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Great tits *Parus major* and blue tits *Cyanistes caeruleus* as indicators of agri-environmental habitat quality

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Abstract

This study examined relationships between habitat and breeding success for two common bird species, the great tit *Parus major* and blue tit *Cyanistes caeruleus*. The aim was to determine the potential of these species to act as indicators of food resource availability for birds in managed semi-natural habitats on farmland and thus a measure of the effectiveness of specific management practices under agri-environment schemes (AES). Breeding success was recorded for four years (2007-10) using 90 nestboxes on arable farmland in central England. Habitat parameters were derived from high spatial resolution airborne Light Detection and Ranging (LiDAR) and hyperspectral data.

Relationships of breeding variables with a range of habitat variables, many of which were influenced by AES management, were evident for both species, despite strong interannual variation in breeding parameters. Relationships were strongest for models using habitat variables within a 100 m radius of the nest, compared to values of 50 and 200 m. Both species showed significant, positive relationships with the area and proximity of tree canopy and, for great tits especially, with hedgerow height and volume.

Therefore, tits may act as indicators of the quality of local habitat, particularly within-hedge trees and hedgerows, managed under agri-environmental provision, and provide insight into the spatial arrangement of AES options at the field scale.

Keywords: Landscape structure, foraging, indicator species

1. Introduction

Over the past century, intensification of agricultural practices, including increased mechanisation, simplification of crop rotation and reduction of non-crop features have led to declines in farmland biodiversity, with population declines even in species which have historically thrived on agricultural land (Donald et al., 2001; Stoate et al., 2001; Henle et al., 2008). Agri-environment schemes (AES) have been cited as the only realistic tools for reversing these decreases (Donald and Evans, 2006). AES vary in their precise aims but all involve offering financial incentives to farmers for undertaking measures designed to benefit the environment or biodiversity (Kleijn and Sutherland, 2003). The Environmental Stewardship scheme, introduced in 2005, is the current AES in the UK, and has a wide range of biological and socioeconomic goals including conserving biodiversity and protecting natural resources (Natural England, 2009).

Despite two decades of study across Europe and the USA, a clear consensus has yet to emerge on the present effectiveness and future potential of AES, with widely varying results depending on the spatial scale and target criteria studied (Klein and Sutherland, 2003; Davey et al., 2010; Batáry et al., 2011). It is therefore important to establish clear links between specific management practices and biodiversity gains in order to monitor and target AES, if they are to meet their objectives in a cost-effective manner (Kleijn and Sutherland, 2003; Vickery et al., 2004).

Great tits *Parus major* and blue tits *Cyanistes caeruleus* are small (around 18 and 10 g respectively), insectivorous passerines that breed sympatrically across much of Europe and provision their young with invertebrates, particularly caterpillars (Perrins, 1991). Although associated primarily with deciduous woodland, both species also occur widely in a range of alternative habitats, including parkland, urban gardens and agricultural land (Hinsley et al., 2008). Both species are tolerant of human disturbance and readily use nestboxes, which allows detailed recording of breeding parameters and avoids some of the risk and difficulties associated with monitoring open nests (James Reynolds and Schoech, 2012). In the UK both species nest in April-June and are

overwhelmingly single-brooded, which simplifies the monitoring of annual reproductive output. The adults typically feed their young several hundred times a day (Cowie and Hinsley, 1987) and are therefore constrained by time and energetic costs to forage within a limited radius around the nest site (Tremblay et al., 2005). This allows realistic assumptions of likely foraging distances around the nest site to be made (Hinsley et al., 2002).

Although it is well known that great and blue tits experience reduced breeding success in habitats other than large deciduous woodlands (Riddington and Gosler, 1995; Hinsley et al., 2008; Marciniak et al., 2007), there has been relatively little research to identify which habitat features influence breeding success at the level of the individual nest, especially within arable landscapes. In contrast to many farmland birds, the increasing populations of great and blue tits (Baillie et al., 2012) do not make them species of conservation concern in Britain. However, if clear relationships between breeding success and specific farmland habitat variables can be identified, tits may prove useful as indicators of local habitat quality and resource availability for other species which are declining or of conservation concern, and thus of the potential for AES management to benefit such species. Several farmland birds of conservation concern, such as the yellowhammer *Emberiza citrinella*, reed bunting *Emberiza schoeniclus* and tree sparrow *Passer montanus*, share a similar insectivorous nestling diet (Wilson et al., 1996) and forage in a range of vegetation including hedges and shrubs which may be used by tits (Hinsley and Bellamy, 2000). There are also species of other taxa which are targets for conservation under Environmental Stewardship, such as bats (Natural England, 2008; Merckx et al., 2009), which share the tits' insectivorous diet and arboreal habits. The dependence of tits on caterpillars also makes their breeding success a potential indicator for abundance of Lepidoptera (Perrins, 1991; Naef-Daenzer and Keller, 1999).

In this study we use a replicated experiment to evaluate the breeding success of great and blue tits as indicators of local habitat quality as provided by specific Environmental Stewardship options. Nestbox monitoring and high-resolution data from remote sensing were used to identify

relationships between breeding performance and habitat variables. This could inform the monitoring, assessment and development of targeted management strategies for the productivity of invertebrates and their insectivorous predators, including those of conservation concern, where diet and habitat overlaps with that of the tits.

2. Methods

The study was conducted on the Hillesden Estate, 1000 ha of farmland in Buckinghamshire, central England (51.95N, 01.00W). The Estate is characterised by arable fields cropped under a rotation of autumn-sown oilseed rape *Brassica napus*, wheat *Triticum aestivum*, and field beans *Vicia faba*, bordered by short (< 2 m), shrub hedgerows dominated by hawthorn *Crataegus spp.*, with scattered, mature trees (mostly English oak *Quercus robur* with some ash *Fraxinus excelsior* and willows *Salix spp*.).

Between 2005 and 2011, the Estate was managed under a large-scale replicated experimental design intended to investigate the effects of Environmental Stewardship on farmland biodiversity, including birds (Hinsley et al., 2010), small mammals, pollinators (Carvell et al., 2012) and invertebrates (Woodcock et al., 2010). Three levels of Environmental Stewardship management were established on plots of between 60 and 90 ha, each replicated five times in a randomised block design (see Hinsley et al., 2010 for further details). The three levels were: Entry Level Stewardship (ELS), Entry Level Stewardship Extra (ELSX) and the control, cross compliance (CC) - the latter representing the minimal obligatory conservation effort required under the European Union Common Agricultural Policy (DEFRA, 2013). Cross compliance field margins were uncultivated areas 2-3 m in width from the centre of a hedgerow, or 1 m from the top of a ditch, with hedges cut annually after harvest. Environmental Stewardship management involved the establishment of a range of non-crop habitats via seed mixes sown as field margins or patches and a biennial hedgerow cutting regime. On ELS treatments, approximately 1% of cultivated land was taken out of production and put into 6 m wide tussocky grass margins and a single patch of winter bird food mix. On ELSX

treatments, approximately 5% of land was removed from production, distributed between 6 or 8 m wide margins (including tussocky grass, pollen and nectar mix, and natural regeneration) and several patches of pollen and nectar mix, wildflower mix winter and bird food mix.

In February 2007, 90 nestboxes were placed in hedgerows throughout the estate. Boxes were mounted 1.5 to 2.5 m above the ground, the majority (86%) on hedgerow trees (68% of which were English oaks) with the remainder attached to bushes or artificial structures (e.g. fenceposts, pylons) within the hedgerow. In addition to five individual boxes, each treatment contained one 'terrace' design consisting of three adjoined boxes, each with its own entrance hole. The latter type was intended for use by tree sparrows but was frequently utilised by either (occasionally both) tit species. There was thus a total of 120 artificial nest sites, all with interior dimensions 160 x 125 x 110 mm and an entrance hole of 32 mm diameter, suitable for use by either tit species. Tits were common breeders on the Estate prior to the provision of boxes, nesting in natural cavities (authors' unpublished data). Thus the comparatively low density of boxes (mean 2 per km of hedgerow across the Estate) was unlikely to have significantly affected the natural tit population density.

2.1. MEASURING BREEDING PERFORMANCE

Measurements of tit breeding performance were gathered for four years (2007 - 2010) from April to June. Boxes were visited at least weekly from early April to determine lay date of the first egg and, subsequently, clutch size and hatch date. Dates are presented from here on as 'April dates', where 1 = April 1st and 91 = June 30th. The number of live and dead nestlings were counted 11 d after hatching, and live nestlings were fitted with a uniquely-numbered British Trust for Ornithology (BTO) alloy leg-ring, weighed (to 0.1 g) and returned to the nest. The number of nestlings successfully fledged was estimated approximately 20 d after hatching by searching vacated nests for nestlings which had died after 11 d. Two primary indicators of breeding success were chosen to reflect likely food supply: mean nestling mass excluding runts (i.e. nestlings too small to ring at 11 d, < 6 and < 12 g for blue and great tits, respectively) and total live nestling biomass (including runts) at 11 d

after hatching. Runts were rare and were excluded from mean nestling mass to prevent them

reducing its usefulness as a measure of overall nestling quality by skewing it downwards. Nestling

mass is a good indicator of nestling condition (Tinbergen and Boerlijst, 1990) so these two measures

were expected to reflect food abundance in the surrounding habitat coupled with the adults'

provisioning abilities, in terms of food supplied to each nestling (mean nestling mass) and total food

supply to the nest (total biomass) (Hinsley et al., 2002). Several additional measures were also

calculated for each nest: lay date of the first egg, clutch size, number of nestlings alive at 11 d, and

nest output (number fledged as a proportion of clutch size).

2.2. COLLECTING AND EXTRACTING HABITAT DATA

Habitat data were obtained from two airborne remote sensed sources, Light Detection and Ranging

(LiDAR) and hyperspectral imaging. These remote sensed data were acquired by the Natural

Environment Research Council Airborne Research and Survey Facility on 28th August 2007, under

conditions of full leaf canopy, from a mean flight altitude of 1190 m. The two sensors used were an

Optech 3033 Airborne Laser Terrain Mapper for LiDAR (scan half angle of 20˚, ground sampling rate

of 1 pulse per square metre, each pulse supplying a first and last return elevation measurement) and

an AISA EAGLE hyperspectral sensor (252 spectral bands across the range 400 -970 nm). Both the

LiDAR and hyperspectral datasets were processed into geo-referenced 0.5 x 0.5 m spatial resolution

grids. LiDAR data were converted from a surface model describing the maximum elevation in each

cell (to 0.01 m vertical resolution) to a canopy height model giving the height above the terrain of

the tallest feature within each cell. A detailed description of LiDAR processing using data from the

same sensor for a similar purpose is given in Hill and Broughton (2009). A subset of 22 bands from

the EAGLE data, selected to cover key spectral regions for vegetation discrimination, was used to

derive 30 land cover classes using a maximum likelihood classification algorithm. These were then

combined with surface height information from the LiDAR data, allowing the subdivision of

spectrally similar land covers by height (e.g. hedges and trees, buildings and roads). This was then

simplified to produce a land use - land cover map consisting of 10 classes (crop, short grass, mixed low vegetation, deciduous trees, field margin, road, hedge, building, water and bare soil/mud). Field margins (i.e. mixed, low, non-woody vegetation bordering arable fields) were subsequently assigned to type by comparing their location with maps of sown ELS and ELSX margins, as margin types could not be distinguished adequately using remote sensed data alone. Handling of the remote sensed data and land use - land cover map was performed in ERDAS Imagine (v 9.0) and ESRI ArcGIS (v 9.3.1).

The extent around the nestbox within which tits forage, and which thus contains the habitat features most influential for breeding success, is likely to vary with habitat and food availability (Stauss et al., 2005; Tremblay et al., 2005). In the absence of precise data on tit foraging patterns in specific habitats, previous studies have frequently assumed that the area within a fixed radius around the nest, based on estimates from radio tracking, represents the core foraging area (Hinsley et al., 2002, 2008; Arriero et al., 2006). Such fixed-radius buffers have proven more effective in assessing the value of habitat parameters around nestboxes than more analytically complex estimates of total foraging area (Wilkin et al., 2007). Tits have been shown to have mean foraging distances of less than 50 m from the nest site in deciduous woodland (Naef-Daenzer, 1994; Naef-Daenzer and Keller, 1999; Stauss et al., 2005; Carpenter, 2008) but foraging distances can be considerably greater in more open, suboptimal habitats (Stauss et al., 2005; Tremblay et al., 2005). To address this issue, habitat data were extracted for three radii around each nestbox (50, 100 and 200 m) based on the range of radii observed or assumed by previous studies, and the resulting models (see section 2.3) were compared to obtain an optimum estimate of core foraging area in an arable landscape (Carpenter, 2008).

Habitat variables likely to provide influential foraging resources for tits were selected for analysis from previous studies examining differences between habitats (e.g. Riddington and Gosler, 1995; Hinsley et al., 2008; Marciniak et al., 2007) or, less frequently, individual nest studies within

woodland (e.g. Wilkin et al., 2007). Habitat variables included several drawn from the tree canopy (proximity index, mean height, maximum height, area and volume). Canopy variables were expected to influence the availability of invertebrate food for tits, because tree canopy forms the major foraging resource in woodland. The canopy proximity index was adapted from Gustafson and Parker (1992) as the sum of every discrete patch of continuous tree canopy (one or more trees) within the buffer divided by its squared distance from the nestbox. Trees were distinguished from hedgerows using a height threshold of 3 m, a criterion used in previous studies on tits (e.g. Arriero et al., 2006; Pedersen et al., 2007). Variables were also derived for hedgerows (length, mean height, area and volume), which provide a widespread alternative foraging resource on farmland (Arriero et al., 2006) and are targeted by AES management. Field margin areas (non-Environmental Stewardship, ELS/ELSX grassy and ELS/ELSX flowering) were also determined, as both tit species also forage in low vegetation and on the ground. Extraction of habitat variables within buffers was performed in ArcGIS using the Analyst, 3D Analyst and Spatial Analyst extensions.

2.3. STATISTICAL ANALYSIS

To reduce the stochastic effects of nest failure due to unrecorded factors such as disease, weather or predation, breeding variables were analysed using only broods which had survived to the stage in question (i.e. zero values were removed from measures of breeding performance). Strongly inter-correlated habitat variables ($p < 0.05$ from Pearson's R correlation) were excluded from analyses, with the variable having the most information content being retained (e.g. volume in preference to length or area, mean height in preference to maximum height).

To examine the relative importance of the different habitat variables in determining breeding success, an initial subset of generalised linear models (GLMs) was constructed for the 'best' 100 combinations of habitat variables, with model selection being performed via a best subsets approach (bestglm, Xu and McLeod, 2010) based on Akaike's Information Criterion (AIC, Akaike, 1971). Since numbers of observations were small in comparison to the number of parameters, AIC was adjusted

to control for bias (AICc, Burnham and Anderson, 2002; Johnson and Omland, 2004). First egg date, mean nestling body mass and nestling biomass were modelled as general linear models assuming a normal distribution, whilst models of counts (clutch size and number of nestlings) and proportions (output) assumed Poisson or binomial distributions respectively. Year and, for all subsequent stages of breeding, first egg date, were included as additional variables, to account for annual variation in breeding parameters and the known effect of lay date on how well peak nestling demand for food coincides with availability (Norris, 1993; Riddington and Gosler, 1995; Naef-Daenzer and Keller, 1999). Given that interannual variation may also occur in the relationships of the breeding variables with habitat, the analyses were repeated for individual years for the two primary breeding variables. These latter analyses used a limited subset of the habitat variables most influential on breeding success across years, to lower the ratio of parameters to samples and lessen the likelihood of overfitting.

Further model comparison and selection was based upon ΔAICc (difference between the AICc of a candidate model and that of the best fitted one) and Akaike weights (w_i) for each model. The latter can be interpreted as the probability that model i is the best model of the candidate set for the observed data (Burnham and Anderson, 2002; Johnson and Omland, 2004). For analysis of the relative importance of the relationships between each habitat variable and breeding variable, a model averaging procedure was followed. Variable selection probabilities were calculated by summing w_i values across all models containing each habitat variable in turn, in order to give a metric comparing the prevalence of habitat variables across all candidate models rather than relying on the selection procedure to identify a single 'best' model (Johnson and Omland, 2004). The mean and standard error of standardised regression coefficients from all candidate models were also calculated for each habitat variable, in order to estimate the model-averaged slope and significance of the relationship with breeding variables. All analyses were undertaken in R (R v2.14.1, R Development Core Team, 2011).

3. RESULTS

Over the four years of study, data were collected for 260 tit nesting attempts (161 great and 99 blue tit). Neither overall nest occupancy (i.e. number of nestboxes reaching at least the first egg stage) nor the proportion of nestboxes occupied by each species varied significantly across years ($\chi 2$ = 0.747, D.F. = 3, p = 0.863; $\chi 2$ = 4.754, D.F. = 3, p = 0.195, respectively).

All breeding variables showed significant interannual variation except number of nestlings for great tits (Table 1). For the majority of breeding variables, these differences between years were most evident between the first two and the latter two years of the study, with the latter being more successful (Table 1).

Comparison of ΔAIC and w_i values from best-subsets GLM showed that the best-fitted model was mostly obtained using variables from the 100 m nestbox buffer (Table 2). For great tits, this was the case for all breeding variables. For blue tits, the trend was less clear, with best fitted models showing lower ΔAIC and w_i values than those for great tits (Table 2), and with some of these obtained using a 50 m buffer. However, as the 100 m buffer produced the best fit models for three of the five breeding variables for blue tits, and was only marginally inferior for a fourth (1st egg date, Table 2), this supported adoption of the 100 m buffer around nest sites as the optimum foraging distance for both species.

Model-averaged results from models of breeding parameters against habitat variables from the 100 m buffer, for all years of the study, showed several consistent effects. As expected from the significant interannual variation described in Table 1, the factor Year showed high variable selection probabilities in models for the majority of breeding variables, with the exception of clutch size and number of nestlings for great tit (Table 3, Fig. S1 supplementary material). Lay date of the first egg showed high selection probabilities, and a significant negative relationship (i.e. early lay date results in increased breeding parameters) for clutch size, number of nestlings and biomass for both species. However, it was only significantly related to output for blue tits (Table 3), and only this species

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showed consistent benefits from earlier lay dates when years were analysed independently (Table 4). For great tits, mean hedge height, mean tree canopy height and the tree canopy proximity index displayed largely consistent high selection probabilities across breeding variables, and largely significant positive relationships (Table 3, Fig. S1 supplementary material). Field margins had some weakly significant positive effects on the later stages of breeding in great tits. For blue tits, the relationships with habitat were less clear, with many variables having similar selection probabilities or high selection probabilities for only a few stages of breeding (e.g. non- Environmental Stewardship margin area on first egg date, hedge height and volume on nest output). However, the tree canopy proximity index did show a significant, positive relationship with three blue tit breeding variables (number of nestlings, mean nestling mass and nestling biomass), as well as a negative relationship with lay date (Table 3).

Some of these relationships remained consistent when relationships with a subset of the habitat variables were analysed independently for each year (Table 4, Fig. S2 supplementary material). The tree canopy proximity index showed a significant, positive effect on great tit nestling biomass in all years, and blue tits always showed increased nestling biomass with earlier lay date of the first egg. However, most other relationships showed substantial interannual variation. The canopy proximity index also had a positive effect on blue tit mean nestling mass, but only in three years. Other variables only showed a significant effect in one or two years. For example, field margin area showed significant positive effects on great tit nestling mass only in 2007 and 2008. In 2009 and 2010 no habitat variables showed a significant relationship with blue tit nestling biomass, the only variable to retain a significant effect being first egg date. In contrast, great tit nestling biomass retained significant relationships with at least one habitat variable in 2009 and 2010.

4. Discussion

As predicted, both tit species demonstrated significant relationships between breeding success and specific farmland habitat variables, most notably tree canopy height, volume and proximity, and

hedgerow height, notwithstanding strong interannual variation. As has been found for many farmland birds (Sparks et al., 1996; Hinsley and Bellamy, 2000), both species benefited from nesting in surroundings which contained the greatest abundance of features most similar to their primary habitat (i.e. woodland), namely large trees and tall shrubs (i.e. hedgerows). The strong links between breeding parameters and habitat features make both tit species potentially useful indicators of the resource value of specific AES management options for other insectivorous farmland species during the breeding season which are of greater conservation concern but more difficult to monitor. Management options best indicated by tits will be those which have a stated aim of providing invertebrate-rich foraging habitats for farmland birds, especially when associated with habitats favoured by tits. Such options within Environmental Stewardship include the conservation of within-hedge trees, reduced hedge cutting of hedgerows and the establishment of non-crop vegetation on arable farmland.

The differences in the majority of breeding parameters between years most likely reflected the fact that 2007 and 2008 had high spring rainfall (mean rainfall for southern England for 2007-2010 respectively: 184, 229, 122 and 108 mm), especially around the period of peak nestling food demand prior to fledging. This resulted in increased nestling mortality and poorer nestling condition for both species. Variation in conditions between years also causes variation in the timing of peak caterpillar emergence, and thus drives the response of first egg date to habitat variables. Where local habitat is suitable, females may obtain sufficient resources to time their breeding to the phenology of their insect prey (Tinbergen and Boerlijst, 1990; Norris, 1993; Naef-Daenzer and Keller, 1999). This has clear advantages, as in both species nests with earlier lay dates produced larger clutches and thus a higher total nestling biomass, although this only translated into a higher nest output for blue tits. In fact, when years were analysed independently, whilst blue tits showed a relationship between lay date and nestling biomass across all four years, great tits showed no such relationship in 2007 or 2008. Blue tits may have been less affected by this problem due to their smaller body size enabling relatively higher energetic returns from smaller food items when compared with great tits (Cowie

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and Hinsley, 1987; Naef-Daenzer and Keller, 1999; Naef-Daenzer et al., 2000). Conversely, when conditions are favourable for promoting invertebrate abundance, breeding success in blue tits may become largely independent of habitat type, with adult birds able to compensate for less productive habitat by increasing foraging effort (Tremblay et al., 2005; Hinsley et al., 2008). This weather-dependant relationship with habitat has been demonstrated for farmland chaffinches *Fringella coelebs*, with oak tree presence only having a positive impact on brood survival in years of poor weather (Whittingham et al., 2001). Thus, as suboptimal conditions affect not only the breeding variables themselves, but also their relationships with habitat, certain habitat features (e.g. field margins) may only be beneficial in years when they are more productive, either in absolute terms or when compared with trees. So, provision such of habitats under AES may well be effective in buffering certain breeding bird species against the effects of unfavourable weather conditions, even if they appear to have little effect in favourable years.

The results suggest that the core foraging area for tits breeding within an arable landscape lies within 100 m of the nest. As this is considerably greater than the radii reported in deciduous woodland (Naef-Daenzer, 1994; Naef-Daenzer and Keller, 1999; Stauss et al., 2005; Carpenter, 2008) it appears that the scattered trees and linear hedgerows of arable farmland comprise suboptimal foraging habitat for tits provisioning young, with adults having to travel further to find sufficient food. Foraging at further from the nest increases predation risk and energy expenditure, and decreases frequency of nestling feeding (Hinsley et al., 1995, 2008). Indeed, the prevalence of the tree canopy proximity index as opposed to total tree canopy volume in the models supports the conclusion that these costs of travel are such that, even within the 100m radius, areas of canopy further from the nest are less preferred as foraging habitat by breeding tits. High costs of travel, as with the tits, may be a common problem for other farmland species which need to access dispersed resources (Merckx et al., 2009; Öckinger et al., 2009). Therefore, the small spatial scale at which local habitat influences breeding success in the tits in the present study suggests that there is a clear

need for careful planning in the placement of AES options at the farm- and field-scale if they are to achieve targets relating to maintaining networks of productive foraging habitat for farmland species.

Mature hedgerow trees can contain high concentrations of invertebrates, especially in comparison to other habitat features in open, arable landscapes (Southwood et al, 1982; Henderson et al., 2007; Merckx et al., 2010). The size and number of trees within a hedgerow has previously been found to be a determinant of overall bird species richness and abundance (Green et al., 1994; Sparks et al., 1996; Hinsley and Bellamy, 2000). Whittingham et al. (2001) found that the number and proximity of mature oak and willow trees influenced the likelihood of nestling starvation in farmland chaffinches, whilst Henderson et al. (2007) demonstrated that barn swallows *Hirundo rustica* feed near mature hedgerow trees due to concentrations of invertebrates around the canopies. Some declining farmland species forage and nest in hedgerow trees, including tree sparrows (Field and Anderson, 2004), although others more usually forage in lower vegetation (e.g. reed bunting, yellowhammer) but may require the presence of trees as songposts (Whittingham et al., 2005). Mature trees with abundant invertebrates may also create a "spill over" of insect food into the surrounding habitat (Henderson et al., 2007; Merckx et al., 2010). The strong link between tits and the tree canopy also suggests that breeding productivity of tits is an indicator of habitat quality for bats, one of the target groups cited in recent additions to Environmental Stewardship which focus on establishment and protection of within-hedge trees (Natural England, 2008).

Despite the prevalence of trees, hedgerow height and volume were also influential, especially for great tits. Hedgerows form a major component of the available semi-natural habitat in arable landscapes (Sparks et al., 1996), with taller and wider hedges potentially supporting more invertebrate food resources, as well as providing nesting habitat and cover (Sotherton et al., 1981; Hinsley and Bellamy, 2000). As a result, hedgerow height and volume are determinants of bird abundance and species richness (Sparks et al., 1996; Hinsley and Bellamy, 2000). Thus tits may be useful indicators of insect abundance relating to hedgerow management (particularly cutting

regimes affecting height and width) under Environmental Stewardship options, especially where trees are scarce. Hedgerow management has been part of Environmental Stewardship since its inception, with options for the establishment, restoration and conservation of hedgerows, and imposition of biennial hedgerow cutting has remained one of the most popular options within the scheme (Natural England, 2009). Merckx et al. (2009) showed that the beneficial effects of tree canopies were greatest when combined with adjacent Environmental Stewardship field margin options, and combinations of hedges and wide field margins have been found to benefit other species (e.g. yellowhammer, Bradbury et al., 2000). However, the generally weak effects and strong interannual variation in the relationship between field margins and tit breeding performance means that tits alone are unlikely to be reliable indicators for field margin quality. Good spatial planning and targeting of options at both farm- and field-scales is essential if conflicts of interest are to be avoided. Most AES have multiple targets, all of which are unlikely to be met by a universally applicable combination of management options. For example, the tall hedges and trees which benefit tits also provide vantage points for corvids and raptors that predate ground-nesters such as skylark *Alauda arvensis*, lapwing *Vanellus vanellus* and grey partridge *Perdix perdix*. Thus monitoring the breeding success of the tits, whilst not a blanket indicator for AES success or failure, may enable assessment of the effects of specific AES management practices on local habitat quality and resource provision.

Acknowledgements

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Table 1 Descriptive statistics of breeding success for both tit species over the four years of the study. Cell contents are mean ± s.e. for nests reaching the relevant stage in breeding, with the number of nests in (). All breeding variables except Number of Nestlings for great tits were significantly different among years ($p < 0.05$, one-way ANOVA).

	Great Tit				Blue Tit			
Year	2007	2008	2009	2010	2007	2008	2009	2010
1st Egg Date	20.69 ± 0.72 (32)	29.91 ± 0.57 (43)	20.55 ± 0.79 (42)	27.02 ± 0.77 (44)	21.13 ± 0.63 (30)	29.38 ± 0.71 (24)	18.40 ± 0.79 (25)	24.05 ± 1.15 (20)
Clutch Size	8.00 ± 0.25 (32)	7.50 ± 0.25 (44)	8.80 ± 0.23 (39)	8.65 ± 0.23 (40)	9.27 ± 0.25 (30)	10.17 ± 0.27 (24)	10.88 ± 0.28 (24)	10.80 ± 0.32 (20)
Number of Nestlings	6.18 ± 0.50 (22)	5.45 ± 0.39 (29)	6.68 ± 0.42 (34)	6.63 ± 0.39 (32)	7.44 ± 0.52 (27)	6.05 ± 0.60 (19)	9.33 ± 0.49 (21)	8.59 ± 0.47 (17)
Mean Nestling Mass (g)	14.85 ± 0.40 (21)	13.43 ± 0.35 (29)	15.03 ± 0.31 (34)	15.39 ± 0.34 (32)	9.35 ± 0.25 (27)	8.85 ± 0.26 (19)	9.48 ± 0.24 (21)	9.93 ± 0.17 (17)
Total Nestling Biomass (g)	90.53 ± 8.22 (21)	72.04 ± 5.53 (29)	98.38 ± 6.31 (34)	102.16 ± 5.85 (32)	70.43 ± 5.55 (27)	52.99 ± 5.54 (19)	87.38 ± 5.21 (21)	84.31 ± 4.44 (17)
Output (%)	66.00 ± 8.06 (13)	50.82 ± 4.82 (26)	70.08 ± 4.07 (32)	74.58 ± 4.73 (30)	52.00 ± 6.70 (21)	45.46 ± 5.91 (18)	79.16 ± 4.17 (20)	71.52 ± 5.76 (17)

Table 2 AIC, ΔAIC (absolute difference from lowest AIC) and w_i (Akaike Weight) for the best-fitted models from each of the three buffer radii, for those breeding parameters showing a significant relationship with habitat

		Great Tit			Blue Tit		
Buffer Radius		50	100	200	50	100	200
1st Egg Date	AIC	482.30	479.24	485.04	268.45	268.61	271.58
	ΔAIC	3.06	-	5.80	-	0.16	3.12
	w_i	0.17	0.79	0.04	0.47	0.43	0.10
Number of Nestlings	AIC	520.62	518.29	518.82	128.64	127.60	129.86
	ΔAIC	2.33	-	0.54	1.04	-	2.25
	wi	0.15	0.48	0.37	0.31	0.52	0.17
Mean Nestling Mass (g)	AIC	131.44	127.51	128.74	13.47	14.66	13.58
	ΔAIC	3.93	-	1.23	-	1.19	0.11
	wi	0.08	0.60	0.32	0.40	0.22	0.38
Total Nestling Biomass (g)	AIC	791.11	785.04	787.01	520.59	520.53	520.57
	ΔAIC	6.07	-	1.97	0.05	-	0.04
	w_i	0.03	0.70	0.26	0.33	0.34	0.33
Output (%)	AIC	640.72	637.00	639.29	484.86	480.72	481.18
	ΔAIC	3.72	-	2.29	4.14	-	0.46
	w_i	0.11	0.68	0.22	0.07	0.52	0.41

Table 3 Model-averaged results from best-subsets generalized linear models for each breeding variable, for great tits and blue tits, against habitat variables from the 100 m buffer. For each habitat variable, the type and number of symbols indicate the direction and significance of the mean slope across all models containing the variable (+ = positive; - = negative; * = factor; +,-,* $p < 0.05$; ++,--,** $p < 0.01$; +++,---,*** $p < 0.001$; EGG = date of first egg; HV = hedge volume; HM = mean hedge height; TV = tree canopy volume; TM = mean tree canopy height; TI = tree canopy proximity index; NES = non-Environmental Stewardship margin area; GM = grass-dominated Environmental Stewardship margins; FM = floral Environmental Stewardship margins).

Species	Habitat Variable Code	1st Egg Date	Clutch Size	Number of Nestlings	Mean Nestling Mass (g)	Total Nestling Biomass (g)	Nest Output
Great Tit	HV	--	--		-		++
	HM	---	++	+++	+	+++	
	TV		++	+	++	+	+
	TM			+	+	++	++
	TI2	--	++	+++		+++	+
	NES				+	+	+
	GM			+		+	
	FM				+		
	YEAR	***			***	***	***
	EGG	NA	---	--		--	
Blue Tit	HV			+			++
	HM	-					+++
	TV						
	TM		+				-
	TI2	-		+	+++	++	
	NES	--	-				+
	GM	-	+				
	FM	-			+		
	YEAR	***	**	*	***	***	***
	EGG	NA	---	---		---	---

Table 4 Model-averaged results from best-subsets generalized linear models for mean nestling body mass and total nestling biomass in each year, for great tits and blue tits, against selected habitat variables from the 100 m buffer. For each habitat variable, the type and number of symbols indicate the direction and significance of the mean slope across all models containing the variable (+ = positive; - = negative; * = factor; +,-,* $p < 0.05$; ++,--,** $p < 0.01$; +++,---,*** $p < 0.001$; EGG = date of first egg; HM = hedge mean height; TV = tree canopy volume; TI = tree canopy proximity index; MP = total field margin area).

Species	Habitat Variable Code	Mean Nestling Mass (g)				Total Nestling Biomass (g)			
		2007	2008	2009	2010	2007	2008	2009	2010
Great Tit	HM		+	+		+		+	++
	TV			+	+				
	TI	+				++	+	+	++
	MP	+	+			+			
	EGG		-	-				--	
		2007	2008	2009	2010	2007	2008	2009	2010
Blue Tit	HM				+		+		
	TV	+							
	TI	+		+	++	+			
	MP				+		+		
	EGG	-				-	---	--	-