

Chapter 2: Nesting and foraging ecology of yellowhammers *Emberiza citrinella*

Abstract

Yellowhammer nesting and foraging ecology were investigated during the breeding seasons of 2006 – 2008. Yellowhammers nested most frequently in hedgerows, with some nests also found in herbaceous vegetation. Mean clutch size was similar to that found in other studies, as was mean fledgling number per successful nest. The percentage of nests successfully fledging at least one chick was similar to both recent (2000) and historic (1960) studies, indicating no evidence of any change in fledging success since the start of the yellowhammer population decline. Predation accounted for the majority of nest failures, followed by abandonment and whole-brood starvation. Mean nest height was significantly greater than that of a study in 1960, being nearly double in the current study: this may indicate either changes in nest site selection or differences in the availability or structure of suitable nesting habitat (nests in vegetated ditches are under-represented in the current dataset). No hedgerow features differed between nest site locations and randomly selected sites within the same territory, indicating that the selection of a territory containing high quality nesting habitat is more important than small-scale habitat selection for nest sites, which is more likely to depend on local habitat features such as suitable support structure in an area of high vegetation cover. When compared with control sites within a similar microhabitat, foraging sites did not differ in terms of vegetation height, density, cover or invertebrate abundance. However, foraging sites had a lower vegetation density, as well as a higher invertebrate abundance at higher vegetation densities than did control sites within a different habitat, indicating that foraging sites are selected according to a vegetation structure that allows a greater accessibility to invertebrates, and that where accessibility at foraging sites is lower and may incur a greater predation risk (through a reduced visibility of predators at higher vegetation densities), there is a payoff in terms of increased invertebrate availability. Parental provisioning rate decreased with increasing vegetation cover at foraging sites in areas of high invertebrate abundance, probably due to an increased amount of time spent scanning for predators; conversely where invertebrate abundance was low, provisioning rate increased with increasing vegetation cover, probably due to a positive correlation between vegetation cover and invertebrate abundance, and suggesting that adults in low food environments may be forced to take more risks when foraging for food for their young.

Introduction

Populations of farmland birds have been declining in recent years due to aspects of farmland management associated with agricultural intensification (e.g. Fuller et al. 1995; Chamberlain and Fuller 2000). The majority of these declines began in the mid to late 1970s (Fuller et al. 1995) but that of one species, the Yellowhammer, is unique (Bradbury and Stoate 1999). This species apparently did not begin its decline until the late 1980s (Kyrkos et al. 1998) but since then it has undergone an estimated population reduction of 54% (Eaton et al. 2008). Unlike populations of many other farmland birds whose populations have now begun to stabilise, yellowhammer populations remain in decline (Eaton et al. 2008).

Nesting habitat appears to be a factor limiting Yellowhammer populations, with population density strongly associated with the densities of hedgerows and vegetated ditches (Kyrkos et al. 1998; Bradbury et al. 2000; Stoate and Szczur 2001; Whittingham et al. 2005). Nests tend to be built in herbaceous vegetation in ditches, or in the base of hedgerows (Bradbury et al. 2000), although Yellowhammer nests in hedges are more susceptible to predation than those in herbaceous vegetation (Stoate and Szczur 2001). Generally, nests with higher levels of vegetation cover are less susceptible to predation by visually-oriented predators such as corvids (e.g. Cresswell 1997; Eggers et al. 2006), which are the main nest predators of birds in the agricultural landscape (Andrén 1992) and also the main nest predator of the Yellowhammer (Bradbury et al. 2000). Depredation is the main cause of nest failure in many farmland species, including the Yellowhammer (Bradbury et al. 2003) and the Reed Bunting (Brickle and Peach 2004).

Yellowhammer breeding population density increases with the proportion of land growing cereals and with increasing crop diversity (Kyrkos et al. 1998). This is likely to be linked to foraging requirements during the breeding season: whilst adult yellowhammers are granivorous, all chicks are fed invertebrates as well as unripe cereal grain (Stoate et al. 1998). Nestling mortality has been linked to weather variables such as cold temperatures and increased rainfall that decrease both numbers and activity levels of invertebrates (Stoate et al. 1998; Bradbury et al. 2003) and a reduction in the growth and body condition of chicks, as well as an increase in brood reduction, has been linked to the use of pesticides during the breeding season, through a decrease in invertebrate populations (Morris et al. 2005; Hart et al. 2006). Habitat type and structure can also influence the availability of invertebrates to foraging birds: grass

margins, hedges and ditches are selected over cropped areas for foraging (Perkins et al. 2002). Within cropped areas, broad-leaved crops and bare ground are favoured, with cereal crops being utilised more often as the cereals ripen (Stoate et al. 1998; Morris et al. 2001) and non-cropped habitats increase in vegetation density, reducing invertebrate accessibility (Douglas et al. 2009).

An interaction between food abundance and accessibility in predicting foraging site suitability, mediated by habitat structure, was proposed by Morris et al. (2001). Whilst Perkins et al. (2002) found no difference in the use of cut and uncut margin patches for foraging, their sample size was small and they suggest that an interaction between prey abundance and accessibility may explain their observations (Perkins et al. 2002). In a larger scale study, Douglas et al. (2009) found cut margins to be used more often than uncut margins by foraging Yellowhammers, indicating that accessibility to prey plays a large part in determining the selection of foraging habitats (Douglas et al. 2009). Predation risk to foraging adults may also play a part in habitat selection: Yellowhammers are sensitive to perceived predation risk (van der Veen 1999) and time exposed to predators is thought more important to survival than an adaptive reduction in body mass to reduce predation risk for this species (van der Veen 1999). Thus, the choice of foraging habitat may be influenced by perceived predation risk mediated by habitat structure (Whittingham et al. 2004; Whittingham and Evans 2004; Whittingham et al. 2006) as well as through food abundance and accessibility.

Neither the abundance of nesting habitat, nor the availability of foraging habitat are sufficient to explain Yellowhammer population declines in areas where cereal cultivation remains predominant (Kyrkos et al. 1998). A study by Whittingham et al. (2005) indicates that winter habitats are important in predicting where birds will locate summer breeding territories, and that the presence of set-aside fields is particularly important (Whittingham et al. 2005). It remains to be seen what effect the reduction in set-aside abundance (Langton 2008) as a result of the lowering of the percentage of compulsory set-aside to 0% in 2008 will have on Yellowhammer populations.

This chapter aims to address some key gaps in knowledge of Yellowhammer nesting and foraging ecology. Firstly, nesting ecology and nest-site selection at the within-hedgerow scale will be examined to determine whether specific microhabitats within a hedge are selected for nesting, and by comparison of nest height data with data from

1960 (Peakall 1960), the possibility that changes in nesting ecology have occurred concurrently with yellowhammer population declines will be examined. Other factors influencing nest survival and fledging success are explored further in Chapter 4.

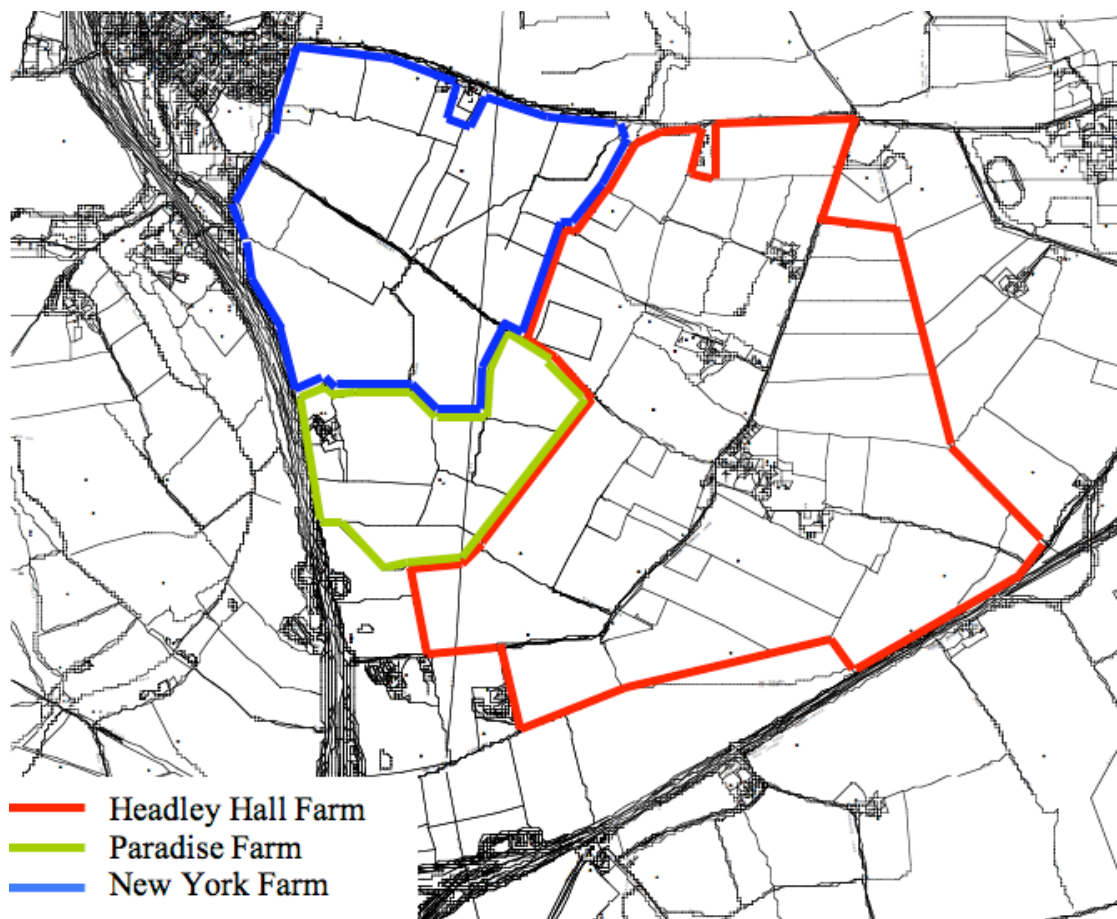
Studies of Yellowhammer foraging site selection have mostly looked at site selection at the habitat scale (e.g. Stoate et al. 1998; Morris et al. 2001; Perkins et al. 2002). Yellowhammer foraging habits have been linked to bare ground and a short sward (Stoate et al. 1998; Douglas et al. 2009) and Yellowhammers are sensitive to predation risk (van der Veen 1999) which can be influenced by foraging habitat structure (Whittingham et al. 2004; Whittingham and Evans 2004). This study compares foraging sites with randomly placed control sites, both within the same microhabitat, for example tramlines within a crop, and within a different microhabitat in order to determine important features influencing habitat choice at the within-field scale. Habitat features of foraging sites will also be linked to parental provisioning rate, to determine whether features of foraging sites may influence foraging success.

Methods

Sites

Fieldwork was carried out between April and August during 2006, and between May and July during 2007 and 2008 on three farms near Bramham, Yorkshire in 2006 (Figure 1) and 12 farms during 2007 and 2008 across Gloucestershire, Hampshire, Wiltshire and West Sussex. Fields were bounded by ditches, hedges, tree-lines, fences, grass margins or green lanes. Land use consisted of a combination of arable crops (spring and winter wheat, spring and winter barley, oilseed rape, vining peas, potatoes, field beans, and sugar beet), grass grown for silage, set-aside (grass-sown and natural stubble re-growth), agroforestry with arable set-aside and pasture grazed by cattle.

Fig. 1. Map showing locations of three farms from which yellowhammer nest and foraging data were collected during 2006. © Crown Copyright/database right 2009. An Ordnance Survey/EDINA supplied service



Nest Data

Territorial pairs were located by repeated observations of singing males and foraging pairs. Once pairs had been located, observations allowed the approximate positioning of a nest to be detected; nests were then located by a systematic search of this region. The height of the nest above ground, and vegetation type within which the nest was built were recorded, along with the height and width of the hedge at the nest site. Distance to the nearest songpost was also recorded: a songpost was defined as a piece of vegetation prominent above the rest of the hedge such as those used by male yellowhammers; these tended to be tree branches, the top of elder bushes, or long hawthorn stems.

To determine whether adult yellowhammers exhibited selection for particular nest site features within hedgerows, measurements were obtained from random sites within 25m either side of the nest. Sites were selected through the use of random numbers marked along a 50m measuring tape; at each site hedge height, width and the distance to nearest songpost (measured as above) were recorded. To establish whether nest positioning may have changed since before the yellowhammer population decline, data on the height distribution of nests were taken from Peakall (1960) and compared to nest height data collected here.

Provisioning and foraging site data

Observations of adult foraging behaviour were carried out on between one and four occasions when chicks were between 2 and 9 days old. The observer was positioned between 50 and 100m from the nest to ensure the birds' behaviour was unaffected by their presence: a previous study observed foraging behaviour from a distance of 30m with no noted effects on behaviour (Stoate et al. 1998). Adults were watched for an hour between 6:00 and 21:00hrs and food provisioning rate was calculated as the number of complete foraging trips per hour. At least one morning and one afternoon watch was carried out for each nest where possible to account for any diurnal variation in foraging patterns. Watches were not carried out during heavy rain or strong winds.

During 2006, data on foraging sites were recorded. The distance of the site from the nest was measured to the nearest 1m using a Bushnell Yardage Pro Sport Laser Rangefinder (Bushnell Performance Optics UK Ltd, Chessington; accuracy ± 1 m). Each foraging site that could be accurately located (n=34, 38% of trips) was paired with two control

sites 5m from the foraging site. The first control was within the same microhabitat (for example, in a crop tramline) and the second control was in a different microhabitat (for example, in the crop if the foraging site was within a tramline) in a randomly selected direction from the foraging site. For each foraging and control site, vegetation height (± 1 cm), vegetation density (as per Douglas et al. in press; ± 1 cm) and vegetation cover were recorded. Vegetation cover was assessed using a fisheye lens attached to a Nikon CoolPix p5000 digital camera placed on the ground facing upwards, using a timer to ensure the observer did not appear in the photograph. Photographs were taken at time of day when the camera was not in direct sunlight, as this would confound the contrast between vegetation and sky. Photographs were subsequently analysed using Gap Light Analyser software (Frazer et al. 1999) to derive the percentage of sky visible in the image.

Invertebrate samples were collected from foraging and control sites using a leaf-vacuum (Ryobi RGBV-3100, Marlow, UK) modified by the use of a fine mesh to trap invertebrates and a 1cm wire mesh to keep vegetation out of the sample. Sampling followed the protocol of Douglas et al. (2009), whereby each sampling site consisted of a 1 m square and 5 x 5s sucks were taken from each corner and from the centre of the square. Samples were frozen and subsequently identified to order (Chinery 1993).

Chick Data

Where first egg date was known, this and clutch size were used to predict hatch date; otherwise nests were visited at maximum intervals of 3 days during incubation in order to determine hatch date and monitor nest failures. Where nest failures occurred and the date was unknown, failure was assumed to have occurred at the mid point between the two final visits to the nest. Where nests were discovered at the chick stage and age was unknown, comparisons were made with the feather tract development of chicks of known age (as per Bradbury et al. 2003).

Chicks were measured on two occasions between two and seven days post-hatching, the period of linear growth for this species (Bradbury et al. 2003). Chicks were individually marked on the leg with a non-toxic marker pen to allow the identification of each nestling and measurements were taken of tarsus length (from the foot to the inside of the knee), mass and length of the leading edge of the wing to allow calculation of growth rate. Measurements of tarsus and wing were taken using digital callipers

(± 0.1 mm) and mass was measured using a pocket scale (± 0.1 g; Satrue, Taiwan). Nests were checked when chicks were 10 days old to determine fledging success: where a nest contained chicks at 7 days and the nest remained intact but was empty at 10 days (making predation of chicks immediately prior to fledging unlikely), the chicks were deemed to have fledged successfully.

Statistical analysis

Statistical analysis was carried out using R version 2.7.1 for Mac (www.r-project.org). Statistics are presented as mean \pm 1 SE throughout.

Nest analyses

To determine whether features of nest sites differed from features of randomly selected sites within the same territory, a generalised linear mixed-effect model with binomial error distributions was used. Site ID (nest site or random site) was designated as the response variable with vegetation height, vegetation width, habitat and distance to the nearest songpost as predictor variables. Nest ID was designated as a random effect to control for differences between territories. Model comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p < 0.05$ remained. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable.

In order to determine whether nest positioning has changed since before the yellowhammer population decline, nest height data were classified according to Peakall (1960) in order to allow direct comparison between the two studies. No difference was found in frequencies of nests in height categories between the three years of this study (Poisson GLM: Year*Height interaction, $Dev_{2,15} = 3.33$, $p = 0.19$) and thus data from these three years were pooled to allow comparisons between the two datasets using a G test.

Foraging analyses

To determine whether or not birds chose foraging sites based on vegetation height, density, cover or invertebrate abundance, two GLMMs with binomial error distributions were constructed using the lmer function within the lme4 package (Bates & Maechler

2009) in R to compare foraging sites to both control sites within the same microhabitat and control sites within a different microhabitat. Predictor variables were vegetation height, density, cover, the abundance of invertebrates >2mm and two-way interactions between invertebrate abundance and vegetation density, height and cover, as well as between vegetation height and density. To control for differences between site localities and between foraging adults, site ID (designated for each pair of foraging and control sites) within Nest ID were designated as random variables.

To determine whether features of foraging sites were associated with parental provisioning rate, a linear mixed-effects model was constructed using the lme function within the nlme package (Pinheiro, 2009) in R. Provisioning rate was designated as the response variable and vegetation cover, height, density, total invertebrate abundance, abundance of invertebrates >2mm in length, distance from nest, trip duration and two-way interactions between invertebrate abundance and vegetation density, height and cover, as well as between vegetation height and density were designated as predictor variables. To control for individual differences, parent ID within nest ID were designated as random factors.

For all models, comparisons using AIC values were used to determine whether terms significantly improved the fit of the model; those that didn't were removed in a stepwise fashion until only those terms that improved the fit of the model at $p < 0.05$ remained. Following model simplification, each term was reinserted into the minimum adequate model (MAM) in turn and compared with the MAM using AIC comparisons to ensure lack of association with the response variable.

Results

Nesting ecology

Fifty-one yellowhammer nests were monitored across three breeding seasons between 2006 and 2008. The majority (65%) of nests were found in hedgerows, mostly in hawthorn (*Crataegus* spp.); 15% were found in bramble (*Rubus* spp.) or herbaceous vegetation and 14% were found in herbaceous vegetation associated with a wall or fence. The remaining 6% were found on the ground amongst grasses. The height of nests above ground ranged from 0 to 210 cm with a mean nest height of 82.71 ± 7.71 cm.

Clutch size varied from 2 to 5 eggs, with a mean of 3.48 ± 0.14 . Brood size ranged from 1 to 4 chicks, with a mean of 2.78 ± 0.14 . From nests that successfully fledged at least one chick, the mean number of fledglings was 2.87 ± 0.20 ; however across all nesting attempts that reached the egg stage, mean fledgling number was 1.375 ± 0.23 fledglings per nest.

Twenty-three nests (45%) successfully fledged at least one chick. Predation accounted for most nest failures (54%), with 19% of nest failures due to starvation of chicks and another 19% of failed nests abandoned during incubation. The remaining 8% of failed nests were destroyed during agricultural operations. Of nests that hatched chicks, brood reduction occurred in 24% of nests; however, when only nests that successfully fledged young were considered, brood reduction affected only 13% of broods.

When nest sites were compared with randomly selected points along the same boundary within 25m of each nest during 2006, none of the features considered differed between nest sites and randomly selected sites (Table 1), indicating that adult yellowhammers do not appear to select for specific features of a hedge when they select nest sites.

In order to determine whether or not yellowhammer nest site positioning might have changed since prior to the yellowhammer population decline, nest height data were compared with that of Peakall (1960). Nest height differed between the two data sets (G test, $G_6=30.26$, $p<0.001$) with more nests at lower heights in the 1960 dataset (Figure 2).

Table 1. Results of a binomial GLMM determining whether adult birds selected for features of a hedge when choosing a nest site: sites were either nest sites or randomly selected sites along the same field boundary within 30m of the nest. All models contained the random effect of Site ID. Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model.

Variable	AIC	Chi sq	p
Null model	79.694		
Habitat	80.139	3.555	0.169
Width	80.378	1.316	0.251
Distance to nearest songpost	81.299	0.396	0.529
Hedge height	81.430	0.265	0.607

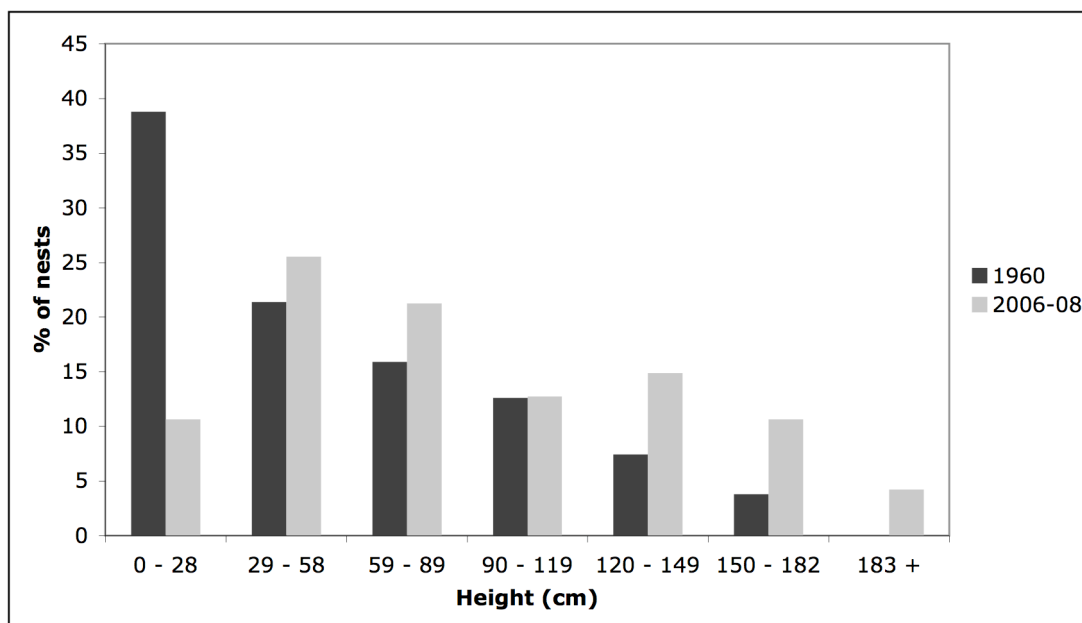


Figure 2. A comparison of nest height data from Peakall (1960) with data from this study (2006-08) indicates differences in nest height between the two datasets (G test, $G_6=30.26$, $p<0.001$)

Foraging ecology

No differences were found between characteristics of foraging sites and control sites of similar microhabitat (Table 2). However, both vegetation density and the interaction between invertebrate abundance and vegetation cover were found to influence whether a site of different habitat was used as a foraging site (Table 3). Foraging sites had both lower vegetation densities, and more invertebrates at higher levels of vegetation cover than control sites (Figure 3b). Invertebrate abundances were higher at foraging sites than at control sites of different microhabitats.

Table 2. Results of a GLMM comparing foraging sites with control sites of similar microhabitats 5m away from the foraging site. All models contain random effects of Site ID within Nest ID to account for the pairwise structure of the data and differences between foraging adults. Statistics presented for non-significant terms are following reinsertion of the term of interest into the minimum adequate model (MAM). *Model comparisons indicated that this term significantly improved the fit of the model (AIC = 89.20, $\chi^2 = 36.47$, $p < 0.01$) and thus the term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Cover * Density ($F_1=0.07$, $p=0.16$), Height * Density ($F_1=0.01$, $p=0.65$), Height * Cover ($F_1 < 0.01$, $p=0.66$), Invertebrate abundance * Cover ($F_1=0.02$, $p=0.42$), Invertebrate abundance * Density ($F_1=0.02$, $p=0.47$) and Invertebrate abundance * Height ($F_1=0.05$, $p=0.28$) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

Variable	df	z	p
Invertebrate abundance	1	-0.649	0.516*
Variable	AIC	χ^2	p
MAM	89.202		
Cover	87.758	3.443	0.064
Density	91.052	0.150	0.699
Height	90.810	0.391	0.531

Table 3. Terms remaining in the minimum adequate model from a GLMM comparing foraging sites with randomly selected control sites of different microhabitats 5m away from the foraging site. All models contain random effects of Site ID within Nest ID to account for the pairwise structure of the data and differences between foraging adults. For significant terms, parameters estimates and SE are also presented; estimates include intercept values. * Model comparisons indicated that this term significantly improved the fit of the model (AIC=73.530, $\chi^2 = 4.10$, $p=0.04$) and thus this term remained in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Density * Invertebrate abundance ($z_1=-0.80$, $p=0.43$) and Density * Height ($z_1=-0.95$, $p=0.34$) did not significantly improve the fit of the model or influence the response variable and thus were removed from the model.

Variable	df	z	p	Estimate	SE
Density	1	-0.143	0.049	-0.418	0.032
Invertebrate abundance	1	-1.963	0.044	-0.455	0.402
Cover	1	0.485	0.628		
Height	1	-0.688	0.491		
Invertebrate abundance * Cover	1	-2.067	0.039	-0.017	0.008
Invertebrate abundance * Height	1	1.905	0.057*		

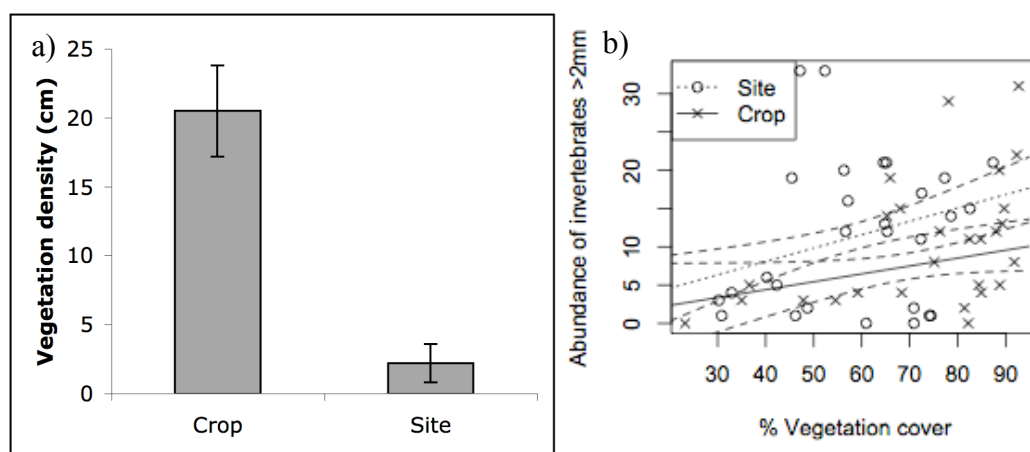


Figure 3. Differences between yellowhammer foraging sites and control sites were influenced by a) Vegetation density and b) An interaction between vegetation cover and invertebrate abundance (Table 3). Bars represent mean ± 1 SE. Lines are predicted from the MAM (Table 3) with mean vegetation density (11.35 cm); dashed lines show ± 1 SE.

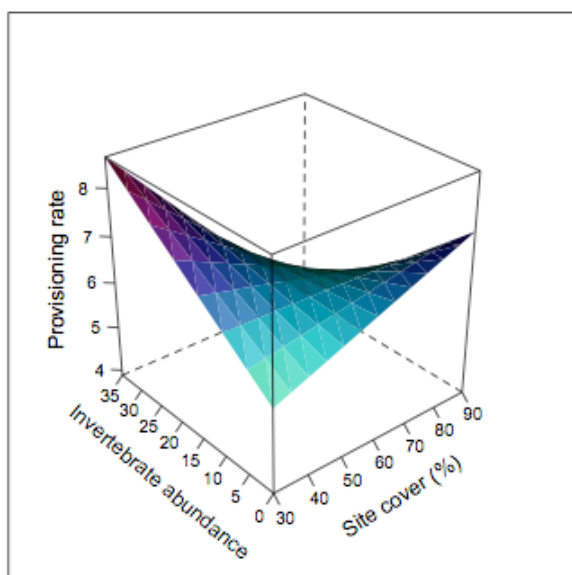


Figure 4. Parental provisioning rate was influenced by an interaction between vegetation cover and invertebrate abundance (LME, $F_{1,10}=13.78$, $p<0.01$). Surface is predicted from the MAM (Table 4) for mean trip duration (15.8 minutes).

Parental provisioning rate was influenced by an interaction between vegetation cover and invertebrate abundance at foraging sites (Table 4; Figure 4). At low invertebrate abundances, provisioning rate increases with increasing vegetation cover, whereas as high invertebrate abundances, provisioning rate decreases with increasing vegetation cover (Figure 4).

Table 4. Minimum adequate model (MAM) from a LMM determining which features of parental foraging sites are associated with provisioning rate. All models contain random effects of Parent ID within Nest ID. Statistics presented for non-significant terms are from model comparisons following reinsertion of the term of interest into the MAM. *Model comparisons indicated that this term significantly improved the fit of the model (AIC=84.71, $\chi^2=11.92$, $p<0.01$) and thus this term remains in the MAM but is not considered to significantly influence the response variable. Two-way interactions of Height * Density (AIC=83.05, $\chi^2=0.22$, $p=0.64$), Height * Invertebrate abundance (AIC=81.27, $\chi^2=0.70$, $p=0.41$) and Density * Invertebrate abundance (AIC = 79.97, $\chi^2=2.81$, $p=0.09$) did not significantly improve the fit of the model or influence the response variable and were thus removed from the model.

Variable	df	F	p	Estimate	SE
Trip duration	1, 10	3.690	0.084*		
Vegetation cover	1, 10	2.170	0.172		
Invertebrate abundance	1, 10	0.594	0.459		
Cover * Invertebrate abundance	1, 10	13.776	0.004	-0.003	0.001
Variable	AIC		χ^2		p
MAM	74.790				
Distance from nest	75.729		1.060		0.303
Vegetation density	76.831		0.001		0.999
Vegetation height	76.558		0.231		0.631

Discussion

Yellowhammer nesting habitat was similar to that found in other studies, with the majority of nests in hedgerows, followed by herbaceous vegetation (Kyrkos et al. 1998; Bradbury et al. 2000; Stoate and Szczur 2001). Preferences appear to differ from the study of Stoate et al. (1998), who state that nests in hedgerows were “located within herbaceous vegetation in field margins, rather than in the shrubby vegetation of the hedge itself” (Stoate et al. 1998): this was not the case in the present study as all nests recorded as in hedgerows were located within hedgerow vegetation, mostly hawthorn. The preference of this species for nesting in vegetated ditches (Bradbury et al. 2000) was not confirmed with this study; however, this is probably a reflection of the paucity of vegetated ditches within the study sites.

The mean clutch size of 3.48 ± 0.14 found in this study compares favourably with the most recent study of Yellowhammer breeding performance: Bradbury et al (2000) found a mean clutch size of 3.27 ± 0.03 from a dataset of over 400 nests within Oxfordshire, Wiltshire and Warwickshire. This figure was significantly lower than that of 3.44 ± 0.70 obtained from the BTO Nest Record Scheme (Robinson 2005) and other datasets with large sample sizes (see Bradbury et al. 2000 for details), and data from this study are more in concordance with these earlier studies (Stoate et al. 1998; Robinson 2005; see Bradbury et al. 2000 for others). Mean fledging success per nest was within the range of Bradbury et al (2000), and 45% of nests successfully fledged at least one chick, compared to 46.5% of nests recorded by Bradbury et al. (2000). When compared with a figure of 45% fledging success in 1960 (Peakall 1960), there appears to have been little change in fledging success since the start of the Yellowhammer population decline.

That predation accounted for the majority of nest failures agrees with other studies (Crick et al. 1994; Bradbury et al. 2000; Hart et al. 2006; but see Stoate et al. 1998 for inter-year variation), and the proportions of other causes of failures are similar (Bradbury et al. 2000), although destruction by agricultural activities is notably lower than recorded by Crick et al (1994), as is the overall failure rate recorded from BTO Nest Record cards pre- 1994 (Crick et al. 1994).

Nest height distribution within this study was found to differ considerably from that of a study by Peakall (1960) undertaken prior to the Yellowhammer population decline, with mean nest height in this study nearly double that found by both Peakall (1960) and more

recently by Stoate et al. (1998). Whilst it is possible that this may be partly due to observer bias leading to a reduction in the number of ground nests found during this study, or a reduction in suitable ground habitat such as vegetated ditches, nests were consistently found at greater heights than by Peakall (1960). Whilst Bradbury et al. (2000), found a higher proportion of nests on the ground than within this study, nests located later in the season were consistently higher above the ground than those analysed by Peakall, especially later in the breeding season when nest height tends to increase (Peakall 1960; Bradbury et al. 2000; Stoate and Szczur 2001). This indicates that nesting habitat has altered since the onset of the Yellowhammer population decline, possibly due to changes in nesting habitat and a reduction in suitable nesting habitat, such as a reduction in ditches leading to an increased use of hedgerows, a possible increase in hedgerow height, and a thinning of herbaceous vegetation at hedgerow bases due to increased use of herbicides (Boatman et al. 1994). However, as nest success is unaltered from that recorded by Peakall (1960) there is unlikely to be a direct link between nest habitat alterations and population decline.

Yellowhammers do not appear to select for any of the hedgerow features examined when choosing a nest site within their territory, as there was no apparent difference between nest sites and randomly selected points within the same territory in terms of habitat, hedgerow height or width, or distance to nearest songpost. As variation within the same length of hedgerow within the extent of a territory is likely to be relatively small, it is probable that the selection of a territory containing a length of high quality hedgerow is more important (Whittingham et al. 2005). Selection of nest sites is more likely to be based upon the presence of a suitable support structure in an area of high vegetation cover, neither of which were assessed within this study. Whilst the presence of a songpost such as a tree has been found to be important in territory selection (Whittingham et al. 2005), this had no influence on the selection of nest sites, probably as there was no shortage of songposts such as emergent hawthorn branches or elder branches that are commonly used as songposts by Yellowhammers (Author, pers. obs.).

There was no difference between foraging sites selected by yellowhammers and control sites of similar microhabitat; however microhabitats used for foraging had lower vegetation density and higher invertebrate abundance than control sites 5m away in a different microhabitat, and higher invertebrate abundances at higher vegetation density. This suggests that Yellowhammers initially select foraging microhabitats according to

vegetation structure, but then according to food availability, with a lower vegetation cover providing a greater visibility of predators (Whittingham et al. 2004; Whittingham and Evans 2004) and a lower vegetation density providing easier access to invertebrates despite their lower abundance. This also suggests that where Yellowhammers take higher risks by foraging in more dense vegetation, where perceived predation risk is higher (Butler et al. 2005), there is a payoff in terms of an increased invertebrate availability within the microhabitats selected for foraging. This concurs with suggestions made by Morris et al. (2001) and studies by Perkins et al. (2002) and Douglas et al. (2009), suggesting that cutting patches within field margins would improve their value for birds by creating a mosaic of cut patches where accessibility is improved, adjacent to uncut patches where invertebrate abundance remains high (Perkins et al. 2002; Douglas et al. 2009), as this would reduce. This also concurs with a recent study by Douglas et al. (in press) which found Yellowhammer foraging sites to be characterised by lower vegetation height, lower vegetation density and a higher proportion of bare earth than control sites within cereal fields, indicating a higher degree of accessibility to foraging sites. However, Douglas et al (in press) found no differences in the abundance of invertebrates between foraging and control sites, indicating no cost to selecting more accessible foraging habitat.

Parental provisioning rate increased with increasing vegetation cover in areas of low invertebrate abundance, indicating that where food availability is low, parents take more risks by foraging where cover (and invertebrate abundance) is higher in order to ensure sufficient food for their chicks. This may increase their own risk of predation by lowering their visibility of predators. Conversely, when invertebrate abundance is high, provisioning rate decreases with increased vegetation cover, expected when increased vegetation cover leads to an increased time spent scanning for predators and thus decreasing prey capture rate (Whittingham et al. 2004; Whittingham and Evans 2004), although the time spent searching for prey is likely to be decreased where prey is abundant.

This work adds to the growing body of literature emphasising the importance of prey accessibility to foraging birds. Here I demonstrate that invertebrate abundance and vegetation cover interact to influence where birds forage, and how efficiently they can provision their chicks. Whilst increased vegetation cover leads to a higher perceived predation risk to the foraging bird, higher invertebrate abundances associated with

increased cover can lead to birds selecting such sites for foraging, with resulting increases in provisioning rates to chicks in areas where invertebrate abundance tends to be low. In areas where invertebrate abundance tends to be higher, provisioning rates to chicks are highest where vegetation cover is low as parents can forage adequately with minimum risk to themselves. This suggests that measures aimed at increasing the abundance of invertebrates in the farmland environment, such as the maintenance of uncropped habitats such as field margins and conservation headlands, can be improved by the establishment of sward heterogeneity within these habitats (Perkins et al. 2002; Douglas et al. 2009) in order to provide a mixture of microhabitats aimed at encouraging invertebrate populations, and microhabitats enabling birds to forage more efficiently.

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