Hart *et al.* 2006). This is most likely due to a variety of factors such as higher plant species richness, greater habitat stability and lower pesticide inputs (uncropped margins generally receive only incidental pesticide drift from spraying of adjacent cropped areas) (Marshall & Moonen 2002). However, insect abundance may show considerable spatial variation within a habitat, and this may have implications for foraging birds. Although habitats such as cereal crops appear relatively homogeneous, many insect distributions are rarely, if ever, uniform in these habitats. Numerous studies have shown that insects in crops and the adjacent margins may be highly aggregated into patches of high and low abundance. Such patterns have been shown for individual species of beetle (Coleoptera) in winter wheat (Holland *et al.* 1999), winter barley (Thomas *et al.* 2001) and oilseed rape (Ferguson *et al.* 2000), and for spiders (Araneae) and springtails (Collembola) in winter wheat (Holland *et al.* 1999; Harwood *et al.* 2001). The size of these patches varies, but strong aggregations have been shown at scales of between 7.5m and 30m for individual species of Coleoptera and Araneae, although clusters of high abundance may extend over areas larger than 1ha. (Holland *et al.* 1999, 2005). However, many previous studies of insect spatial distributions (such as those described above) have focussed on only a small number of species per study. As a result little is known about the underlying spatial and temporal distribution of a range of insect taxa important in the diet of granivorous passerines in the birds' primary foraging habitats. In addition, there are insufficient data on the effect of different crop management regimes (e.g. spring-sown versus autumn-sown) on insect distributions within cereal crops. Such data are required across a temporal scale encompassing the duration of the birds' breeding season, which for granivorous passerines in the UK generally occurs between April and August (Snow & Perrins 1998).

ii) The foraging patterns of farmland birds in relation to food abundance and accessibility

The farmed landscape represents a mosaic of habitat types, both cropped and uncropped, which may potentially be exploited by foraging birds. At the habitat scale, numerous studies have shown that granivorous passerines select foraging habitat non-randomly during the summer, with cereal crops and field margins consistently favoured by a range of species (Stoate *et al.* 1998; Brickle *et al.* 2000; Wilson 2001; Morris *et al.* 2002). This habitat selection has been shown to be positively related to insect abundance (Brickle *et al.* 2000; Morris *et al.* 2002; Brickle & Peach 2004). Birds must also select foraging patches at a fine-scale within habitats. At this patch scale, birds may select areas containing higher insect abundance than surrounding non-foraged areas (e.g. for yellowhammers, Morris *et al.* 2002). However, food accessibility, mediated by vegetation structure, may be of equal or greater importance than abundance in determining patch selection. A study of skylarks foraging in barley crops found that birds' preferred to forage along tractor tramlines and other bare patches within the fields, despite the crop itself supporting higher insect abundance (Odderskaer *et al.* 1997). This was thought to be due to the short, sparse vegetation offering greater accessibility and detectability of insect prey, but at a cost of lower abundance. Foraging yellowhammers have also been shown to select patches in winter wheat with shorter, more open vegetation than non-foraged patches (Morris *et al.* 2002). Vegetation structure is known to be an important determinant of food availability for foraging birds and may influence foraging efficiency in a number of ways. Tall vegetation may reduce the accessibility and detectability of prey (Brodmann *et al.* 1997; Nystrand & Granstrom 1997; Butler & Gillings 2004; Stillman & Simmons 2006) and may also restrict forager mobility (Brownsmith 1977; Devereux *et al.* 2004). In addition vegetation structure may also affect perceived predation risk for many small passerines (Whittingham *et al.* 2004, 2006; Butler *et al.* 2005), and can impact on foraging efficiency through a trade-off between time allocated to feeding and time allocated to vigilance to predators (Whittingham & Evans 2004; Wilson *et al.* 2005).

The summer is a period of rapid vegetation growth, both in crops and other habitats, and changes in vegetation structure have the potential to alter the accessibility of insect food and hence the suitability for foraging birds. However few studies have investigated whether foraging habitat preferences of granivorous passerines vary during the course of the breeding season. Stoate *et al.* (1998) showed seasonal variation in habitat use by yellowhammers, however this study covered only the first half of the breeding season. In addition, seasonal variation in the underlying insect and vegetation characteristics of foraging habitats was not investigated in parallel, meaning that it was difficult to identify the causes of seasonal variation in habitat selection.

Few studies, therefore, have investigated foraging behaviour simultaneously at both the habitat and patch scale, and in relation to the underlying insect and vegetation characteristics. There are also little data on whether habitat selection varies over the course of the breeding season, and the relative importance of insect abundance and vegetation structure in determining any such variation.

iii) and iv) Manipulation of foraging habitat to improve food availability, and potential benefits for the productivity of breeding birds

Enhancing the value of farmland as foraging habitat for birds could be achieved through increasing prey abundance or accessibility, or both. Several recent studies have investigated the benefits of manipulating stubbles for foraging birds during the winter (Butler *et al.* 2005; Whittingham *et al.* 2006), however few have investigated the manipulation of foraging habitat during the breeding season.

One recent study assessed the benefits of creating open patches within winter wheat for breeding skylarks (Morris *et al.* 2004; Donald & Morris 2005). Small undrilled patches or 'Skylark plots' were created to mimic some of the advantages of shorter, less dense spring-sown cereals during the crucial phase of the birds breeding season. Skylark nestling body condition and productivity were higher in fields containing undrilled plots, with these benefits most likely arising from increased food accessibility for foraging adults in the sparsely vegetated plots (Morris *et al.* 2004). In a further analysis of this work it was suggested that the population decline of skylarks in England could be stabilised if just 15% of winter cereals held skylark plots (Donald & Morris 2005).

Given that tall vegetation generally supports high abundance and diversity of insects (Vickery *et al.* 2001; McCracken & Tallowin 2004), but may restrict food accessibility relative to short vegetation, several authors have suggested that creating heterogeneity in vegetation height within a habitat may provide optimum benefits for foraging birds, by maximizing both food abundance and accessibility (Devereux *et al.* 2004; Tallowin *et al.* 2005; Wilson *et al.* 2005). Perkins *et al.* (2002) created cut and uncut areas in close proximity within field margins and studied the response of foraging yellowhammers. No differences in use of cut and uncut margin were detected, however the authors acknowledge that small sample sizes may have reduced the statistical power to detect a difference in use. The benefits of creating a mosaic of vegetation heights for foraging birds therefore remain largely untested. There is scope for examining the response to such manipulations in a variety of habitats such as cereal crops and/or field margins during the summer, and assessing any potential benefits on productivity, through potential increases in adult foraging efficiency.

Conclusions and thesis outline

The availability of protein rich insects for breeding granivorous passerines has declined on farmland over recent decades through a range of direct and indirect effects. Adult foraging efficiency, mediated by the abundance and accessibility of insects, may be a key determinant of current and future measures of productivity and survival of granivorous passerines. Maximising the value of foraging habitats for breeding birds may therefore be an important means of stimulating population recovery for farmland birds. However, data are currently lacking in several key aspects relating to the foraging ecology of granivorous passerines:

i) The underlying spatial and temporal distribution of insect and vegetation characteristics in primary foraging habitats of granivorous passerines during the breeding season

ii) How the foraging patterns of birds' at different spatial scales (habitat and patch) are influenced by food abundance and accessibility, and whether seasonal variation in vegetation structure influences foraging patterns

iii) Whether vegetation structure within foraging habitats can be manipulated to improve food availability for foraging birds

iv) Whether such manipulation has beneficial effects on the productivity of breeding birds

The aim of this thesis is to investigate these aspects of foraging ecology on arable farmland for a key granivorous passerine, the yellowhammer.

Yellowhammer breeding biology

Yellowhammer was chosen as the study species for a variety of reasons. It is a red-listed species of high conservation concern, having declined by 54% from 1970-2005 (Eaton *et al.* 2007). However, despite this decline the yellowhammer remains a widespread farmland species (Gregory *et al.* 2002), ensuring reasonable sample sizes for field studies. A major factor associated with this decline has been the removal of cereals from pastoral landscapes, although populations have also declined markedly in arable areas due to more subtle changes in management (Kyrkos *et al.* 1998). Studies of yellowhammer demography indicate that nestling production per breeding attempt appeared to be higher during periods of population decline than during periods of increase or stability (Siriwardena *et al.* 2000a). In addition, annual survival rates of both adults and juveniles have been shown to be lower during periods of population decline (Siriwardena *et al.* 1998b). However, variation in survival and productivity per nesting attempt alone are insufficient to explain observed changes in yellowhammer abundance (Siriwardena *et al.* 2000a). This suggests that changes to other demographic rates such as post-fledging survival rates and/or the number of breeding attempts per season may also be important (Siriwardena *et al.* 2000a).

Yellowhammer nestling growth, body condition and fledging probability are known to be influenced by insect abundance within the foraging radius of the nest (Boatman *et al.* 2004; Morris *et al.* 2005; Hart *et al.* 2006). The yellowhammer is therefore a priority species for studies of adult foraging behaviour in relation to insect availability.

In addition the yellowhammer shares similar habitat requirements and life-history with a number of other declining farmland granivorous passerines (e.g. skylark, reed bunting *Emberiza schoeniclus* and corn bunting, Brickle *et al.* 2000; Wilson 2001; Brickle & Peach 2004). This makes the yellowhammer a good model species and may help to ensure that management recommendations are applicable across a range of species.

The yellowhammer has been the subject of a number of previous studies during the breeding season (e.g. Stoate *et al.* 1998; Bradbury *et al.* 2000; Morris *et al.* 2001; Perkins *et al.* 2002). Whilst there is still considerable scope for further studies as outlined above, this previous research provides an excellent resource for the general breeding biology of yellowhammers on UK farmland.

Yellowhammer diet is chiefly cereal and weed seeds, although the nestlings require protein-rich invertebrates, many of which have undergone long-term declines in abundance (Ewald & Aebischer 1999: Benton *et al.* 2002). Breeding males establish and defend territories from early spring, and the first breeding attempts are usually initiated from mid to late April (Snow & Perrins 1998). The breeding season in the UK often lasts until late August, and pairs may have young in the nest into September (C. Wright, *pers. comm.*). Pairs may have 1-4 breeding attempts per season, although the maximum number of successful broods raised in a season is generally 3 (Snow & Perrins 1998). British farmland yellowhammers typically build their nests along field boundaries, either on the ground in ditches or grassy margins, or in hedges and isolated bushes (Bradbury *et al.* 2000). Clutch sizes average 3.3-3.55 (range 2-6), and the mean number of chicks fledged per successful attempt averages 2.6-2.72 (Snow & Perrins 1998; Stoate *et al.* 1998; Bradbury *et al.* 2000). The nestlings are provisioned by both adults (Murray 2004) and typically fledge after 11-13 days in the nest (Snow & Perrins 1998).

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Chapter 2: The spatial and temporal distribution of insects in barley under varying management

Abstract

Insects perform a variety of important roles on farmland, such as natural agents of pest control and as food for farmland birds. Managing insect populations for these purposes requires data on the spatial and temporal distribution and abundance of insects in crops and the effect of management practices on this distribution. Insects were sampled during one summer from fields of barley under two management regimes (winter-sown and spring-sown). The timing of crop development and harvesting had a strong influence on insect abundance between crop types, with winter barley supporting significantly higher abundance in early summer, and spring barley significantly higher in late summer. Insect abundance and distribution exhibited considerable spatial heterogeneity within fields, and counts of total insects showed positive spatial autocorrelation over scales of 5-10m, suggesting the presence of localised aggregations. These results have implications for studies of the foraging behaviour of farmland birds and for the targeted application of pesticides.

Introduction

Invertebrates, especially insects, are a vital component of agricultural ecosystems. They may act as either pests or natural agents of pest control, key elements of food chains, major contributors to biodiversity and general indicators of ecosystem health (Holland *et al.* 2005). One such role is as a major food source for farmland birds.

Adults of many farmland bird species consume insects, and their high protein content means they are particularly important for nestling growth and development (Holland *et al.* 2006). One group of birds requiring insects during the breeding season are granivorous passerines such as yellowhammer *Emberiza citrinella* and corn bunting *Emberiza calandra* (Brickle *et al.* 2000; Hart *et al.* 2006). Both granivorous passerines and many of the insect taxa important in their diet have declined markedly over recent decades, and there is evidence linking these declines to agricultural intensification (Chamberlain *et al.* 2000; Benton *et al.* 2002). For insects, one of the main impacts has been the development of more efficient pesticides and an increase in the proportion of farmland which is sprayed (Ewald & Aebischer 1999; Robinson & Sutherland 2002). The availability of invertebrates may influence the nestling growth and productivity of a number of farmland birds (Brickle *et al.* 2000; Brickle & Peach 2004; Hart *et al.* 2006) and declining granivorous birds have been shown to rely significantly more on insect food than those species not in decline (Wilson *et al.* 1999). In addition a link has been shown between invertebrate abundance, bird population size and measures of farm management (Benton *et al.* 2002). Granivorous passerines are altricial breeders, and as such the nestlings are dependent on adults for food provisioning. Cereal crops are a common foraging habitat (Stoate *et al.* 1998; Brickle *et al.* 2000; Morris *et al.* 2001) and measures to enhance insect availability within cereals are an important component of agri-environment schemes designed to aid farmland bird recovery (Vickery *et al.* 2004; Grice *et al.* 2007). However, maximizing the value of cereal crops for foraging birds whilst maintaining, as far as possible, crop yields, requires a detailed understanding of the underlying spatial and temporal distribution of insects.

A number of insect taxa are known to exhibit highly aggregated distributions in cereal crops and the adjacent margins (Holland *et al.* 1999a, 2005; Ferguson *et al.* 2000; Thomas *et al.* 2001). However, determining how the foraging patterns of farmland birds are linked to the underlying insect distribution requires a better understanding of factors such as the scale over which insect aggregations occur and temporal variation in insect abundance in cereal crops. Many previous studies of insect distributions have focussed on only a particular species or family. As a result there are few data on the spatial and temporal distribution of a wide range of insect orders in cereal crops, including those important in the diet of farmland birds. In addition, there are insufficient data on insect distributions under varying crop management regimes (e.g. spring-sown versus winter-sown). Such data are required across a temporal scale encompassing the duration of the birds' breeding season. A more detailed understanding of insect distributions in cereal crops could, potentially, allow populations to be more effectively managed for diversity and pest control within sustainable farming (Barker *et al.* 1999). For example, more effective spatial targeting of pesticides may help to minimise the effects on non-target insect species (Ferguson *et al.* 2000).

In the present study insects were sampled from barley under two management regimes (spring-sown and winter-sown) and the adjacent uncropped margins during the summer, with the aim of answering the following questions;

i) How does insect abundance differ between 2 crop types: spring and winter barley?

ii) How does the spatial distribution of insects vary seasonally within barley crops and uncropped margins?

iii) Are insects spatially aggregated within barley crops? And if so over what scale?

Methods

Study sites and insect sampling

Insect sampling was conducted from April-August 2004 on four farms in Aberdeenshire, North-East Scotland, ranging in size from 98 to 292 ha. This sampling period was chosen to encompass the normal duration of the yellowhammers' breeding season (Snow and Perrins 1998). All sites were typical of local farmland, with all arable crops under conventional management (i.e. with routine use of agrochemicals).

Insects were sampled from fields of spring- and winter-sown barley (the dominant cereal crops on the study sites, comprising 59% and 27% of the total area of cereals respectively) and the adjacent uncropped margins. Field margins comprised permanent grass margins adjacent to the crop edge (varying in width from 1-12m), with small areas of ditches, hedgerow and roadside verge. Sampling was conducted only from the permanent grass margin adjacent to the crop edge.

Five fields of each crop type and the adjacent margins were sampled at four-weekly intervals (five visits to each field in total). Sampling was conducted along parallel transects across the entire width of each field, perpendicular to the longest boundary of the field. Transects were spaced 100m apart and there were between two and five transects per field. Transects ranged from 82-253m in length, reflecting differences in field size. Sampling was conducted at the same points along each transect on each visit. Each sampling point was treated as a $1m^2$ patch, marked by placing coloured tape around several crop stems at each point. Insects were sampled at two spatial scales within each field: one transect within each field was randomly selected for fine-scale sampling and sample points were located in the margin, 1m into the crop, then at every 5m interval across the field and again in the opposite margin. The remaining transects within each field were sampled at a coarser scale, with sample points located in the margin, 1m into the crop, then at every 30m interval across the field and again in the opposite margin. The number of individual sample points within a field ranged from 23-55, with a total of 193 and 241 sample points for spring- and winter barley respectively. Insects were sampled using a modified petrol-motor leaf vacuum (Ryobi RGBV-3100, Marlow, Bucks, UK). Suction sampling was considered to be the single most efficient method of sampling the widest range of invertebrate taxa known to be important in yellowhammer nestling diet that are diurnally active in the vegetation layer and on the soil surface (Thomas & Marshall 1999).

One invertebrate sample was taken at each sampling point on each visit, and consisted of 5 x 5 second sucks, which were combined to form a single sample. Samples were stored in polythene bags and frozen the same day. Invertebrates were later sorted and identified to order to give a measure of total abundance and the number of individuals at order level.

Analysis

All analyses were conducted in S-Plus 7.0 (Insightful Corporation 2005). Temporal variation in the abundance of insects between the two crop types was firstly examined. The mean abundance at each sampling visit within each crop type (excluding sample points located in margins), was calculated for each of the eight insect groups below:

- total insect abundance;
- chick-food: a combined measure of those invertebrate orders comprising a mean of at least 10% of yellowhammer nestling diet across three studies of UK yellowhammer populations (Stoate *et al.* 1998; Moreby & Stoate 2001; Macleod *et al.* 2005);

The four orders comprising chick-food analysed individually;

- Coleoptera;
- Diptera;
- Araneae;
- Lepidoptera;

Two additional orders for which sufficient numbers were collected to permit analysis:

- Hemiptera;
- Collembola

The significance of differences in abundance between the two crop types at each sampling visit was assessed by constructing bootstrapped 95% confidence intervals around the means, employing 10000 permutations. The five fields of each crop type were each sampled from two different farms (three fields and two fields per farm respectively per crop type). It was therefore possible that additional variation in insect abundance could have been introduced between farms as well as between individual fields. However preliminary analyses revealed that, within each crop type, variation between individual fields within a farm was comparable with that between farms. In addition as field identity would have been confounded by farm identity, it was not considered necessary to control for farm identity in the analyses.

To visualise the within-field spatial distribution of insects, contour plots of insect abundance were created in S-Plus 7.0. One field of each crop type was selected at random and total insect abundance at each of the five sampling visits was categorised by interpolated contouring into shaded density classes.

Variation in crop insect abundance with increasing distance from the margin was then examined. Data were utilised only from the single transect per field sampled at 5m intervals. Within this transect the first ten sample points along the transect, in the crop only (excluding the sample point in the margin), were selected. These points were located at distances of 1-41m from the field boundary. Data were analysed for each transect separately. A linear regression was fitted to each dataset, with a response variable of total insect abundance at each sample point, versus explanatory variable of distance from the boundary. Therefore, for spring barley at visit 1, for example, five separate linear regressions were fitted to the data, corresponding to the transects from each field. The coefficients intercept a, and slope b, were extracted from each regression. The mean intercept from the five regressions was calculated. The mean slope was calculated and the significance of the slope estimate assessed by constructing bootstrapped 95% confidence intervals, employing 10000 permutations, around the mean slope estimate. This procedure was repeated for the five transects per crop type on each of the five sampling visits.

The within-field distribution of insects was then examined for evidence of aggregations. An aggregated distribution would be characterised by high insect counts across a number of neighbouring sample points at the spatial scale in question. This was assessed by calculating spatial autocorrelation using the S+SpatialStats package in S-Plus 7.0 (Insightful Corporation 2005). Significant positive spatial autocorrelation would be expected in the presence of aggregations, where a high insect count at a sample point was correlated with a high count at a neighbouring location. Data were utilised only from the single transect within each field sampled at 5m intervals (i.e. the fine scale sample), within the crop only (excluding sample points located in margins). The analyses described below were conducted within each transect individually, and mean autocorrelation estimates were then calculated per crop type at each sampling visit as described below. Transect lengths differed between individual fields, and between crop types. Therefore to ensure equal numbers of sample points between crop types for the autocorrelation estimates, transect lengths were standardised between crop types. The five transects within each crop type were firstly ranked in order of length. The longest transect from each crop type was then compared, and the longer of the two cropped to the length of the shorter. Transects were cropped by removing sample points from a randomly selected end of the transect in question. This was repeated for each ranked pair of transects between the two crop types.

Autocorrelation was assessed between paired sample points located along a transect at varying spatial scales. The first stage required identifying all pairs of sample points at each spatial scale, by creating spatial neighbour matrices following the methods of Kaluzny *et al.* (1997). The location of sample points was identified using coordinates analogous to easting and northing: x (the same value for each sample point along a transect) and *y* (distance from the boundary, 0m being the field margin). Fifteen neighbour matrices were created for each individual transect. The first matrix was used to identify all pairs of sample points located 5m apart along a transect i.e. all neighbouring sample points. Neighbour pairs were identified in both directions along a transect i.e. a single sample point could form two neighbour pairs, one on either side. The second matrix identified all pairs of sample points located 10m apart i.e. alternate sample points along a transect. Each successive neighbour matrix identified paired sample points at increasing increments of 5m i.e. 15m, 20m, etc up to 75m between sample points in the fifteenth neighbour matrix. As the number of available pairs of sample points along a transect decreased with increasing distance interval, 75m was judged to be the largest spatial scale at which there would be sufficient sample sizes for meaningful analysis. As all pairs of neighbours within a particular matrix were located the same distance apart, default neighbour weights of 1 were assigned within all matrices (Kaluzny *et al.* 1997). The fifteen neighbour matrices per transect were then combined to create a single spatial neighbour object per transect, containing information on all pairs of neighbouring sample points at varying spatial scales. Spatial autocorrelation of total insect abundance was then calculated at each spatial scale within the neighbour object using the function *spatial.cor*. This was repeated within each spatial neighbour object at each sampling visit. Hence for each crop type and each sampling visit, five spatial autocorrelation estimates were obtained at each spatial scale between sample points from 5-75m. The mean of the five autocorrelation estimates at each spatial scale was then calculated per crop type/visit. Bootstrapped 95% confidence intervals employing 10000 permutations were constructed around the means. This allowed the determination of whether the autocorrelation estimates at each spatial scale were significantly greater than, or less than, zero (significant positive or negative spatial autocorrelation respectively).

Results

Temporal insect abundance in different crop types

The majority of insect groups showed a general trend of increasing abundance from April, peaking in June or July, before declining in August (Fig. 1). There was however considerable variation in the abundance of different taxa between the two crop types. Total insect abundance was significantly higher in winter barley than spring barley from April-June (Fig. 1a). In July there was no significant difference between the two crop types, and by August spring barley supported significantly higher abundance (Fig. 1a). There was a similar pattern of relative abundance between crop types for chick-food insects (Fig. 1b). Abundances of the six individual insect orders varied considerably between the two management regimes over the summer (Figs. 1c-h). However a general trend was that winter barley supported significantly higher abundance of many orders in early summer, particularly from April-June.

Spatial distribution

There was evidence of spatial heterogeneity in the within field distribution of insects. Inspection of the contour plots (Fig. 2) revealed that in early summer (April-May) the field of spring barley supported few insects in the cropped area, with the majority of insects concentrated around the field boundary (Figs. 2a-b).

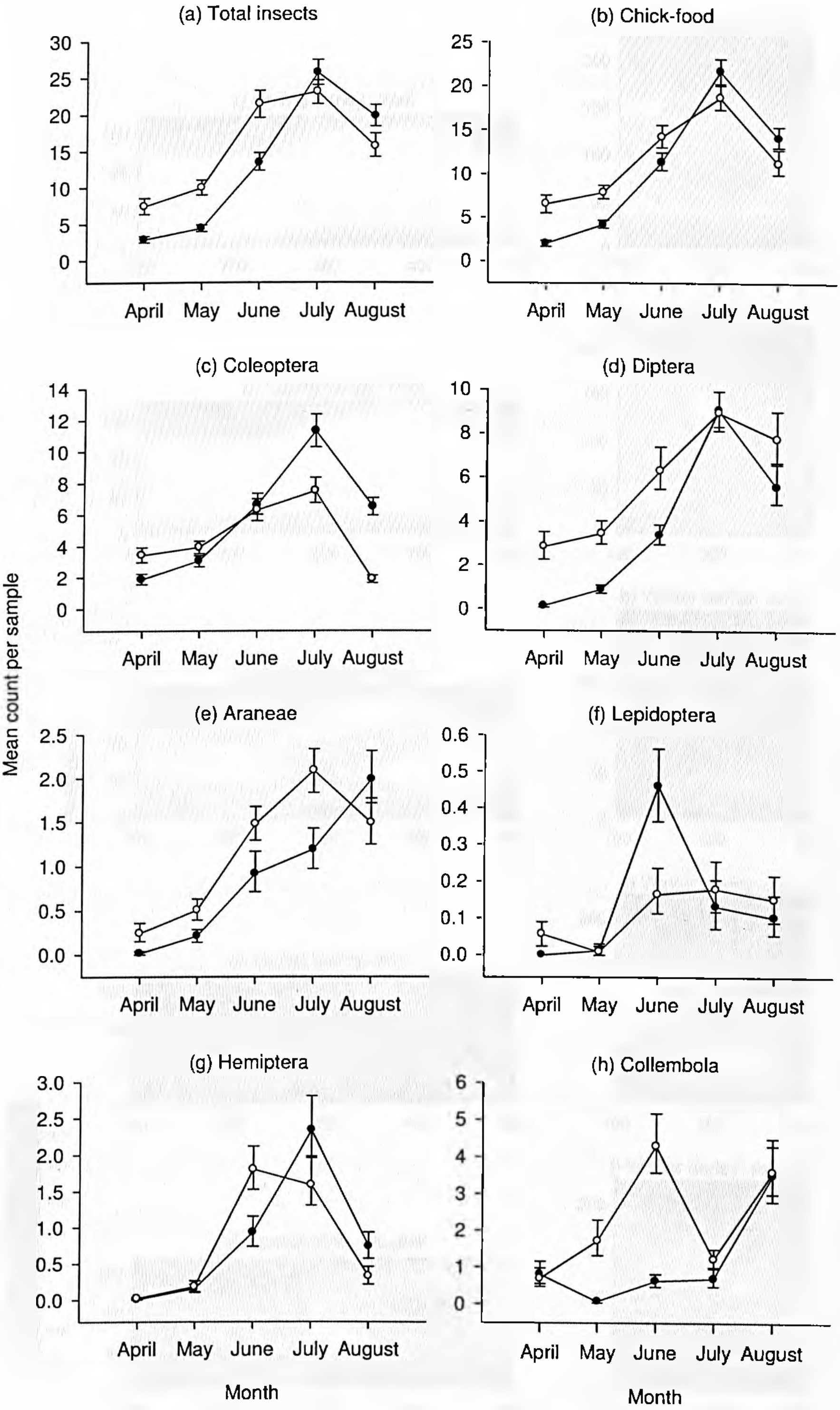

Fig. 1. Temporal abundance of insects in barley under two management regimes; winter barley (open circles) and spring barley (filled circles). Shown are mean count per crop type (derived from five fields of each crop type sampled at monthly intervals), with 95% confidence intervals estimated by bootstrapping.

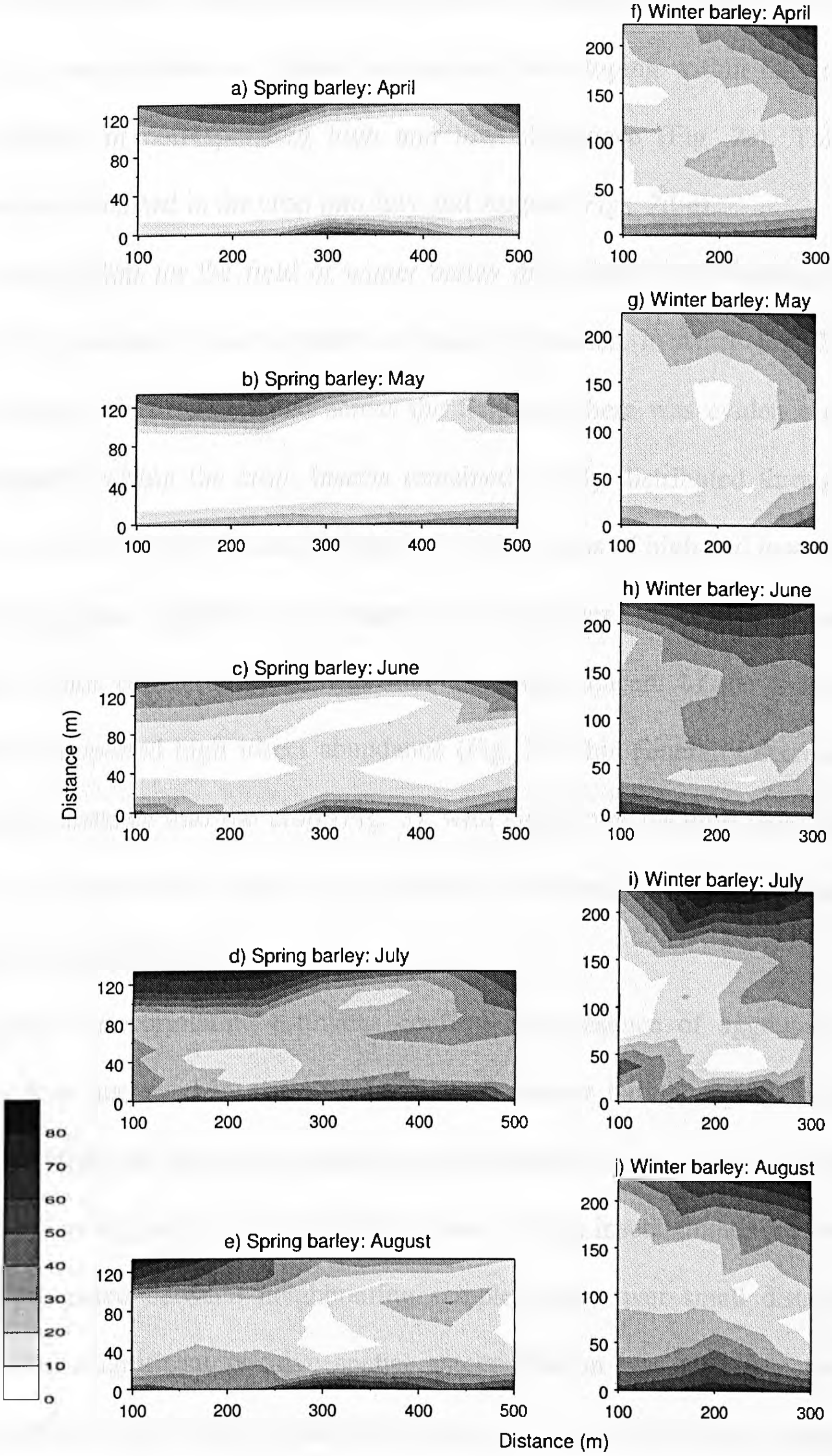

Fig. 2. Total insect abundance sampled at monthly intervals within barley fields, categorised by interpolated contouring into shaded density classes. Plots a-e show a single field of spring barley and f-j show a single field of winter barley. Sampling was conducted at multiple scales (5m and 30m intervals) along transects spaced 100m apart within fields (transect locations on *x* axes, with field width on *y* axes).

By June insects were widely distributed across the cropped area within spring barley, and there was evidence of spatial heterogeneity developing within the crop itself, with patches of corresponding high and low abundance (Fig. 2c). This patchy distribution persisted in the crop into July and August (Figs. 2d-e).

The contour plots for the field of winter barley differ from that of spring barley in terms of spatial and temporal pattern of insect abundance. In April (Fig. 2f) insects were already widely distributed across the field and there was evidence of spatial heterogeneity within the crop. Insects remained widely distributed throughout the field over the whole of the sampling period, with regions of high and low abundance of differing areas apparent at all stages of the summer (Figs. 2g-j). A consistent pattern within both crop types was that the crop adjacent to the field margins generally supported high insect abundance (Fig. 2). This generally decreased with increasing distance into the crop (Fig. 3), with significant declines detected over a scale of ca 40m into the crop in spring barley in May and June, and in winter barley in April and July (Fig. 3).

The spatial autocorrelation estimates confirm the presence of aggregated insect distributions suggested by the contour plots. In winter barley, significant positive autocorrelation was detected at scales of 5-10m between sample points (Figs 4a-e). This suggests the presence of localised patches of high insect abundance, with high counts correlated between neighbouring sample points over small distances (see Discussion). Significant positive spatial autocorrelation was also detected within spring barley, however the estimates were generally weaker and less consistent than those in winter barley. Significant positive autocorrelation was detected within spring barley at the 5m scale in June and July (Figs. 4h and 4i) and intermittently at larger sampling scales: at 15m in April (Fig. 4f) and 35m in May (Fig. 4g).

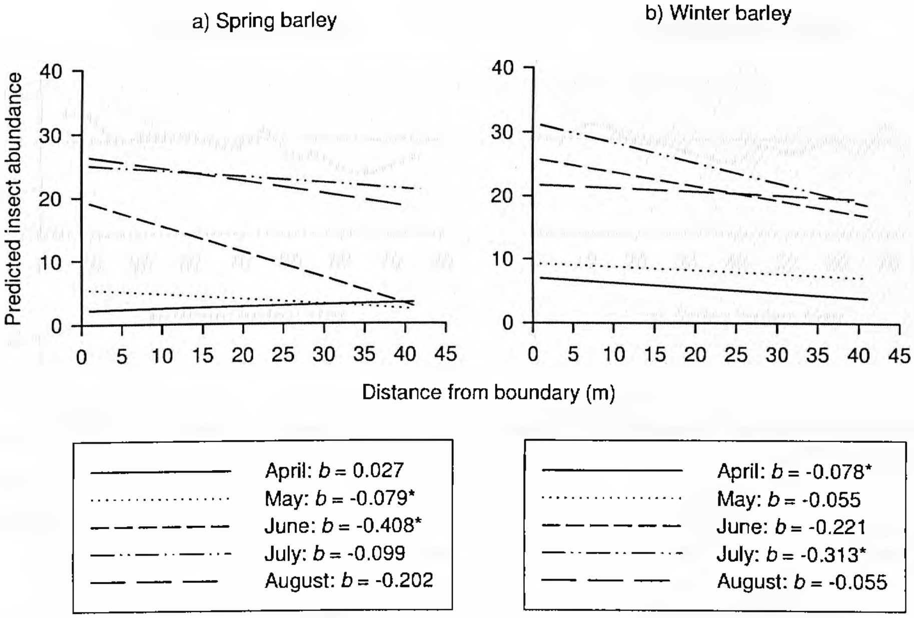

Fig. 3. Variation in crop insect abundance with increasing distance from the field margin. Plots show predicted total insect abundance per crop type from five fields of each crop sampled at monthly intervals. Key shows slope estimates (*b*) per sampling visit, with an asterisk denoting a slope significantly different from zero, assessed by bootstrapping slope estimates.

The significant results at the larger scales may represent artefacts, possibly associated with the statistical techniques, rather than consistent patterns of spatial association in insect distributions (see Discussion below).

Significant negative autocorrelation within insect counts was also detected within both crop types. Although there was considerable noise in the patterns, a general trend was that negative autocorrelation occurred at greater distances between sampling points than the positive autocorrelation estimates. In winter barley, such trends were detected at scales varying from 45-75m between sampling points (Figs. 4a-e). Within spring barley, significant negative autocorrelation was detected over sampling scales varying from 25-75m (Figs. 4f-j).

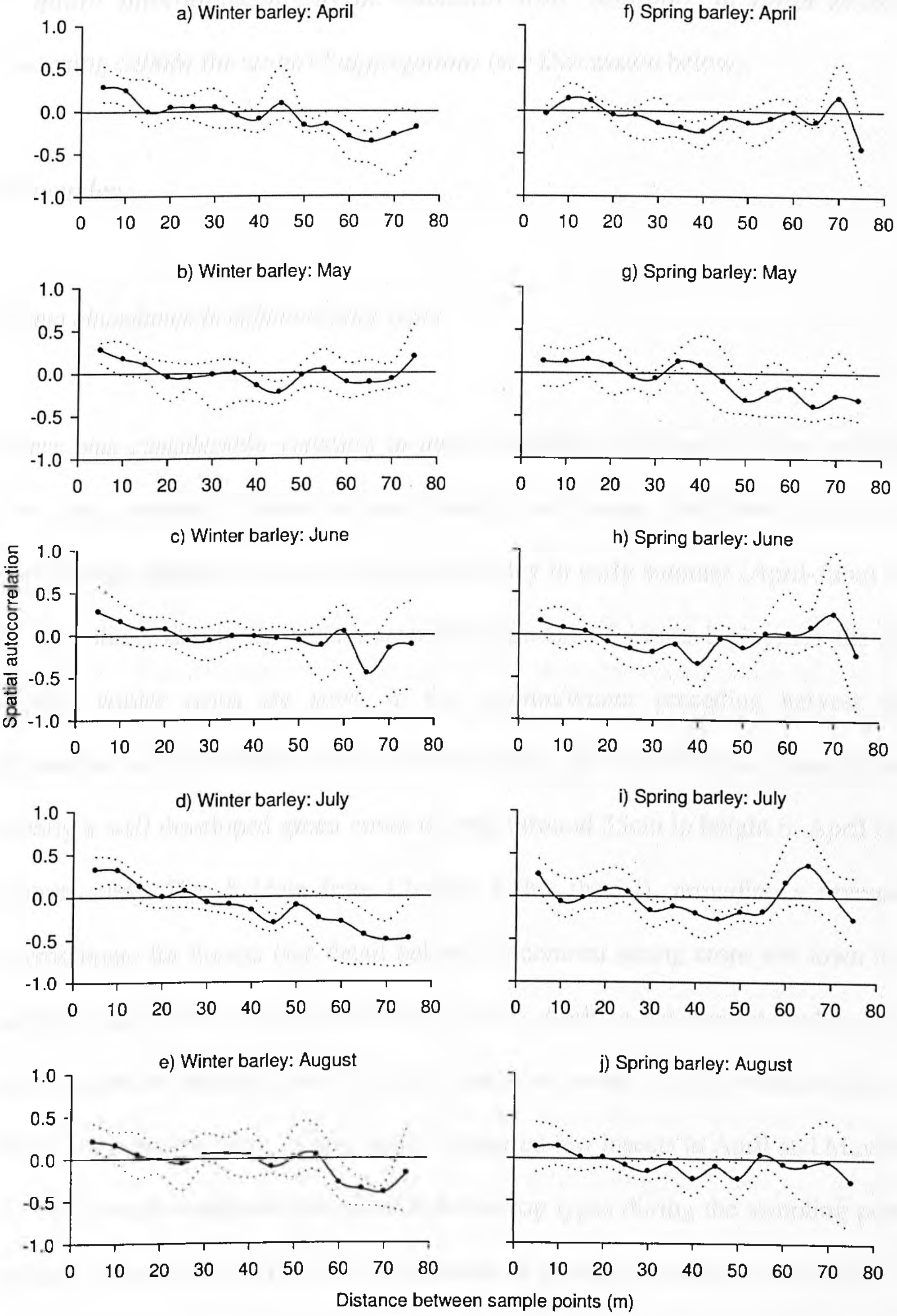

Fig. 4. Within-field spatial autocorrelation of total insect abundance in different crop types at varying distance intervals between sampling points: a-e) Winter barley; f-j) Spring barley. Five fields of each crop type were sampled at monthly intervals. Trends are shown using a smoothing spline and dotted lines indicate 95% confidence intervals estimated by bootstrapping.

Negative autocorrelation may be consistent with ‘coldspots’ of insect abundance occurring outside the range of aggregations (see Discussion below).

Discussion

Insect abundance in different crop types

There was considerable variation in insect abundance between the two crop types over the summer. Counts of total insects and many individual orders were significantly higher in winter- than spring barley in early summer (April-June). This is most likely due to the earlier crop development of winter barley. As the name implies winter crops are sown in the autumn/winter preceding harvest (mid-September to late October in the present study). By the following spring there is usually a well developed green cover of crop (around 35cm in height in April in the present study, Fig. 5 [data from Chapter 3 this thesis]), providing a favourable microclimate for insects (see detail below). In contrast spring crops are sown in the spring of the harvest year (mid-March to early April in the present study). Spring crops therefore generally provide little vegetative cover in early summer (Fig. 5), hence in the present study spring barley supported few insects in April and May (Fig. 1). Total insect abundance increased in both crop types during the sampling period, peaking in both in July (Fig. 1). Colonisation of a crop by insects occurs chiefly via spring migration from the field boundaries and by emergence from pupation directly into a field (Coombes & Sotherton 1986; Ferguson *et al.* 2000; Thomas *et al.* 2002), although some taxa may over winter in winter sown crops (Sotherton 1984; Thomas *et al.* 2002). The timing of migration into the crop varies between different taxa, with 'waves' of dispersal evident at different stages during the spring and summer (Coombes & Sotherton 1986).

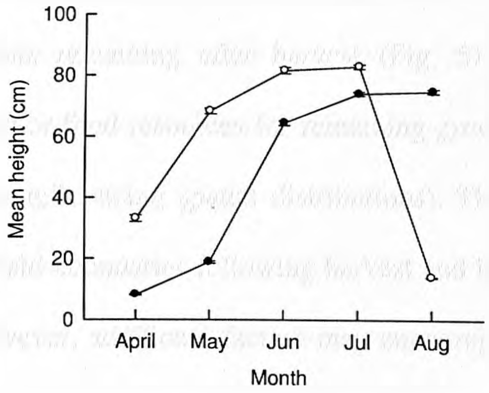

Fig. 5. Vegetation height in winter barley (open circles) and spring barley (filled circles) during the summer. Winter barley was harvested prior to the final measurement in August. Five fields of each crop type were sampled at monthly intervals. Values shown are mean per crop type ±1SE. For further details see Chapter 3.

In April and May insects in the field of spring barley were virtually restricted to the field edges, with little dispersal into the crop until June (Figs. 2a-c). In contrast, insects were already widely dispersed in the field of winter barley by April (Fig. 2f). Different insect taxa may differ in the extent of their migration into the crop, and dispersal from field boundaries does not always result in populations penetrating all the way to field centres (Holland *et al.* 1999a). This may explain why insect abundance generally remained higher in the crop immediately adjacent to the boundary and declined with increasing distance from the boundary (Fig. 3). The implications of seasonal variation in insect abundance between crops and margins for foraging birds are discussed in more detail in Chapter 3 of this thesis.

Insect abundance declined in both crop types in August (Fig. 1). The decline in abundance in winter barley is consistent with harvesting of the crop, which took place in early August prior to the final sampling visit mid-month. Harvesting is likely to cause considerable direct insect mortality, in particular to foliar dwelling taxa. In addition the stubble remaining after harvest (Fig. 5) may offer poor microclimatic conditions and/or food resources for remaining ground dwelling taxa (see detail below on factors influencing spatial distributions). This may stimulate insect migration back into field boundaries following harvest and hence a decline in within crop abundance. However, additional factors may encourage emigration out of the crop in late summer, such as migration back into field boundaries prior to hibernation (Thomas *et al.* 2002). In addition, some taxa including phytophagous groups and their predators are known to decline in abundance as the crop matures (Holland *et al.* 2000), becoming less suitable as a food source. These factors may explain the decline in insect abundance in spring barley in August (Fig. 1), which was not harvested until early September after sampling had ceased.

Few previous studies have examined differences in insect abundance between the same crop under varying management. Holland *et al.* (2002) found few differences in insect abundance between spring- and winter-sown barley over the summer. However, samples collected over several months were pooled prior to analysis, and this may have masked any temporal differences in abundance such as those found in the present study.

Insect abundance may also vary between crop types due to the intensity of agrochemical applications. Cereal crops are sprayed with a variety of chemical pesticides and fertilizers, many of which affect insect abundance (Campbell *et al.* 1997; Ewald & Aebischer 1999). None of the crops in the present study received any insecticides. However, fields of winter barley received a mean of 2.2 herbicide, 1.8 fungicide and 3 fertilizer applications (n = 5 fields). This was greater than the mean of 1.4 herbicide, 1.2 fungicide and 1.6 fertilizer applications to fields of spring barley (n = 5 fields). These figures are consistent with other studies showing that winter cereals generally receive higher pesticide inputs than spring cereals (Robinson & Sutherland 2002). Herbicides and fungicides generally cause only low levels of direct insect mortality (Moreby 1995). However herbicides may have significant indirect effects on insect populations, by reducing weed host plants within the crop that provide food and/or a favourable microclimate for insects (Campbell *et al.* 1997; Holland & Luff 2000). Fungicides may also affect insect abundance indirectly, by reducing the amount of fungal food available to fungivorous species (Ewald & Aebischer 1999). The effects of fertilizer applications on insect abundance are unclear and somewhat contradictory. Lower fertilizer inputs may promote greater heterogeneity in crop structure, providing a more diverse range of environmental conditions suitable for a wider diversity of species (Holland & Luff 2000). However, Moreby (1995) suggests that reduced fertilizer may lead to lower nutritional quality of crops, making cereals a poorer host plant. Therefore whilst apparently receiving higher pesticide inputs over the course of the growing cycle, winter barley supported significantly higher insect abundance than spring barley for a large proportion of the summer (April-June). However, the relative intensity of pesticide applications between crop types should be compared with caution, as the differing brands applied to the two crop types may have varied in efficacy and the concentration they were applied in (Ewald & Aebischer 1999). Regardless of any differences in agro-chemical inputs, the data suggests that the timing of sowing (and hence the stage of crop development at a particular time of year) and harvesting are important influences on temporal variation in insect abundance between crop types (see Conclusions).

Spatial distributions

Visualising within-field patterns of insect abundance using contour plots suggests that insects were patchily distributed, with concentrations of high abundance and corresponding areas containing few insects. Significant positive spatial autocorrelation within insect abundance was detected along individual transects over scales varying from 5-10m. The presence of positive spatial autocorrelation suggests some measure of dependence between insect counts at neighbouring sample points at the spatial scale in question. This would be expected where a high insect count at a particular location gives rise to a high count at a neighbouring location. This in turn suggests the presence of aggregated insect distributions within cereal fields in the present study, with localised 'hotspots' of high abundance occurring over scales of 5-10m between sample points. This is consistent with a range of previous studies of insect distributions in cereal crops. Within Coleoptera, individual species of carabid beetle and counts of total carabids have been shown to be aggregated over a range of fine to medium sampling scales (7.5m, 16m and 30m) in winter wheat, although some clusters of high abundance may extend over areas larger than 1ha (Holland *et al.* 1999a, 2005; Bohan *et al.* 2000). For Araneae, aggregations at 7.5m and 30m have been shown for the family Lycosidae in winter wheat (Holland *et al.* 1999a). Aphid distributions in winter wheat may also be highly aggregated (Winder *et al.* 2001, 2005). Few previous studies have examined the spatial distribution of counts of total insects across a range of orders, including those known to be important in the diet of farmland birds. However, Holland *et al.* (1999b) found evidence of significant clustering of total arthropod counts in winter wheat at the 30m scale.

Trends in positive spatial autocorrelation were more consistent within winter barley than spring barley, with significant associations only detected in spring barley at the 5m scale in June and July. One explanation for this may be differing temporal patterns of insect dispersal into the crop, due to variation in sward development. There were few insects within the crop itself in spring barley in April and May (Figs. 1 and 2). Any insect aggregations, if indeed present, may therefore prove difficult to detect. Despite insect abundance being comparable within spring barley and winter barley by July-August, the later dispersal of insects into spring barley may mean that aggregated distributions never develop to the same extent as in winter barley.

Significant positive autocorrelation was detected intermittently at larger sampling scales within spring barley (at the 15m scale in April (Fig. 4f) and at 35m in May (Fig. 4g). However this may possibly reflect artefacts of the analysis, producing erroneous significant estimates, rather than consistent associations in abundance between sample locations: evidence of significant autocorrelation at smaller spatial scales would be expected in the presence of true aggregations at larger scales, but there was no such evidence in spring barley in either April or May. A further caveat should be applied to the interpretation of the positive spatial autocorrelation estimates as the analyses did not control for variation in insect abundance between field edges and centres. Insect abundance was generally higher around field edges (Figs. 2 & 3) and therefore whilst the autocorrelation estimates utilised data from across the whole width of the fields, the detection of aggregations may have related predominantly to the clustering of insects around field boundaries. This could be investigated by more intensive sampling along the length of the field at equal distances from the field boundary.

Significant negative autocorrelation was also detected within insect distributions in the present study. These patterns were generally found at greater distances between sampling points than the scale of positive autocorrelation. This pattern is consistent with an aggregated insect distribution, where 'coldspots' containing few insects occur beyond the scale of aggregations. For example, negative autocorrelation would be expected between a sample point located within a 'hotspot', having high insect abundance, and a sample point located within a 'coldspot', having lower insect abundance, beyond the scale of the aggregation. This is consistent with the heterogeneous distributions shown in the contour plots, with patches of low abundance surrounding 'hotspots' (Fig. 2). Negative autocorrelation was generally detected at smaller spatial scales in spring barley then winter barley. This is consistent with the smaller spatial scale at which aggregations were detected within spring barley. Any trends detected over larger distances between sample points may be less reliable than localised patterns at small spatial scales. This is because sample sizes in the autocorrelation calculations declined with increasing distance between sampling points. The considerable widening of the confidence intervals at larger scales suggests that, in the present study, the autocorrelation estimates may become unreliable above scales of approximately 50-60m between sampling points (Fig. 4).

A wide variety of interacting factors determine the spatial distribution of insects within cereal fields. Environmental variables play an important role, and it is their combined effect, in conjunction with inter- and intra-species relationships that gives rise to heterogeneous distributions (Holland *et al.* 1999a; Thomas *et al.* 2001, 2002). Numerous insect taxa are predatory and are known to aggregate in response to prey items (Bryan & Wratten 1984; Harwood *et al.* 2001; Winder *et al.* 2001, 2005). Complex multispecies aggregations may also occur in response to food resources. For instance, carabid beetles may respond to aggregations of cereal aphids either because they are attracted to the aphids as prey or because they are attracted to alternative prey which aggregate around the honeydew produced by the aphids (Monsrud & Toft 1999). Many insects are also phytophagous and may aggregate in response in plant food. A range of taxa including Coleoptera, Lycosidae (Araneae) and Collembola may be positively related to weed cover within cereal fields (Speight & Lawton 1976; Coombes & Sotherton 1986; Holland *et al.* 1999a). However, the influence of weed cover may be two-fold as vegetation will also influence the microclimate. Groups including carabid beetles are known to have optimal microclimatic ranges and may aggregate in areas where conditions are most favourable (Thomas *et al.* 2002). The most important factors are thought to be temperature, humidity and light, mediated by vegetation and soil conditions. These can vary at the spatial scale of an individual field (Thomas *et al.* 2002). Additional abiotic factors associated with soil conditions such as moisture, organic content and pH may also give rise to heterogeneous insect distributions (Thomas *et al.* 2002).

The spatial associations shown by combined measures of total insect abundance across taxa in the present study may therefore reflect the presence of multispecies aggregations similar to those described above, where favourable microclimatic and/or food resources lead to a variety of taxa aggregating in the same locations within a field.

The scale at which insect sampling is conducted may bias the scale at which aggregations are detected (Holland *et al.* 1999a; Thomas *et al.* 2002). This is unavoidable to some extent when sampling is conducted at regularly spaced intervals. However any bias in the present study is likely to have been minimised as the analyses allowed the testing of spatial autocorrelation over the widest reasonable range of spatial scales.

Conclusions

This study has, for the first time, demonstrated marked differences in the temporal abundance and spatial distribution of insects in a cereal crop managed under two differing regimes, and quantified the patchy nature of insect abundance within crops. A key factor underlying this variation appears to be differences in the timing of crop development and, as predicted, proximity to margin vegetation. The sampling period covered by the study encompasses the breeding season of many farmland bird species. These results suggest that spring- and winter-sown crops offer differing levels of insect resources for foraging birds at different stages of the summer, with winter barley supporting more insects in early summer, and spring barley more in late summer. A major change to farming practices over recent decades has been the large-scale switch from spring to autumn sowing of cereal crops (Robinson & Sutherland 2002). This has resulted, generally, in a negative impact on farmland birds in terms of reducing the quality of foraging habitat in winter (through loss of winter stubble) and nesting habitat in summer for some species such as skylark. The results of the present study suggest that winter sown crops may still provide better foraging habitat for farmland birds, in terms of higher insect resources than spring crops, in early summer but poorer quality in late summer. A heterogeneous mix of spring and winter sown cereals in close proximity (with over winter stubbles retained where appropriate) is likely to provide optimum benefits for farmland birds, by ensuring a range of insect and seed resources at different stages of the year. It is also possible that timing of sowing is a potentially important management tool that could be promoted as a means of enhancing the abundance of insects in crops for foraging birds during the summer. However, although earlier sowing of spring crops may enhance food availability in the crop earlier in the season, it may have the undesired effect of reducing food available in late winter by ploughing in stubbles earlier. This late winter period is increasingly recognised as a 'gap' in food resources for birds such as yellowhammers (e.g. Evans *et al.* 2004).

This study found evidence of localised insect aggregations within cereal crops at scales of 5-10m and reinforces the particular value of crop edges and margins in terms of supporting insect prey. There is evidence that foraging yellowhammers can detect and exploit patches of high insect abundance in cereal crops (Morris *et al.* 2002) and there may be potential for a more targeted approach to crop management that would benefit foraging birds. This might, however, require more knowledge on the factors underlying the patchiness observed e.g. whether it is driven by edaphic factors such as soil type or soil moisture. Accessibility of insects, mediated by vegetation structure, may also be an important determinant of patch selection in cereals for foraging birds (Odderskaer *et al.* 1997).

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Chapter 3: Foraging habitat selection by breeding yellowhammers at two spatial scales: food abundance versus accessibility.

Abstract

Farmland bird populations have undergone dramatic declines across much of Europe and sympathetic management of foraging habitats is a key means of population recovery. Maximizing the value of habitats for foraging birds requires detailed knowledge of the factors influencing habitat selection and foraging efficiency at multiple spatial scales. Foraging habitat selection by breeding yellowhammers *Emberiza citrinella* was investigated at two scales, habitat (field, margin etc) and patch, in relation to the invertebrate and vegetation characteristics of these habitats and patches. At the habitat scale, field margins and cereal crops were the primary foraging habitats but there was a clear seasonal shift in their relative use. Margins were used less than crops in late summer, despite consistently supporting significantly higher abundance of important chick-food invertebrates. Vegetation height increased in all habitats during the summer, but did so to the greatest extent in margins, suggesting that this seasonal shift may be due to reductions in food accessibility within field margins. At the patch scale, yellowhammers selected patches with shorter, sparser vegetation and higher invertebrate abundance than random non-foraged patches. Bare patches such as tractor tramlines were favoured within cereal fields. These patches are likely to allow greater access to prey than the dense swards of intensively managed cereal crops.

This study suggests that vegetation structure is an important determinant of habitat selection at both the habitat and patch scale. Dense vegetation in field margins and

cereal crops may offer poor foraging opportunities for a range of farmland bird species and greatly reduce the value of these margins for birds breeding later in the summer. Provision of invertebrate-rich field margins is a core component of agri-environment schemes, however, vegetation growth of many such margins may result in them having limited value in late summer. More active management, such as more frequent cutting, may be required to maximize the benefits for foraging birds by creating patches of shorter, more open vegetation. The cost-effectiveness of such management needs to be assessed but measures to increase accessibility to invertebrates on farmland will benefit a range of farmland bird species.

Introduction

Animals foraging in patchy landscapes must select habitats at a number of spatial scales, and a variety of factors will influence this selection, including food availability and perceived predation risk. For animals such as altricial birds, breeding requires food to be delivered to a central place (the nest) and adult foraging efficiency is an important influence on nestling weight and subsequent survival (Magrath 1991; Wright *et al.* 1998). Parents must balance the energetic costs of collecting food against the effect on body condition, which may affect both survival and future reproductive effort (Nur 1984a, b, 1988). In poor environments parents may work harder to provision nestlings with an equal amount, or less, of food (Tremblay *et al.* 2005). This leads to a trade-off between maximizing nestling growth and minimizing parental foraging costs. Foraging efficiency will be determined, in part, by the abundance and accessibility of prey. Vegetation structure is an important determinant of food availability and can affect foraging efficiency in a number of ways. Vegetation structure affects the accessibility and detectability of food items (Brodmann *et al.* 1997; Butler & Gillings 2004; Stillman & Simmons 2006), forager mobility (Brownsmith 1977; Devereux *et al.* 2004) and also the perceived risk of predation (Whittingham & Evans 2004; Whittingham *et al.* 2006a), and hence is likely to be a major influence on foraging habitat selection.

The yellowhammer *Emberiza citrinella* has shown a marked decline in the UK since the 1980s (Gregory *et al.* 2002) and, like many declining farmland birds requires protein-rich invertebrates for nestling growth and development (Brickle *et al.* 2000; Hart *et al.* 2006). Intensification of farmland management has led to reductions in invertebrate availability, directly through reductions in abundance (Ewald & Aebischer 1999; Benton *et al.* 2002) and indirectly through changes in sward structure, reducing accessibility to invertebrates (McCracken & Tallowin 2004; Wilson *et al.* 2005). The availability of invertebrates has been shown to influence the nestling growth and productivity of a number of farmland birds (Brickle *et al.* 2000; Brickle & Peach 2004; Hart *et al.* 2006) and a link has been shown between invertebrate abundance, bird populations and measures of farm management (Benton *et al.* 2002).

One key aim of agri-environment schemes designed to aid population recovery is the provision of suitable foraging habitats for farmland birds (Vickery *et al.* 2004), often through measures such as the creation and maintenance of invertebrate-rich field margins. However, deriving the maximum benefit from these measures requires detailed knowledge of how and when birds use different habitats to collect food. We investigated foraging habitat selection of yellowhammers, a bird that shares similar foraging habits with a number of other declining farmland passerines such as corn bunting *Emberiza calandra* and skylark *Alauda arvensis* (Brickle *et al.* 2000; Wilson

2001). A number of previous studies have examined foraging habitat selection by this species (Stoate *et al.* 1998; Morris *et al.* 2001, 2002; Perkins *et al.* 2002) but none have considered habitat selection at multiple spatial scales and in relation to detailed measurements of invertebrates and vegetation throughout the breeding season.

The aim of this study was to determine how foraging habitat selection by yellowhammers at two spatial scales varied in relation to (i) invertebrate abundance, (ii) vegetation characteristics and (iii) stage in the breeding season. The scales studied are termed habitat and patch. The former relates to relatively coarse scale differences between habitat types (cropped, natural and semi natural etc) and the latter to fine scale differences within a habitat type. The implications of these findings for the cost-effectiveness and development of margin options within agri environment schemes are considered.

Methods

Study sites

Fieldwork was conducted from May-August 2004-2006 on five farms in Aberdeenshire, ranging in size from 98 to 292 ha. All sites were typical of local farmland, comprising a mix of arable and grassland habitats under conventional management (i.e. with routine use of agrochemicals). The dominant arable crops were cereals, mainly spring- and winter-sown barley *Hordeum* spp., with small areas of winter wheat *Triticum* spp.

Invertebrate and vegetation sampling from cereals and margins

Previous studies indicated that field margins and cereal crops are two of the most frequently used habitats by foraging yellowhammers (Stoate *et al.* 1998; Morris *et al.* 2001; Perkins *et al.* 2002). Invertebrate and vegetation characteristics were therefore sampled from fields of spring- and winter-sown barley (the dominant cereal crops on the study sites, comprising 59% and 27% of the total area of cereals respectively) and the adjacent margins from May-August 2004. Field margins were defined as the strip of semi-natural boundary habitat separating cropped fields. Margins on the study sites were dominated by permanent grass margins adjacent to the crop edge (varying in width from 1-12m), with small areas of ditches, hedgerow and roadside verge. Five fields of each crop type were sampled at 4-weekly intervals (four visits to each field in total). Sampling was conducted along parallel transects across the entire width of each field, perpendicular to the longest boundary of the field. Transects were spaced 100m apart and there were between 2 and 5 transects per field. Sampling was conducted at the same points along each transect on each visit. Each sampling point was treated as a 1m^2 patch, marked by placing coloured tape around several crop stems at each point. Sample points were located in the margin, 1m into the crop, then at every 30m interval across the field and again in the opposite margin. Insects were sampled using a modified petrol-motor leaf vacuum (Ryobi RGBV-3100, Marlow, Bucks, UK). Suction sampling was considered to be the single most efficient method of sampling the widest range of invertebrate taxa known to be important in yellowhammer nestling diet that are diurnally active in the vegetation layer and on the soil surface (Thomas & Marshall 1999). One invertebrate sample was taken at each sampling point on each visit, and consisted of 5 x 5 second sucks, which were combined to form a single sample. Samples were stored in polythene bags and frozen the same day. Invertebrates were later sorted and identified to Order to give a measure of total abundance and the number of individuals at Order level.

Vegetation height (to the nearest 5cm) was recorded at each sampling point on each visit (the mean of 5 measurements, one taken from each corner and one in the centre of the sampling patch).

Foraging watches

Foraging behaviour of breeding yellowhammers was studied from May-August in 2005 and 2006. Nests were located by mapping territorial males and watching for signs of breeding behaviour. Three hour foraging watch observations were conducted on 60 nests (30 nests in 2005 and 2006 respectively [one per nest]) with nestlings aged 6-11 days. Observations were carried out from 0700-1100 to control for the effect of diurnal variation. Periods of adverse weather, e.g. heavy rain, were avoided. During a watch the location of all foraging flights made by parents to collect food for nestlings were recorded, marking sites on sketch maps. If a parent visited more than one site during a foraging flight the location of the last site was recorded as the foraging site and multiple visits to the same site were recorded. Foraging sites were considered to be separate if spatially separated by at least 20m from another site. Adults returning to the nest with food frequently perched before entering the nest, and whenever possible the food items provisioned to chicks were identified using a 30x telescope.

Invertebrate and vegetation sampling at foraging sites

At 25 of the nests for which foraging observations were made in 2005, fine-scale foraging patches were sampled for vegetation and invertebrates. Foraging sites were treated as $1m^2$ patches located in the centre of the site where the bird was observed foraging, and were marked with canes immediately following a watch. The distance of each foraging patch from the nest was recorded using a hand-held GPS (accuracy ± 5m). Each foraging patch was paired with a random non-foraged control patch, located 50m from the foraging site, but the same distance from the nest as the foraging site. At each foraging and control site, invertebrates were sampled using the same Ryobi suction device and protocols as described above, with one sample from each site, comprising 5 x 5 second sucks, combined to a single sample. These were stored and then processed as described above. All invertebrate sampling was conducted on the same day as the foraging watch.

A number of measurements of vegetation structure were also taken at each foraging and control site: Habitat type (margin, spring-barley, winter-barley, winter-wheat, grass fields, set-aside), vegetation height (mean of 5 measurements, each to the nearest 5cm, one in each corner of the patch and one in the centre); vegetation density (mean of 5 measurements). Vegetation density was measured at the same time as height, by looking down the measuring stick and recording the lowest 5cm band that could be seen. Percentage cover of bare earth (to the nearest 10%) was estimated within each patch. For those foraging and control sites located in cereal fields, three additional characteristics were recorded: the percentage of non-crop vegetation (grass and weed spp.); the number of crop stems in a 0.25m x 0.25m quadrat thrown randomly in the foraging site, and; the presence/absence of a tramline.

Foraging habitats

Habitat types surrounding each nest were mapped onto Ordnance Survey 1:10000 maps. Three habitat categories were defined: field margins, cereals (spring- and winter-sown barley, winter wheat) and other (set-aside, grass fields, winter oilseed rape, potatoes, woodland, houses, farmyards, roads/tracks). The area of each habitat type available within a 333m foraging radius of each nest (the 95th percentile of all mapped flights across all nests in this study) was calculated.

Analysis

All analyses were conducted in R v2.3.1 (R Development Core Team 2006). All probabilities quoted are two-tailed. Means and SE are presented in the form mean ± 1 SE.

Abundance of invertebrates sampled in 2004 in margins, spring-barley and winter-barley was compared using a generalised linear mixed model (GLMM), with poisson error structure and log-link. The response variable was total invertebrate abundance at each sampling point on each visit, with habitat (a three level factor) and visit (four level factor) as explanatory variables, with an interaction term included. Visit and field identity were specified as random terms, to control for temporal and spatial pseudoreplication respectively. This model was repeated with a response variable comprising abundance of those invertebrates known to be important in yellowhammer nestling diet. This measure of chick-food included those taxonomic groups comprising a mean of at least 10% of nestling diet using data from three studies of UK yellowhammer populations (Stoate *et al.* 1998; Moreby & Stoate 2001; Macleod *et al.* 2005) and consisted of Coleoptera, Diptera, Lepidoptera and Arachnidae.

Vegetation height in margins, spring barley and winter barley was examined using a linear mixed effects model (LME), with mean vegetation height at each sampling point on each visit as the response variable. Habitat and visit were specified as factors, including an interaction term. Visit and field identity were declared as random terms. Broad-scale habitat usage by foraging adults in 2005 and 2006 was investigated using a GLMM with poisson error structure and log-link. The response variable was the number of foraging visits to each habitat per nest. Habitat type and season (early or late, to examine temporal changes in usage of different habitats) were included as explanatory variables, testing for an interaction. Each nest was assigned to either early or late season according to the midpoint between the earliest and latest foraging watches across both years (hence early = 20th May-2nd July and late = 3rd July-14th Aug). Nest identity was specified as a random term, rather than individual bird ID, as it was not always possible to distinguish between the sexes within each pair at a nest. Log_e (area) of each habitat type, within a 333m radius of a nest, was declared as an offset. This allowed the number of foraging visits to each habitat per nest to be expressed as foraging densities (Morris *et al.* 2001).

The significance of all terms in the models above was assessed by removing terms one at a time and assessing the change in deviance, which is distributed asymptotically as χ^2. The fit of all GLMM's described above to the assumptions of a poisson distribution was assessed using the ratio of residual deviance / residual d.f.

(Crawley 2002). A ratio close to one indicates a reasonable fit, but ratios greater than 1.5 indicate a poor, overdispersed fit (Crawley 2002). The LME of vegetation height was assessed for normality of the residuals.

Fine-scale patch selection was analysed by comparing invertebrate and vegetation measurements between paired foraging and control sites. A number of GLMM's were constructed, all with binomial error structure, logit-link and including nest as a random term. The first model examined differences between all paired foraging and control sites across all habitats, using a binary response variable (foraging or control site). Six explanatory variables were included: total invertebrate numbers; chick-food abundance; vegetation height; vegetation density; percentage of bare earth and habitat. Paired foraging and control sites were grouped by ranking each pair within a nest in order of increasing distance from the nest, and adding this covariate of "Site pair rank" to the model. A minimum adequate model (MAM) was obtained by manual stepwise deletion from a full model containing all main effects and first order interaction terms. At each step the least significant term in the model was removed, beginning with interaction terms, and the term discarded if its removal resulted in a non-significant change in deviance at the $P<0.05$ level (Crawley 2002). Non-significant factors that featured in significant interactions were not removed from the MAM (Crawley 2002). In a second model this analysis was repeated on a subset of the data using a binary response variable of just those paired foraging and control sites that were located in cereal fields. The explanatory variables *vegetation density* and *habitat* from the first model were replaced with three additional explanatory variables; *crop stem density* (number of stems counted in a 0.25 x 0.25m quadrat thrown randomly in the patch); *percentage of non-crop vegetation* (grass and weed spp.) and; *presence/absence of a tramline* at the site. The model was simplified as described above. A third model was constructed to examine differences between those foraging sites visited once with those visited two or more times across all habitats, using a binary response variable (1 or $\geq$2 visits). Eight explanatory variables were included: total invertebrate numbers; chick-food abundance; vegetation height; vegetation density; percentage bare earth; distance from the nest; mean trip duration (the mean length of time spent visiting the patch per visit), and habitat. Model simplification was conducted as above. Whilst mean trip duration included the flight time to and from the nest to the patch, this was considered to be only a small fraction of the total trip duration, hence mean trip duration is a good indicator of time spent foraging at the patch. The significance of all terms retained in the minimum adequate models was assessed by removing terms one at a time and assessing the change in deviance, which is distributed asymptotically as χ^2. Models containing binary response variables are not subject to overdispersion (Crawley 2002) so correct fit of these models was assumed. The robustness of the three MAMs described above was assessed to ensure that deleting terms from the full model and utilising the full data-set for each respective analysis resulted in the 'best-fitting' models (an approach yielding results comparable to alternative model selection techniques such as IT-AIC, Whittingham *et al.* 2006b). Various simplifications of the MAMs were fitted and the significance of variables of interest tested to ensure that they remained significant in the simplified models, which proved to be the case. In all cases the AIC value of the simplified models was considerably larger than for the respective MAM. This indicated that the MAMs, despite containing a relatively large number of significant terms and interactions provided a better fit to the data than the various simplifications (Crawley 2002).

Results

Broad scale habitat use by foraging adults

A total of 1549 foraging flights to known destinations were recorded during the observations of foraging behaviour. The number of foraging flights to known destinations varied from 15-45 per watch (range 7-21 different foraging sites identified per watch). Fig. 1 shows the percentage of visits to field margins and cereals, the two most frequently visited habitats.

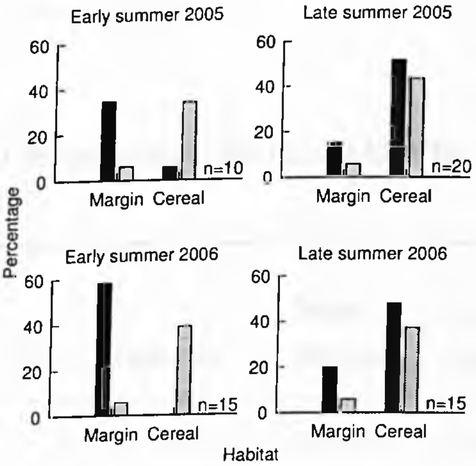

Fig. 1. Foraging habitat use by breeding yellowhammers. Data shown are percentage of visits to the two primary foraging habitats (black bars) relative to area available (grey bars). Area of habitat available was calculated within a 333m radius of each nest (the 95th percentile of all foraging flights recorded in the study).

In early summer field margins were used heavily, with little or no use of cereal crops. Late in summer, use of field margins declined markedly, with a large increase in the use of cereal fields. There was a significant change in overall habitat use between early and late season (habitat x season interaction, Table 1); a significant decrease in use of field margins between early and late season ($z = 4.49$, $P<0.001$) and a significant increase in the use of cereal fields ($z = 12.31$, $P<0.001$). There was also a significant decrease in use of "other" habitat types between early and late season ($z = 3.37$, $P<0.001$). However this category consists of numerous habitat types each present and visited in relatively small proportions, making interpretation of any patterns difficult, and the use of "other" habitats is not considered further. There was a significant interaction between habitat and year (Table 1), probably due to small differences in the use of margins and cereals between years, but the overall pattern of seasonal habitat use did not differ significantly between years (season x year, $\chi^2 = 1.8$, d.f = 1, $P = 0.18$).

Table 1. Sequential deviance table for the GLMM for the effects of season on habitat usage

Term	df	Deviance	Mean deviance	Deviance ratio	P
Habitat	2	859.72	429.86	304.87	<0.001
Season	1	1.80	1.80	1.27	0.180
Year	1	3.97	3.97	2.92	0.046
Habitat*Season	2	423.98	211.99	155.88	<0.001
Habitat*Year	2	26.02	13.01	9.57	<0.001
Residual	169	229.84	1.36		
Total	178	1545.39			

Non-significant term removed from model:					
Season*Year	1	1.80			0.180

Vegetation structure and arthropod abundance in cereals and margins

There was a trend for total invertebrate abundance to increase in all habitats from May-July and then decline in August (Fig. 2a). Over the entire summer total invertebrate abundance differed significantly between habitats (Table 2a, Fig 2a); field margins supported significantly more invertebrates than either spring- (z = 37.59, P<0.001) or winter-barley (z = 21.22, P<0.001) at all months over the summer.

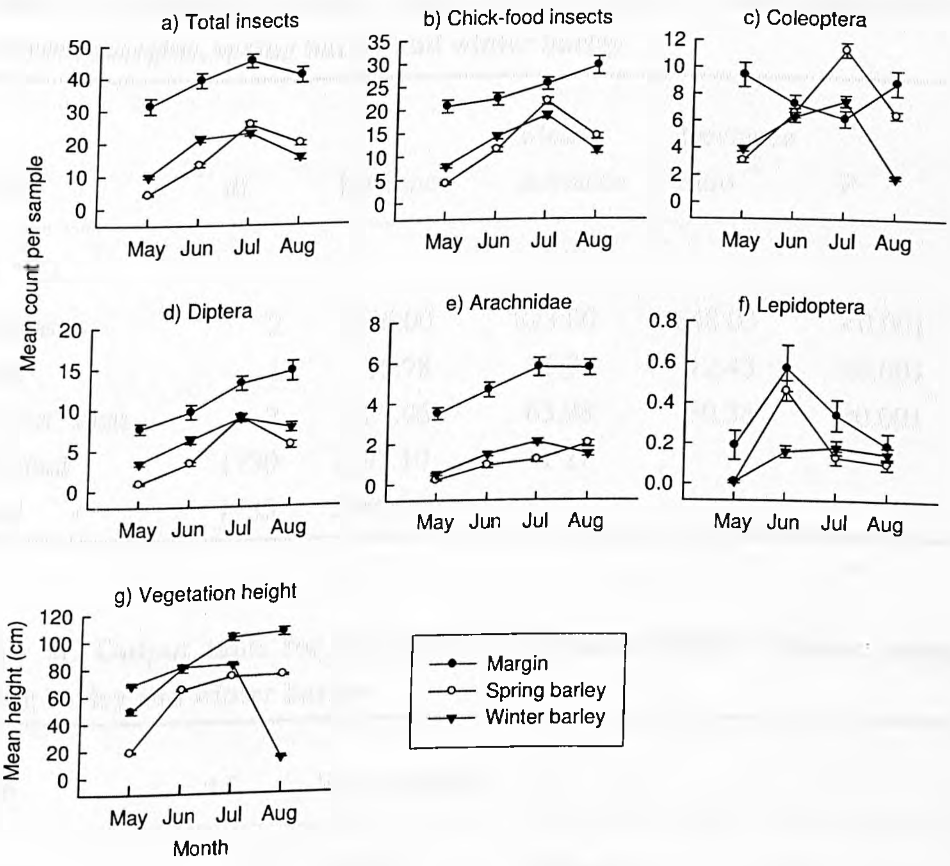

Fig. 2. Insect abundance and vegetation height in primary foraging habitats of breeding yellowhammers. Measures of insect abundance are: a) Total insects; b) Chick-food insects; c-f) the four orders comprising chick-food. Data were collected from five fields of each crop type and adjacent margins at monthly intervals during the breeding season.

Table 2a. Sequential deviance table for the GLMM of total invertebrate abundance between margins, spring barley and winter barley

Term	df	Deviance	Mean Deviance	Deviance ratio	P
Habitat	2	1373.90	686.95	494.21	<0.001
Visit	1	13.97	13.97	10.05	<0.001
Habitat*Visit	2	354.00	177.00	127.34	<0.001
Residual	1730	2404.70	1.39		
Total	1735	4146.57			

Table 2b. Sequential deviance table for the GLMM of chick-food abundance between margins, spring barley and winter barley

Term	df	Deviance	Mean deviance	Deviance ratio	P
Habitat	2	1646.00	823.00	648.03	<0.001
Visit	1	15.78	15.78	12.43	<0.001
Habitat*Visit	2	127.96	63.98	50.38	<0.001
Residual	1730	2197.10	1.27		
Total	1735	3986.84			

Table 2c. Output table for the LME of vegetation height between margins, spring barley and winter barley

Term	d.f.	Wald statistic	P
Habitat	2	237.02	<0.001
Visit	1	0.45	0.503
Habitat*Visit	2	455.91	<0.001
Residual	1730		
Total	1735		

This was also true when considering only chick-food invertebrates (Table 2b, margins>spring-barley [z = 24.40, P<0.001], margins>winter-barley [z = 11.89, P<0.001). However, seasonal patterns of chick-food abundance differed from that of total invertebrates. Numbers of chick-food invertebrates increased in all habitats from May-July, and then declined markedly in cereals in August, whilst continuing to increase in margins in August (Fig. 2b). Different orders of chick-food invertebrates also showed differing seasonal patterns of abundance between the three habitats (Figs. 2c-f).

Vegetation height increased in all three habitats over the summer (Fig. 2g). There was a large reduction in height in winter-barley in August, corresponding with harvesting of the crop. Vegetation height in margins and spring-barley increased during August. Overall vegetation height differed significantly between habitats (Table 2c), being significantly greater in margins than either spring- (t = 3.18, d.f = 1721, P = 0.002) or winter-barley (t = 16.72, d.f = 1721, P = 0.001), particularly in July and August (Fig. 2g).

Fine-scale patch selection

Across all habitats foraging patches were characterised by significantly shorter vegetation, more bare earth (Table 3a, Figs. 3a, 3b) and significantly greater abundance of chick-food invertebrates than control sites (Table 3a, Fig. 3c).

Foraging sites within cereal fields were characterised by shorter, more open vegetation than control sites, with significantly lower crop height, a greater area of bare earth and significantly lower crop stem density (Table 3b, Figs. 3a, 3b, 3d).

Table 3a. MAM for the GLMM for the comparison of invertebrate and vegetation characteristics between all paired foraging and control sites (n = 25 nests, 297 paired sites)

Term	d.f.	Deviance	Mean deviance	Deviance ratio	P
Chick-food invertebrates	1	23.89	23.89	22.97	<0.001
Vegetation height	1	28.17	28.17	27.08	<0.001
Vegetation density	1	0.01	0.01	0.01	0.909
Percentage bare earth	1	20.54	20.54	19.74	<0.001
Habitat	2	18.02	9.01	8.66	<0.001
Vegetation height*Vegetation density	1	29.28	29.28	28.15	<0.001
Vegetation height*Habitat	2	11.53	5.77	5.54	0.003
Vegetation density*Habitat	2	20.53	10.27	9.87	<0.001
Residual	579	602.23	1.04		
Total	593	754.20			

Table 3b. MAM for the GLMM for the comparison of invertebrate and vegetation characteristics between paired foraging and control sites in cereal fields (n = 16 nests, 128 paired sites)

Term	d.f.	Deviance	Mean Deviance	Deviance ratio	P
Total invertebrates	1	4.15	4.15	4.55	0.042
Chick-food invertebrates	1	8.21	8.21	9.01	0.004
Vegetation height	1	12.10	12.10	13.28	<0.001
Crop stem density	1	4.13	4.13	4.54	0.042
Percentage bare earth	1	6.46	6.46	7.09	0.011
Percentage non-crop vegetation	1	0.86	0.86	0.95	0.353
Tramline	1	10.03	10.03	11.01	0.002
Total invertebrates*Vegetation height	1	3.89	3.89	4.27	0.049
Total invertebrates*Tramline	1	6.85	6.85	7.52	0.009
Chick-food invertebrates*Vegetation height	1	7.82	7.82	8.59	0.005
Chick-food invertebrates*Tramline	1	6.36	6.36	6.98	0.012
Vegetation height*Percentage bare earth	1	7.32	7.32	8.03	0.007
Vegetation height*Tramline	1	5.82	5.82	6.39	0.016
Percentage bare earth*Percentage non-crop vegetation	1	7.48	7.48	8.21	0.006
Residual	239	217.81	0.91		
Total	255	309.31			

Table 3c. MAM for the GLMM for the comparison of invertebrate and vegetation characteristics between foraging sites visited once and those visited twice or more (n = 25 nests, 1 visit = 156 sites, ≥2 visits = 70 sites). Mean trip duration is a combined measure of foraging time at the patch and travel time to and from the patch to the nest per visit.

Term	d.f.	Deviance	Mean deviance	Deviance ratio	P
Chick-food invertebrates	1	10.68	10.38	11.37	0.001
Mean trip duration	1	83.86	83.86	89.27	<0.001
Residual	223	209.47	0.94		
Total	225	304.01	1.35		

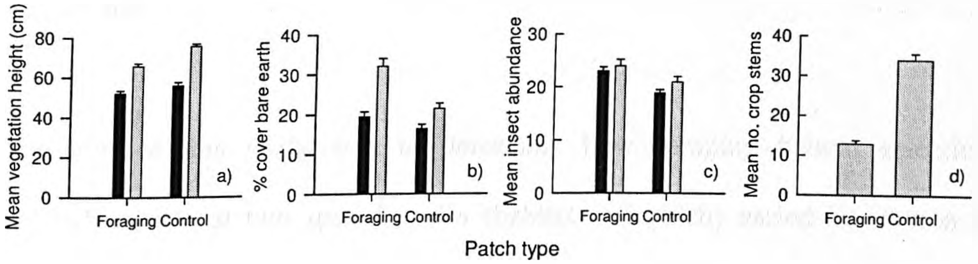

Fig. 3. Characteristics of foraging and control patches across all habitats (black bars) and within cereal crops (grey bars): a) vegetation height; b) percentage cover of bare earth; c) abundance of chick-food invertebrates; d) crop stem density (cereal crops only). Foraging patches were identified from observations of adult yellowhammers provisioning nestlings, and each foraging site was paired with a random non-foraged control site (all habitats: n = 25 nests, 297 paired sites; cereal crops: n = 16 nests, 128 paired sites). Bars show pooled means ± 1 SE.

Abundance of chick-food invertebrates was also significantly higher at foraging patches (Table 3b, Fig. 3c). Foraging yellowhammers showed a significant preference for tractor tramlines within cereal fields (Table 3b), with 87.5% of all foraging sites located along a tramline, compared to 21.1% of control patches.

Across all habitats, foraging patches visited two or more times had significantly higher abundance of chick-food than those visited just once (Table 3c, 1 visit = 22.0 ± 0.77, ≥2 visits = 25.68 ± 1.68). In addition, mean trip duration was significantly shorter at patches that were re-visited (1 visit = 5.72 ± 0.33 mins, ≥2 visits = 4.27 ± 0.28 mins).

Discussion

The aim of this study was to determine how foraging habitat selection by yellowhammers at two spatial scales (habitat and patch) varied in relation to (i) invertebrate abundance, (ii) vegetation characteristics and (iii) stage in the breeding season.

At the habitat scale yellowhammers selected field margins, where invertebrates were most abundant, early in the season but switched to cereals late in the season despite the fact that invertebrates remained more abundant in the margins. Seasonal vegetation growth was more pronounced in the margins than the crops and the observed switch may be a response to invertebrate prey becoming less accessible in the margins, reducing the quality of the habitat for foraging birds. Further evidence for the importance of the interaction between invertebrate abundance and accessibility was apparent from the habitat selection at the patch scale. Across all habitats foraging patches were characterised by higher invertebrate abundance and sparser vegetation than non-foraging sites and those sites used had significantly higher abundance of key chick prey items than non-foraging sites. In the discussion below the habitat and then the patch scale selection of foraging sites are considered.

Habitat selection by foraging yellowhammers

The importance of grass field margins for foraging yellowhammers, as well as other passerines, is well known (Brickle *et al.* 2000). This has usually been attributed to higher abundance of insects (both total numbers and important chick-food groups) than adjacent cereal crops (Dennis *et al.* 1994; Thomas & Marshall 1999; Hart *et al.*

2006), a finding supported by the present study. The present study is the first to have identified a clear seasonal switch in the relative use of margins and crops by yellowhammers, with the latter used to a much greater extent late in the summer. There are several possible explanations for this. Firstly, although yellowhammer nestlings are provisioned predominantly with invertebrates, they are also fed unripe cereal grain (Stoate *et al.* 1998; Moreby & Stoate 2001; Macleod *et al.* 2005) and this has been cited as the cause of increasing use of cereals in mid to late summer (Stoate *et al.* 1998). However, in the present study increases in the amount of grain fed to nestlings do not seem to adequately explain the increase in use of cereal fields. Opportunistic observations suggest that although the proportion of cereal grain fed to chicks increases through the summer (from 0% to 25.7% of visits to the nest from a cereal field in early and late season respectively) it still only accounts for a relatively small proportion of the dietary items fed to nestlings. The vast majority of visits to a cereal field late in the season (almost 75%) were to collect invertebrates. Furthermore, unripe grain is considered to be a sub-optimal food source (Hart *et al.* 2006) and its exploitation may imply limited availability of invertebrates elsewhere. A more likely reason for the observed switch may be a reduction in the accessibility of invertebrates in margins associated with seasonal vegetation growth. Vegetation height increased in all habitats over the summer, but the increase was greatest in field margins. Taller and denser vegetation will make prey more difficult to find and capture, as well as perhaps increasing perceived predation risk (see detail below). One past study has suggested that dense plant growth in field margins late in the season may reduce accessibility to food (Hart *et al.* 2006) but the present study is the first to quantify the effect.

Fine-scale patch selection

Across all habitats and within cereal fields, foraging yellowhammers showed a preference for patches with shorter, more open vegetation and higher abundance of important chick-food invertebrates than non-foraged patches. Previous studies have shown a similar pattern of foraging patch selection in cereal crops by yellowhammers (Morris *et al.* 2002) and also corn buntings (Brickle *et al.* 2000). In the present study, within cereal fields, the majority of foraging visits were to tramlines where short, sparse vegetation would allow improved accessibility and detectability of prey than the adjacent crop. Foraging yellowhammers also generally flew up from the tramline before returning to the nest, suggesting that foraging occurred mainly along the tramline rather than in the crop itself. A study of foraging skylarks found a similar preference for tramlines within cereal fields, even though the crop itself supported higher invertebrate abundance (Odderskaer *et al.* 1997). In the present study invertebrate abundance appeared higher in tramlines than the crop itself. A comparison of chick-food abundance at foraging sites located along tramlines with paired control sites located in the crop revealed significantly higher abundance at tramlines (GLMM with nest as random term, $\chi^2 = 28.0$, d.f = 1, $P<0.001$, n = 85 paired sites), so tramlines offer higher abundance and accessibility. The former could be due to the presence of weedy vegetation in the tramlines (e.g. grasses), providing a microhabitat for invertebrates (Coombes & Sotherton 1986). It could, however, reflect a sampling bias as vegetation height and density can influence the efficiency of vacuum samplers (Southwood 1978). Regardless of any differences in invertebrate abundance, the consistent selection of tramlines with short, sparse vegetation suggests that vegetation structure is an important determinant of patch selection within cereal fields, particularly as tramlines and other open patches are estimated to cover only 5% by area of cereal fields (Odderskaer *et al.* 1997). There was also evidence that yellowhammers revisit patches with high invertebrate abundance, consistent with the findings of Morris *et al.* (2002). Foraging times were significantly lower at these patches, compared to those visited just once. These patches were selected independently of distance from the nest. Previous research suggests that insects may be aggregated within cereal crops, with localised patches of high abundance extending over scales of approximately 5-10m (see Chapter 2). The results of the present study suggest that foraging yellowhammers may detect and exploit such insect 'hotspots'. This provides further evidence that yellowhammers optimize foraging efficiency by selecting patches that allow increased prey intake rates per unit time.

The importance of vegetation structure in determining food availability

This study has shown that vegetation structure is an important determinant of foraging habitat selection at both the habitat and patch level. Numerous studies in both arable and grassland habitats have shown that passerine birds often prefer to forage on shorter swards (Whitehead *et al.* 1995; Atkinson *et al.* 2004; Butler *et al.* 2005a). Vegetation height is known to have a large effect on foraging efficiency, through influences on food availability and the perceived risk of predation. Increases in sward height can reduce the accessibility and detectability of prey (Brodmann *et al.* 1997; Nystrand & Granstrom 1997; Butler & Gillings 2004; Stillman & Simmons 2006), restrict forager mobility (Brownsmith 1977; Devereux *et al.* 2004) and, when damp, may impose greater energetic demands on foraging birds, by wetting the plumage (Dawson *et al.* 1992). Tall vegetation may also increase perceived predation risk for many small passerines (Whittingham *et al.* 2004, 2006a; Butler *et al.* 2005b).

Management recommendations

The importance of invertebrate-rich field margins as foraging habitat for farmland birds is well documented (Marshall & Moonen 2002; Vickery *et al.* 2002). The provision of field margins is a core component of agri-environment schemes (AES) designed to aid recovery of farmland bird populations, such as the UK's Entry Level Stewardship (ELS) (Vickery *et al.* 2004). Current guidelines for the management of such field margins allow farmers to cut, or top the margins at intervals, normally to control woody growth (Anon 2005). However these cutting requirements are variable and often infrequent, and give no consideration to the requirements of foraging birds. For example, under the ELS, 2m and 4m wide buffer margins may be cut only once every five years (one year in ten where adjoining woodland) after the first 12 months (Anon 2005). More frequent cutting of margins may therefore be required in order to increase accessibility to invertebrates and maximize the benefits for foraging birds. Short swards, however are generally associated with lower abundance and diversity of invertebrates (Vickery *et al.* 2001; McCracken & Tallowin 2004). Therefore within margins a mosaic of tall patches of vegetation for reservoirs of invertebrates, and shorter more open patches for foraging may benefit birds such as the yellowhammer. A single annual cut of the outer portion of field margins, adjacent to the crop, around the 1st July, may alleviate the problem of dense growth reducing access to invertebrates. A follow-up experiment to the present study was conducted to test the response of foraging yellowhammers to cut patches in field margins (see Chapter 4). There was a significant increase in the use of cut patches between early and late summer, supporting the hypothesis that late in the summer dense growth within margins reduces accessibility to invertebrates. In a larger scale study, examining the use of experimentally managed margins by farmland birds, breeding season densities were significantly higher on grass margins where the sward had been opened up through scarification and graminicide use rather than cutting, though the underlying mechanisms were not examined (Henderson *et al.* 2007). Future work should investigate the cost effectiveness of creating these patches through a range of methods and the number required within a territory to enhance productivity.

A recent study suggests that targeting AES options at the cropped area of farmland rather than field margins may deliver greater benefits for farmland birds (Butler *et al.* 2007). However more active management of grass margins (and other margin types) would undoubtedly increase their value for birds by extending their 'useful lifetime' into late summer, and may reduce the reliance on cropped areas by some species. Such management will, of course, impose additional costs, and so might demand higher payment levels. In the UK, for example, this may be more suitable for inclusion in Higher Level Stewardship (HLS) rather than ELS. However, management is likely to increase the overall cost-effectiveness of margins as an AES option and may 'buffer' birds from deleterious effects of crop management, such as pesticide spraying, later in the season (Hart *et al.* 2006). In addition, the high uptake of margin options by landowners within AES (e.g. Grice *et al.* 2007) suggests that improving the value of margins may benefit a considerable proportion of farmland birds within the UK and elsewhere in Europe.

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Chapter 4: Vegetation height influences the use of field margins by foraging yellowhammers

Abstract

Uncropped field margins are important foraging habitats on farmland for many declining bird species, and are a key component of agri-environment schemes. However vegetation growth within margins may restrict accessibility of invertebrate food in late summer, reducing their use by, and value for, breeding birds. Vegetation height within field margins was experimentally manipulated by cutting patches, and the response of foraging yellowhammers *Emberiza citrinella* tested. Use of cut patches by birds increased between early and late summer, and patches were used more frequently with increasing vegetation height in the adjacent margin. These results suggest that open patches within tall swards may increase accessibility of food for foraging birds and extend the 'valuable lifetime' of margins as foraging habitats. The creation of fine-scale heterogeneity in vegetation structure within a habitat is likely to be a general tool for enhancing foraging opportunities for birds.

Introduction

Recent decades have seen drastic declines in European farmland bird populations and it is now widely accepted that agricultural intensification is the primary cause of these declines (Krebs *et al.* 1999; Chamberlain *et al.* 2000; Donald *et al.* 2001). Many declining songbirds such as yellowhammer *Emberiza citrinella* and corn bunting *Emberiza calandra* require protein-rich invertebrates for nestling growth and development (Brickle *et al.* 2000; Hart *et al.* 2006). Agricultural intensification has led to reductions in invertebrate availability, directly through reductions in abundance (Ewald & Aebischer 1999; Benton *et al.* 2002) and indirectly through changes in sward structure, reducing accessibility to invertebrates (McCracken & Tallowin 2004; Wilson *et al.* 2005). The availability of invertebrates has been shown to influence the nestling growth and productivity of a number of farmland birds (Brickle *et al.* 2000; Brickle & Peach 2004; Hart *et al.* 2006) and a link has been shown between invertebrate abundance, bird populations and measures of farm management (Benton *et al.* 2002).

One key aim of agri-environment schemes (AES) designed to aid population recovery is the provision of suitable foraging habitats for farmland birds (Vickery *et al.* 2004), often through measures such as the creation and maintenance of invertebrate-rich field margins. Such margins may buffer birds from the deleterious effects of crop management such as pesticide spraying, which can severely reduce the abundance of invertebrates in cropped fields (Boatman *et al.* 2004; Hart *et al.* 2006). The creation and maintenance of field margins has little or no detrimental impact on economically important cropped areas, thereby providing a potentially cost-effective means of conserving biodiversity within intensive agricultural systems. Optimising the benefit of field margins for biodiversity, through modifications in establishment or management for example, could provide a significant tool by which to mitigate the detrimental effects of intensive management within cropped areas.

A recent study showed that use of field margins by foraging yellowhammers declined in late summer, with a shift to cereal crops, despite margins supporting significantly higher invertebrate abundance (Chapter 3 this thesis, Fig. 1). This was attributed to a response to increasing vegetation height within margins in late summer (Fig. 1), reducing accessibility to invertebrates.

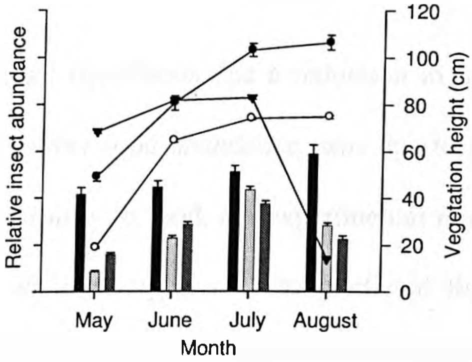

Fig. 1. Insect and vegetation characteristics in primary foraging habitats of adult yellowhammers during the breeding season. Bars indicate mean monthly count of chick-food insects sampled from five fields of spring-barley (light grey bars), winter-barley (dark grey bars) and adjacent margins (black bars). Lines show mean monthly vegetation height measured at the same sampling locations (open circles=spring-barley, triangles=winter-barley, filled circles=margins) (after Chapter 3).

Vegetation height is known to have a large influence on food availability for birds and can affect foraging efficiency in a number of ways. Tall vegetation may reduce the accessibility and detectability of food items (Brodmann *et al.* 1997; Butler & Gillings 2004), restrict forager mobility (Brownsmith 1977; Devereux *et al.* 2004) and/or increase the perceived risk of predation (Whittingham & Evans 2004; Whittingham *et al.* 2006). As a result many passerine birds prefer to forage on shorter swards (Whitehead *et al.* 1995; Morris *et al.* 2002; Butler *et al.* 2005a), despite the fact that such swards are generally associated with lower abundance and diversity of invertebrate food (Vickery *et al.* 2001, McCracken & Tallowin 2004). Therefore a mosaic of taller vegetation, which serves as a reservoir of invertebrates, and short vegetation, where prey becomes more accessible, may enhance the overall value of foraging habitat for birds (Devereux *et al.* 2004; McCracken & Tallowin 2004).

This study aimed to test the hypothesis that a reduction in margin use by foraging yellowhammers, despite higher food abundance, was due to vegetation growth and therefore decreased accessibility to food. An experimental mosaic of short and long vegetation was created within margins. It was predicted that this mosaic would stimulate greater margin use by foraging birds, especially late in the breeding season when uncut vegetation was tallest. If the hypothesis is correct, it would have considerable implications for the management of biodiversity in an agricultural setting.

Methods

Study area

Fieldwork was conducted from May-August 2006 on five farms in Aberdeenshire, North-East Scotland ranging in size from 98 to 292 ha. All sites were typical of local farmland, comprising a mix of arable and grassland habitats under conventional management (i.e. with routine use of agrochemicals). The majority of fields were bordered by margin habitat, defined as the strip of uncropped semi-natural boundary habitat between the crop and field boundary. Field margins on the study sites were dominated by permanent grass margins adjacent to the crop edge (varying in width from 1-12m), with smaller areas of ditches, hedgerow and roadside verge. All margin manipulations in this study were conducted on permanent grass margins adjacent to the crop edge.

Nest location and margin manipulation

Yellowhammer nests were located by mapping territorial males and watching for signs of breeding behaviour. Margin manipulation was conducted at 30 nests containing nestlings aged 0-8 days old. Nests were selected to fall into two groups (15 early summer [$\leq$ 2nd July] and 15 late summer [$\geq$ 3rd July], as per Chapter 3). At each nest, ten patches each measuring 15 x 1m were cut in the margins surrounding each nest. These were sited so that five patches were cut in each of two margins around a nest. Where there were more than two margins adjacent to a nest (e.g. when the nest was situated at the junction of several fields), all available margins were numbered and two selected at random. Patches in each margin were cut at the following distances from the nest; 30-45m, 60-75, 90-105, 120-135 and 150-165. Where cutting at the required distance was not possible due to features such as gates/tracks crossing the margin, the relevant patch was cut in the nearest available length of margin. Vegetation in cut patches was topped down to ground level (the soil-vegetation interface) using a petrol-motor brushcutter (Stihl KM85R/KM-MB CombiTool, Camberley, UK), and the cut vegetation raked off. The location of each patch was marked by placing a 2m long cane at either end, to enable patches to be identified from a distance during subsequent foraging watches. The canes were marked at the top with coloured tape, using a different colour for each of the ten patches per nest. The height of uncut vegetation in the margin immediately adjacent to each patch was measured to the nearest 10cm using a measuring stick.

Foraging watches

A minimum interval of three days (mean 4.3 ± 0.3 days, range 3-7) was left between cutting of patches and conducting observations of adult foraging behaviour at each nest. This was to ensure that any selection of cut patches was not due to exploitation of temporary flushes of foliar invertebrates following cutting (Eiserer 1980; Vickery *et al.* 2001). A single foraging watch lasting three hours was conducted on each of the 30 nests containing nestlings aged 4-11 days. Observations were carried out from 0700-1100 to control for the effect of diurnal variation. Periods of adverse weather, e.g. heavy rain, were avoided. During a watch the location of all foraging flights made by parents to collect food for nestlings were recorded, marking sites on sketch maps. Foraging sites in margins were recorded as either cut (treatment) or uncut. The location of foraging sites in non-margin habitats was also recorded to enable calculation of the typical foraging radius around the nest. Multiple visits to the same site were recorded. Following a watch each foraging site was visited and the distance from the nest measured using a hand-held GPS (accuracy ± 5m).

Calculating margin areas

The length and width of all field margins surrounding each nest were measured *in situ* and mapped onto Ordnance Survey 1:10000 maps. The area of cut and uncut margin at a radius corresponding to the distance of the furthest cut patch from each nest (mean 162 ± 8m) was calculated. The area of cut and uncut margin within the typical foraging radius around a nest (320m, the 95th percentile of all mapped flights to all habitats in this study) was also calculated.

Analysis

Seasonal variation in the use of cut and uncut margins was assessed using a generalised linear mixed model (GLMM) in R v2.3.1 (R Core Development Team 2006). The model examined usage within the radius of cut patches at each nest, with a response variable of the number of foraging visits to each margin type (cut or uncut) per nest. A poisson error structure and log-link were specified. Margin type (cut or uncut) and season (early or late) were included as explanatory variables, testing for an interaction. Nest identity was specified as a random term, rather than individual bird ID, as it was not always possible to distinguish between the sexes within each pair at a nest. Log_e (area) of cut and uncut margin, within the radius of cut patches at each nest, was declared as an offset. This allowed the number of foraging visits to the two margin types to be expressed as foraging densities (Morris *et al.* 2001). The significance of all explanatory terms in the model was assessed by removing terms one at a time and assessing the change in deviance, which is distributed asymptotically as χ^2. The fit of the model to the assumptions of a poisson distribution was assessed using the ratio of residual deviance / residual d.f. (Crawley 2002). A ratio close to one indicates a reasonable fit, but ratios greater than 1.5 indicate a poor, overdispersed fit (Crawley 2002). The above model was repeated to include all margin visits within the typical foraging radius around a nest. However the results were very similar to that obtained when examining usage within the radius of cut patches, and the results presented below refer only to margin use within the radius of cut patches around a nest.

The frequency of visits to cut patches in relation to the height of the adjacent uncut margin was also examined. Heights of uncut margin adjacent to each patch were assigned to five height categories (0-30cm, 31-60, 61-90, 91-120, 121-150). The expected frequency of visits (the number of cut patches in each height category) was compared to the observed frequency (number of visits to patches in each height category) using the chi-square goodness of fit. Means are expressed as mean ± 1 SE. All probabilities quoted are two-tailed.

Results

A total of 841 foraging flights were recorded in the study, of which 339 (40.3%) were to margins (mean 11.3 ± 1.7 margin visits per nest, range 0-37) (Table 1). Thirty-one of these margin visits were to cut patches. As predicted the use of cut and uncut margins differed significantly between early and late summer (Table 2), with a significant increase in the use of cut patches in late summer ($z = 5.14$, $P<0.001$, Fig. 2). In early summer margin vegetation surrounding the nests was generally short in height (Fig. 3a). During this period the difference between cut patches (0cm vegetation height) and the adjacent uncut margin rarely exceeded 60cm (Fig. 3a) and 2.2% (n=5) of all margin visits were to cut patches (Fig. 2). In late summer margin height increased, leading to a greater difference in height between cut and uncut margin (generally greater than 60cm, Fig. 3b). During this period the use of cut patches increased to 23.9% (n=26) of all margin visits (Fig. 2).

The frequency of visits to cut patches in relation to the height of adjacent uncut margin differed significantly from that expected under the null hypothesis that patch use was not influenced by vegetation height ($\chi^2 = 53.26$, df = 4, $P<0.001$). When combining data from early and late summer there was a bias for greater use of patches in tall margins (Fig. 3), with 84% of visits to cut patches recorded in margins with swards >60cm tall.

Table 1. Foraging habitat use by breeding yellowhammers in early and late summer

	Percentage of foraging visits		
Habitat	Early summer	Late summer	Total summer
Margin (uncut)	57.5	18.4	36.6
Margin (cut patches)	1.3	5.8	3.7
Non-margin	41.2	75.8	59.7
Total no. visits	391	450	841

Table 2. Sequential deviance table for the GLMM for the effects of experimental margin manipulation (cut or uncut) and season (early or late summer) on use of margins by foraging adults within the radius of cut patches at each nest

Term	d.f.	Deviance	Mean deviance	Deviance ratio	Approximate χ-square probability
Margin type	1	149.48	149.48	134.67	<0.001
Season	1	4.70	4.70	4.23	0.030
Margin type*Season	1	54.76	54.76	49.33	<0.001
Residual	56	62.16	1.11		
Total	59	271.10			

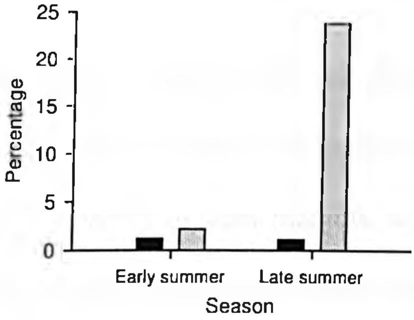

Fig. 2. Seasonal use of experimentally cut margins by adult yellowhammers. Black bars show area of cut margins as a percentage of total margin area available within the radius of cut patches at a nest (162±8 m). Grey bars show frequency of visits to cut patches expressed as a percentage of total margin visits within the same radius. Early summer (May-June): n=15 nests; Late summer (July-August): n=15 nests.

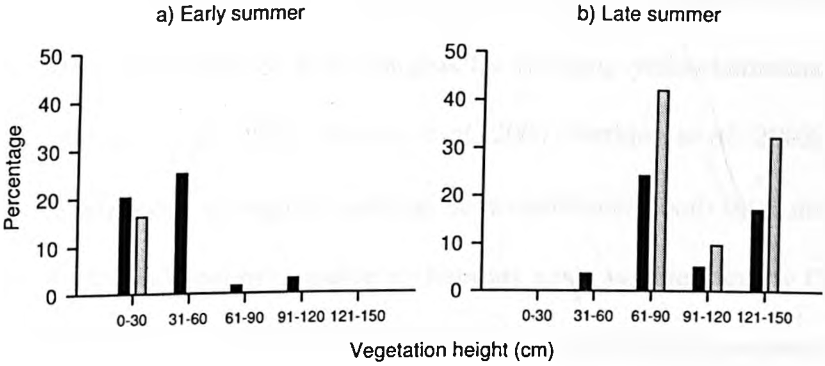

Fig. 3. Frequency of use of cut patches (grey bars) by foraging adult yellowhammers in different height categories of adjacent uncut margin, in relation to frequency of patches available (black bars) in a) Early summer (May-June); b) Late summer (July-August).

Discussion

This study found a significant increase in the use of experimentally cut patches in margins between early and late summer by foraging yellowhammers. In addition, patches were used more frequently in taller margins, with little use of cut patches in short (<60cm) vegetation. These findings support the prediction that yellowhammers foraging in margins would become more dependent on open patches, as a means of accessing invertebrates, in tall vegetation, particularly in late summer. Fine-scale variation in vegetation structure is an important determinant of patch selection for farmland birds (Odderskaer *et al.* 1997; Chapter 3 this thesis) and the creation of such heterogeneity within a habitat may be an important general tool for enhancing the value for foraging birds (Wilson *et al.* 2005).

Field margins were important foraging habitats for breeding yellowhammers in the present study, comprising 40.3% of all foraging visits. Previous studies have also highlighted the importance of field margins for foraging yellowhammers and other passerines (Brickle *et al.* 2000; Morris *et al.* 2001; Perkins *et al.* 2002). This has usually been attributed to high abundance of invertebrates (both total numbers and important chick-food groups) relative to habitats such as cereal crops (Thomas & Marshall 1999; Hart *et al.* 2006; Chapter 3 this thesis). However accessibility of food may be of equal or greater importance in determining habitat selection. The results of this study support recent findings that tall vegetation in unmanaged margins may reduce accessibility to invertebrates in late summer, resulting in a shift in habitat use by foraging yellowhammers to cereal crops, despite lower food abundance in cereals (Fig. 1) (Chapter 3). Whilst overall margin use in the present study declined between early and late summer, margins accounted for a greater proportion of all foraging visits by yellowhammers in late summer than on the same sites in the previous year, when no margin manipulation was undertaken. In the previous year 15.2% of all foraging visits made by yellowhammers in late summer were to margins (Chapter 3), compared to 24.2% in the present study. Whilst data from two different years may not be directly comparable these results suggest that manipulating only a small proportion of margin area may lead to a marked overall increase in margin use by foraging birds in late summer.

A previous study of yellowhammers foraging in experimentally manipulated field margins found no difference in use of cut and uncut margins, however the authors acknowledge that small sample size may have reduced the power of the analysis to detect a difference (Perkins *et al.* 2002). Vegetation height is known to have a large effect on foraging efficiency, through influences on food availability and the perceived risk of predation. Increases in sward height can reduce the accessibility and detectability of prey (Brodmann *et al.* 1997; Butler & Gillings 2004; Stillman & Simmons 2006), restrict forager mobility (Brownsmith 1977; Devereux *et al.* 2004) and, when damp, may impose greater energetic demands on foraging birds, by wetting the plumage (Dawson *et al.* 1992). Tall vegetation may also increase perceived predation risk for many small passerines (Whittingham *et al.* 2004, 2006; Butler *et al.* 2005b). Numerous studies in both arable and grassland habitats have shown that passerine birds often prefer to forage on shorter swards (Whitehead *et al.* 1995; Morris *et al.* 2002; Atkinson *et al.* 2004; Butler *et al.* 2005a). Short swards are, however, generally associated with lower abundance and diversity of invertebrates (Vickery *et al.* 2001; McCracken & Tallowin 2004). The benefits of open patches are therefore likely to arise from an increase in food availability at the interface between long vegetation, which serves as a reservoir of invertebrates, and short vegetation, where prey becomes more accessible. Early in the summer margins were generally short in height, and the low use of cut patches suggests that when the difference between adjacent cut and uncut vegetation is relatively small (e.g. <60cm), food accessibility for foraging birds is not constrained by vegetation height. In late summer, however, when margins are taller, birds are likely to become more dependent on open patches as a means of accessing food, resulting in the observed increase in the use of cut patches. The analysis of seasonal variation in margin patch use included *season* rather than *vegetation height* as an explanatory term. The two measures are likely to be confounded as height of adjacent uncut margin increased during the summer, and therefore it was not considered necessary to include both terms in the model. However doing so would have allowed the testing of the relative importance of changes in vegetation height on patch use rather than a seasonal effect *per se*.

Conclusions and management recommendations

The importance of invertebrate-rich field margins as foraging habitat for farmland birds is well documented (Marshall & Moonen 2002; Vickery *et al.* 2002). The provision of such margins is a core and frequently adopted component of agri-environment schemes (AES) designed to aid recovery of farmland bird populations, such as the UK's Entry Level Stewardship (ELS) (Vickery *et al.* 2004, Grice *et al.* 2007). Current guidelines for the management of such field margins allow farmers to cut, or top the margins at intervals (Anon 2005). However these cutting requirements are variable and often infrequent, and give no consideration to the requirements of foraging birds. For example, under the ELS, 2m and 4m wide buffer margins may be cut only once every 5-10 years following a 12 month establishment period (Anon 2005). We suggest that more frequent cutting of margins may be required in order to increase accessibility to invertebrates and maximize the benefits for foraging birds. Such cutting would provide optimum benefits if targeted to create fine-scale heterogeneity in vegetation structure, ensuring a mosaic of tall and short vegetation in close proximity to optimize both food abundance and accessibility. There is continuing debate about the effectiveness of AES in delivering biodiversity benefits (Kleijn and Sutherland 2003), and improving habitat quality (through increasing access to food) has been highlighted as a target for AES (Whittingham 2007). The results of the present study provide a means for improving the quality of a key AES option for farmland birds.

Although this work focuses on field margins, the findings are equally applicable to a wide range of habitats used by foraging birds, both on farmland and within other systems. One consequence of agricultural intensification has been the loss of sward structural heterogeneity both within and between habitats (Benton *et al.* 2003). Creating within-field sward heterogeneity has shown benefits for skylarks *Alauda arvensis* foraging in cereal fields (Morris *et al.* 2004) and has been suggested as a means of improving the value of grasslands for foraging birds (Tallowin *et al.* 2005; Atkinson *et al.* 2005). We suggest such management may be a general tool for enhancing foraging opportunities for a wide range of bird species across a range of foraging habitats.

In a recent larger scale study, examining the use of experimentally managed margins by farmland birds, breeding season densities were significantly higher on grass margins where the sward had been opened up through scarification and graminicide use rather than cutting, though the underlying mechanisms were not examined

(Henderson *et al.* 2007). Future work should investigate the cost effectiveness of creating these patches through a range of methods and the optimal number and spatial arrangement required within a territory to enhance productivity via effects on increased foraging efficiency.

It has been suggested that targeting AES options at the cropped area of farmland rather than field margins may deliver greater benefits for farmland birds (Butler *et al.* 2007). However more effective management of grass margins (and other margin types) would undoubtedly increase their value for birds by extending their 'useful lifetime' into late summer, and may reduce the reliance on cropped areas by some birds. Such management will, of course, impose additional costs, and so might demand higher payment levels. In the UK, for example, this may be more suitable for inclusion in Higher Level Stewardship (HLS) rather than ELS. However, the uptake of margin options by landowners is often high (e.g. Grice *et al.* 2007) suggesting that improving the value of field margins may benefit a considerable proportion of farmland birds within the UK and elsewhere in Europe. From a wider perspective, maximizing the benefits of field margins for birds and other taxa may help to balance the conflicting demands of efficient food production and biodiversity conservation within agricultural ecosystems (i.e. 'land sparing' versus 'land sharing', Green *et al.* 2005): field margins occupy a relatively small land area, thereby providing a means for conserving biodiversity within intensive agricultural systems whilst minimizing the impact to economically important cropped areas.

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Chapter 5: Productivity of farmland yellowhammers in the presence of experimentally manipulated foraging habitat

Abstract

Insect availability for breeding granivorous passerines has declined on farmland, through a range of direct and indirect effects. Such reductions may impact on demographic rates via reduced adult foraging efficiency. Measures to enhance insect availability on farmland for granivorous birds may therefore play an important role in promoting population recovery. In a previous experiment field margins were manipulated to increase insect accessibility for breeding birds and foraging yellowhammers showed a positive response to these manipulations. In the present study the potential benefits on yellowhammer productivity were assessed. Nestling provisioning rates and body condition were significantly higher at nests with experimentally cut margin patches in the foraging radius, relative to nests without such patches but there was no effect on overall productivity per nesting attempt. Improved nestling condition may reflect the influence of increased adult foraging efficiency within margin patches and represents a potential mechanism by which future survival rates and reproductive output of juveniles may be enhanced. Although comparisons were made between years, so the effect of additional unmeasured variables cannot be excluded, the results provide a basis for further research into the benefits of manipulating sward structure on farmland to increase productivity of breeding birds.

Introduction

European farmland bird populations have declined dramatically over recent decades and it is now widely accepted that agricultural intensification is the primary cause of these declines (Krebs *et al.* 1999; Chamberlain *et al.* 2000; Donald *et al.* 2001). For many declining songbirds such as yellowhammer *Emberiza citrinella* and corn bunting *Emberiza calandra*, protein-rich invertebrates are essential for nestling growth and development (Brickle *et al.* 2000; Hart *et al.* 2006). Agricultural intensification has led to reductions in invertebrate availability, directly through reductions in abundance, driven by factors such as increased pesticide applications and the loss of non-cropped habitat (Ewald & Aebischer 1999; Benton *et al.* 2002) and indirectly through changes in sward structure, reducing accessibility to invertebrates (McCracken & Tallowin 2004; Wilson *et al.* 2005). Declining granivorous birds have been shown to rely significantly more on insect food than those species not in decline (Wilson *et al.* 1999) and a general link has been shown between invertebrate abundance, bird population size and measures of farm management (Benton *et al.* 2002).

However to date an effect of insect availability on breeding success has been shown to have contributed to population decline for only one farmland bird species in the UK. The grey partridge *Perdix perdix* has declined in part because of the effect of pesticides on the availability of chick-food invertebrates in cereal crops, leading to lower chick survival (Southwood & Cross 1969; Potts & Aebischer 1995). The grey partridge is precocial, and it is therefore not surprising that a link between insect abundance, productivity and population size has proved easier to detect than for altricial passerines, as precocial chicks will bear any costs of low food abundance directly.

For granivorous passerines, insect abundance may influence the number of chicks fledging per nesting attempt [e.g. for yellowhammer and corn bunting (Boatman *et al.* 2004)]. However for many species there is little evidence of a decline in measures of reproductive output per nesting attempt over the period of population decline (e.g. (Siriwardena *et al.* 2000a). However, reproductive success depends not just on the number of young that fledge from a nest, but more importantly the number that survive after fledging to breed successfully. This may be reduced if parents maintain offspring quantity at the expense of offspring quality, as nestling growth and body condition are known to have important effects on future survival and lifetime reproductive success (Magrath 1991; Wright *et al.* 1998; Lindstrom 1999; Blount *et al.* 2006).

Alternatively, for altricial breeders, any effects of reduced food availability may be 'buffered' by the adults through higher work rates to provision nestlings with food (Tremblay *et al.* 2005). Indeed, in short-lived passerine species, where many individuals may have only one breeding season in their lifetime, this strategy is more likely than in longer-lived species where birds may simply not breed in poor conditions (Clutton-Brock 1988). Reproduction imposes costs on parents, and under conditions of increased food stress e.g. low food abundance in natural conditions or through experimentally increased brood sizes, parents increase their work rate (Drent & Daan 1980; Dijkstra *et al.* 1990; Tremblay *et al.* 2005). However, this may have consequences for adults in terms of reduced survival and reproductive output in current and future years (Nur 1984; Roskaft 1985; Martin 1987; Daan *et al.* 1996).

This leads to a trade-off between maximizing nestling growth and minimizing parental foraging costs.

In contrast to the lack of evidence for declines in productivity of farmland passerines over the period of population decline, a number of studies have shown that falls in survival rate are more often associated with population declines (e.g. Peach *et al.* 1999; Siriwardena *et al.* 1999, 2000b). Declines in survival rates are often attributed to reductions in food availability outside the breeding season, such as winter seed supplies (e.g. Peach *et al.* 1999; Robinson & Sutherland 2002). However, as described above, the delayed effects of conditions during the breeding season cannot be ignored when considering survival rates of both adults and juveniles.

As a result measures to increase insect availability on farmland for breeding birds may be important in stimulating population recovery of granivorous passerines. Chapter 4 of this thesis describes the results of an experiment manipulating sward structure within field margins, a key foraging habitat for breeding yellowhammers. The creation of patches with short, open vegetation was shown to stimulate greater use of field margins by foraging adults, most likely via increased insect accessibility. Such measures may enable greater foraging efficiency for breeding adults and therefore any potential benefits on productivity need to be assessed. In this chapter the impact of experimental manipulations of field margins on various measures of current and potential future productivity and survival of yellowhammers are assessed in terms of nestling provisioning rates, nestling and adult body condition and productivity per nesting attempt

Methods

Study sites and nests

Fieldwork was conducted from May-August 2005-2006 on five farms in Aberdeenshire, ranging in size from 98 to 292 ha. All sites were typical of local farmland, comprising a mix of arable and grassland habitats under conventional management (i.e. with routine use of agrochemicals). The dominant arable crops were cereals, mainly spring- and winter-sown barley *Hordeum* spp., with small areas of winter wheat *Triticum* spp.

Nests of yellowhammer were located as described in Chapter 3. Nests containing eggs were visited every three days to determine the hatching date. In 2005 no manipulation of foraging habitat was undertaken at any nests. In 2006, experimental patches were cut in the field margins surrounding each nest (see Chapter 4 for details). For the present study only those nests containing nestlings aged ≤4 days old on the day of patch cutting were utilised for measurements. This was to ensure there was a minimum time interval of 3 days (range 3-7) between the cutting of patches within the foraging radius and nestling measurements at age 7 days old [the oldest age at which yellowhammer nestlings could be safely handled without the risk of prematurely leaving the nest (Redfern & Clark 2001)]. This time interval was required as the aim of the present study was to assess whether creating margin patches within the foraging radius of the nest had any measureable benefits on yellowhammer productivity, via increased adult foraging efficiency. Sample sizes were 43 broods (26 broods in 2005 with no manipulation and 17 in 2006 with manipulation).

Nestling measurements

The age, in days, of the nestlings was known from the hatching date or, when this was not known, was estimated by comparison of feather development with known-age broods. Nestlings aged 7 days old were weighed (to the nearest 0.1g) using a Pesola spring balance. Tarsus length - from the distal point of the intertarsal joint to the last complete scale before the toes diverge - was measured (to the nearest 0.5mm) using a butted rule. Nestling provisioning rates were obtained from the observations of foraging adults described in Chapters 3 and 4. Data on the use of experimental margin patches by foraging adults in 2006 were obtained from the foraging observations outlined in Chapter 4. Foraging watches had been conducted, wherever possible, in the period prior to or on the day of nestling measurements. This was to ensure that provisioning rates were representative of those influencing nestling condition over the period of development prior to measurements. This was achieved for 13 out of the 17 nests from 2006, where foraging watches were conducted when nestlings were aged 4-7 days. However, due to logistics, foraging observations at the remaining 4 nests were conducted after nestlings had been measured (nestling age 8 (n=2) and 9 (n=-2) days old). However, these were considered to be close enough to the date of nestling measurements for the provisioning rates to be representative of those experienced prior to the measurements of body condition. In any case, the effect of nestling age on provisioning rates was examined in subsequent analyses (see below).

Adult body condition

In 2005 attempts were made to trap provisioning adults to determine body condition in relation to provisioning effort. In the latter stages of the nestling rearing period (nestlings aged 7-11 days) mist nets were erected in the vicinity of the nest in the typical flight paths of adults entering and leaving the nest. Nets were sited a minimum of 5m from the nest to reduce disturbance to nestlings and minimise trampling of vegetation (to reduce the likelihood of predators detecting the nest). If the presence of the nets was judged to be deterring adults from returning to the nest with food, the nets were removed after a maximum of 30 minutes. Only 4 adults were trapped, and in 2006 no further trapping attempts were made. These results are therefore not considered any further.

Analysis

All analyses were conducted in R 2.3.1 (R Core Development Team 2006). All means are presented as mean ± 1 SE.

Nestling provisioning rates were examined in relation to the presence and/or use of experimental margin patches by foraging adults. A General Linear Model (GLM) was constructed with a response variable of provisioning rate per nest, corrected for brood size (nest visits chick^{-1} hour^{-1}). Experimental margin patch use by foraging adults was specified as a three level factor (1 - no experimental margin patches present in the foraging radius [all 26 broods from 2005]; 2 - margin patches present but not visited by adults during foraging observations [8 broods from 2006]; 3 - margin patches present and visited during foraging watches [1-5 visits to margin patches in 3 hour observation period, 9 broods from 2006]). Additional explanatory variables were brood size, nestling age on the day of the foraging watch, mean foraging distance per trip per nest and a two level factor or "early" or "late" season. Broods were assigned to either early (20th May-2nd July) or late (3rd July-14th Aug) season according to the date of the foraging watch as per Chapters 3 and 4. A minimum adequate model (MAM) was obtained from a full model containing all main effects and interactions by manual stepwise deletion (Crawley 2002). If the *patch use* factor was found to have a significant effect on provisioning rates, differences between factor levels were assessed using post hoc contrasts following the methods of (Crawley 2002). Contrasts were specified by combining two of the factor levels into a single level for testing against the remaining factor level. This new two level factor was then inserted into the MAM in place of the original *patch use* factor. The fit of the two models was compared using F tests (Crawley 2002). A non-significant change in model fit indicated that the two factor levels that had been combined together did not differ significantly in their effect on provisioning rates.

Nestling body condition was assessed in relation to the presence/use of experimental margin patches by foraging adults. A GLM was constructed with mean nestling mass per brood at 7 days old as the response variable. Margin patch use by foraging adults was specified as a three level factor described above. Additional explanatory variables were nestling provisioning rate (nest visits chick^{-1} hr^{-1}), brood size and season (two level factor of early or late season as described above). Tarsus length was included as a covariate to control for variation in nestling size. A MAM was obtained as described above. Differences in nestling mass between the three levels of the *patch use* factor were assessed using post hoc contrasts as described above. The fit of all models described above were assessed for normality of the residuals.

The number of chicks fledging from successful nests (38 out of the 43 nests) in relation to the presence/use of experimental margin patches was then examined. A Generalized Linear Model was constructed with a response variable of number of chicks fledging per nest, specifying a poisson error structure. Explanatory variables were patch use (three level factor as above) and season (as above), testing for an interaction between the two. The significance of each term in the model was assessed by removing terms one at a time and assessing the change in deviance, which is distributed asymptotically as χ^2. The fit of the model to the assumptions of a poisson distribution was assessed using the ratio of residual deviance / residual df. A ratio close to 1 or below indicates a good model fit, but ratios of 1.5 or above indicates overdispersion and a poor model fit (Crawley 2002).

Results

Nestling provisioning rates

When controlling for significant interactions in the model, the presence/use of experimental margin patches by foraging adults had a significant effect on nestling provisioning rates (Table 1, Fig. 1a). Post hoc contrasts revealed that, within broods from 2006, there was no significant difference in provisioning rates between broods where margin patches were visited by adults during foraging watches versus those where no patches were visited ($F_{5,22} = 1.26$, $P = 0.314$).

However, provisioning rates within these two factor levels combined (i.e. all broods with margin patches present) were significantly higher than nests from 2005, when no margin manipulation had been undertaken. ($F_{1,27} = 47.70$, $P < 0.001$). This was equivalent to testing for a year effect, and indicates that provisioning rates were significantly higher in 2006 than in 2005.

Table 1. MAM for the GLM of yellowhammer nestling provisioning rates in relation to the presence/use of experimental margin patches by foraging adults. Margin patch use was categorised as a three level factor (1 - no experimental margin patches present in the foraging radius [26 broods from 2005]; 2 - margin patches present but not used by adults during foraging observations [8 broods from 2006]; 3 - margin patches present and used during foraging watches [1-5 visits to margin patches, 9 broods from 2006]).

Term	df	Sum of squares	F	P
Patch use	2	29.62	27.47	<0.001
Brood size	1	34.36	63.74	<0.001
Chick age	1	1.82	3.38	0.080
Foraging distance	1	3.56	6.61	0.017
Season	1	1.35	2.50	0.128
Patch use*Brood size	2	7.72	7.16	0.004
Patch use*Chick age	2	0.31	0.29	0.751
Patch use*Foraging distance	2	1.13	1.05	0.368
Patch use*Season	2	0.47	0.43	0.655
Brood size*Chick age	1	0.82	1.53	0.230
Brood size*Foraging distance	1	0.86	1.60	0.219
Brood size*Season	1	0.67	1.25	0.276
Chick age*Season	1	1.31	2.42	0.134
Foraging distance*Season	1	0.04	0.07	0.796
Patch use*Brood size*Season	1	5.09	9.43	0.006
Residuals	22	11.86		
Adjusted $R^2 = 0.78$				

There was a significant effect of brood size on provisioning rates per nestling (Table 1), with a trend of decreasing provisioning rates with increasing brood size (Fig. 1b). Provisioning rates were also significantly negatively influenced by mean foraging distance per foraging trip (Table 1, Fig. 1c).

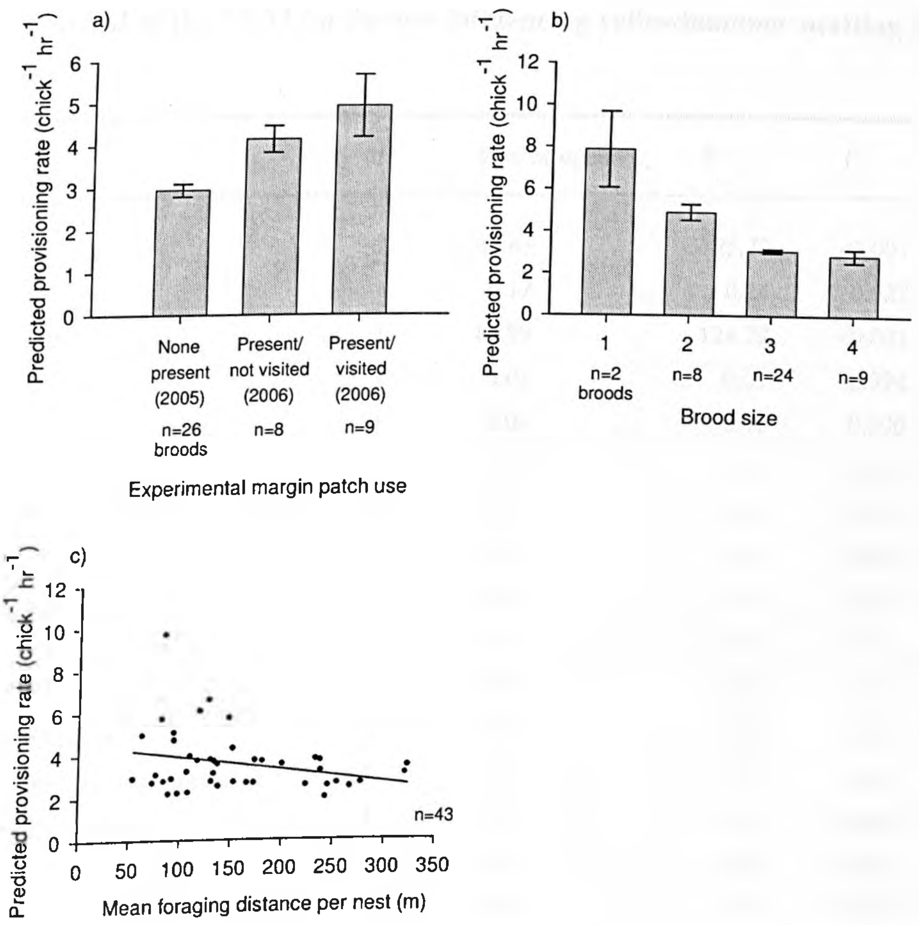

Fig. 1. Predicted provisioning rates of adult yellowhammers in relation to a) the presence/use of experimental margin patches; b) brood size; c) mean foraging distance per nest.

Nestling body condition

Nestling body condition was significantly influenced by the presence/use of experimental margin patches by foraging adults (Table 2). Post hoc contrasts revealed a similar effect between factor levels to that found for provisioning rates.

Table 2. MAM of the GLM for factors influencing yellowhammer nestling body condition

Term	df	Sum of squares	F	P
Patch use	2	35.43	25.72	<0.001
Brood size	1	0.17	0.24	0.627
Tarsus length	1	85.95	124.79	<0.001
Provisioning rate	1	0.01	0.01	0.994
Season	1	0.01	0.01	0.990
Patch use*Brood size	2	0.23	0.16	0.850
Patch use*Tarsus length	2	1.71	1.24	0.311
Patch use*Provisioning rate	2	4.03	2.93	0.078
Patch use*Season	2	1.63	1.18	0.327
Brood size*Tarsus	1	0.07	0.10	0.751
Brood size*Provisioning rate	1	2.03	2.95	0.102
Brood size*Season	1	2.73	3.97	0.061
Tarsus length*Provisioning rate	1	2.59	3.75	0.068
Tarsus length*Season	1	0.40	0.57	0.458
Provisioning rate*Season	1	1.15	1.66	0.212
Patch use*Brood size*Provisioning rate	2	6.78	4.92	0.019
Brood size*Provisioning rate*Season	1	3.26	4.74	0.042
Residuals	19	13.09		

Adjusted $R^2 = 0.82$

Within broods from 2006, there was no significant difference in nestling body condition in relation to observed use of margin patches by foraging adults ($F_{6,25}$ =

0.85, P = 0.548, Fig. 2a). However, nestling body condition across all 2006 broods was significantly higher than broods measured in 2005 ($F_{1,25} = 53.09$, $P < 0.001$, Fig. 2a). Tarsus length was a highly significant predictor of nestling body mass (Table 2), with a strong positive relationship (Fig. 2b).

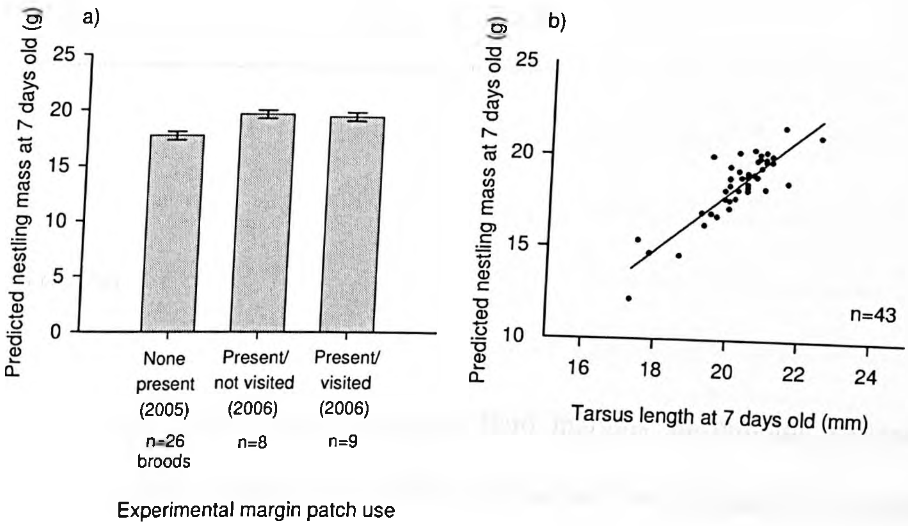

Fig. 2. Predicted yellowhammer nestling mass at 7 days old in relation to a) presence/use of experimental margin patches by foraging adults; b) nestling tarsus length

Yellowhammer productivity

The mean number of chicks fledging from successful nests was 2.95±0.13 across all nests. There was no significant effect of the presence/use of experimental margin patches by adults on productivity per nest (Table 3). In addition, testing for a year effect revealed no significant difference in the number of chicks fledging per nest between years ($\chi^2 = 0.10$, 1df, $P = 0.751$).

Table 3. Output table for Generalized Linear Model for effects of experimental margin patch use on the number of nestlings fledging from successful nests (n=38)

Term	df	Deviance	P
Patch use	2	0.67	0.716
Season	1	0.02	0.896
Patch use*Season	2	0.03	0.983

Discussion

In a previously described experiment, field margins surrounding yellowhammer nests were experimentally cut to create open patches (see Chapter 4). The aim was to increase accessibility to insect food and stimulate greater use of margins by foraging adults. Yellowhammers showed a positive response to these patches and in the present study the potential benefits of these manipulations on productivity were assessed. Nestling provisioning rates and body condition were significantly higher among broods with cut patches present, in 2006, than broods on the same sites in 2005, when no margin manipulation was undertaken.

The short, sparse vegetation within cut patches may have enabled greater adult foraging efficiency through a variety of mechanisms. Short vegetation is often associated with greater accessibility and detectability of prey for foraging birds (Nystrand & Granstrom 1997; Butler & Gillings 2004; Stillman & Simmons 2006), and may permit greater forager mobility (Devereux *et al.* 2004). In addition, predator vigilance levels exhibited by passerines are generally lower in short vegetation, resulting in increased foraging rates (Devereux et al. 2004; Whittingham *et al.* 2004; Butler *et al.* 2005). It therefore seems plausible to assume that the availability of open patches within the foraging radius of a nest may permit greater adult foraging efficiency, thereby allowing greater rates of prey delivery to nestlings. This provides a possible explanation for the observed increases in provisioning rates and nestling body condition in 2006, relative to nests from 2005. However, these results should be interpreted with caution. Firstly, the use of experimental margin patches by foraging adults was relatively low. For those broods where cut patches were both present and visited by foraging adults (9 out of 17 broods in 2006), the mean number of visits to these patches was 2.1±0.48 (range 1-5) during a 3 hour foraging watch. The use of cut patches during these watches comprised a mean of 9.8% of all foraging visits. It is therefore difficult to assess whether the level of margin patch use recorded would be likely to influence changes in provisioning rates and nestling body condition. However, the foraging watches covered only a single 3 hour period during the entire nestling rearing period. It is possible that the level of use of the margin patches by adults may have varied during the nestling provisioning period. This may apply both to those nests where patch use was observed during the watches, and those where no margin patch visits were recorded. This may explain why nestling provisioning rates and body condition were significantly higher in the presence of margin patches (i.e. all 2006 nests) compared to nests in 2005, irrespective of whether patches were visited during a foraging watch.

Secondly, nests without and with margin patches present in the foraging radius were observed in two consecutive years. This may have influenced the reliability of any comparisons. Due to the number of nests required for meaningful analyses, all available nests in 2006 were utilised for the experimental manipulation of margins. It was therefore not possible to compare nestling body condition between nests with and without margin patches within the same year. The effect of additional, unmeasured variables between years therefore cannot be ruled out. Such effects may include weather and variation in habitat quality, influencing insect availability and hence adult foraging efficiency. However, weather has been shown to be a poor predictor of nestling body condition (Bradbury *et al.* 2003). This suggests that during periods of adverse weather, when insect availability may be low, adults may compensate by adjustments to their foraging strategy (Bradbury *et al.* 2003). However, attempts to trap adults during the nestling rearing period unfortunately proved unsuccessful. It was not therefore possible to examine whether adult body condition varied in relation to provisioning effort. Previous studies have shown that adults of a range of bird species may increase their work rate in poor environments, and that increased provisioning effort may lead to reduced future survival and reproductive output (Nur 1984; Roskaft 1985; Martin 1987; Daan *et al.* 1996).

In terms of variation in habitat quality, the majority of fields on the study sites were managed under the same crop type between years (D. Douglas, unpublished data). This may have minimised any variation in underlying insect resources at the scale of individual territories between years. Food availability may have varied between years due to differing levels of pesticide use. Pesticides have been shown to negatively affect the availability of insects for breeding yellowhammers, leading to impacts on nestling growth and body condition (Boatman *et al.* 2004; Morris *et al.* 2005). However, any differences in pesticide use between years are likely to be expressed at the scale of individual fields or crop types, rather than across the entire farmed landscape encompassed by the study sites. The most obvious change in habitat between years was that deliberately created within field margins by the experimental cutting of patches. Therefore whilst additional between-year effects cannot be ruled out, the presence of experimentally cut margin patches provides a plausible explanation for the observed increase in nestling provisioning rates and body condition between years, via increased adult foraging efficiency.

The detection of any effect of margin patches in the present study assumes that the time interval between cutting and nestling measurements was sufficient for any benefits to be translated to growing nestlings. In the present study this time interval varied from 3-7 days. This represents a period of rapid nestling growth: a subset of nestlings weighed at age 4 as well as age 7 days old reveals average daily weight gain of 2.5±0.1 g day^{-1} over this period. It might be predicted that the earlier in the nestling rearing period that patches were cut, the greater any benefits for nestlings. This was assessed by fitting a linear regression of nestling mass at 7 days old (mean per brood) against the interval in days between cutting of patches and nestling measurements at 7 days old. There was no significant effect of time interval on nestling mass ($F_{1,15} = 0.42$, $P = 0.529$). However the regression slope ($b = 0.14$), indicated a weak, positive relationship between the timing of cutting and nestling body condition.

Provisioning rates per nestling decreased with increasing brood size. This did not appear to impact on nestling body condition directly (neither brood size nor provisioning rate had significant main effects on body condition; Table 2). However, both provisioning rate and brood size were present in significant high-order interactions, suggesting more complex influences on nestling body condition (Table 2). Parents may compensate for increased brood size through adjustments to load sizes (Wright *et al.* 1998) which were not measured in the present study.

Recent work on breeding skylarks supports the hypothesis that the presence of patches of sparse vegetation can enhance provisioning rates and nestling body condition. For this species, small, undrilled patches in winter wheat crops are an agri-environment scheme (AES) option created to mimic some of the nesting and foraging advantages of later developing spring, compared to winter, cereals (Morris *et al.* 2004; Grice *et al.* 2007). These undrilled plots have shown considerable benefits for breeding skylarks, including enhanced nestling body condition in plots containing undrilled patches compared to control plots without such patches (Morris *et al.* 2004). In addition, nests within undrilled plots produced a greater number of chicks per nest than control nests. These benefits are most likely to have arisen through increased accessibility to food in the short, sparse vegetation within the undrilled patches (Morris *et al.* 2004). These improvements in skylark productivity have been shown purely in relation to the presence of undrilled patches, rather than observed use of the patches *per se*. In the present study there was no significant effect of the presence and/or use of margin patches on yellowhammer productivity per nesting attempt, but sample sizes were small and patches were only present for a relatively short period of time, compared with Skylark plots that are created at sowing. The apparent increase in nestling body condition in the presence of margin patches suggests a method by which productivity of yellowhammers may be enhanced. Although there are little data on post-fledging survival rates of granivorous farmland passerines (Siriwardena 2000a), work on other songbirds suggests that increased nestling body condition may lead to improved survival and lifetime reproductive success (Magrath 1991; Wright *et al.* 1998; Lindstrom 1999; Blount *et al.* 2006). Given the importance of field margins as foraging habitat for yellowhammers and other granivorous passerines (Brickle *et al.* 2000; Morris *et al.*

2001), and the traditionally high uptake levels of margin options among landowners within AES (e.g. Grice *et al.* 2007), measures to enhance insect accessibility within margins may have considerable benefits for breeding birds, and may potentially help stimulate population recovery. Future work should focus on the optimal number and spatial arrangement of margin manipulations required to enhance productivity across the farmed landscape, and the cost-effectiveness of introducing such management within agri-environment schemes. In addition, post-fledging survival rates of farmland passerines remain a key demographic rate for which data are lacking.

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Chapter 6: Discussion

Insect distributions in crops and margins

Insects were sampled from cereal crops under two management regimes (spring-sown and autumn-sown barley) and the adjacent uncropped margins over the duration of the yellowhammers breeding season. Insect abundance was significantly higher in field margins than either crop type at all stages of the summer. These results are consistent with a number of previous studies (Dennis *et al.* 1994; Thomas & Marshall 1999; Hart *et al.* 2006). Higher abundance of insects in field margins relative to cereal crops may be expected for several reasons. Margins generally contain greater plant species richness than cropped fields (Marshall & Moonen 2002), and many margins, such as those in the present study, are permanent or semi-permanent, thereby providing a more stable habitat for insects than annually cultivated crops. In addition, margins do not generally receive direct pesticide inputs, although spray drift from adjacent cropped fields may negatively affect margin biodiversity (Marshall & Moonen 2002). Margins were a rich source of insects to adjacent cropped areas. This was particularly apparent in early summer, with insect dispersal from field margins into the adjacent developing crop.

Insect distributions within barley fields exhibited considerable spatial heterogeneity. There was evidence of localised aggregations or ‘hotspots’ over scales of 5-10m. These results are consistent with a number of previous studies showing that insects are often highly aggregated within cropped fields, with patches of high and low abundance occurring over a range of spatial scales (Holland *et al.* 1999, 2005; Ferguson *et al.* 2000; Thomas *et al.* 2001). The collection of detailed data on the spatial and temporal distribution of insects in crops has a variety of potential applications, potentially aiding the conservation of insects within agricultural systems. There is current interest in the use of beneficial insect taxa to control crop pest outbreaks within integrated farming systems (e.g. Ferguson *et al.* 2000; Holland *et al.* 2005). A detailed knowledge of the temporal patterns of insect distributions may therefore allow temporal targeting of insecticide treatments to avoid the main immigration period of beneficial taxa into the crop (Ferguson *et al.* 2000; Holland *et al.* 2000). In addition, a detailed knowledge of the spatial distribution of insects would allow effective spatial targeting of insecticides to areas where pests are most abundant, reducing the level of insecticide required to control pest outbreaks, and minimising effects on beneficial non-target species (Ferguson *et al.* 2000). However, this may require the identification of insects to a taxonomic level below that of order, which due to time constraints was not possible in the present study.

Crop management practices may have an important effect on insect spatial distributions, with implications for foraging patch selection in birds'. The results of the present and previous studies (e.g. Morris *et al.* 2002) suggest that foraging yellowhammer may detect patches of high insect abundance in cereal crops. These patches are often revisited, suggesting that foraging yellowhammers optimize prey intake rates. Insecticides have been shown to disrupt the spatial distribution of insects in crops, including groups important in the diet of granivorous passerines (Holland and Luff 2000; Holland *et al.* 2000). Such pesticide applications may therefore reduce the value of cereal crops as foraging habitat for yellowhammer and other species, by depressing overall abundance of insects, but also by disrupting localised aggregations, reducing the efficiency with which insects can be collected in crops. The implications of pesticide-induced reductions in insect abundance for breeding yellowhammer include reduced nestling body condition and lower numbers of chicks fledging per attempt (Boatman *et al.* 2004; Morris *et al.* 2005; Hart *et al.* 2006).

Food availability for foraging yellowhammers

Field margins and cereal crops were the two most frequently visited habitats by adult yellowhammers foraging during the nestling period. These findings are consistent with previous studies of yellowhammer and other granivorous passerines during the breeding season (Brickle *et al.* 2000; Morris *et al.* 2001; Wilson 2001; Perkins *et al.* 2002). However, the present study is the first to quantify a seasonal decline in the use of field margins by foraging yellowhammers, showing a marked switch to cereal crops in late summer. This switch was almost certainly due to tall vegetation in field margins in late summer, reducing accessibility to insects. This is consistent with a number of studies showing that tall vegetation may restrict the accessibility and detectability of food for foraging birds (e.g. Butler & Gillings 2004; Stillman & Simmons 2006) and reduce foraging efficiency through impeding mobility (Devereux *et al.* 2004) and via a trade-off between foraging rate and vigilance levels (Whittingham & Evans 2004; Whittingham *et al.* 2004).

Reduced prey accessibility may explain why yellowhammers selected cereal crops, with shorter vegetation, more frequently than margins in late summer, despite margins supporting higher insect abundance. Vegetation structure was also an important determinant of fine-scale patch selection. Yellowhammers' favoured patches with short, sparse vegetation. This pattern was particularly apparent within cereal fields, where tractor tramlines were frequently selected, and is consistent with a previous study of skylarks foraging in barley crops (Odderskaer *et al.* 1997). These results highlight the importance of accessibility to food, mediated by vegetation structure, for foraging birds. One consequence of agricultural intensification has been the loss of habitat heterogeneity on farmland at multiple spatial scales (Benton *et al.* 2003). At the scale of the foraging radius of a typical farmland passerine, this may mean fewer habitat types available, due to factors such as the decline of mixed farming systems, simplified crop rotations and the loss of noncropped areas (Benton *et al.* 2003). However, perhaps the most pertinent change for foraging birds has been the loss in sward structural heterogeneity at the within field scale. For example, in cereal crops, advances in crop breeding, increased fertilization and greater use of herbicides to eliminate weeds have resulted in dense swards favouring only the crop species itself (Wilson *et al.* 2005). Similarly, in grass swards, reseeding with competitive species and increased fertilization may result in dense monocultures (Vickery *et al.* 2001; McCracken & Tallowin 2004). The result of these changes has been an increase in structural uniformity within a habitat. Such habitats generally offer poor foraging opportunities for farmland birds, as the dense, uniform swards may reduce accessibility to insects (Vickery *et al.* 2001; Atkinson *et al.* 2004; Wilson *et al.* 2005). The selection of tramlines within cereal fields by yellowhammers in the present study is consistent with this.

As a result, measures that create heterogeneity in sward structure within a habitat have been suggested, but rarely tested, as a means of enhancing the value for foraging birds (Devereux *et al.* 2004; Tallowin *et al.* 2005; Wilson *et al.* 2005). This was examined in the present study by creating a mosaic of short and long vegetation in close proximity within field margins. The use of short, open margin patches by foraging yellowhammers increased between early and late summer, and patches were used more frequently as vegetation height increased in the adjacent margin. It seems likely therefore that open patches within such margins may enhance food availability at the interface between long vegetation, which serves as a reservoir of invertebrates, and short vegetation, where prey becomes more accessible.

From a general perspective, the positive response of yellowhammers to margin manipulations suggests that creating heterogeneity in vegetation structure within a habitat may be a general tool for enhancing the value of tall, dense arable or grass swards for foraging birds. This is supported by recent research focussing on skylarks in cereal crops. The creation of small, undrilled plots within winter wheat has shown benefits for breeding skylarks (Morris *et al.* 2004; Donald & Morris 2005). These benefits most likely arise from increased accessibility to food in the short, sparse vegetation within undrilled plots.

Field margins are important habitats on farmland for foraging passerines, and the creation and maintenance of margins is an important prescription within agri-environment schemes (AES) designed to aid farmland birds (e.g. Grice *et al.* 2007). However, the results of this study suggest that margins that are left uncut may become poor foraging habitat for birds in late summer. More frequent cutting of margins within AES may therefore be required to increase the value of margins as foraging habitat in late summer. Future work should investigate the optimal area, spatial arrangement and timing of margin cutting required within the farmed landscape to benefit foraging birds, and also the range of species that might utilise such manipulations. In addition, the cost effectiveness of such management would need to be assessed.

Yellowhammer productivity

The presence of experimental margin patches within the foraging radius of a nest appeared to show benefits for breeding yellowhammers. Nestling provisioning rates and body condition were significantly higher at those nests having margin patches present than nests without margin patches on the same sites in the previous year. The effect of between-year variation in additional unmeasured variables on the observed patterns cannot be ruled out. However, margin patches with short, open vegetation may enhance adult foraging efficiency, via effects on food accessibility, forager mobility and perceived predation risk described above. Therefore the presence of such patches within the foraging radius of a nest provides a plausible reason for the observed increased in provisioning rates and nestling body condition between years. If these findings represent a true effect of the presence of margin patches, it would be consistent with the benefits shown by undrilled plots in winter wheat for breeding skylarks (Morris *et al.* 2004; Donald & Morris 2005). The authors showed that nestling body condition increased in the presence of skylark plots during the breeding season, whilst decreasing in control plots having no skylark plots present. These results were thought likely to have arisen due to increased food accessibility, resulting in adults foraging closer to the nest than in control plots. Furthermore, it was suggested that the population decline of skylarks in arable areas in England could be stabilised if just 15% of winter cereal crops contained skylark plots (Donald & Morris 2005). No effect of margin patches was shown on yellowhammer productivity per nesting attempt in the present study. However, increased nestling body condition provides a potential mechanism by which future survival rates and reproductive output of juvenile birds may be enhanced (e.g. Magrath 1991;

Lindstrom 1999). Further research into the potential benefits of margin manipulations on productivity of yellowhammer and other species would be desirable.

Conserving farmland biodiversity

The use of experimental margin patches in late summer by foraging yellowhammers led to an increase in the proportional use of those margins in late summer. This resulted in a reduction in the magnitude of the switch to cereals relative to the previous year in the absence of margin manipulation. This may be beneficial for birds by stimulating greater use of margins supporting higher food abundance than cereals. However, reducing the extent to which birds are required to forage in cereal crops during the summer may have wider implications for biodiversity conservation on farmland and agricultural management practices. Field margins have traditionally proved popular AES options as measured by uptake levels (Butler *et al.* 2007; Grice *et al.* 2007). Maximising the value of margins throughout the summer may have the added benefit of allowing more flexible crop management, as work here suggests that the presence of suitable margins (structurally complex and invertebrate rich) reduces the use of the crop as a foraging habitat. This is important in the context of recent debates about the value of land sparing (where habitat is removed or spared from agriculture) versus land sharing (where agricultural land is managed under reduced intensity) (Green *et al.* 2005). Maximising the value of uncropped land such as margins could be seen as sharing or sparing depending on the scale at which biodiversity is measured. The retention and sympathetic management of uncropped margin habitat provides a means for which to maintain a 'reservoir' of biodiversity in intensive agricultural systems, as field margins occupy only a small percentage of total land area. Managing field margins for biodiversity may therefore reduce the reliance on cropped areas for some taxa, allowing cropped areas to be managed intensively to maximize crop yields. This would reduce the need for conservation measures applied to cropped areas, with the resulting loss in crop yields. Despite recent emphasis on the value and need for in field options within AES (Butler *et al.* 2007) there is almost certainly unrealised potential of field margins in terms of enhancing foraging habitat for birds on farmland in the form of well managed margins. There is clearly scope for innovation in the design of margins that offer enhanced structural complexity that will benefit invertebrates and also enhance food availability for foraging birds.

Conclusions

This study makes a further contribution to knowledge of the factors influencing food availability and foraging habitat selection by a key granivorous bird species on farmland. A seasonal decline in the use of insect-rich field margins by foraging yellowhammers is quantified for the first time, and linked to the effect of seasonal vegetation growth reducing accessibility to insects. A solution to this problem, namely the creation of patches of short vegetation, was tested and a positive response shown to the creation of heterogeneity in vegetation structure within field margins. Although this study focussed on yellowhammers, the implications of the findings and management recommendations may apply to a number of other granivorous farmland passerines sharing similar habitat requirements and life-history with yellowhammers.

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