

RESEARCH ARTICLE

Linking agri-environment scheme habitat area, predation and the abundance of chick invertebrate prey to the nesting success of a declining farmland bird

Niamh M. McHugh^{1,2}  | Patrick J. C. White³  | Steve Moreby² | John Szczur² | Chris Stoa² | Simon R. Leather⁴ | John M. Holland²

¹Imperial College London, Silwood Park Campus, Ascot, Berkshire, UK

²The Game and Wildlife Conservation Trust, Fordingbridge, Hampshire, UK

³Centre for Conservation & Restoration Science, Sighthill Campus, Edinburgh Napier University, Edinburgh, UK

⁴Crop and Environment Sciences, Harper Adams University, Newport, UK

Correspondence

Niamh M. McHugh, The Game and Wildlife Conservation Trust, Fordingbridge, Hampshire, UK
Email: nmchugh@gwct.org.uk

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Abstract

1. Across Europe, farmland bird populations have continued to decline since the 1970s owing to the intensification of farming practices. Studies of such declines have tended to focus specifically on either the impacts of habitats (nesting and foraging), nest predators or prey availability on bird demographics. The study presented here provides new insights into the relative effects of each of these factors on yellowhammer nest survival. The yellowhammer was selected for this study as it is a UK Red-Listed bird species whose population is in decline across much of Europe.

2. We use a long-term dataset of 147 nests, monitored between 1995 and 2007, to provide an insight into how yellowhammer nest survival is influenced by nesting habitat (nest concealment and nest height), foraging habitats (habitat coverage within 100 m of nests), the removal of nest predators (magpie *Pica* abundance as an inverse measure of avian predator removal through gamekeeping) and food availability (measured with a D-vac invertebrate suction sampler).

3. Our results indicated that yellowhammer hatching success was negatively related to the coverage of spring agri-environment scheme habitats, a group which represents invertebrate-rich agri-environment habitats, but hatching success increased with nest height. Fledging success was positively related to the coverage of the seed-rich habitat wild bird seed mixture. The farm-level abundance of yellowhammer chick-food invertebrates declined over the study period.

4. Our results highlight the importance of simultaneously considering multiple agents that shape avian breeding success, that is their ability to produce offspring, to inform conservation management. Our key finding for land managers relates to the positive relationship between the proportion of seed rich foraging habitat within the yellowhammer's average foraging range and yellowhammer fledging success, which shows that a habitat intended primarily to provide winter food resources is also

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important to breeding birds. Chick food abundance in this habitat was, however, similar to broadleaf and cereal crops. We recommend that this habitat should be provided near to potential yellowhammer nesting sites and adjacent to invertebrate-rich agri-environment scheme habitats such as beetle banks and conservation headlands to further boost invertebrate resources for a declining farmland bird.

KEYWORDS

agro-ecology, common agricultural policy, conservation, farmland birds, Insect

1 | INTRODUCTION

Over the past several decades, farmland management and mechanization have dramatically intensified worldwide. This intensification has been linked to declines in many elements of farmland biodiversity including arable plants, invertebrates and birds (Newton, 2004; Powney et al., 2019; Richner et al., 2017; Stanton et al., 2018). The causal factors of these declines relate to key changes that took place over this period including an increase in farm size and a decline in the number of individual farms in the United States (Stanton et al., 2018). Other changes in Europe and the United States include shifts in the timing of farming activities (e.g. a move from spring to winter cropping and the consequent loss of over winter stubbles), the use of non-traditional crops (e.g. oilseed rape *Brassica napus* in Europe), a trend from rotational mixed farming to farm and regional specialization, increased tillage, field enlargement, the use of agrochemicals and a reduced area of uncropped land (Newton, 2004; Sotherton et al., 2000). These aspects of agricultural intensification occurred concurrently, making it hard to isolate their individual impacts (Newton, 2004).

The link between agricultural intensification and periods of major avian decline is well established in Europe where, since the 1980s, the abundance of common farmland birds has on average halved (BirdLife International, 2018; IUCN, 2021; Vorisek, 2005). In response to these large-scale changes in biodiversity, agri-environment schemes (AES) payments were introduced in Europe. Payments were/are based on estimates of income foregone to enable farmers to undertake environmental management at zero net cost as well as providing novel solutions to biodiversity declines, for example sowing floristically diverse habitats such as pollen and nectar mixture (Kleijn & Sutherland, 2003; Natural England, 2013a, 2013b). The environmental objectives of AES are varied; on lowland farmland in England, habitat bundles may be selected by landowners depending on whether management is aimed at farmland birds, arable plants, small mammals (e.g. bats), brown hares *Lepus europaeus* or nectar-feeding insects (e.g. bees; Natural England, 2013a, 2013b).

Short-term studies have provided limited evidence for associations between AES habitat prescriptions and bird demographics at a local level (but see Bright et al., 2015; McHugh et al., 2017), suggesting that AES habitats may not have been in place for long enough to

detect such effects or that the unmeasured impact of habitat quality may be influencing results. Similarly, long-term studies on the impacts of AES habitats on bird populations (e.g. Baker et al., 2012) have provided little evidence that summer foraging options provide benefits to farmland birds (but see Potts, 2012). Such studies have, however, demonstrated that winter conditions are critical in most resident farmland passerine declines and that winter management often has positive effects, particularly on species that are dependent on seed as a food resource for at least part of their life cycle (Baker et al., 2012; Peach et al., 1999; Siriwardena et al., 2007). Others have highlighted the importance of collecting productivity measurements in understanding the demographic parameters that underline population changes in a farmland context (Newton, 2004).

Currently, implementation of AES on English farmland (Country-side Stewardship and Environmental Stewardship, the latter of which closed to new applicants in 2014) is based on a menu system, where a range of management prescriptions can be chosen by landowners under the schemes (Natural England, 2013a, 2013b). The aims of these habitat options are varied, with options available to farmers including grass margins, beetle banks, wild bird-seed mixtures (WBSM) and conservation headlands (see Appendix S1 in the Supporting Information for detailed habitat descriptions). WBSM is a commonly chosen AES option, whereas within crop features such as conservation headlands (now known as cereal headlands for birds) and beetle banks are less frequently adopted.

Subsidies for predator control are not available under English AES (Natural England, 2013a, 2013b), but in Scotland predator removal via AES may be implemented on sites where Black Grouse *Lyrurus tetrix* leks are active to improve their conservation status (RPS, 2021). In England, however, game management across lowland farmland routinely combines sympathetic habitat management measures with the reduction or removal of predators which commonly predate game birds. There is limited evidence of large-scale population-level impacts of avian predators on passerine populations (Newson et al., 2010) but studies involving manipulation of the abundance of a broader suite of predators have indicated that predator control can have significant effects on passerine nest success rates and subsequent populations at a local level (e.g. White et al., 2008) and may have the potential to contribute towards the conservation of threatened farmland passerines. The effects of predator removal may, however, also vary between

prey species depending on their population status and trends (White et al., 2008, 2014). For some species, predation can be reduced through non-lethal methods, for example protecting nests with electric fencing, but this has been more commonly used for colonial nesters such as northern lapwing *Vanellus vanellus* and is unlikely to be effective for passerine species (Malpas et al., 2013). Therefore, assessing the potential for predator reduction to have a biologically significant benefit to a variety of prey species is essential.

The study presented here focuses on the nesting success of yellowhammer *Emberiza citrinella* using an 11-year dataset from the Game and Wildlife Conservation Trust's 'Allerton Project' research and demonstration farm in Leicestershire, England (Lat, Long = 52.6132, -0.8353). The yellowhammer is a red-listed species in the United Kingdom and has suffered >50% population decline since the mid-1980s (British Trust for Ornithology, 2022). They are lowland habitat specialists which frequently exploit both AES and crop habitats (Douglas et al., 2009). Yellowhammers are a field boundary nesting species and are dependent on grain and wild plant seed throughout their life cycle, relying on protein-rich invertebrate food only for rearing young (Moreby & Stoate, 2001). Overwinter survival and seed food resources are critical for yellowhammer population sustainability, but little is known on the importance of invertebrate food resources (Siriwardena et al., 2008). Invertebrate taxa are essential in the diet of their chicks and resource availability will directly impact chick growth and development along with their ability to resist chilling (Potts, 2012). Assessments of the availability and susceptibility of different food taxa to the aspects of agricultural change are therefore essential.

The aim of this paper is to inform future conservation management for the yellowhammer by examining annual variation in yellowhammer chick-food items over time and between arable habitats; and to identify how to nest success interacts with chick food provisions, predator removal and AES coverage. To investigate our aim we propose the following working hypotheses:

1. The presence of spring AES (habitat group comprising beetle banks, conservation headlands and grass margins) and WBSM foraging habitats (habitat coverage within 100 m of nests (Perkins & Anderson, 2002) provides better quality territories and feeding conditions for adults and provisioning chicks, so influences nest success at both stages. The influence of crop and pasture cover will also be investigated, due to their dominance in the landscape.
2. We expect hatching and fledging success (i.e. the proportion of a clutch to hatch and the proportion of hatchlings to fledge) to be negatively impacted by nest predation. Our study uses magpie *Pica pica* abundance as a proxy for game-keeping effort and as a direct measure of nest predator abundance.
3. Our study includes two measures relating to nest concealment: (A) nest exposure and (B) nest height. We expect that nest concealment will influence detection by predators at both the egg and chick stage and/or the suite of potential nest predators, with more exposed/lower nests suffering higher predation rates.
4. Invertebrate food availability (measured with a D-vac invertebrate suction sampler) was measured in the agricultural habitats sur-

rounding nests, and we predict that chick-food abundance within a feasible distance for foraging from nests will be positively related to fledging success. We did not expect this measure to influence hatching success as adults are dependent on grain and wild plant seeds (Moreby & Stoate, 2001). Variation in invertebrate chick-food abundance over time and between habitats will also be examined, and we expect that invertebrate chick-food abundance will be highest in AES habitats, particularly those designed to benefit invertebrates and that invertebrate abundance will decline over the study period as previously reported for other farmland systems (Ewald et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study site

Data were collected at the Allerton Project Loddington Estate, a 3.33-km² lowland (mean altitude = 144 m) research and demonstration farm in Leicestershire, England. The main crops present over the 11-year survey period were wheat *Triticum aestivum*, barley *Hordeum vulgare*, oats *Avena sativa*, oilseed rape and field beans *Vicia faba*. The standard 4-year crop rotation over this period was wheat, oilseed rape, wheat, oats or beans. Crops were winter sown with the exception of field beans which moved from winter to spring sowing in 2003.

Since 1993, AES management has taken place on the estate with the aim of enhancing breeding and overwintering populations of Galliformes and passerines (Stoate & Szczur, 2001a). The AES habitats on-site include boundary options such as wildflower margins, conservation headlands, non-rotational WBSM strips and in-field beetle banks. In addition, there was supplementary feeding for pheasants using 140 grain hoppers across the farm, filled weekly.

Between 1993 and 2001, a gamekeeper was employed to legally control nest predators. Foxes *Vulpes vulpes* were controlled from February, with the use of a rifle and spotlight at night, in combination with snares when necessary. Small mammals including brown rats *Rattus norvegicus*, stoats *Mustela ermine* and least weasels *Mustela nivalis* were managed between April and July, using a network of 200 Fenn traps. From April to July corvids (Eurasian magpies and carrion crows *Corvus corone*) were controlled by a combination of shooting and Larsen trapping. After 2001 predator control ceased on the estate. Magpie territory mapping was conducted annually as an inverse measure of avian predator removal through gamekeeping, under the assumption that gamekeeping activity, rather than resource availability or habitat suitability, limits magpie abundance. At the farm scale and over the 11-year study period considered here, this is a reasonable assumption because background conditions remained similar. It is, however, unlikely to be true generally or at larger spatial scales. At Loddington, magpie territory densities were reduced to zero each year that predator control took place, but recovered to pre-control levels a few years after control stopped (White et al., 2008).

TABLE 1 Habitat codes used in analysis and details of their component habitat categories

Habitat code	Component
Cereal	Winter wheat, winter barley, oats
Pasture	Permanent pasture
Broadleaf	OSR, linseed, winter beans, spring beans
Spring AES	Grass margin, grass set aside, beetle bank, conservation headland
WBSM	Set aside strips planted with wild bird seed

2.2 | Nesting data

Yellowhammer nesting data were collected between 1995 and 2007 (excluding 1999–2001). Two field workers collected nest data following the code of practice outlined by the British Trust for Ornithology (BTO; Crick, 1999); field boundaries were systematically searched between March and August each year. Nest contents were checked every 3–4 days until the nest either succeeded (at least one chick fledged) or failed (no chick fledged). During nest monitoring, a score for nest concealment was recorded on a scale from 1 to 3 (well hidden, part hidden or exposed; British Trust for Ornithology, 2021) and the nest height (to the nearest 5 cm) from the ground. Yellowhammer nest monitoring did not require a license, but counts of eggs and chicks in nests followed the BTO's code of conduct.

2.3 | Habitat mapping and data extraction

Digital maps of the site were produced using Arc GIS v10.2.1 (ESRI, 2015). Polygons representing areas of contiguous landcover were assigned to five categories of interest by identifying potentially important foraging habitats for breeding yellowhammer (Table 1). Maps were specific to year, so crop type per field changed between years and where any features were changed (such as the addition of WBSM cover strips) this was updated in the maps. To aid analysis, some structurally or functionally similar habitat types were pooled into broader habitat groups (e.g. cereal crops). Points were added to maps representing yellowhammer nest sites, and the habitat composition within 100 m of nest sites was extracted. Yellowhammers can forage up to 300 m from their nest site (Stoate et al., 1998), but 100 m represents 60–90% of foraging flights for yellowhammer when feeding nestlings (Perkins & Anderson, 2002; Stoate et al., 1998). The extracted data were then used to estimate the annual yellowhammer chick food abundance in each habitat type within this radius.

2.4 | Invertebrate abundance data

Invertebrate data were collected annually in late June from each of the habitat categories listed in Table 1. Samples were taken using

a D-vac suction sampler from fixed locations. Two crop headland sampling sites (A and B) were monitored in each field between 1995 and 2007, in 1995 and 1996 two samples are taken at A and B, and from 1997 one sample was taken at A and B. Two mid-field (M) samples were taken each year from 1995 to 2007. Each sample comprised five sucks lasting 10 s each, with the motor idling between sucks, corresponding to a sampling area of 0.5 m².

Cereal conservation headlands were rotational within the farm and were included on approximately one third of crop fields annually. These headlands were sampled indirectly as they were represented by A and B sampling sites; therefore, where conservation headlands were present cereal invertebrate samples had to be divided accordingly, resulting in the cereal field being represented by only one mid-field sample (M) and conservation headlands by two samples (A + B). Between 1995 and 1997, WBSM samples could not be distinguished from grass set-aside samples as both were labelled set-aside. Therefore, samples that could not be identified as WBSM were excluded from analysis. No grass set-aside samples were included in our analysis.

The abundance of yellowhammer chick food items was calculated at each sampling location. Moreby and Stoate (2000) and Hart et al. (2006) identified Araneae, Diptera, Coleoptera, Hemiptera (Sub-order Heteroptera), Hemiptera (Sub-order Homoptera) and Lepidoptera larvae as important elements in their diet. The average abundance of these taxa in the sampled habitat is presented in Appendix 2 in the Supporting Information. For analysis relating to nesting success a measure of yellowhammer, invertebrate food abundance surrounding the nest was calculated by multiplying the area of each habitat type (Table 1) by the mean annual chick-food abundance per square metre of that habitat across the estate, similar to the approach used by Ponce et al. (2014) and McHugh, Prior, Leather et al. (2017b).

2.5 | Data analysis

Rv3.5.0 was used to explore the data and perform all statistical analyses (R Core Development Team, 2020). Potential co-linearity between explanatory variables present in the hatching and fledging success data was measured using a combination of Pearson's correlation plots (Appendix 3 in the Supporting Information) and variance inflation factors (VIFs). A Pearson's correlation plot revealed a high correlation between broadleaf and cereal crops (−0.70) and high VIFs for broadleaf crops (5.82) and cereal crops (5.26). By excluding cereal crops from the set of continuous predictors, VIFs were reduced to between 1.37 and 1.59, values below 3 are considered to indicate an acceptable level of co-linearity (Zuur et al., 2013). The spread of the data was investigated using Cleveland dotplots and histograms and resulted in the natural log (+1) transformation of the variables nest height, magpie territory density and chick-food abundance. Habitat extent data were arcsin squareroot transformed.

We modelled the hatching success data using a generalized linear mixed-effects model (GLMM) with a year specified as a random effect, as temporal trends were identified in the data but were not of direct interest to the study. The hatching success GLMM included logit link functions and binomial errors, as overdispersion was not evident. The model comprised all nests with information on clutch size and the number of hatched eggs ($n = 147$). The model response variables were dual vectors of the number of eggs which hatched successfully, and the number that did not. Explanatory variables included in the hatching success model were: the proportion of permanent pasture, proportion of broadleaf crops, proportion of spring AES habitats (those designed to supply chick food, i.e. beetle banks, conservation headlands and grass AES) and proportion of WBSM within 100 m of nests, a score for nest concealment (1 = well hidden, 2 = part hidden and 3 = exposed; BTO, 2021), nest height (to the nearest 5 cm) and annual magpie territory density (as an inverse measure of avian predator removal through gamekeeping). This model did not include the chick-food abundance variable since it was not expected to influence nest success during laying and incubation. Furthermore, cereal crops were excluded from our hatching success analysis due to the strong negative correlation of this variable with broadleaf crops. We present all coefficients estimated by the full model, regardless of their statistical significance.

Initially, a GLM was built to determine if temporal trends needed to be accounted for in fledging success models, this included the term year as a factorial explanatory variable. The model response variables were dual vectors of the number of chicks which fledged successfully and the number that did not. Fledging success was not found to vary between years, and survey year was therefore not included in later fledging success models. Our fledging success models only considered nests that had hatched at least one chick ($n = 69$) and due to the sample size inclusion of all response variables ($n = 8$) in a maximal model would have been overparameterized. Three fledging success GLMs were therefore built, focused on (1) habitat availability (explanatory variables included the proportion of permanent pasture, broadleaf crops, spring AES habitats and, separately, WBSM within 100 m of nests); (2) predation (included the explanatory variables nest concealment, nest height and annual magpie territory density) and (3) food abundance (included a measure of yellowhammer chick-food abundance). The dispersion was measured in GLMs using the ratio of residual deviance to residual degrees of freedom (Lindsey, 1999).

Variation in chick food abundance between sampled habitat types (broadleaved crops, beetle banks, cereal crops, conservation headlands, permanent pasture and WBSM) and year, as a continuous variable, was investigated using a quasipoisson distributed GLM, to account for overdispersion present in a Poisson distributed model. A threshold of 3 was set for dispersion ratios of residual deviance to residual degrees of freedom for the chick food abundance model (Lindsey, 1999). We present all coefficients and standard errors estimated by the full model, regardless of their statistical significance. Differences in chick-food abundance between the sampled habitat types were then tested post hoc using a Tukey HSD test (function `glht`, package `multcomp` (Hothorn et al., 2008).

TABLE 2 GLMM model estimates for the effect of habitat extent (permanent pasture, -broadleaf crop, spring AES and WBSM cover within 100 m of nests), nest site selection (nest exposure and nest height) and predator abundance (magpie territory density) on yellowhammer hatching success

Response	Estimate \pm SE	z-value	p
Intercept	2.34 \pm 0.60	3.91	<0.001
Permanent pasture	-1.04 \pm 0.61	-1.70	0.08
Broadleaf	0.01 \pm 0.42	0.02	0.99
Spring AES	-2.82 \pm 0.96	-2.96	<0.01
WBSM	-0.10 \pm 0.85	-0.12	0.90
Log (height + 1)	1.39 \pm 0.61	2.26	<0.05
Exposure (part hidden)	0.11 \pm 0.44	0.25	0.81
Exposure (exposed)	0.16 \pm 0.55	0.29	0.77
log (magpie territory density + 1)	-0.11 \pm 0.17	-0.62	0.53

Note: The model response variables were dual vectors of the number of eggs which hatched successfully and the number that did not.

3 | RESULTS

3.1 | Nesting success

In total, 147 nests (mean 15.70 \pm 7.03 SD per year; range 5–27) were monitored at Loddington between 1995 and 2007. 94.9% of yellowhammer nests were recorded in boundary habitats (ditches or hedges), and 79.2% of nests recorded in boundary habitats were adjacent to spring AES habitats. The mean \pm SD clutch size per nest was 3.5 \pm 0.06 (range 2–5), mean number of hatchlings produced per nest was 2.92 \pm 0.08 (range 0–5) and the mean \pm SD number of fledged young, from nests where at least one chick hatched, was 2.51 \pm 0.14 (range 0–5). The mean \pm SD number of successful nests per year was 7.2 \pm 5.41 (range 0–15).

Annual variation in hatching success was apparent, and survey year was therefore included as a random effect in the hatching success model. Between year differences in fledging success were not evident (Appendix 4 in the Supporting Information). Yellowhammer hatching success was significantly positively related to nest height (Figure 1) and negatively related to spring AES habitat cover (Figure 1 and Table 2). No relationship between yellowhammer hatching success and magpie territory density was detected (Table 2)

Yellowhammer fledging success was significantly positively related to the area of WBSM within 100 m of a nest and negatively related to permanent pasture (Figure 2 and Table 3). Neither magpie territory density nor chick-food abundance was found to influence the fledging success (Table 3)

3.2 | Chick food abundance

1357 invertebrate samples measuring yellowhammer chick-food abundance were taken over the 13-year period between 1995 and

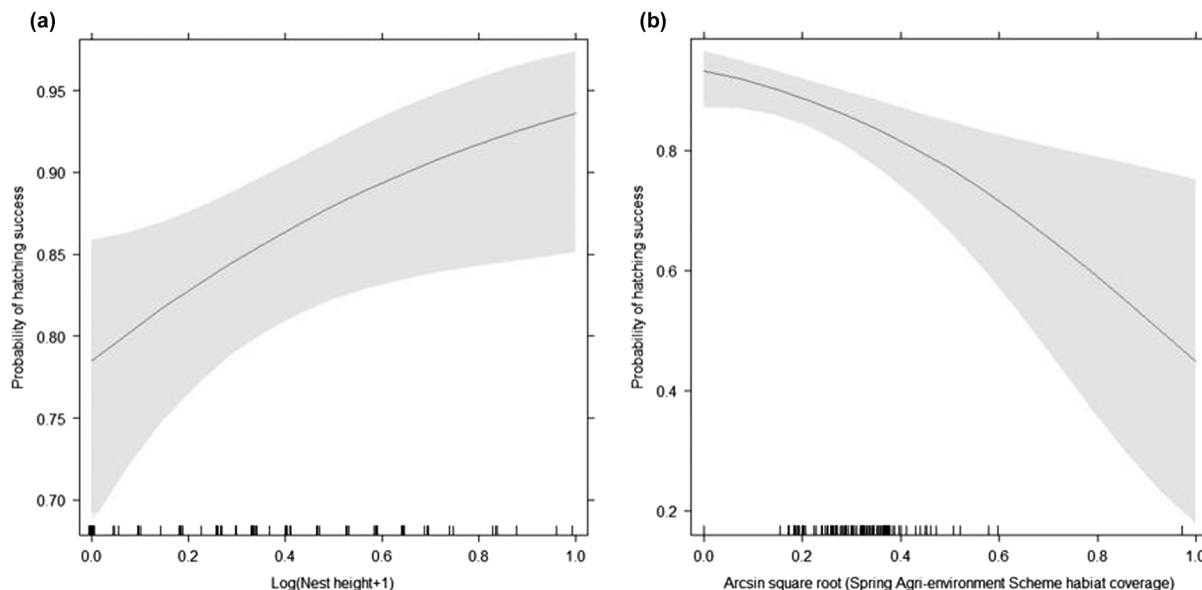


FIGURE 1 Predicted relationship between (a) yellowhammer hatching success and nest height above the ground (m) and (b) yellowhammer hatching success and spring AES habitat coverage from a generalized linear model. The vertical axis is labelled on the probability scale, and a 95% confidence interval is drawn around the estimated effect. A rug plot has been used to display the distribution of the data

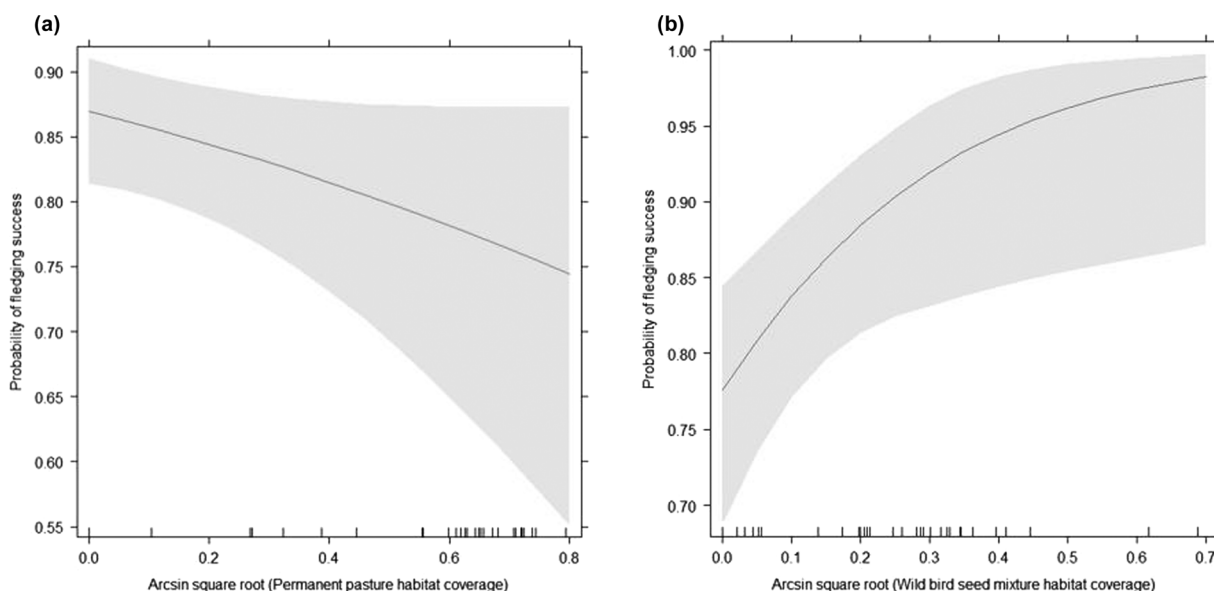


FIGURE 2 Predicted relationship between (a) yellowhammer fledging success and permanent pasture habitat coverage and (b) yellowhammer fledging success and WBSM habitat coverage from a generalized linear model. The vertical axis is labelled on the probability scale, and a 95% confidence interval is drawn around the estimated effect. A rug plot has been used to display the distribution of the data

2007 (average invertebrates per 1 m² sample per year ranged from 278.5 to 918.2, from beetle banks (median 457, IQR (interquartile range) 315–667.5); broadleaf crops (287, 169.5–483.5), cereal crops (294, 176–423), conservation headlands (408, 241–585), pasture (124.5, 70–235) and WBSM (197, 72–368). A post hoc Tukey test revealed that yellowhammer chick food abundance was significantly higher in beetle banks than in cereal crops (-0.39 ± 0.12 , estimate \pm SE; $p < 0.05$), permanent pasture ($-0.98 \pm$

0.15 ; $p < 0.001$) and WBSM (-0.48 ± 0.15 ; $p < 0.05$) (Figure 3). Conservation headlands held significantly higher abundances of yellowhammer chick food items compared to broadleaf crops (0.24 ± 0.07 ; < 0.05), cereal crops (0.37 ± 0.07 ; < 0.001), permanent pasture (-0.96 ± 0.11 ; < 0.001) and WBSM (-0.46 ± 0.11 ; < 0.001) (Figure 3). Finally, permanent pasture held lower invertebrate abundances compared to WBSM (0.50 ± 0.14 ; < 0.01) and cereal crop (-0.59 ± 0.11 ; < 0.001) (Figure 3). Yellowhammer chick food

TABLE 3 GLM model estimates for three models assessing relationships with yellowhammer fledging success: (A) The habitat model focused on measures of habitat extent (permanent pasture, broadleaf crop, spring AES and WBSM cover within 100 m's of nests); (B) predation model estimated effects of nest-site selection (nest exposure and nest height) and predator abundance (magpie territory density) measures and (C) the chick-food density model estimated the effect of yellowhammer chick food abundance within 100 m's of nests. The model response variables were dual vectors of the number of chicks which fledged successfully and the number that did not

Response	Estimate ± SE	z-value	p
(A) Habitat model			
Intercept	1.64 ± 0.56	2.96	<0.01
Permanent pasture	-1.47 ± 0.74	-1.99	<0.05
Broadleaf	-0.28 ± 0.60	-0.47	0.64
Spring AES	-0.25 ± 1.31	-0.19	0.85
WBSM	3.99 ± 1.70	2.35	<0.05
(B) Predation model			
Intercept	0.84 ± 0.71	1.18	0.24
log (height +1)	1.98 ± 0.87	2.29	<0.05
Exposure (part hidden)	0.09 ± 0.70	0.13	0.90
Exposure (exposed)	1.28 ± 1.01	1.27	0.21
log (magpie territory density +1)	-0.16 ± 0.17	-0.93	0.35
(C) Chick-food density model			
Intercept	-6.44 ± 5.57	-1.16	0.25
log (yellowhammer chick-food density)	0.50 ± 0.35	1.43	0.15

Note: The model response variables were a dual vectors of the number of chicks which fledged successfully and the number that did not.

abundance also showed a significant decline at a farm level between 1995 and 2007 ($-0.04 \pm 0.01, p < 0.001$) (Figure 4).

4 | DISCUSSION

4.1 | Nesting success

Yellowhammer fledging success was positively related to WBSM coverage and to our knowledge this study is the first to identify breeding benefits of this habitat, which is intended primarily to provide winter food resources. The provision of sown bird food is well known to attract foraging birds (Perkins et al., 2008), but positive associations with fledging success are contrary to what we would expect since this habitat contained a similar level of chick-food resources as broadleaf and cereal crops and significantly less than beetle banks and conservation headlands. It may be that yellowhammer's preferred to forage in this habitat because the invertebrate food was more readily accessible and/or the vegetation structure provides protection from predators. Douglas et al. (2012) showed that consuming a lower proportion of

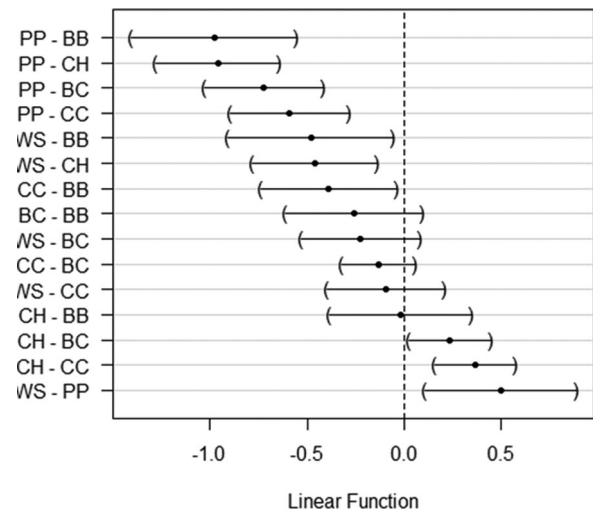


FIGURE 3 Effect size and 95% confidence intervals from chick-food abundance post hoc tests: BC, broadleaf crop; BB, beetle bank; CC, cereal crop; CH, conservation headland; PP, permanent pasture; WS, wild bird seed mixture. The linear function represents the mean differences between pairs. A negative estimate for BC-BB means that BB was selected above BC. A positive estimate for BC-BB means that BC was selected above BB. Effects are significant if there is no overlap with zero

invertebrates relative to plant-based food items led to reduced growth rates and depressed body conditions in yellowhammer chicks.

Baker et al. (2012) reported that the population growth rates of yellowhammer were positively associated with the presence of WBSM management at the 1-km² scale, a finding which is likely to reflect the non-breeding season benefits of WBSM. We therefore hypothesize that WBSM may benefit yellowhammer by improving adult fitness, resulting in improved overwinter survival and the population growth reported by Baker et al. (2012). Improved fitness may also result in adults being able to forage for longer and, where necessary, further for chick-food invertebrates resulting in improved fledging rates.

The positive relationship that we observed between nest height and both hatching and fledging success is likely to relate to predation pressure. One explanation for the positive relationship detected here may be that the gamekeeper was particularly effective in removing avian predators, such as carrion crows and magpies and, as these predators' impact more on higher nests than ground predators, higher nests did disproportionately better (Söderström et al., 1998; Weidinger, 2002). The absence of a relationship between magpie territory density and yellowhammer hatching and fledging success was, however, unexpected, in particular due to the trends in magpie territory density recorded during the study. Magpie territory densities were reduced to zero each year that predator control took place, but recovered to pre-control levels a few years after control stopped (White et al., 2008). We recommend that future studies consider using a proxy representing both mammalian and avian predation pressure, which may more accurately represent predation pressure.

We detected a negative relationship between spring AES habitats and yellowhammer hatching success. A negative relationship between

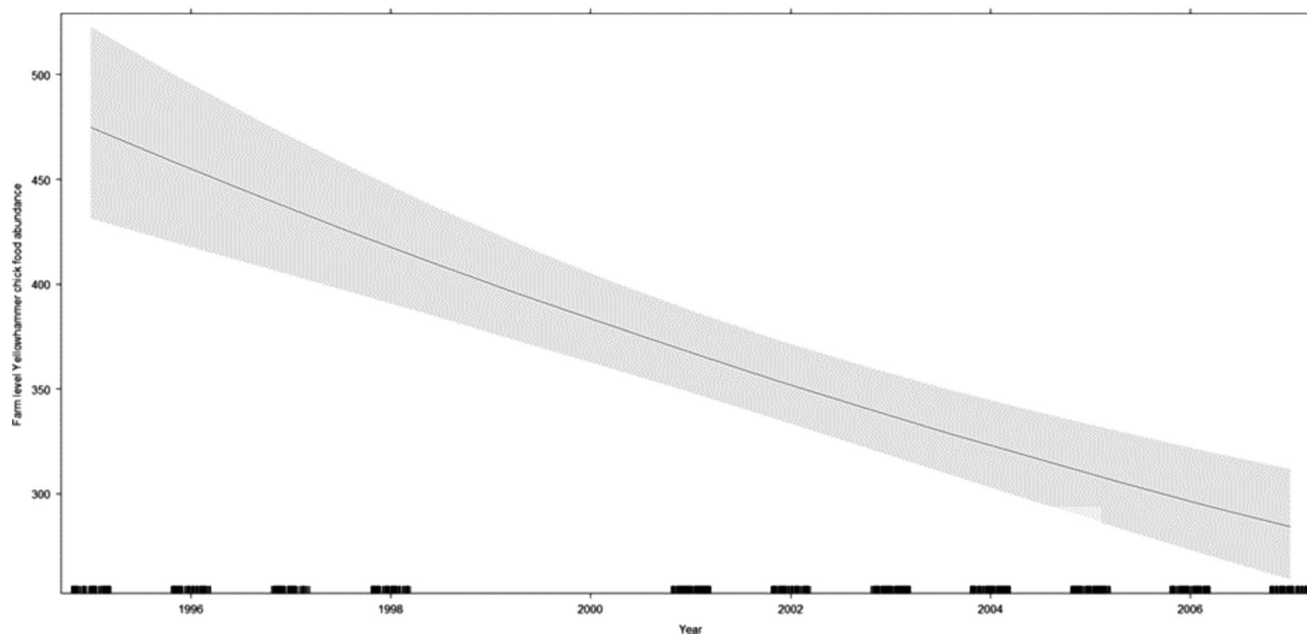


FIGURE 4 Predicted relationship between farm-level yellowhammer chick food abundance and year from a generalized linear model. The vertical axis is labelled on the probability scale, and a 95% confidence interval is drawn around the estimated effect. A rug plot has been used to display the distribution of the data

hatching success and margin AES habitats was also detected in a study of tree sparrow *Passer montanus* nest success (McHugh et al., 2017a). The authors suggested that this relationship may be a result of the low abundance of seed resources these habitats supply for granivorous adults, resulting in poor adult conditions. We suggest an alternative explanation that, as with nest height, this finding may relate to predation pressure because the habitat types which comprised the spring AES habitat category, typically narrow linear strips which are located along field edges, are more likely to be used by foraging carnivores in a fragmented agricultural environment (Šálek et al., 2009, 2010). Carnivores, such as foxes and badgers *Meles meles*, are thought to be drawn to these field edge habitats due to the high numbers of rodent prey they support and because they can use them as travel lines across agricultural landscapes (Šálek et al., 2009). These narrow habitat edge strips have been found to act as an ecological trap for hare leverets in Switzerland (Hummel et al., 2017) and may impact ground-nesting birds in a similar way. Common mammalian predators of farmland, such as foxes, may not primarily target ground-nesting bird nests of eggs but chicks are often killed as by-catch when encountered by predators which typically hunt for abundant prey such as rodents (Hummel et al., 2017). We suggest that further research be conducted to identify the factors linking nest success to predator foraging behaviour, that is how they use the habitat to forage for egg or chick prey, across AES habitats in agricultural landscapes.

4.2 | Chick food abundance

At a farm level, there was an overall downward trend in chick food abundance, echoing trends reports in previous studies. This negative

trend was first identified in a similar longer-term study of invertebrates on ca. 100 fields in Sussex, UK, approximately 170 km south of our study site, using the same sampling methodology. The Sussex study showed that when Collembola was excluded from counts, the total number of invertebrates sampled had almost halved between 1979 and 1989 (Aebischer, 1990). A more recent analysis of this study showed that many taxa have stabilized since 1990, although there are some that have increased whilst others have decreased (Ewald et al., 2015). Pesticide use was identified as the primary cause of invertebrate declines, with variation in climate causing short-term changes (Ewald et al., 2015). The overall declines in our study and of that in Sussex, where annual sampling has been conducted, indicate that total numbers of invertebrates have declined in crops, but not to the same extent as reported elsewhere (Sánchez-Bayo & Wyckhuys, 2019). Nevertheless, unless fewer pesticides are used this reduction of farmland invertebrates is likely to persist. This may mean that adults have to sacrifice their own condition by working harder to feed chicks, at a possible cost to their own survival and reproduction (Bright, 2004).

In this and other studies, the arable crops contained low levels of invertebrates (Holland et al., 2012), far below the amount needed to sustain the grey partridge *Perdix perdix* for which there is an index indicating the required chick food level (Potts & Aebischer, 1991), emphasizing the importance of AES habitats in the farmed landscape. WBSM was, however, linked to increased fledgling success and therefore invertebrate abundance alone may not always indicate the value of a habitat, and the accessibility of invertebrates within the vegetation may also be important. Birds may also show a preference for the types of habitat in which they are willing to forage, dependent on, for example, the risk of predation. For example Signorell et al. (2010) showed

that female black grouse lead chicks to suboptimal feeding areas if young trees provide cover from avian predators.

Beetle banks were found to be a rich source of yellowhammer chick-found items, but they are included on arable farms as supplementary overwintering sites for beneficial arthropods (Thomas et al., 2001). Secondary benefits of AES options have been recorded on several other occasions, for example, the density of female corn bunting *Emberiza calandra*, was positively influenced by low input extensively managed cereal resources (Setchfield et al., 2012). Ornithological research relating to beetle banks has focused on the benefit of this habitat to the widely studied grey partridge showing that it is a preferable foraging habitat compared with pollen and nectar mixtures, which are generally too dense and damp for foraging partridge chicks (Phillips et al., 2010). They also increase grey partridge over wintering densities when compared to nesting cover (Thomas et al., 2001). For passerines, a study of foraging habitat use on the same site revealed that skylarks *Alauda arvensis* used beetle banks significantly more than unmanaged set-aside; however, they were not favoured by yellowhammer (Murray et al., 2002). Differential use by these two species was attributed to habitat accessibility since skylarks were regularly seen foraging around the edges of beetle banks but yellowhammer were not (Murray et al., 2002). Considering the structural and compositional similarities between grass margins and beetle banks (Vickery et al., 2009) further research is necessary to examine why habitat use may differ and, for beetle banks, how this could be improved.

For conservation headlands, the high level of invertebrates recorded supports the results of previous studies (e.g. Sotherton, 1991). But the benefits of cereal headlands to passerines such as yellowhammer are not well understood. Green et al. (1994) showed that the abundance of European robin *Erithacus rubecula*, European greenfinch *Chloris chloris* and song thrush *Turdus philomelos*, occupying hedgerows adjacent to crops receiving reduced levels of pesticides was lower than their abundance beside headlands that were fully sprayed. The remaining species showed non-significant differences in the same direction. Cole et al. (2007), also reported that passerines did not use reduced input cereal headlands more than conventionally managed ones, concluding that this was linked to habitat structure. The opposite has also been reported, however, with suggestions that corn bunting, whitethroat *Sylvia communis*, chaffinch, greenfinch and yellowhammer distribution are related to in-field areas receiving limited or no agro-chemical input (Stevens & Bradbury, 2006). This is supported by Frampton and Dorne's (2007) meta-analysis which showed that herbicide restriction on crop edges most positively influenced chick food populations. Disagreement between the studies outlined above implies that further research is needed in this area.

4.3 | Management implications

The 14-year-old dataset analysed here offers what we believe is the first in-depth analysis of the relative effects of habitats (nesting

and foraging), nest predators and prey availability on yellowhammer nest survival. The results are still of relevance today since a similar suite of AES habitats is offered under England's current AES scheme, Countryside Stewardship.

For land managers, our most important finding is the positive relationship between WBSM cover and the fledging success of the yellowhammer. To our knowledge, this study is the first to identify the breeding benefits of this a habitat, which is intended primarily to provide winter food resources. Although seed food is known to attract foraging birds (Perkins et al., 2008) positive impacts on fledging success were not expected since this habitat contained a similar level of chick-food resources as broadleaf and cereal crops. It may be that invertebrates are more accessible to foraging yellowhammer in WBSM or that the seed resources it supplies improve adult fitness. In future, we recommend that WBSM plots are implemented on farmland in areas yellowhammer are likely to nest (e.g. near song posts used by male yellowhammer; McHugh et al., 2016) and that invertebrate rich habitats (e.g. beetle banks) are sown along WBSM habitats to help boost their invertebrate populations. Of course, for the adoption of these AES to aid yellowhammer breeding success, the financial incentives need to outweigh the bureaucratic and logistical challenges of implementing them, and their optimal placement requires access to good quality advisory information.

However, the negative relationship detected between hatching success and spring AES habitats is a cause for concern and highlights the importance of considering how mammalian predators may hunt across arable farmland. We suggest that further research should be conducted to identify the factors linking nest success to predator foraging behaviour across AES habitats in agricultural landscapes. This work will be essential if predator control measures are to be considered in the UK's new AES, the Environmental Land Management Scheme.

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AUTHOR CONTRIBUTIONS

John Szczur, Steve Moreby, Patrick White and Chris Stoate collected the data; Niamh McHugh analysed the data with support from Patrick White; Niamh McHugh led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.vmcvdcnw0> (McHugh et al. 2022)

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ORCID

Niamh M. McHugh  <https://orcid.org/0000-0001-6659-7266>

Patrick J. C. White  <https://orcid.org/0000-0002-9349-8447>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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