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The Impact of Landscape Level Arable Reversion on Invertebrate Feedstock for Yellowhammers

By

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ABSTRACT

The yellowhammer (*Emberiza citronella*) has suffered a severe decline in the United Kingdom over the last five decades (McHugh *et al.,* 2013). Attempts to halt the decline by changing farming practice and land use patterns have had mixed results (Sutherland, 2004). Very little is known about the value of landscape level arable reversion schemes to yellowhammers. It is expected that such schemes increase local invertebrate abundance- an important summer food resource for yellowhammer chicks. This study aims to test this hypothesis and provide insights into possible resource trade-offs yellowhammers may be experiencing as ecological succession occurs on re-wilded land at the Knepp Castle Estate, by investigating invertebrate and yellowhammer populations in fields set aside in different years. Invertebrate abundance was found to be higher in older fields and those with a tall sward. However, invertebrate abundance failed to be a strong predictor of yellowhammer density. Instead, yellowhammer call density and sighting numbers were negatively correlated with the percentage cover of woody scrub species and the sward height, indicating increasingly adverse foraging conditions or increasing competition as avian diversity increases. Wheat fields on a control farm were found to have higher call densities and number of yellowhammer sightings than most fields within the re-wilded land. A more extensive analysis of the changing habitat value to species considered to be farmland specialists is advised.

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1. INTRODUCTION

1.1 Background

Billions of euros are annually invested into agri-environment schemes under the European Common Agricultural Policy (CAP). These schemes are a key policy mechanism for mitigating the reductions in biodiversity that result from certain types of agricultural practice (Baker *et al.,* 2012). It is essential that these schemes are well targeted both spatially and temporally, in order to yield the greatest possible return in biological capital. To achieve this goal, studies must be undertaken investigating the impact of different projects operating under agri-environment schemes on particular groups of species currently under threat. Information gleaned could then inform future management practice. Not all schemes are targeted at increasing the population or range of particular species, but, through monitoring, may still provide useful insights into potential conservation strategies in the future. These types of studies are increasingly critical in the light of impending CAP reviews. This study will examine one specific conservation strategy, re-wilding, with respect to a red-listed bird species, the yellowhammer.

1.2 The Yellowhammer

Rapid changes in agricultural systems over the twentieth century have caused a decline in the abundance and range of many once common bird species across Europe (Fuller *et al.*, 1995)(Newton, 2004)(Donald *et al.,*2006). The yellowhammer (*Emberiza citrinella)* is a distinctive bird found widely across the agricultural landscape of lowland Britain. Since the 1960s yellowhammer populations have suffered a continuing decline tempered only by its ability to feed extensively on grain crops through much of the year (Morris *et al.,* 2002). The rapidity of the decline has led to the yellowhammer being red listed by IUCN (IUCN, 2012);

however the still extensive range precludes this species from being listed as vulnerable as yet (McHugh *et al.*, 2013).

Traditionally the yellowhammer has been viewed as a farmland bird. Predominantly a seed eater, the yellowhammer feeds on cereal crops where available (Gregory *et al.*, 2004), only taking insects in the summer months for the young- a protein source that is essential for healthy feather development (Savory, 1989)(Borg & Toft, 2000). Landscape level changes in land use are likely to present trade-offs in resource distribution, with some resources becoming more abundant while others become scarce or temporally unstable.

Conservation research has largely focussed on the perceived weak points in the yellowhammer life cycle, aiming to improve understanding of the mechanisms underpinning the reduction in survival and productivity of the species. Bradbury & Stoate (2000) collated feedback from a variety of studies on the yellowhammer decline. Two dimensions of the yellowhammer niche were considered- nest site availability and dietary resource availability. Loss of quality hedgerow nesting sites combined with low invertebrate availability due to modern farming practices may prevent the successful raising of chicks to adulthood in sufficient quantity to retain a stable population.

Detailed studies into the impacts of particular management strategies on yellowhammer densities are rare (Morris *et al.,* 2005) and can provide part of a vital evidence base on which to build management prescriptions for future conservation work. The timing of such research is critical; the breeding season and chick raising period are potentially the most vulnerable points in the yellowhammer life cycle. The impacts of farm management decisions such as applying herbicides and insecticides may be felt most keenly during the summer months of June and July (Morris et al., 2005).

One focus of such research has been the indirect impacts of herbicide and pesticide use on crops within yellowhammer foraging territories (*fig.*1) (Moreby & Southway, 1999)(Morris *et al.,* 2001)(Morris *et al.,* 2005). To mitigate the damage from these changes a range of agri-environment schemes (AES) have been implemented, financially incentivising environmentally sensitive management of agricultural land. Documented population gains have been made in response to land management changes made under environmental stewardship schemes; provision of a species rich field boundary and boundary features are thought to be of particular importance in providing a strong invertebrate feedstock and adequate nesting sites respectively (Goodwin *et al.,* 2013)(McHugh *et al.,* 2013). However, the changes in invertebrate assemblages associated with agricultural reversion, or 're-wilding', have not been examined in relation to the yellowhammer diet.

1.3 Re-wilding

Re-wilding at a landscape level is an uncommon but developing approach to conservation land management (Sutherland *et al.,* 2006) (Hodder & Bullock, 2009). One such pioneering project is underway at the Knepp Castle Estate in rural West Sussex. Using a combination of naturalistic grazing (using extant substitutes for extinct mega fauna in order to recreate past grazing relationships as closely as possible) and a disturbance regime delivered by a small herd of Tamworth pigs, the project attempts to recreate the system that may have existed before the land was ever farmed. The land was under increasingly intensive arable production throughout the latter half of the 20th Century but still retains its traditional features, including small fields and networks of hedgerows. The grassland restoration is described by the HK16 option for Higher Level Stewardship (HLS) and includes an increase in habitat beneficial to 23 UK Biodiversity Action Plan (UK BAP) species including the yellowhammer, although with potential for a shift in species composition as the project progresses.

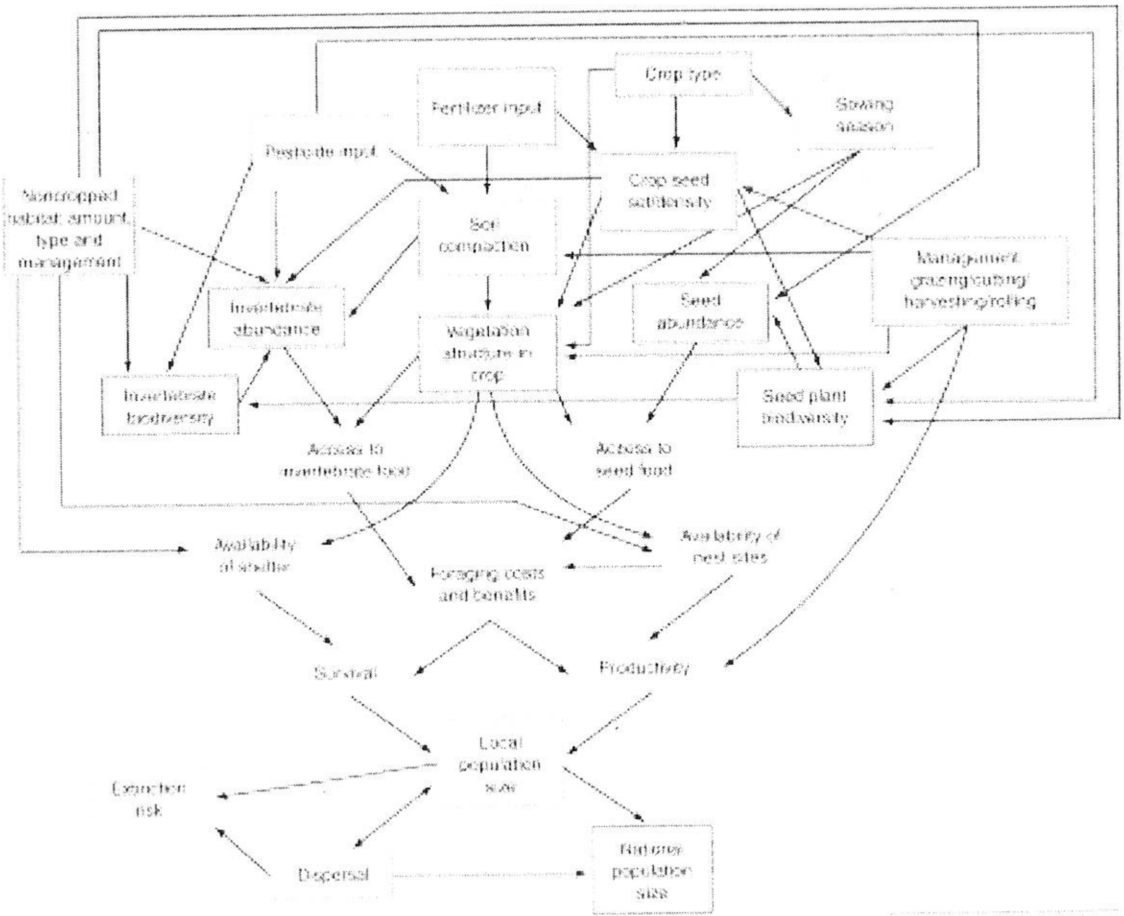
In contrast to targeted conservation work the project has no distinct ecological goal, but rather is deemed to be experimental. Hughes *et al.,* 2011, discuss the intricacies of monitoring a quagmire of ecological inheritance, attempting to pry apart the effects of current factors and ecological forces from the remnants of past management methods and residual population dynamics. As many institutions including UK wildlife trusts increase their focus on landscape level management (The Wildlife Trusts, 2013), combined with increasing uptake of stewardship schemes in the UK (Hodge & Reader, 2010), it is important to investigate the ecological trade-offs for farmland species that could benefit or suffer from the changes as the land undergoes ecological succession.

With this in mind, the southern block of the Knepp Castle Estate, an area of approximately 470 hectares (over 1160 acres), has been used to host a broad scale scoping investigation into potential relationships between standing vegetation, insect diversity and abundance and yellowhammer populations during the yellowhammer breeding season. This study will aim to determine the key features in an evolving landscape that influence the level of yellowhammer activity by making a record and analysis of vegetation, insects and yellowhammer populations throughout the month of June 2013. This study should provide a species specific but timely insight into the value of a 'living landscape' approach to conservation land management. The yellowhammer is an ideal species to examine- being threatened enough to cause international concern, yet still abundant enough to monitor with relative ease in the field (McHugh *et al.,* 2013). Sampling will be carried out to determine how the re-wilding project has affected invertebrate and yellowhammer populations, and the relationship between the two.

2. LITERATURE REVIEW

2.1 The mechanisms behind the yellowhammer decline

Changes in methods of agricultural production have had widespread effects on land and biota across the world. Relatively recent developments in cropping systems and pest management have altered the farmed landscape in the UK considerably; agriculture has intensified, increasing use of broad-spectrum herbicides and pesticides are some of the most ecologically significant components of the intensification.



TRENDS in Ecology & Evolution

Figure 1: *A representation of the many variables influencing survival and productivity of local yellowhammer populations on lowland farms (Benton et al.,*

2003). The amount of non-cropped habitat available combined with pesticide input ultimately affects the balance of costs and benefits in foraging behaviour.

The indirect effects of chemical pest control are far-reaching- impacts have been demonstrated across entire food webs, with detrimental impacts at community and even ecosystem level in terrestrial and marine systems (Haynes *et al.,* 2000). The inter-connectedness of agricultural and natural systems is reflected in the scale of the conservation problems that result from agricultural intensification. The effect of particular farm management decisions on either survival or productivity of yellowhammers can be seen in the representation above (*fig.* 1).

The specific mechanisms causing the indirect effects of both herbicides and pesticides on farmland bird populations have been investigated by the Game Conservancy Trust. Moreby & Southway, 1999, investigated the indirect impact of autumn herbicide application on the available invertebrate feedstock for birds with territories around a winter wheat crop over a period of three years. Herbicide application was found to significantly decrease floral diversity and thus abundance of invertebrates within a number of taxonomic groups thought to be of importance in the nestling diet of several farmland bird species. The reduction in plant diversity, specifically the loss of the weed species in crop headlands, had a disproportionate impact on invertebrate abundance- highlighting the significance of the ecological role played by weed species in the agricultural landscape. In this respect many farmland communities, with a few species that interact with many others in ecological networks- the keystones of the system- can be managed with conservation goals in mind by the protection of just a few of the most important weed species. The value of specific weed species to invertebrate orders and hence avian fauna was found to be difficult to elucidate due to the low abundance of individuals caught within particular invertebrate orders. It was found that dichotomous weed cover had a strongly positive significant relationship with the abundance of rove beetles (*Staphylinidae*) and flies (*Diptera*). Both of these orders have been found in the diet of yellowhammer chicks (Stoate *et al.,* 1998).

Insecticides may also directly reduce food availability, especially within particular groups. Morris *et al.,* 2005, note that groups widely considered not to be pests, within the orders *Araneae, Staphylinidae* and *Hymenoptera,* are often adversely affected by pesticide application (all of these having been noted as important in the yellowhammer chick diet (Stoate *et al.,* 1998)). The target species of pesticide applications include aphids, which are of comparatively little value in the yellowhammer diet unless higher protein content food is unavailable (Wilson *et al.,* 1996).

Some difficulty has been had in the demonstration of a causal link between reduced invertebrate abundance and impaired chick development. To record feeding and development within the nest the methodology required is either intrusive, such as neck collars on nestlings (preventing swallowing so that items brought to nest can be examined), or requires intensive monitoring over an extended time period. Morris *et al.,* 2005, failed to conclusively show any evidence of a strong relationship between insecticide application during the breeding season and chick starvation; however a drop in body condition was demonstrated effectively. Hart *et al.,* 2006, located and monitored nests twice weekly over a three year period. Other investigations have found that it is simpler and equally valuable to conservation goals to show a strong association between invertebrate abundance and habitat selection during territory selection- Dale & Manceau, 2003, found that yellowhammers in a burned forest area of Norway tended to set up territories near areas of high quality farmland food resources. The value of invertebrates to farmland birds has been widely accepted despite difficulties in showing a causal link; the HLS farmland bird package, for example, has been designed to deliver spring-summer invertebrate food by a variety of possible methods including crop headlands, sown margins, beetle banks and strips of sown nectar mix (Natural England, 2012).

2.2 Conservation efforts- agri-environment schemes

Environmental stewardship schemes, being context dependant in their application, vary widely. The methods that can be used to generate spring-summer invertebrate food should be appropriately placed and managed for maximal benefit- Baker *et al.*, 2012, point out the potential for mismanagement and variation in scheme efficacy due to differences in landscape context. A well placed resource, when mature, should demonstrate quantifiable results that can be used to inform future practice. This is reinforced by the findings of Davey et al., 2010a - a broad assessment of the impact of Entry Level Stewardship (ELS), including specific management options, on lowland farmland birds in the UK (using Breeding Bird Survey (BBS) data and spatially referenced ELS uptake data over 2000 1 km^2 sites). Davey *et al.* reported that there was only negligible evidence for positive associations between specific management options and the abundance of the target bird species- although it is noted that a snapshot of current population dynamics may not reflect the long term value of the schemes, some of which have yet to mature. A wealth of data was available to supplement that taken by the authors in the field; however, to standardise sampling methods across the entire 2000 sites the complexity of the sampling was constrained to recording birds seen along a single 2km long transect at each site, on two separate occasions. It seems possible that the lack of any strong associations between agri-environment schemes and abundance of particular species could be due to the relatively low amount of variation that could be captured by the sampling process.

Baker *et al.*, 2012, further developed the on-going ELS monitoring project using BBS data but focussing on particular management actions (as part of stewardship schemes) grouped by the intended biological result and examined at multiple spatial scales over a longer time period (2002-2010, rather than just a single year). A negative relationship was found between yellowhammer population growth rates and hedgerow management under ELS. This is somewhat conflicting with previous work with the opposite findings; that implementation of ELS measures may increase yellowhammer abundance in boundary habitats specifically (Davey *et al.*, 2010b). This conflict is potentially due to competition with other bird species, but seems more likely to be an artifice of the analysis- the areas where the hedgerow schemes were implemented are likely to have been those with the most rapid declines in yellowhammer population initially; thus, a continuing yellowhammer decline would result in the negative association. A study with a narrower focus would not tend to suffer from this problem.

Goodwin *et al.,* 2013, investigated the extent to which schemes specifically providing invertebrate rich habitat successfully improve foraging territories for yellowhammers during the summer months. This was a simple preliminary study to see whether stewardship sites have any impact on territory choice by making a presence/ absence comparison of sites. It is noted that invertebrate availability is one among many factors determining territory quality; breeding habitat is likely to require vegetation structure and community population dynamics (e.g. competing species) that fall within tolerable ranges. Furthermore, variation can be expected to stem from the differences in time since initial implementation- positive associations may be demonstrated based on short term, highly volatile population dynamics that have yet to settle. Goodwin *et* al. therefore aim to identify basic features of the habitats that have the strongest associations with yellowhammer presence across three arable farms in Hampshire. It was found that over all three farms the only habitat type to be significantly higher in abundance within the recorded yellowhammer foraging ranges were those associated with environmental stewardship schemes- suggesting a measure of success in producing a valuable breeding season food resource as a mitigation measure against intensification. Provision of additional summer food resources should buffer against instability and reduction in yellowhammer populations due to low productivity.

Recent research by Dallimer *et al.,* 2010, has aimed to investigate the value of landscape level implementation of agri-environment schemes rather than small scale, single farm application. In this case 346 fields on 29 farms in one region of the Peak District were sampled for all avian fauna at single field level. This particular example involves an extensive pastoral system rather than intensive arable; as such the stewardship options in place are somewhat different to those examined by Davey *et al.,* for example. The scheme in place was the Environmentally Sensitive Area (ESA) Scheme, a precursor to ELS in some regions. Dallimer *et al.* do not specify the options in place, although traditional farming practices and maintenance of small field size and boundaries was key to the ESA scheme's general approach to the Peak District (DEFRA, 2002). The drivers of avian decline in this region are more likely to be linked to nesting site availability than to summer food resources, however it is pointed out that reversion from improved to semi-natural grasslands could improve invertebrate availability, benefitting specific bird species. Indeed, the implementation of the ESA scheme was found to be a good predictor of the abundance of upland specialists and species of conservation concern (in effect, the scheme's target species), rather than a predictor of total avian abundance.

The somewhat mixed results of studies into the response of avian fauna, particularly yellowhammers, to environmental stewardship are possibly due to differing spatial scales at which the research was carried out. High resolution studies may be able to capture individual behaviour patterns and strong associations at habitat/ field level. This information may be lost at low resolution, especially if the behaviour patterns are not consistent across the landscape, perhaps due to inadequate understanding of target species niche resulting in poor spatial planning and ineffective implementation of agri-environment scheme measures. The timescale of sampling is also important; contrasts between the three studies by Davey *et al.* demonstrate the effect of a longer study time period on the conclusions that can be made.

So far the majority of reports on the effectiveness of environmental stewardship, whether at landscape level or not, or short or long term, have focussed on 'broad and shallow' stewardship methods. This 'traditional' stewardship is really the very widespread implementation of low effort measures rather than more extreme management types such as re-wilding. Few re-wilding projects are financially feasible in the UK, except where supported by subsidies under agri-environment schemes (English Nature, 2005). As a measure to mitigate problems such as unsustainable agricultural intensification re-wilding is somewhat controversial; such a complete habitat change involves many trade-offs for many species that provide services. Thus these types of schemes are equally in need of monitoring and assessment as any other; certainly landscape level changes must be validated in order to inform future projects. Hughes *et al.,* 2011, review the challenges associated with the assessment and continual monitoring of open-ended projects that are not targeted at particular species or even groups of species. It is pointed out the goals set for these types of project should be the restoration of natural processes, dynamics and landscape characteristics rather than the promotion of a particular ecological state. The theory of island biogeography (Wilson & MacArthur, 1967) and meta-population dynamics suggest that the large size and high connectivity of landscape scale re-wilding projects should provide more stable ecosystem services than small scale implementation of conservation measures.

The Knepp Castle Estate's re-wilding project is discussed with reference to the initial baseline assessment and monitoring strategy (Greenaway, 2007) and subsequent status assessments (Greenaway, 2009-2011). Hughes *et al.* then propose the evaluation of ecosystem function and service provision through time with regular status updates as a way to monitor the changes experienced in an open ended project such as that at the Knepp Castle Estate. One method described is the use of indicator species to assess the shifts in habitat from the original condition at the commencement of the project. Macro- invertebrates are cited by the authors as potentially useful as indicators of changing ecosystem function in terrestrial habitats such as the Knepp Castle Estate. As the expected process here is a transition from arable production to semi-natural habitat it may be expected that species that thrive in farmland will be displaced to some extent as the landscape changes by succession, although overall diversity should increase with increasing habitat heterogeneity (Benton *et al.*, 2003). Hughes *et al.* recommend evaluation at a variety of spatial and temporal levels and over a long time period as biodiversity gains are likely to fluctuate; populations of key species will be exceptionally dynamic through the initial stages of succession. It is worth noting that the yellowhammer, traditionally considered a farmland bird, is likely to face considerable trade-offs in various aspects of its niche as the land reverts to a semi-natural condition under a naturalistic grazing regime, and so may provide a useful indicator of floristic and invertebrate change.

3. METHODOLOGY

3.1 Field Study Location

The study was carried out on the southern block of the Knepp Castle Estate, West Sussex. The southern block is a single ring fenced parcel of just over 470 hectares, the majority of which has previously been in arable production, but is now in mixed stages of agricultural reversion (fields were consigned to the re-wilding project in different years in a stepwise fashion). The southern block is managed using a naturalistic grazing regime (a herd of approximately 230 English Longhorn cattle graze alongside Exmoor ponies and a small number of Tamworth pigs). Field size is relatively small in comparison to modern farming enterprises and the original hedgerows have been retained (Greenaway, 2005).

A chrono-sequence will be used to capture the ecological succession over time since fields were first set aside. As individual fields were set aside in different years and field boundaries are still easily recognisable sampling will be carried out at field level. Plant, invertebrate and yellowhammer population data will be collected from fields re-wilded in consecutive years, creating a chrono-sequence that can be used to examine the effect of succession on the provisioning of summer food for yellowhammers.

A conventional arable farm was included as a control site- this was Prior's Byne Farm, Partridge Green, West Sussex. The fields sampled at the control site were intensively managed wheat fields with 6m field borders as required under an existing stewardship agreement.

The two parcels of land are approximately 2.5km apart, within the Adur river valley. All fields included in the study, including those at the Prior's Byne site, have very similar underlying geology- the Weald Clay formation. Treatment when in agriculture was also very similar- farm reports show that all the fields included in this study were managed using fertiliser, herbicides, fungicides and insecticides (either as a field dressing or as a post emergence application in some cases). To control for as many variables as possible the fields chosen were of similar size and were distributed evenly across the southern block. Three field replicates were chosen for each of 8 years: 2000, 2001, 2002, 2003, 2004, 2005, 2006 and 2013.

Sampling was undertaken in each field over six weeks from 13/5/2013-30/6/2013. To minimise the effect of temporal variation in the results the fields were organised into three separate chrono-sequences, one replicate from each year group in each sequence. These sequences were sampled consecutively, with the fields within each sequence sampled in random order. The habitat characteristics that were recorded as potential predictors of yellowhammer abundance are listed below (*tab.*1). Sampling was not undertaken on rainy days to maintain consistency across all samples, both in terms of sampling efficiency, yellowhammer behaviour patterns and invertebrate abundance.

The farm maps used were digitised using Quantum GIS 1.8.0 (QGIS Development Team, 2012). The fields chosen as sample sites were identified through consultations with the land owners and an initial survey to confirm accessibility and the year of entry into the project of each field in the southern block. See *appendix 1* for a map of the sample fields chosen for this study.

3.2 Sampling Methods

Table 1: Variables recorded for during the sampling process.

Vegetation Sampling	Invertebrate Sampling	Yellowhammer Sampling	Abiotic Conditions
% cover of five most dominant plant species	Abundance (N) - mean of 12 transects in each field.	Calls/hr	Air temperature (°C)
Mean sward height (cm)	Abundance within orders (mean of 12 transects in each field.	Sightings/hr	Soil moisture content ($m^{-3}m^{-3}$)
	Mean dry mass of 12 transects in each field.	Sighting locations- 4 levels.	Years since last crop

Vegetation sampling

Twelve 30m transects were sampled within each field. Vegetation sampling as carried out by an assessment of the percentage cover of the five most dominant plant species within five 1m^2 quadrats spaced evenly along the 30m transect. To ensure capture of in-field variation sampling was stratified; transects were placed in four categories- field boundary (sample hedgerow itself), field edge (sample 5m from the boundary feature), intermediate (15m from boundary) and middle (equidistant from all boundary features where possible). Three transects were taken within each category. This was necessary because of the discrete characteristics of these sections of each field- the tree or hedgerow borders, combined with past border management, had profound implications on the vegetative structure alongside the field border.

Sward height was then sampled within each of the five quadrats used along each transect. Sward height was sampled using the drop disc method (Holmes, 1974). A 200g, 30cm diameter disc with a central slot is drooped down a ruler from the height of 1m. This is repeated three times within the quadrat and the mean height at which the disc rests on the surface of the vegetation recorded. This method is considered the most suitable for large scale recording of sward height when monitoring agri-environment schemes under a grazing regime (Stewart *et al.,* 2001) due to the high correlation with dry weight of the vegetation when compared to alternative techniques (O'Riorden, 2000).

Yellowhammer sampling

To sample the yellowhammer response to vegetation and invertebrate variables in each field response variables were recorded using a point-count method (sampling was carried out from a single point at the centre of each field for one hour). These response variables were the number of yellowhammer calls heard and the number of sightings within or on the boundaries of each field (both recorded between 09:00 and 10:00 for every field in the sample). The location, either boundary, edge, intermediate or middle (the same protocol with respect to categories as outlined in the vegetation sampling section) was recorded alongside each sighting. Categorisation of yellowhammer sightings by location within the field also enabled the analysis to include an element of yellowhammer habitat use. Only activity clearly within the boundaries of the field being sampled was recorded. Invertebrate sampling was carried out directly after bird recording.

These methods of yellowhammer recording are not ideal- no causative link between invertebrate abundance and yellowhammer densities can be proven; however, it may be possible to show strong spatial associations. A causal link could be demonstrated by assessing chick performance directly and intrusively using measures of nestling condition such as mass (Hart *et al.,* 2006). The landscape scale of this investigation necessitates a less labour and time intensive measure of the yellowhammer response to habitat type. Risk of bias arising from the point-count methodology is considerable- high variability in vegetation across the site means that visibility for yellowhammer sightings was very different in each field, resulting in reduced yellowhammer activity recorded in habitats with a greater degree of succession (Bibby & Buckland, 1987) (Buckland, 2006). Issues regarding the use of population indices and the problem of non-constant detectability will be considered at greater length in the discussion (section 5.3); the nature of the terrain and the limited scope of the study precluding the use of more robust methods including correction for detectability.

As a quality control the number of calls per hour will be recorded and compared to the number of sightings to assess the two factors as measures of yellowhammer abundance. A strong positive correlation between the two indices of abundance would suggest that they are valid indicators of yellowhammer activity within each field. Using the timed sampling method an upward bias in the yellowhammer density estimate is more likely than if a snapshot method was used, however a more detailed representation of yellowhammer habitat use through time is desirable, rather than a potentially unrepresentative snapshot that could influence the analyses. A recording time of more than 1 hour would not have been feasible given time constraints.

Invertebrate sampling

Invertebrate sampling was carried out along the same 12 transects in each field used to sample for vegetation. Sampling was carried out using three methods along each transect. These were sweep netting, vacuum sampling and the use of a drop sheet to sample hedgerows and scrub. To confirm a requirement for all three methods a preliminary investigation was undertaken to examine intrinsic bias in the techniques and to confirm capture of the invertebrate groups thought to be key in yellowhammer nestling diet (section 3.3). To avoid bias due to diurnal variation in invertebrate diversity and abundance sampling was carried out directly after yellowhammer sampling, approximately between the hours of 11:00 and 12:00 daily. All invertebrates caught were killed using 70% IMS and retained in sealed plastic pots for identification to order level. Once identified samples were naturally dried and weighed using a fine balance. Mass was recorded for analysis- invertebrate abundance and orders alone provide an incomplete representation of food quality.

Abiotic variables

Air temperature was recorded at each transect at 1m above the ground. Soil volumetric moisture content ($m^3.m^{-3}$) was recorded 10cm below the surface using a moisture meter (Delta T Devices Ltd). Field area and boundary length were recorded by creating polygons and using the 'measure' function in QGIS.

Data analysis

All statistical analyses were carried out in the R statistics package, version 2.13.2. Analysis of the influence of habitat on indices of yellowhammer abundance site selection was carried out using generalised linear models (GLMs) after mean percentage cover data for vegetation had undergone an arcsine transformation. The GLMs were carried out with poisson family errors (quasipoission where correction for over-dispersion was required). Analysis of the in-field location data (proportions of invertebrates or yellowhammers within the four sections of the field) was carried out using Pearson's chi square test.

3.3 Preliminary Study

The sheer heterogeneity in vegetation structure across the southern block necessitated the use of multiple sample techniques in order to include as many taxonomic groups of invertebrates as possible and minimize bias toward particular groups. A preliminary study was carried out to compare the effectiveness of three arthropod sampling techniques in terms of total catch (N) and the distribution of the catch across taxonomic groups. The three techniques chosen were sweep netting, drop sheet and a handheld cyclonic vacuum. Although yellowhammers are thought to forage from the ground or base of plants, making vacuum sampling most appropriate (Morris *et al.*, 2005) (Wilson *et al.*, 2005), this is not always the case- Fuller *et al.*, 2004, note that Yellowhammers may have strong associations with young plantations and scrub for both nesting and feeding.

It is important to understand the relative advantages and disadvantages of these techniques in the field; but also to be aware of potential sampling bias towards particular invertebrate groups. With this goal in mind sampling was carried out at one site (Waterworks West) that contained roughly equal cover of rough grazing and scrub. Ten 10m transects were sampled using each technique: five radiating from the centre of the field, five along the field boundaries. Five sweeps were carried out along each transect using the same wrist action consistently throughout, while the vacuum sampling was carried out for 5 minutes along each transect. The drop sheet method was only used under scrub and along the field boundary transects- the sheet being placed below the vegetation every 2m along the transect. The vegetation was the vigorously shaken five times. Catches were placed in polythene bags before being killed using 70% IMS. Catches were then analysed to discover potential bias in sampling techniques towards groups of invertebrates with particular life history strategies. An element of bias is inevitable, and indeed desirable, in this case- only invertebrates of dietary value to yellowhammers are required in the sample. It is likely that these mainly include larger, foliar invertebrates rather than very small, high flying invertebrates (Morris *et al.*, 2001).

Each transect was covered by sweeping, vacuum sampling and finally by the use of a drop sheet under scrub, hedgerows or trees.

The invertebrate samples demonstrated a non-normal distribution (as shown by a Shapiro-Wilks normality test). Wilcoxen t-tests were used to make a comparison of the mean numbers of invertebrates within each of the orders caught using the three sampling methods. It was found that the sweep net selected for foliar and flying groups- especially the orders *Hemiptera*, *Hymenoptera* and *Diptera*, for all of which the mean catch using the sweep net was significantly higher than the catches using the other two methods (p<0.01). The vacuum sampling selected against these groups in favour of *Coleoptera*- the mean number caught being significantly higher than those caught in the sweep net (p<0.01), but not the drop sheet. The drop sheet method was found to select for species that could not fly, with significantly more *Araneae* being caught than all other groups. It is worth noting the value of the drop sheet method in sampling *Lepidoptera* and *Symphyta* in their larval stages (*fig.* 3) - the sweep net and vacuum methods were poor in this respect due to the ability of the larvae to adhere strongly to branches.

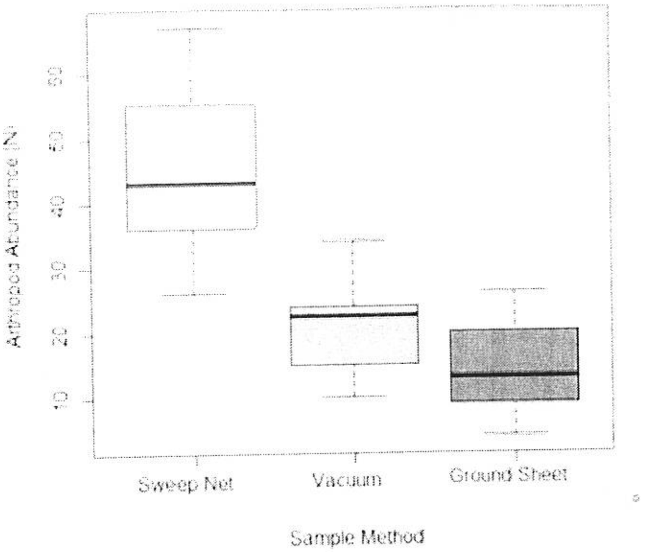


Figure 2: *Abundance of invertebrates caught on transects using each sample method.*

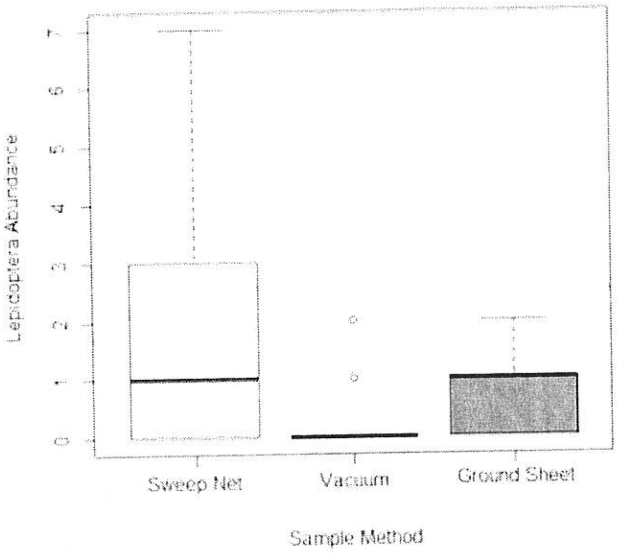


Figure 3: *Abundance of moths (Lepidoptera) caught on transects using each sample method. All those caught using the ground sheet were larvae, demonstrating the importance on including this sampling method.*

With the combined use of all three techniques on a single transect the majority of invertebrate groups of greatest importance to yellowhammer chicks- *Araneae*, *Lepidoptera*, *Coleoptera* and *Diptera* can be sampled effectively (invertebrate preferences based upon the faecal analysis and collar work of Moreby & Stoate, 2000). However, potential biases will remain- sites with high scrub cover necessitate the use of the vacuum and drop sheet sampling, biasing the sample towards smaller invertebrates and this reducing the biomass sampled.

4. RESULTS & ANALYSIS

4.1 Vegetation changes since re-wilding

Few plant species responded to the number of years since last crop as an explanatory variable. However, the number of years since last crop did explain significant variation in the percentage cover of some scrub species recorded (*tab.* 2). Sward height could not be adequately explained by the number of years since last crop.

Table 2: *Test statistics for GLM analysis of mean percentage cover of the significant plant species against the age of field.*

Species	t value	d.f	p value
P.spinosa	2.122	23	<0.05
Q.robur	0.543	23	<0.05
R.fruticosa	1.958	23	<0.05

4.2 Associations between invertebrates and vegetation

There is a clear association between the mean invertebrate abundance in fields and the year in which they were set aside. Positive relationships were also found between the mean abundance of both spiders and flies with the set aside year (*tab.* 3). Tests were then carried out to check for associations between sward height and invertebrates (*tab.* 4).

Table 3: *test statistics for GLM analysis of results for which a significant amount of the variation in invertebrate groups could be explained by the age of the field.*

	t value	d.f	p value
Abundance (N)	2.293	23	<0.05
Araneae	2.152	23	<0.05
Diptera	2.259	23	<0.05

Table 4: *test statistics for GLM analysis of results for which a significant amount of the variation in invertebrate groups (some at order and some at family level) could be explained by the mean sward height. Note the association between aphids and the interaction between sward height and sallow cover.*

	t value	d.f	p value
Abundance (N)	1.905	23	<0.05
Hemiptera	3.241	23	<0.01
Aphididae	6.603	23	<0.001
Aphididae*~Sward:*Salix	6.161	23	<0.001
Lepidoptera	2.454	23	<0.05
Bibionidae	3.325	23	<0.01

Table 5: *test statistics for GLM analysis of results which had a significant association with the mean invertebrate dry mass caught in fields. Trifolium repens and Holcus lanatus are both relatively low growing plant species common in pastures.*

	t value	d.f	p value
Air temperature	3.422	23	<0.01
T. repens	-2.091	23	<0.05
H. lanatus	-2.131	23	<0.05

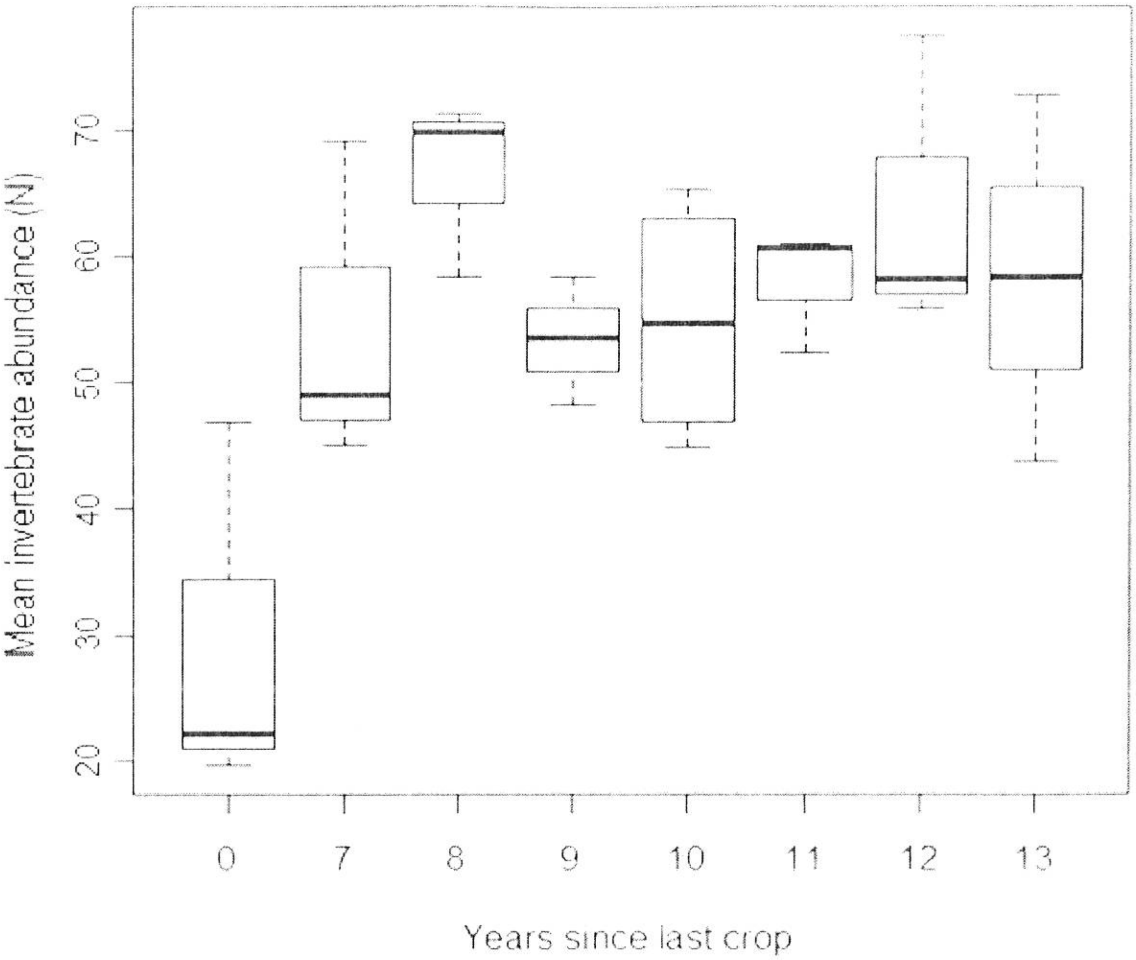


Figure 4: *Invertebrate abundance as a function of the number of years since last crop. See tab. 2 for test statistics.*

4.3 Associations between Yellowhammer density, Invertebrates and Vegetation

A total of 61 individual yellowhammers were sighted and 1139 calls recorded across all sites. Generalised linear models were used to test whether any of the habitat predictors explained significant variation in these two measures used as proxies for yellowhammer abundance. Yellowhammer call density and sightings correlate strongly with each other (t= 5.79, d.f = 23, p<0.001), thus should provide reasonable indicators of yellowhammer activity within each field sampled.

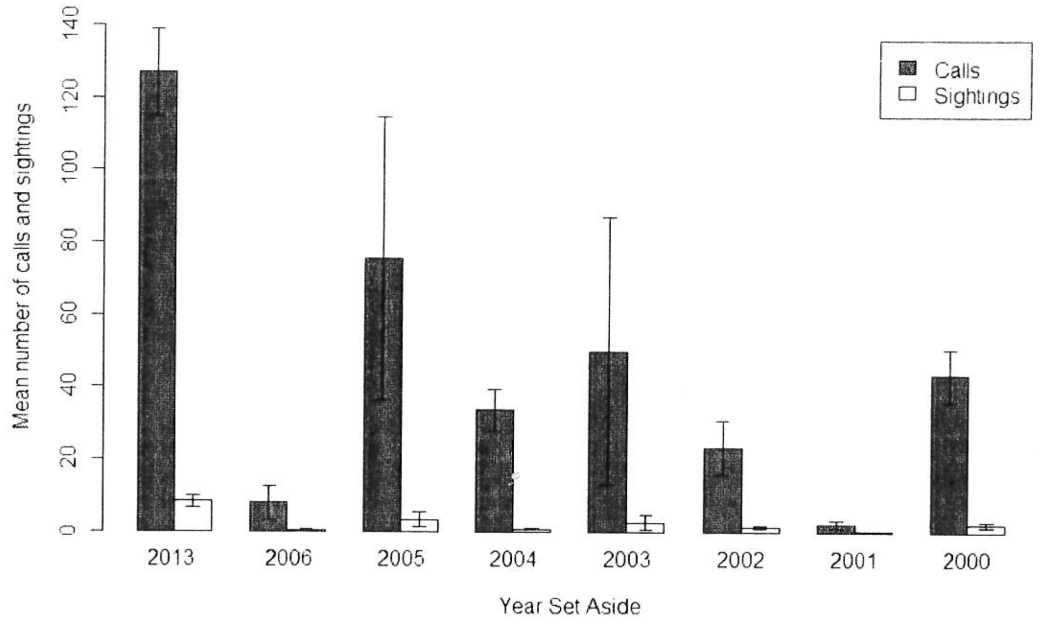


Figure 5: *The mean number of calls and sightings recorded within fields set aside in different years. Those recorded in 2013 were the control fields still in arable production.*

No significant association was found between yellowhammer call density and the year in which fields were entered into the re-wilding scheme (*fig. 5*); however, a negative trend, though not statistically significant, can be seen.

Table 6: *Tests statistics for GLM analysis of factors explaining a significant amount of the variation in Yellowhammer call density between fields. These include indicators of succession such as sward height and scrub cover.*

Factor	**t value**	**d.f**	**p value**
Mean sward height	-2.018	23	<0.05
% Cover *R.canina*	2.172	23	<0.05
Araneae	2.619	23	<0.05
R.canina:Araneae	3.004	23	<0.01
% cover *Q.robur*	-2.794	23	<0.01
% cover *C.monogyna*	2.018	23	<0.05
% cover wheat Crop	2.297	23	<0.05

Associations can be demonstrated between yellowhammer call density and indicators of ecological succession such as sward height and the percentage cover of various scrub species (*tab.* 6).

Mean sward heights within each field have a significant negative association with yellowhammer call density. A fitted loess curve suggests an optimal sward height possibly around 21cm (*fig.* 6a).

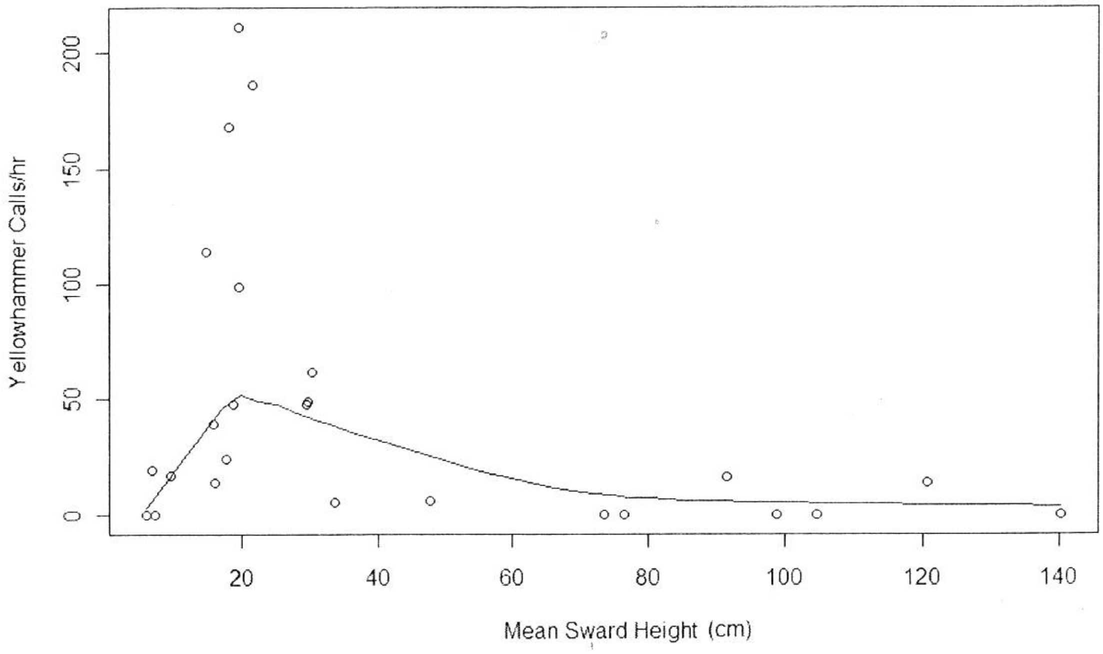
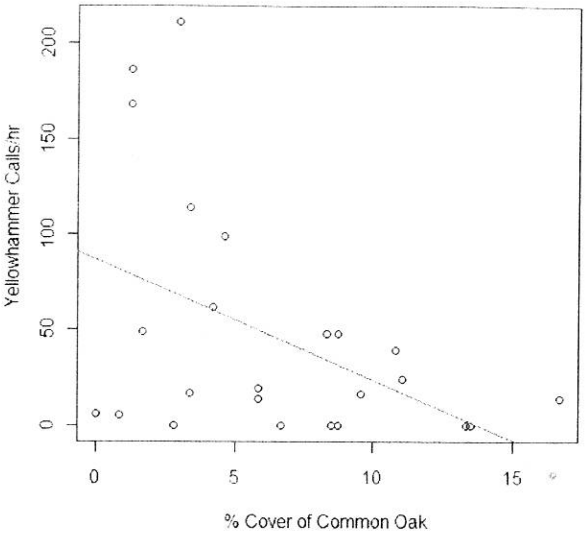
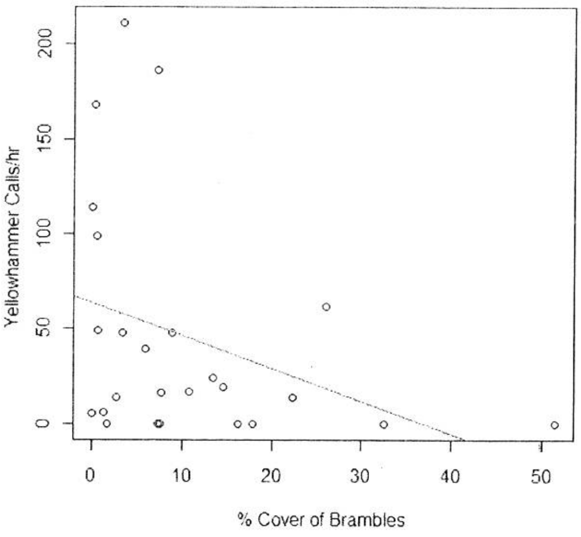


Figure 6a: *A negative relationship was demonstrated between sward height and call density; however, an optimal sward height (around 21 cm) may exist before which the relationship is positive.*





Figures 6b & 6c: *Scatter plots demonstrating the significant negative associations between yellowhammer call density and the percentage cover of common oak (Q. robur) and brambles (R. fruticosa) respectively. Test statistics can be seen in tab. 6.*

No significant associations were found between field size, border length, air temperature or soil moisture any indices of yellowhammer abundance. However, air temperature was found to significantly influence the invertebrate biomass (*tab.* 5).

A ctions Analysis

u out to see if there were any significant differences in the s of yellowhammer sighted in each section of the fields (*tab.* 7). It was found that the sighting distribution was significantly different than could be expected under a null hypothesis- that all field sections would be selected equally ($\chi=101.3$, d.f=3, $p<0.001$).

Table 7: *The number of yellowhammer sightings recorded in each field section (all fields included).*

Field Boundary	Edge	Intermediate	Middle
49	8	3	1

An association was not found between invertebrate abundance in each field section and yellowhammer sightings in each section. When all fields are included the null hypothesis (that the location in which yellowhammers were sighted is independent of invertebrate abundance) cannot be rejected.

A separate analysis of the 36 transects taken on Prior's Byne farm revealed a close positive association between the mean number of invertebrates caught and the number of yellowhammers sighted in each section of the wheat field ($\chi=17.4$, d.f=3, $p<0.0001$).

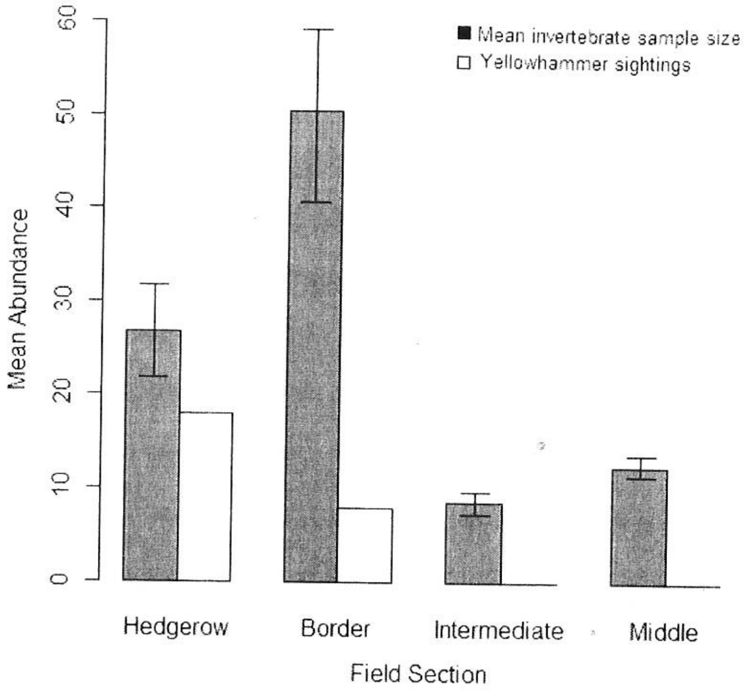


Figure 7: *Mean invertebrate abundance caught in transects in each section of 3 wheat fields at Prior's Byne Farm. Numbers of yellowhammers sighted in each section are also included.*

No yellowhammers and very few invertebrates were recorded within the crop itself; invertebrate abundance was highest within the 6m borders, while yellowhammers were seen both in the borders and the boundary features. Thus the null hypothesis can be rejected- there is a significant likelihood that the section of the wheat field in which yellowhammers were sighted is dependent upon invertebrate abundance.

Note that the samples taken were included as the 2013 (non-rewilded control) in the above analyses, but have been treated separately for the purposes of a comparison to the arable reversion management methods in terms of a species specific management for yellowhammers.

5. DISCUSSION

5.1 The effect of succession on invertebrate availability

The case for ecological trade-offs resulting from landscape level re-wilding is strongly supported by the yellowhammer habitat associations demonstrated in the analysis. Although the maturation of the re-wilding project may provide increasing supplies of invertebrates during the summer months (invertebrate abundance (N) was shown to increase with the height of the sward and the 'age' of the re-wilded land (*tab.* 3 & 4, *fig.*4)), the continuance of ecological succession to a relatively stable point determined by the near-natural grazing regime also provided species and structures that had a negative relationship with yellowhammer sightings and call density at field level (*tab.* 6).

Firstly, the use of a chrono-sequence within the southern block failed to enable significant differences in plant communities between fields of different ages to be recognised. Significant increases in the mean percentage cover of three species of woody scrub (blackthorn (*P. spinosa*), oak (*Q. robur*) and brambles (*R. fruticosa*)) were demonstrable (*tab.* 2); otherwise no strong associations with time could be made. The rate of ecological succession seems to be uneven across the southern block- the number of years since the last crop was harvested failed to explain significant amounts of variation in sward height or the mean percentage cover of other scrub species such as hawthorn (*C.monogyna*), dog rose (*R.canina*) and sallow (*Salix* spp.). This is potentially due to heterogeneity in abiotic conditions and residual population dynamics- development of sallow stands was noticeably heterogeneous even at and below field level.

In contrast to the difficultly in discerning a clear succession in the plant communities, invertebrate communities are markedly different across the southern block and show a relatively clear response to the number of years since the land was set aside (*fig.* 4).The highest number of invertebrates caught in any transect at Prior's Byne was lower than the median abundance within any set-aside year in the re-wilding project. Variation in the mean invertebrate abundance between fields could be significantly explained by the age of the communities as well as by the height of the vegetation. The strong positive response in mean invertebrate abundance to sward height (*tab.* 4) is to be expected- increasing vegetation biomass should provide more structurally complex habitats allowing high abundance and diversity of invertebrates to survive and reproduce (Wilson *et al.*, 1999). However, as sward height cannot be adequately explained by age, other factors must also underpin the increase in invertebrate abundance over time. This could be explained by the lack of a measure of sward structure- sward height fails to adequately incorporate the complexity of the vegetation- thus, lower but more mature, species-rich swards might support higher numbers of invertebrates than a taller but less diverse and less complex sward. The increase in invertebrate abundance in response to field age should evoke an increase in productivity in many avian species that rely on invertebrates as a protein source in the summer months (Doulgas *et al.*, 2009).

The mean biomass of invertebrates caught in transects (using all three sampling methods) was not found to correlate with the sward height. A significant amount of the variation in invertebrate biomass could be explained by the mean percentage cover of particular plant species- again, possibly a more representative measure of sward structure than the sward height. Negative associations were seen with low growing, simple structure species such as clover (*T. repens*) and a perennial grass species, *H. lanatus* (*tab.* 5). Morris, 2000, discusses the importance of microclimate, oviposition sites and food resources in determining invertebrate abundance in grasslands. The relatively low stocking density used to create naturalistic grazing and disturbance regime on the Knepp Castle Estate could be an important influence on the sward structure- intensive grazing reduces standing plant biomass and so reduces niche space (including the aspects listed by Morris) for invertebrates. Unpalatable plant species are often more architecturally complex than palatable species (Morris, 2000), so some grazing pressure may be responsible for allowing increases in percentage cover of scrubby species.

The variation in the abundance of invertebrates within certain specific orders could also be explained by the number of years since fields were set aside. Spiders

(*Araneae*) are the clearest example of this- having a strong positive relationship not only with the number of years but also with the percentage cover of dog rose (*R.canina*) along transects. The mean abundance of *Hemiptera* caught along transects was strongly correlated with the percentage cover of sallows- aphids specifically had an exceptionally strong relationship with the young sallow stands in fields (*tab. 4*).

Bearing in mind these patterns in the plant and invertebrate communities it is unsurprising that no strong relationship was found between the years in which fields were set aside and the yellowhammer abundance (as represented by call density and number of sightings). It is, however, possible to demonstrate the effect of succession in the fields on yellowhammer abundance by analysing relationships with particular floral species present and the height of the vegetation.

5.2 Predictors of yellowhammer density

The number of years since the last crop was grown on the land seems to be a relatively poor predictor of yellowhammer abundance (*fig.* 5). This could be because time does not really represent the level of ecological succession within each field; thus it is likely that a chrono-sequence may not be the most appropriate method to explain the shifting population dynamics through time. Instead, variation in yellowhammer call density and sightings can better be explained by vegetation and invertebrate differences between sites. It was not possible to demonstrate a relationship between invertebrate abundance and yellowhammer density at any spatial scale. Reasons for this are further discussed below.

The increase in scrub across fields in the southern block has had a mixed effect on yellowhammer distribution. Batary *et al.,* 2012, emphasize the importance of diverse yet isolated hedgerow structures rather than scrub and woodland in farmland bird territory selection, possibly to avoid competition with species better adapted to woodland conditions. This is supported by the findings of this study; *figs.* 6b. & c. demonstrate the negative correlation between the percentage cover of common oak (*Quercus robur)* and brambles (*Rubus fruticosa*), both in fields and along borders, with the number of yellowhammer calls recorded in an hour. Furthermore, the strong negative relationship between the height of the sward and yellowhammer call density suggests that sward height is an important component of feeding habitat selection.

Avian foraging site selection can be considered as a trade-off between energy intake rates and the risk of predation (Buckingham & Peach, 2005) (Buckingham *et al.*, 2006). Thus, a tall sward may provide more or better quality invertebrate food, but may be less accessible with a greater risk of predation (Whittingham & Evans, 2004). Prey accessibility may be greatly reduced by complex, taller swards for several farmland bird species (Butler & Gillings, 2004). Douglas *et al.*, 2009, found that cut grass margins were used more intensively by foraging yellowhammers than taller, structurally complex margins- possibly due to inaccessibility or reduced visibility, increasing predation risk.

Although the combined results of this and previous investigations suggest invertebrate abundance increases with sward height, the efficiency of yellowhammer foraging efforts is likely to be greatly reduced in certain taller vegetative structures. The majority of the individual yellowhammers sighted were in or beside the boundary hedges, with very few being sighted within scrubby areas in the middle of fields (*tab. 7*). A possible optimum mean sward height could be around 21 cm- above this call density is negatively correlated with increasing sward height. The mechanism behind the association with sward height is difficult to demonstrate. Other than ease of foraging, it could be due to relationships with particular invertebrates that thrive in certain swards made up of particular floral species. This could help explain the lack of an association between yellowhammer abundance and invertebrate abundance; although invertebrate numbers increase with the amount of time since the land was re-wilded (*fig.* 4), other factors prevent yellowhammers from exploiting these increases.

A sward below the optimum height, perhaps due to intensive grazing or trampling (this being very unevenly distributed across the southern block, the cattle having particular behavioural patterns), could have been avoided for a number of reasons;

reduced invertebrate availability (*tab.* 4) but also reduced winter food availability- Buckingham *et al.,* 2006, found that wintering yellowhammers avoided fields that had been grazed heavily during the summer by cattle. The change from arable production to increasing scrub cover serves to continually decrease winter food availability over time (in lowland UK winter food for yellowhammers is thought to largely comprise seed foraged from cereal stubbles- left over cereal grains, or regenerated cereals in set-aside land. These are thought to provide greater foraging benefits than the lower seed availability provided by grass leys or scrub (Bradbury *et al.*, 2000). Increasing plant diversity, progressing to scrub in some places, is likely to provide seeds at densities below the required thresholds for efficient foraging behaviour- around 50 seeds m^{-2} for yellowhammers in autumn and early winter according to Moorcroft *et al.,* 2002.

Previous research into the yellowhammer's ecological niche suggests a strong affinity with arable land with hedgerows and grassy borders, while pasture and woodland tend to be avoided (Bradbury *et al.*, 2000). Indeed, the yellowhammer is considered to be a hedgerow specialist (Fuller *et al.*, 1995) (Fuller *et al.,* 2001). Hedgerows continue to thrive throughout the southern block of the Knepp Castle Estate (with an estimated total hedgerow length of 65 km, increasing in width and height as hedgerows in the southern block remain unmanaged). The results of this study confirm the value of hawthorn (*C.monogyna*) as a dominant species in lowland hedgerows (*tab.*6), possibly as a nesting resource.

Previous research is divided on the nutritional value to the yellowhammer diet provided by invertebrates in hedgerows. Generally hedges are regarded as being a nesting resource rather than a source of invertebrates (Stoate *et al.,* 1998). However, Thomas & Marshall, 1999, point out that an enormous diversity and abundance of invertebrates can be found in florally diverse hedgerows, such as those on the Knepp Castle Estate. The results of this study confirm that invertebrate abundance was high in the hedgerows generally (*fig.* 7). Furthermore, the majority of yellowhammer sightings were within hedgerows or along field borders. However, the association may be due to nesting rather than foraging- hedgerows are too structurally complex for efficient foraging, yellowhammers being better adapted to forage in grassy margins than the hedgerow itself despite high invertebrate abundances being present (Fuller *et al.,* 2001). Although no specific aspects of hedgerow structure were investigated in this study, it is apparent that the developing hedgerow structure around the southern block could be of considerable habitat value to avian fauna. The light grazing regime allows (without any other hedgerow management) the slow formation of a thorny mantle along the edges of the existing hedgerows. This structure was reflected by transects along the field edges in this study (where yellowhammer sightings were highest after the field boundary hedgerows themselves (*tab.* 7)).

Other than those previously mentioned (oak and hawthorn), few plant species could explain significant variation in yellowhammer call density or the number of sightings. The positive relationship found between dog rose (*R.canina*), spiders (*Araneae* spp.) and yellowhammer call density suggests the importance of sward structure in the provision of spiders in the yellowhammer diet. A positive association with some low density scrub species suggests an optimum where the foraging costs due to a reduction in sward accessibility do not outweigh the benefits gained by increases in invertebrate abundance (specifically spiders- known to be an important component of nestling diet (Stoate *et al.,* 2010)(Perkins *et al.,* 2002)). Although the cover of dog rose could not be shown to significantly dependent upon the time since set-aside, this is likely because fields were not available to sample that had entered the re-wilding scheme less than seven years ago- thus the early stages of succession, including dog rose colonisation, were not available for inclusion in the analysis. However, a strong positive correlation between spider abundance and field age was shown, and so the relationship between yellowhammers, spiders and dog rose seems to be an important component of the summer food provision by a large scale reversion scheme.

Yellowhammers seem to exhibit flexible rather than narrow foraging strategies, having strong associations with different invertebrate groups depending on availability- aphids, for example, are not thought to be a primary choice of prey but form a large proportion of diet where other prey groups are depleted due to pesticide application (Wilson *et al.,* 1996) (Morris *et al.,* 2005). Some yellowhammer habitat associations were found to differ between the re-wilded land and the control land (cereal crops with 6m borders and hedgerows). These differences are of great interest when considering species specific conservation strategies, such as the most appropriate strategies for locations in which yellowhammer populations are particularly vulnerable.

The crop borders at Prior's Byne farm were shown to be successful in providing a summer food resource to yellowhammers- invertebrates were higher in abundance than either the hedgerow or the crop (*fig.* 7) but limited in diversity at order level; reflecting the floral species composition of the borders. The success here is demonstrable- invertebrate abundance was exceptionally low in all transects taken within the wheat crop itself (*fig.* 7), yet yellowhammer call density and sightings within the borders and hedgerows are high. This suggests that the borders are the important resource pool in the summer, while the crop may be a resource throughout the rest of the year. The association between the section of the field in which yellowhammers were sighted and the invertebrate abundance suggests a strong dependency; however, there are many possible confounding variables. The lack of biological diversity within the crop itself would tend to confine both the invertebrates and yellowhammers to the borders and boundary features whether they were interdependent or otherwise.

Fuller *et al.,* 2004, suggest that arable farmland specialists breeding in a non-arable habitat (as the southern block could be described) are likely to be dependent on arable farmland at some point within the year for provision of a resource type. A relationship has been demonstrated between the winter habitat location and where farmland birds set up summer territories (Whittingham *et al.,* 2005). The relatively high densities of yellowhammer encountered on fields at Prior's Byne farm when compared to the majority of fields on the southern block suggests this may be an important factor to consider when designing landscape level conservation enterprises aimed at particular species- although heterogeneity within the southern block is able to support yellowhammers territories, equally high densities may be supported on arable land (provided adequate hedgerow and border requirements are met). Landscape complementation seems likely; the southern block of the Knepp Castle Estate may act as a large summer resource pool for birds that utilise nearby farms during the winter months.

Previous biodiversity records from the Knepp Castle Estate show an initial rise in yellowhammer abundance on the estate. This could be expected as the availability of summer invertebrate feedstock rises over time (*fig.* 4). An initial rise in yellowhammer abundance until saturation, limited by competition for winter food resources.

5.3 Limitations of this study

There are several methodological limitations to this study, largely due to constraints imposed by the scale and scope of the investigation and the highly heterogeneous terrain that was adverse to unbiased sampling methods.

Firstly, as mentioned previously there are limitations to bird studies using abundance indices generated from single point, timed surveys; although this is a conventional and widely used method, it can lead to an upward bias in the population estimates as birds move around while the sampler remains in place (Buckland, 2006). It is accepted that abundance estimates gained from point sampling are relative and not absolute; this does not, however, overcome the issue of non-constant detectability within the sampling radius. Habitat heterogeneity, especially important in the southern block, limits the value of the data- variation in the level of succession results in different levels of visibility within fields (see Bibby & Buckland, 1987, a study of detectability in conifer plantations of various ages). This could theoretically explain the lower yellowhammer abundance experienced in older fields despite higher invertebrate abundances; these fields were less open than the wheat fields, for example- thus, more yellowhammers may have escaped detection. A point-count sample is defendable in this instance. It was desirable to demonstrate close spatial associations between habitat characteristics, invertebrates and yellowhammers across relatively small plot areas- in many of which yellowhammer counts, and certainly call counts, can be considered absolute (Buckland *et al.,* 2008). However, it is worth noting that accounting for bird movement in and out of the fields being sampled is more difficult and could have resulted in upward bias in both sightings and call density. The irregular shape of some fields also caused detectability to be non-constant both within and between sample sites that was not corrected for.

The use of call density as a proxy for yellowhammer abundance is not so limited by varying detectability; on site it was found to be relatively simple to record yellowhammer calls from within the boundaries of a single field. The yellowhammer call is distinguishable from a long range regardless of scrub cover, so detectability is not likely to have caused bias in call density due to varying levels of succession in different fields. Yellowhammer detectability may also vary temporally- this was accounted for by the maintenance of a fixed time for bird sampling and reverse order sampling for each chrono-sequence to mitigate bias from seasonal effects (i.e. the fields in the second chrono-sequence were sampled in the opposite order to those in the first).

To investigate landscape level ecological changes over 13 years of re-wilding in only one month required the use of an imperfect experimental design. To create a chrono-sequence of fields, each having been brought out of arable in different years, required the use of individual fields as experimental units. This creates difficulty in formulating a robust method for sampling- fields vary in size and shape, thus boundary lengths differ as well as a variety of abiotic conditions. It is more difficult to achieve a representative sample in larger fields than the small fields. The fields chosen were as similar in these respects as possible; the majority of fields included were between 3 and 5 hectares, although some sites originally left fallow in sections along the boundaries of larger fields were significantly smaller. When field size is included in the analysis there is no significant explanation of the variation in yellowhammer call density or sightings. It seems that other factors have more influence on local yellowhammer densities than the field size and correspondingly, hedgerow availability. Initially this seems to conflict with other results (*tab. 7*). Although hedgerow seems to be the most used habitat type this does not infer that it is the limiting factor in determining the local population size. Large fields with extensive networks of hedgerows were found to have little or no yellowhammers, while others had exceptionally high densities- it is clear that while nesting space may explain patterns at some spatial scales, other factors are deciding the macro-level patterns in yellowhammer distribution.

An improvement to the method applied in this study would be the use of sonograms to recognise individual yellowhammers allowing a more absolute estimate of abundance rather than a relative index. Call density is subject to an upward bias due to high activity individuals that could be recognised using sonograms.

6. CONCLUSIONS

Opportunities to study the effects of agricultural reversion are rare; this is a pioneering study into yellowhammer habitat associations across a large-scale mosaic of succession and disturbance. The evidence gained by this study suggested the existence of seasonal trade-offs for yellowhammers as a result of the evolving landscape. The most evident trade-off seems to be the increasing scrub cover in place of grasslands, and in the more distant past, crops. The project at Knepp may be a valuable provision for yellowhammers in comparison to its previous state under agriculture- no data exists for yellowhammer densities prior to the beginning of the re-wilding project; however, the current spatial patterns suggest a preference for conditions that arise with limited levels of succession only- tendency towards a high sward, scrub or woodland community results in very low estimates of yellowhammer abundance.

This could help inform conservation efforts at landscape scale. Project objectives are key when deciding the type and scale of conservation projects; re-wilding of agricultural land is rarely driven by specific goals; instead it is seen as a journey with a likely result of a net increase in biodiversity. The result of this study suggests that higher densities of yellowhammer may be supported on wheat farms practicing bird-oriented conservation schemes than in scrub, rough grazing and woodland, although at a local patch level this may not always be the case.

The value of crop borders and hedgerows to maintaining yellowhammer populations is confirmed; continued implementation of diverse borders on arable farms in lowland Britain should be an aspect of conservation schemes continually promoted if such schemes are to be targeted at specific avian species such as the yellowhammer. This study confirmed some known yellowhammer habitat associations despite flaws in method. The strong association with spider abundance confirms the compositional analysis carried out by Moreby & Stoate, 2001, who found that spiders made up 11.1% of food found in yellowhammer nests when using the neck collar method. Associations with other orders thought to make up large proportions of the diet, such as moths, could not be confirmed, perhaps due to methodological constraints or foraging patterns particular to local conditions.

While net gains in biodiversity are being experienced on the Knepp Castle Estate, re-wilding results in a succession in the types of species that are most abundant; the results of this study suggest that the future is unlikely to hold large gains for predominantly granivorous avian species adapted to the conditions provided by traditionally managed arable farmland. With these species in mind, recommendations for yellowhammer conservation remain the provision of small scale mosaics of land use within a farmed landscape, retaining hedgerows, grass borders and managing in a temporally sensitive manner. This study demonstrates the complexity and inter-connectedness of ecological relationships in the farmed landscape, highlighting the need for evidence-backed strategy and review when planning conservation land management actions. In a wider context, stakeholder responses to the potential declines seen in particular farmland species in arable reversion schemes should be monitored (Hughes *et al.,* 2011) to avoid social constraints to ecologically valuable projects that lack a definition of success or failure.