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Drivers of songbird territory density in the boundaries of a lowland arable farm

Megan E. Tresise[a], Sofia Biffi[a], Rob H. Field[b], Les G. Firbank[a]

[a] School of Biology, University of Leeds, Leeds, United Kingdom, LS2 9JT

[b] RSPB, The Lodge, Sandy, SG19 2DL, rob.field@rspb.org.uk

Abstract

Conventional farming in the UK has had adverse effects on farmland biodiversity, particularly during post-war intensification of agriculture. Efforts have been made in the reversal of these effects, with much of the literature reporting a mixture of findings. At a localised scale, these efforts have been noticeable with RSPB Hope Farm observing a 200% increase in bird territory numbers from 2000-2012, achieved with the wide implementation of agri-environment schemes (AES) on the farm. We aimed to investigate the spatio-temporal drivers of territory density in four hedgerow specialist bird species using a thirteen year (2000-2012) dataset of hedgerow management, in-field cropping and field boundary habitat records. Territory maps were used to calculate territory counts for each hedgerow across the time period. Generalised Linear Mixed Models were used to model territory counts for each habitat variable. These findings demonstrate that for *Emberiza citrinella*, *Carduelis cannabina* and *Sylvia communis*, presence of oilseed rape (OSR) is a strong predictor of higher territory numbers, leading to a doubling in territory density compared to absence of OSR. However, tree presence in hedgerows was a negative predictor of territory numbers for these species. Opposing trends were observed for *Carduelis chloris*, which exhibited significantly greater territory numbers in roadside hedgerows, hedges with trees and when adjacent fields were not sown with a main crop. Management of hedges was a weak predictor of *S. communis* territories. This demonstrates that crop type, AES features, tree presence and location of hedgerows are drivers of farmland bird territory numbers. These findings validate the usefulness of more sustainable, wildlife-friendly farming under previous CAP rules and have important implications for post-Brexit farming policy, such as the Agriculture Bill.

Keywords

Agri-environment schemes; farmland birds; hedgerow management; mixed cropping; passerines

1. Introduction

The intensification of post-war conventional arable farming negatively impacted biodiversity in Europe through homogenisation of the land, increased agrochemical usage and removal of semi-natural boundaries (Kyrkos et al., 1998; Wilson et al., 1999; Donald et al., 2001; Winspear & Davies, 2005). Farmland specialist bird species have declined by 70% in the UK since the 1970s (Hayhow et al., 2016; DEFRA, 2018). Species including yellowhammer (*Emberiza citrinella*) and linnet (*Carduelis cannabina*) were once common across British lowland agricultural landscapes yet are now among the 12 red-listed farmland birds of conservation concern (Eaton et al., 2015). Newer reforms of the Common Agricultural Policy (CAP) have increased efforts to make conventional farming more sustainable and environmentally friendly in the long term, for example, by incentivising farmers to increase cropping diversity and heterogeneity of boundary habitats (Pe'er et al., 2014; Batáry et al., 2015). It is important that these measures draw on the best evidence of how to promote farmland birds. Much of the literature concerned with this focusses on the responses of farmland birds to changes in crop management (Siriwardena et al., 2000; Benton et al., 2003; Henderson et al., 2009; Batáry et al., 2010; Fahrig et al., 2015), boundary characteristics and management (Arnold, 1983; Green et al., 1994; Sparks et al., 1996; Hinsley & Bellamy, 2000; Morris et al., 2010), habitat diversity (Benton et al., 2003, Firbank et al., 2008) and presence of various agri-environment schemes (AES) and Entry Level Stewardship (ELS) trials (Morris et al., 2004; Morris et al., 2010; Vickery et al., 2009; Batáry et al., 2015). However, there is still a need for finer scale, long term research into avian response to changes in the arable landscape to understand what mechanisms drive these trends.

The Royal Society for the Protection of Birds' (RSPB) Hope Farm is a conventional and predominantly arable research farm (see section 2.1) with large populations of birds and fine-scale data records of farming operations dating back to 2000. This makes it one of the few available settings for research aiming to understand these mechanisms. A variety of research-led trials and management techniques have been employed to aid the reversal of farmland bird decline. The purpose of these research trials has been an attempt to improve both avian and invertebrate abundance and richness on commercial arable farmland through the provisioning of adequate nesting habitat, summer chick food and winter food and refugia (RSPB, 2012) and to inform agri-environment scheme development (Morris et al., 2010; Aebischer et al., 2016). The field boundaries at Hope Farm, including hedgerows, ditches and trees, have been managed to produce a more heterogeneous habitat for breeding bird species in compliance with the ELS agreement enacted in 2007 (Morris et al., 2010). Various AES based trials were added to the farm after a two-year initial baseline data collection period starting in 2000. Examples include beetle banks, in-field wild bird cover, floristically enhanced margins and ponds (Morris et al., 2010). The results of these efforts include a 226% increase in the Hope Farm Breeding Bird Index species from 2000 (117 territories of 10 index species) to 2017 (271 territories of 16 index species) (RSPB, 2017) and remains at roughly double the farms' baseline survey record (RSPB, 2018).

The aim of this study was to identify the main drivers of songbird territory density by modelling the effects of different spatio-temporal habitat variables related to hedges, including management, adjacent cropping to hedgerows and field boundary features (e.g. AES features and trees) at the hedgerow level on the territory count data of four passerine species recorded at Hope Farm.

This investigation builds upon previous work into the monitoring of wildlife-friendly and environment-focussed farming in a commercial setting, by using a thirteen-year (2000-2012) dataset of detailed farming operations and territory map records from RSPB Hope Farm. Territory data for four songbird hedgerow specialist (Fuller et al., 2001) species with consistent data were chosen, including yellowhammer, linnet, common whitethroat (*Sylvia communis*) and greenfinch (*Carduelis chloris*). Whitethroats are an insectivorous species, migrating between Sub-Saharan Africa over winter and arable farmland in Europe during the summer breeding season (Fransson, 1998), whereas the other species are all mostly resident and granivorous, although rely on invertebrate food during the breeding season (Cramp et al., 1994; Winspear & Davies, 2005).

2. Methods

2.1 Study Site

Hope Farm is a 181 ha, predominantly arable, research farm owned by the nature conservation charity RSPB, located on the calcareous clay soils of Knapwell, Cambridgeshire, UK (0° 3′ 15″ W, 52° 14′ 44″ N). The farm was purchased in 1999 by the RSPB for the purpose of trialling novel wildlife friendly farming practices and to identify methods of reversing farmland biodiversity declines whilst inhibiting the impact of these conservation measures on commercial farming (Morris et al., 2010; RSPB, 2012; Aebischer et al., 2016; Field et al., 2015). Between 2005 and 2012, Hope Farm employed a four-year crop rotation of wheat (*Triticum aestivum*) – oilseed rape [OSR] (*Brassica napus*) – wheat – field beans (*Vicia faba*). Prior to 2005 only a three-year wheat – wheat – OSR rotation was in place; the field beans introduced more recently have reduced the nitrogen requirement from fertilisers. There are roughly 10.3 km of hedgerow at Hope Farm bordering eighteen fields, alongside other boundary types including grass margins and woodland copses (total 1 ha). Hope Farm is bordered by two small towns, as well as the arable and pastoral fields of other landowners for which no crop records were available.

2.2 Territory density and habitat variables

Breeding bird surveys of hedgerow-nesting yellowhammers, linnets, common whitethroats and greenfinches, recorded between April and mid-June from 2000 to 2012, were used in this study to identify the number of territories per hedgerow and estimate ‘territory density’ (TD). Territories were identified using Common Bird Census methods (as in Marchant et al., 1990; Bibby et al., 2000), typically involving between eight and twelve surveys, and maps of breeding bird activity and location information were digitised. Territories for each species were separately assigned to the closest hedgerow by measuring the distance between the individual sightings within a territory and nearby hedges using the measure tool in ArcGIS 10.6 ArcMap; the closest hedge to a territory was recorded as the site of occupancy. Larger territories that spanned multiple hedgerows were recorded at each hedge. Each observation of the dataset corresponds to a territory count on a unit of hedgerow (see Supplementary Information Figure A.1 for hedgerow unit example) in a particular year (*y,* i.e. the 'current' year). All sample sizes given are the number of observations across the 13 year dataset. TD per 100 m was also calculated by taking the total number of territories for each individual hedgerow unit (e.g. B1a in SI Fig. A.1), dividing this by the length of the section and multiplying by 100 to get a standardised TD (following Shepherd, 2014; see also Macleod et al., 2004). 101 hedgerow sections were recorded for the farm (Figure A.2 in SI), although 21 were excluded due to inconsistent recording, or due to no territories or no hedgerow management being recorded during the study period. Thus the final sample size for each year is n = 80 (n = 1040 across the 13 year dataset).

Hedgerow management records were used to create a 'time since management' variable, by identifying those with no previous management ('no management'; n = 325), management in a particular year ('management'; n = 254), '1 year since management' (n = 151), '2 years since management' (n = 112), '3 years since management' (n = 94), '≥4 years since management' (n = 104). In-field land use data, e.g. crop types, was recorded as dichotomous presence/absence variables. Some land use types were grouped for their biological similarities and to account for differing sample sizes (Table 1). Where 'No crop' is recorded, this indicated that no main crop had been sown, thus the field was either in fallow, bare ground, grass or had wild bird cover. The group 'Edge' was used to describe hedgerows that ran along the perimeter of the farm, where data for the other side of the hedgerows was unavailable but largely consisted of cropped fields and residential gardens, so remained in the models to identify buffer effects from neighbouring land. Some hedgerow boundaries had trees (Table 1) and these were used to compute a tree presence variable that also included the managed woodland copses (n = 5). Tree species at Hope Farm, including those in hedgerows, are native and typical of the British countryside, as well as having been replanted to replicate ancient hedgerows and copses. Similarly, a presence and absence record for boundaries where an AES trial or related research, e.g. floral margins, was occurring in a particular year was created. The ‘no crop’ and ‘AES trials’ variables have been recorded to reflect the location-based elements that they comprise, rather than ecological benefits. For example, all ‘no crop’ elements relate to in-field uncropped habitat, whereas AES trials occur more often at the field boundary, which is where the passerine species nest.

Table 1 *Habitat variables used in GLMM analyses with descriptions of how they were coded*

Independent variable	Details
Time since management	
No management (n = 325)	No management has occurred since 2000
Management that year (n = 254)	Management in that year
1 year since management (n = 151)	Managed the previous year
2 years since management (n = 112)	No management for 2 years
3 years since management (n = 94)	No management for 3 years
≥4 years since management (n = 104)	No management for 4 or more years
Wheat	Wheat present = 599, absent = 441
OSR	Oilseed rape present = 314, absent = 726
Beans	Beans (spring/winter) present = 215, absent = 825
No Crop	In-field fallow, bare ground, grass, wild bird cover, set-aside present = 306, absent = 734
Road	Roadside hedge present = 130, absent = 910
Edge	Hedgerow that runs along the edge of the farm, where only one side has a data record; present = 465, absent = 575
Trees	Tree presence (n = 429) in the hedgerow, i.e. Hedge with trees, Hedge with trees and a ditch, Woodland. Tree absence (n = 611), i.e. Hedge, Hedge with ditch.
Field margin AES trials	Agri-environment trials present = 565, e.g. pollen & nectar, floristic/grass margins, beetle bank. Agri-environment trials absent = 475
Year	Year used as a 'dummy' variable in the modelling analyses to account for differences among years, e.g. weather, pathogens.

2.3 Statistical analysis

Generalised Linear Mixed Models (GLMMs) were used to analyse the effects of hedgerow management and in-field land use on territory number of the four study species (see Table 1). Each species was analysed separately, with time since management, crop type, tree presence, AES presence, roadside location and perimeter location (i.e. edge) as fixed factors. Year was included as a random factor to account for between year fluctuations in territory number at the farm scale due to external factors such as weather, pathogens, and population growth. Hedgerow ID was also included as a random effect, to account for species preference towards hedgerows based on their location, size, plant species composition, etc. Spatial autocorrelation of data was tested using the DHARMa package (Hartig, 2019) with all four species models returned as non-spatially autocorrelated.

GLMMs with Poisson error distribution and log link function were modelled using the *glmer* function in the lme4 package (Bates et al., 2015). Homogeneity of residuals was checked with plots of standardised residuals against fitted values. Marginal and conditional R^2 were calculated to evaluate goodness-of-fit for each species GLMM by describing fixed and random factor variance in territory counts, respectively (Nakagawa & Schielzeth, 2013). All statistical analyses and graphics were performed and produced in R version 1.2.1335.

3. Results

3.1 Trends in territory density between species

A total of 1901 territories were included in the analysis: 553 yellowhammer territories (annual mean = 42.5 ± 11.4), 334 linnet territories (25.7 ± 10.0), 672 whitethroat territories (51.7 ± 10.9) and 342 greenfinch territories (26.3 ± 9.06). See Figure 1A for territory counts for each species per year.

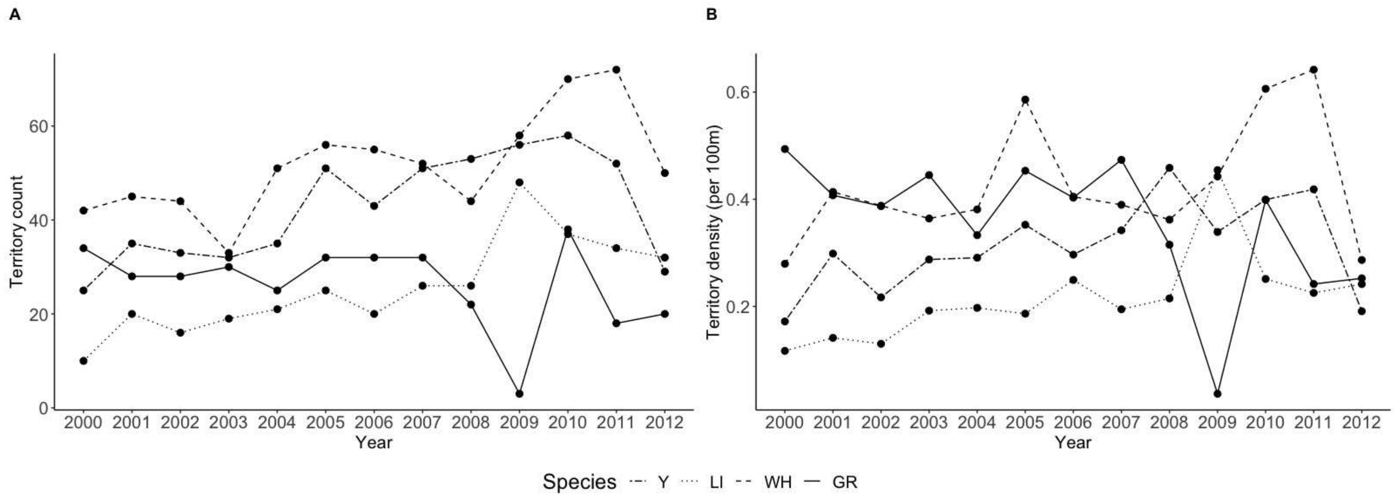

Figure 1 *Territory counts (A) and density per 100m (B) for yellowhammers (Y; two dash), linnets (LI; dotted), whitethroats (WH; dashed) and greenfinches (GR; solid) between 2000 and 2012 at RSPB Hope Farm.*

Territory density, measured as number of territories per 100m of hedgerow, increased for three of the species between 2000-2012 (Fig. 1B). Yellowhammer territories doubled between 2000 (0.17 territories/100m) and 2005 (0.35 territories/100m), although by 2012 had declined to 0.19 territories/100m. Linnets, despite having the lowest overall TD of all four species (Table 2), showed a similar gradual increase with time from 0.12 territories/100m in 2000 to 0.25 territories/100m by 2012. Whitethroats occupied the most territories overall (Table 2) and showed similarities in TD pattern with yellowhammers, more than doubling in TD between 2000 (0.28 territories/100m) and 2005 (0.59 territories/100m). This species showed a peak TD of 0.64 territories/100m in 2011. Greenfinch TD declined with time, halving from 0.49 territories/100m in 2000 to 0.25 territories/100m by 2012. The year 2009 showed a peak in territory density for linnets (0.45 territories/100m) and a steep decline for greenfinches (0.04 territories/100m), which may have been linked to the trichomoniasis outbreak that caused a strong decrease in the British greenfinch population in the late 2000s (Lawson et al., 2012). For overall mean species TD see Table 2 and see SI Table A.1 for annual mean TD across species.

Table 2 *Mean territory density (TD) per 100m hedgerow (± SE) of each species.*

Species	**Mean TD ± SE**
Yellowhammer	0.31 ± 0.63
Linnet	0.22 ± 0.64
Whitethroat	0.43 ± 0.83
Greenfinch	0.36 ± 0.71

3.2 Habitat effects on territory numbers

The GLMM analyses revealed some possible drivers of territory density in the songbird species studied, mainly in the type of crop sown, spatial location of and features associated with hedgerows, with interspecies differences and differences in model variation.

The time since management parameter was significant in the whitethroat model ($p < 0.05$), although the coefficient achieved was small, indicating some increase in the number of territories with increasing time intervals since the last management event (SI Table A.2). Whitethroat TD was highest when it had been at least 2 years since the last management event (mean ± SE = 0.69 ± 0.11; Figure 2; SI Table A.3). Although the other species models showed no significant effects of management frequency, yellowhammer and linnet territory counts and TD also responded positively to more frequent management, whereas for greenfinches infrequent management was better (SI Table A.3).

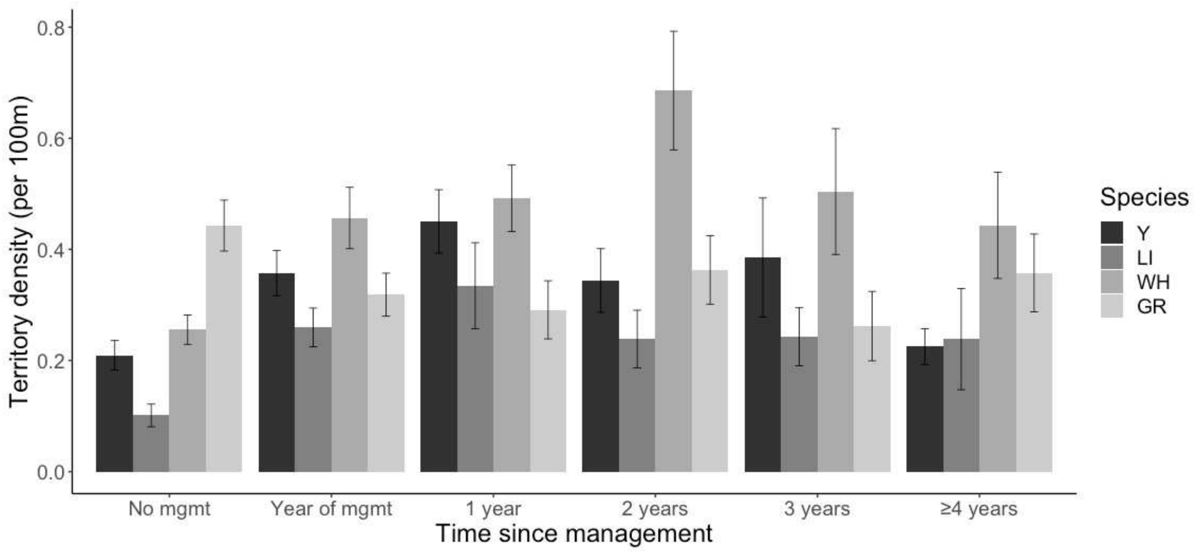

Figure 2 *Mean territory density per 100m hedgerow (±SE) for yellowhammers (Y), linnets (LI), whitethroats (WH) and greenfinches (GR) for the time since last management of a hedgerow. 'No mgmt' = no management has occurred since 2000, 'Year of mgmt': management occurred that year, '1 year': 1 year since management, '2 years': 2 years since management, '3 years': 3 years since management and '≥4 years': 4 or more years since management.*

Wheat and field beans were not significant predictors of territory count for any of the four species modelled ($p > 0.05$; Fig. 3A & C; SI Table A.2), although generally the mean TD of yellowhammers, linnets and whitethroats was greater than for greenfinches under wheat and field bean cultivation (SI Table A.4). The presence of oilseed rape was a significantly positive predictor of yellowhammer, linnet and whitethroat territory count ($p < 0.05$; Fig. 3B; SI Table A.2) and achieved an increase in mean TD by 102%, 138% and 92%, respectively (SI Table A.4). The effect of leaving fields without a main crop sown, e.g. when left for fallow or as grassland, were significant for greenfinch territory numbers shown as a trebling of mean TD but was found to be a significant negative predictor of counts in the linnet model (89.7% decrease in mean TD) (Figure 3D; SI Table A.2).

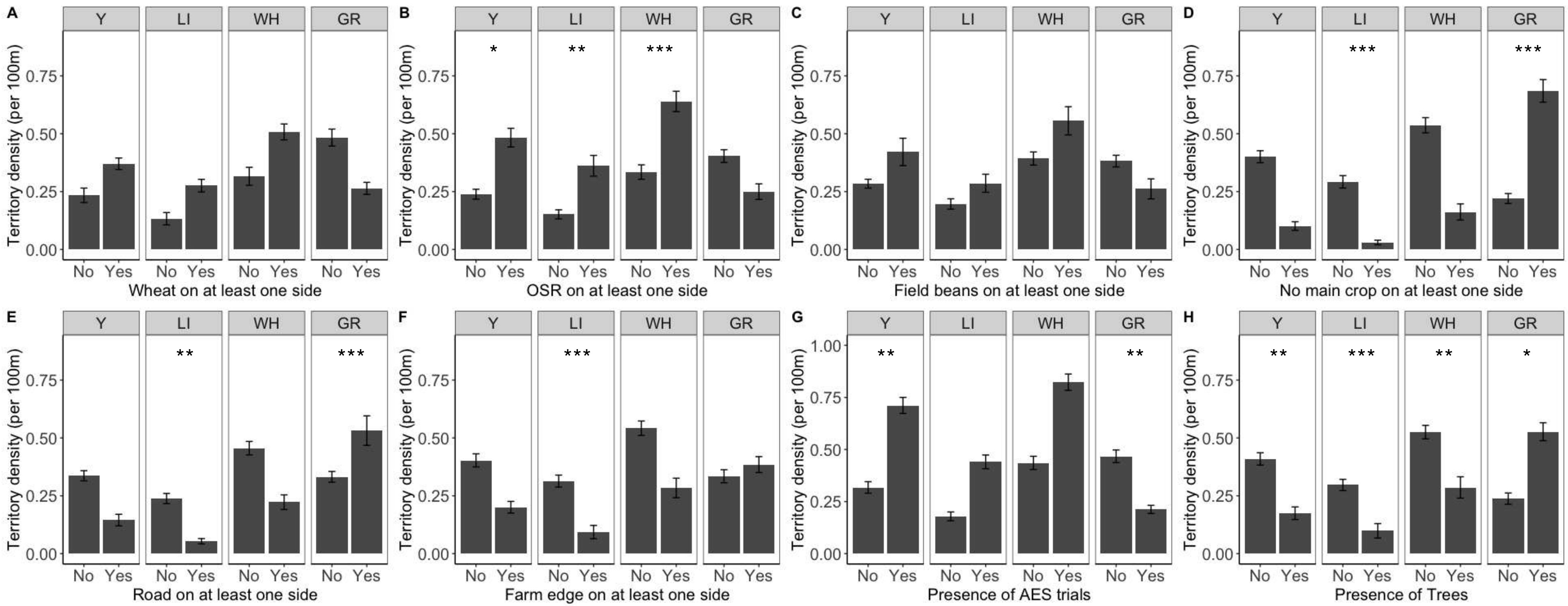

Figure 3 *Mean territory density per 100m hedgerow (± SE) of yellowhammers (Y), linnets (LI), whitethroats (WH) and greenfinches (GR) for different in-field crops (A-C) or no crop (D), roadside (E) and perimeter (F) hedgerows, and in hedgerows with AES trials (G) or trees (H). OSR = oilseed rape; AES = agri-environment scheme. * = p < 0.05, ** = p < 0.01, *** = p < 0.001 (SI Table A.2).*

Tree presence in the hedgerow resulted in significant ($p < 0.01$; Fig. 3H) predicted declines in yellowhammer, linnet and whitethroat territory counts, with percentage decreases in mean TD of 56%, 67% and 55% respectively (SI Table A.2). However, trees were a significant ($p < 0.05$) positive predictor of greenfinch territory counts, more than doubling mean TD (Figure 3H). Similar species-specific patterns were observed for the presence of AES features, although the effects were reversed. There was a significant ($p < 0.01$) increase in yellowhammer territory numbers, with a 43.6% rise in mean TD, when AES trials were occurring close to the hedgerow. Conversely, a substantial decrease ($p < 0.01$) in count was found for greenfinches under these conditions, resulting in a 152.4%) decrease in mean TD (Fig. 3G).

Similar interspecies patterns in territory counts and mean density were observed when looking at the effects of roadside and perimeter hedges. Both parameters resulted in significant negative ($p < 0.01$) effects on linnet territory numbers, with a 79.2% and 71% decrease in mean TD for roadside and farm edge hedgerows respectively (SI Table A.2; Figure 3E-F). Roadside hedgerows were associated with a strong, significant ($p < 0.001$) increase in greenfinch territory counts and showed a 60.6% increase in mean density compared to non-roadside hedgerows (Figure 3E).

For all four species models achieved, the conditional R^2 values calculated were higher than the marginal R^2 values, indicating that the random effects added to the model (year and hedgerow ID) were not negligible (see SI Table A.2). The greenfinch model achieved the lowest R^2 values overall, thus, the results of this model should be considered with caution.

4. Discussion

The sustainable management of conventional arable systems for farmland biodiversity conservation requires the maintenance of highly productive crop yields, whilst being able to allocate space and resources for biodiversity (Batáry et al., 2015). Farmland birds rely on semi-natural boundaries, such as hedgerows, and in-field crops for invertebrate and seed food provision and nesting space (Wilson et al., 1999; Winspear & Davies, 2005). The results of this study indicate that variables linked to the surrounding habitat of hedgerows were the stronger drivers of territory numbers than the timing of hedgerow management. Interspecies differences were found and attributed to differences in species' behavioural ecology and territoriality.

Crops emerged as an important driver of territory number. There were significant positive effects of oilseed rape (OSR) being sown on the number of yellowhammer, linnet, and whitethroat territories. OSR provides seed-rich foraging grounds for granivorous species (i.e. yellowhammers and linnets), but also offers sites of increased invertebrate richness to insectivorous species, such as whitethroats (Winspear & Davies, 2005; Henderson et al., 2009). Previous research from Whittingham et al. (2009) found similar yellowhammer territory associations for Brassica fields, which were mostly sown with oilseed rape and earlier research from Green et al. (1994) corroborates this and the findings from this paper. Winter wheat, instead, was not a significant driver of territory number in any of the species models. Previous research has found negative effects of cereals on avian abundance, for example Firbank et al. (2003) and Henderson et al. (2009) observed consistently lower densities of foraging granivores and insectivorous birds in winter wheat plots.

Fields not sown with a main crop, for example when left as set-aside, in fallow or as grassland, were highly beneficial to greenfinches. However, the GLMM achieved suggests that less than a fifth of the variance in the greenfinch territory count data could be explained by the habitat variables used in the model and therefore these results should be interpreted carefully. Grassland areas provide a good source of invertebrate food during the breeding season and previous research on conventional arable farms showed mostly positive effects of set-aside on farmland bird abundance (Firbank et al., 2003; Whittingham et al., 2005). However, the findings of this paper suggest that both yellowhammer and whitethroat territory counts responded negatively to uncropped fields and that linnets showed a significant negative response. Research from Bracken and Bolger (2006) found similar results for whitethroats, suggesting that more individuals were found in agricultural fields compared to those used as set-aside. On the other hand, research from Davey et al. (2010) and Murray et al. (2002) suggests that linnets and yellowhammers, respectively, do utilise uncropped fields, particularly those with wild bird cover mix. Overall it is evident that diversifying crop rotations through the inclusion of break crops, such as OSR, and set-aside, grassland or fallow periods has numerous positive impacts on both invertebrate and bird abundance (Benton et al., 2003; Henderson et al., 2009; Davey et al., 2010) and should be an integral part of sustainably-managed conventional farming under future policy reforms.

Hedgerow management has been an integral part of farmland management policy, as hedgerow characteristics and management have been shown to be important to support farmland birds in arable landscapes (e.g. Arnold, 1983; Hinsley & Bellamy, 2000; Field et al., 2010; Morris et al., 2010). Our results, however, suggest that the management of hedgerows was not an important driver of territories for the four hedgerow specialists studied at Hope Farm, with only a weak, positive impact on whitethroat counts on a three-year management cycle. Similar findings were observed by Davey et al. (2010), where no significant associations between hedgerows managed under ELS and farmland bird numbers were found. Hedgerow management is integral to its functionality; in pastoral and mixed farming systems hedges are managed as stock fences and can provide shelter, in arable systems hedges are often managed to prevent shading of and water competition with adjacent crops (Barr et al., 1995) amongst other reasons. Our results indicate that the focus of future AESs should be on increasing the flexibility of time intervals between management events for hedgerows, such as four or five year management rotations, rather than every 2 or 3 years (Natural England, 2018). A farm-scale medium term hedgerow management practice may increase farmers' management flexibility (Siebert et al., 2006) and still be beneficial habitat for territory settlement for farmland birds.

The presence of trees or AES features in the field margins (e.g. nectar mixes, floral margins), was found to be a strong driver of territories, with different impacts for the species studied. For example, the presence of AES trials increased yellowhammer TD (>40% compared to without AES trials), whereas greenfinches responded negatively to AES features. Hinsley and Bellamy (2000) suggested that hedgerow value can be improved when associated to other boundary features, such as floristic margins, which could explain the results from the yellowhammer model. Moreover, Redhead et al. (2018) found an increase in the abundance and number of territories of breeding farmland bird species when AES features, including grass margins, wild bird seed and stubbles, were managed well over the previous winter (see also Field et al., 2010). Similar findings, but more specifically for yellowhammers were also observed by Burgess et al. (2014). The negative impact that AES trials appeared to have had on greenfinch territory numbers was likely a spatial effect, as their territories were often clustered near smaller fields left as grassland and where fewer AES trials were occurring. Hedgerows with trees were a significant driver of higher greenfinch territories number (120% increase in TD compared to without trees), whereas the other three species exhibited strong decreases in territory numbers in hedgerows with trees (45-67% drop in territory density). The effect of trees on territory numbers was evident even after including Hedgerow ID as a random effect. Greenfinches are farmland 'generalists' (Hinsley & Gillings, 2012), thus they are more likely than the other three species studied to utilise woodland copses and hedgerows with trees for nesting and foraging purposes. This supports previous research by Green et al. (1994) who found evidence of this particular finch species exhibiting preferences for boundaries with many trees when compared with yellowhammers, linnets and whitethroats, which prefer hedges with very few trees. These supporting findings indicate that interspecies differences in hedge tree preference are likely to drive territory numbers and density.

The effects of roadside hedgerows and hedges located at the farm perimeter were noticeable amongst all of the species considered. Hedges that ran alongside the main road were found to be optimal for greenfinch territories (61% increase in TD), but incurred a significant decrease in yellowhammer, linnet and whitethroat territories. Previous research from Green et al. (1994) and Fuller et al. (2001) also found that greenfinches formed territories in roadside hedgerows, attributing this to the close proximity of nearby residential gardens that may have left out bird seed. It has also been suggested that 'double hedgerows', the result of two hedges separated typically by a road, are important for birds visiting their nests whilst avoiding predators and that hedgerows close to villages may be avoided due to disturbance (David Buckingham, personal communication). Yellowhammers, linnets and whitethroats instead prefer hedges in open farmland, which could be the result of predator avoidance and disturbance in roadside and perimeter hedgerows.

The results observed suggest several driving forces in songbird territory numbers at Hope Farm and the interspecies differences found can be attributed to differences in behavioural ecology and territoriality. Yellowhammers, linnets, and greenfinches are resident species on arable farmland in the UK and can hold territories in field boundaries year-round (Hinsley & Gillings, 2012), whereas whitethroats are migratory (Fransson, 1998). Whittingham et al. (2005) showed that summer territory occupancy patterns of yellowhammers may be influenced by winter habitats, such as set-aside. This issue of latency in bird territory analysis is known, as birds often choose a territory and nest in it for the rest of their lives (Ambrosini et al., 2002).

Hope Farm, despite being a one-site sample, provides a unique insight into the possibilities of conventional arable farming being linked with wildlife-friendly practice and improved farmland biodiversity. Using a thirteen year time-series of hedgerow management, cropping rotation and various boundary characteristics, it has been possible to narrow down the major drivers of songbird territory density to boundary-specific habitat features, such as hedgerow trees and AES trials, and the use of diversified cropping rotations that include oilseed rape. There were clear interspecies differences in hedgerow habitat territory density, which suggests that future farm management and policy implementation should consider species-specific preferences for foraging and nesting habitat. The four passerines studied are found throughout the UK and across Europe during the breeding season (Cramp et al., 1994). Therefore, these findings may be representative of patterns occurring in conventional arable landscapes elsewhere in Europe, where loss of semi-natural habitat and rotation simplification have also been widely documented (Butler et al., 2010; Batáry et al., 2015), and of species with similar habitat requirements (Donald et al., 2001). Our study identifies OSR as important for several species, thus, we recommend its introduction as a component of future agri-environmental policy. Ideally, arable landscapes should present both crop and field margin heterogeneity within the territory limits of the target bird species, while the growth of trees should be limited to smaller areas at the farm edge, to favour species that benefit from the cover of trees, such as greenfinches.

Although the results of the modelling analysis suggest that hedgerow management was not an overly important driver of songbird density, with only weak positive associations found for whitethroats, the mean TD results (Fig. 2) indicate that whitethroats and greenfinches may benefit more from less frequent management (i.e. a 3-year cutting regime or no management at all, respectively), which is also a more cost-effective solution to future wildlife-friendly conventional farming. If the territoriality of farmland birds is significantly unaffected by the management of the hedgerows they nest and forage in, then perhaps attention should be shifted towards influencing more diverse cropping rotations, improving

AES features on-farm and keeping the farmed landscape more heterogeneous in future policy (e.g. Agriculture Bill).

Conclusions

Owing to the consistency and longevity of the dataset used, it has been possible to determine that AES implemented features, diversified cropping rotations and the presence of trees have been the major drivers of songbird territory densities over time, accruing both positive and negative effects on the passerines studied. These findings have potential impacts for changes in management on conventional commercial farms, such as reducing the frequency of hedgerow management and increasing the prevalence and protection of agri-environment practices, such as, floristic margins and mixed cropping, particularly with set-aside or grass in the rotation. These are important drivers to be considered under future post-Brexit agricultural policy (i.e. the Agriculture Bill).

Author Contributions

Megan Tresise: Conceptualisation, Methodology, Software, Validation, Formal analysis, Writing – Original draft, Writing – Review & editing, Visualisation, Project administration; **Sofia Biffi:** Conceptualisation, Methodology, Software, Validation, Formal analysis, Data curation, Writing – Review & editing; **Rob Field:** Conceptualisation, Resources, Writing – Review & editing, Supervision; **Les Firbank:** Conceptualisation, Writing – Review & editing, Supervision

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Drivers of songbird territory density in the boundaries of a lowland arable farm

Megan E. Tresise, Sofia Biffi, Rob H. Field, Les G. Firbank

Supplementary Information

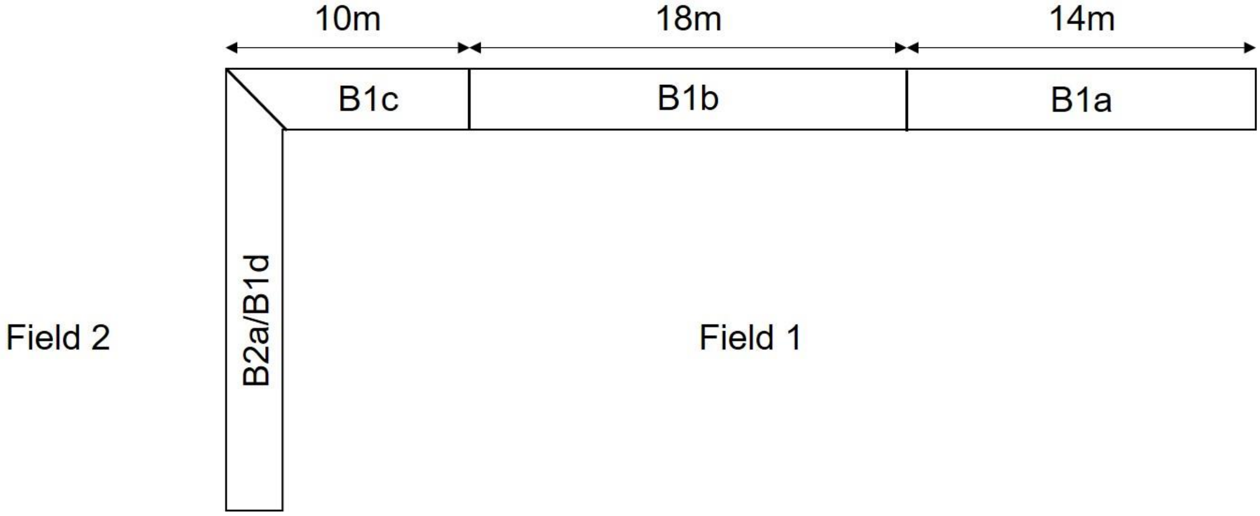

Figure A.1 *Schematic diagram of example hedgerow sections found at RSPB Hope Farm. Hedgerow boundaries are labelled according to the fields they partition. Hedgerow management was not applied uniformly along a hedgerow in every year, thus some hedges were divided into sections (e.g. B1a, B1b, B1c).*

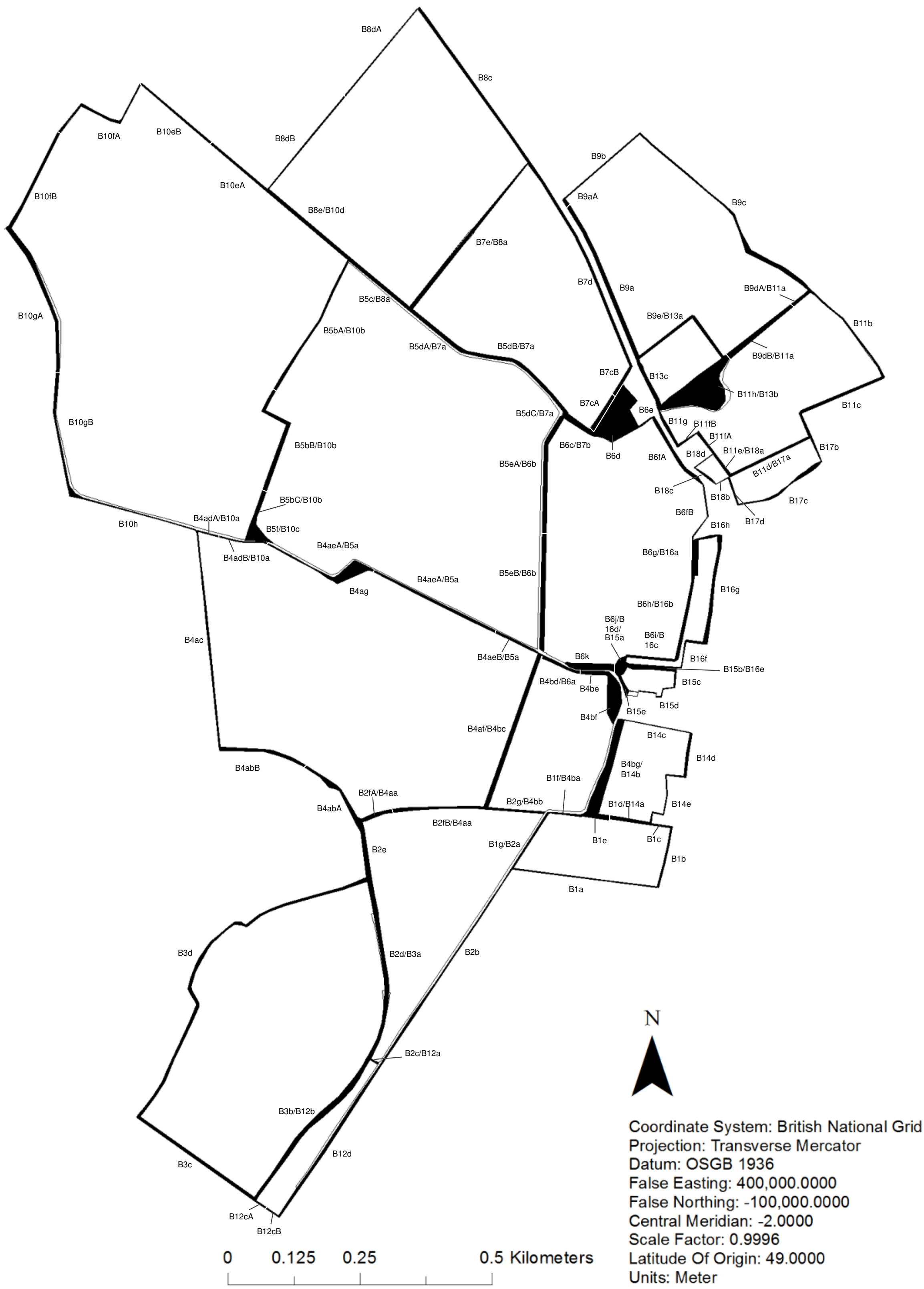

Figure A.2 *Map of RSPB Hope Farm showing boundary labels (n=101). Data provided by RSPB*

Table A.1 *Annual mean TD ± SE for each species*

Species	***2000***	***2001***	***2002***	***2003***	***2004***	***2005***	***2006***	***2007***	***2008***	***2009***	***2010***	***2011***	***2012***
YH	*0.17 ± 0.41*	*0.30 ± 0.60*	*0.22 ± 0.46*	*0.29 ± 0.67*	*0.29 ± 0.54*	*0.35 ± 0.60*	*0.30 ± 0.59*	*0.34 ± 0.58*	*0.46 ± 0.77*	*0.34 ± 0.48*	*0.40 ± 0.66*	*0.42 ± 1.09*	*0.19 ± 0.44*
LI	*0.12 ± 0.47*	*0.14 ± 0.44*	*0.13 ± 0.40*	*0.19 ± 0.52*	*0.20 ± 0.53*	*0.19 ± 0.41*	*0.25 ± 1.08*	*0.19 ± 0.50*	*0.21 ± 0.51*	*0.45 ± 1.14*	*0.25 ± 0.57*	*0.23 ± 0.47*	*0.24 ± 0.56*
WH	*0.28 ± 0.49*	*0.41 ± 1.09*	*0.39 ± 0.68*	*0.36 ± 1.11*	*0.38 ± 0.62*	*0.59 ± 1.22*	*0.40 ± 0.67*	*0.39 ± 0.61*	*0.36 ± 0.63*	*0.44 ± 0.66*	*0.61 ± 0.82*	*0.64 ± 1.20*	*0.29 ± 0.45*
GR	*0.49 ± 0.86*	*0.41 ± 0.75*	*0.39 ± 0.69*	*0.45 ± 0.82*	*0.33 ± 0.65*	*0.45 ± 0.77*	*0.40 ± 0.76*	*0.47 ± 0.86*	*0.32 ± 0.66*	*0.04 ± 0.26*	*0.40 ± 0.67*	*0.24 ± 0.59*	*0.25 ± 0.55*

Table A.2 *Results from the Generalised Linear Mixed Model likelihood analyses for each passerine species testing the effects of farm habitat variables on territory count. * = $p < 0.05$. ^ = marginal R^2, † = conditional R^2.*

Parameter		Coefficient ± SE	z-value	p-value
Yellowhammer	*14.3%^, 53.0%†*			
Time since management		-0.003±0.03	-0.09	0.9293
Wheat		0.17±0.15	1.12	0.2611
OSR		0.34±0.13	2.54	0.0111*
Field beans		0.20±0.14	1.45	0.1461
No Crop		-0.30±0.24	-1.25	0.2123
Road		-0.93±0.62	-1.50	0.1343
Edge		-0.55±0.39	-1.42	0.1569
AES trial presence		0.36±0.13	2.85	0.0044*
Tree presence		-1.06±0.39	-2.70	0.0070*
Linnet	*21.7%^, 31.2%†*			
Time since management		0.06±0.05	1.38	0.1664
Wheat		0.04±0.20	0.20	0.8399
OSR		0.43±0.15	2.78	0.0054*
Field beans		0.19±0.16	1.14	0.2537
No Crop		-1.83±0.37	-4.98	<0.001*
Road		-1.25±0.46	-2.72	0.0065*
Edge		-1.10±0.31	-3.53	0.0004*
AES trial presence		0.32±0.17	1.87	0.0609
Tree presence		-1.05±0.31	-3.36	0.0008*
Whitethroat	*14.9%^, 46.8%†*			
Time since management		0.08±0.03	2.62	0.0088*
Wheat		0.15±0.14	1.11	0.2690
OSR		0.41±0.11	3.55	0.0004*
Field beans		0.15±0.12	1.22	0.2231
No Crop		-0.43±0.22	-1.93	0.0540
Road		-0.60±0.48	-1.26	0.2092
Edge		-0.55±0.31	-1.76	0.0779
AES trial presence		0.07±0.10	0.65	0.5179
Tree presence		-0.94±0.31	-3.01	0.0026*
Greenfinch	*6.3%^, 11.9%†*			
Time since management		-0.01+0.04	-0.29	0.7713
Wheat		0.13±0.18	0.73	0.4685
OSR		0.14±0.19	0.74	0.4586
Field beans		-0.30±0.24	-1.26	0.2078
No Crop		1.25±0.24	5.30	<0.001*
Road		1.45±0.37	3.98	<0.001*
Edge		0.37±0.25	1.44	0.1492
AES trial presence		-0.44±0.16	-2.79	0.0052*
Tree presence		0.50±0.22	2.29	0.0220*

Table A.3 *Mean TD ± SE (per 100m) for all species under the different management time intervals. Corresponding to Figure 2.*

Species	***Time since management***	***Mean TD ± SE***
Yellowhammer	No management	**0.21 ± 0.03**
	Management that year	**0.36 ± 0.04**
	1 year since management	**0.45 ± 0.06**
	2 years since management	**0.34 ± 0.06**
	3 years since management	**0.39 ± 0.12**
	≥ 4 years since management	**0.23 ± 0.03**
Linnet	No management	**0.10 ± 0.02**
	Management that year	**0.26 ± 0.03**
	1 year since management	**0.33 ± 0.08**
	2 years since management	**0.24 ± 0.05**
	3 years since management	**0.24 ± 0.05**
	≥ 4 years since management	**0.24 ± 0.07**
Whitethroat	No management	**0.26 ± 0.03**
	Management that year	**0.46 ± 0.06**
	1 year since management	**0.49 ± 0.06**
	2 years since management	**0.69 ± 0.12**
	3 years since management	**0.50 ± 0.11**
	≥ 4 years since management	**0.44 ± 0.10**
Greenfinch	No management	**0.44 ± 0.05**
	Management that year	**0.32 ± 0.04**
	1 year since management	**0.29 ± 0.05**
	2 years since management	**0.36 ± 0.06**
	3 years since management	**0.26 ± 0.06**
	≥ 4 years since management	**0.36 ± 0.07**

Table A.4 *Mean TD* ± SE *(per 100m) for all species in hedgerows adjacent to in-field crops (wheat, OSR, beans), by roadsides or the farm perimeter, in hedges adjacent to AES trials or with trees. Corresponding to Figure 3.*

Species	*Parameter*	*Presence/Absence*	*Mean TD ± SE*
Yellowhammer	**Wheat**	Yes	**0.37 ± 0.02**
		No	**0.23 ± 0.03**
	OSR	Yes	**0.48 ± 0.04**
		No	**0.24 ± 0.02**
	Field beans	Yes	**0.42 ± 0.06**
		No	**0.28 ± 0.02**
	No crop	Yes	**0.10 ± 0.02**
		No	**0.40 ± 0.03**
	Road	Yes	**0.15 ± 0.03**
		No	**0.34 ± 0.02**
	Edge	Yes	**0.20 ± 0.02**
		No	**0.40 ± 0.03**
	AES trials	Yes	**0.71 ± 0.04**
		No	**0.32 ± 0.03**
	Trees	Yes	**0.18 ± 0.03**
		No	**0.41 ± 0.03**
Linnet	**Wheat**	Yes	**0.28 ± 0.03**
		No	**0.13 ± 0.03**
	OSR	Yes	**0.36 ± 0.04**
		No	**0.15 ± 0.02**
	Field beans	Yes	**0.29 ± 0.04**
		No	**0.20 ± 0.02**
	No crop	Yes	**0.03 ± 0.01**
		No	**0.29 ± 0.03**
	Road	Yes	**0.05 ± 0.01**
		No	**0.24 ± 0.02**
	Edge	Yes	**0.09 ± 0.03**
		No	**0.31 ± 0.03**

	AES trials	Yes	**0.44 ± 0.03**
		No	**0.18 ± 0.02**
	Trees	Yes	**0.10 ± 0.03**
		No	**0.30 ± 0.02**
Whitethroat	**Wheat**	Yes	**0.51 ± 0.03**
		No	**0.32 ± 0.04**
	OSR	Yes	**0.64 ± 0.04**
		No	**0.33 ± 0.03**
	Field beans	Yes	**0.56 ± 0.06**
		No	**0.39 ± 0.03**
	No crop	Yes	**0.16 ± 0.03**
		No	**0.54 ± 0.03**
	Road	Yes	**0.22 ± 0.03**
		No	**0.46 ± 0.03**
	Edge	Yes	**0.28 ± 0.04**
		No	**0.54 ± 0.03**
	AES trials	Yes	**0.82 ± 0.04**
		No	**0.44 ± 0.03**
	Trees	Yes	**0.29 ± 0.05**
		No	**0.53 ± 0.03**
Greenfinch	**Wheat**	Yes	**0.26 ± 0.03**
		No	**0.48 ± 0.04**
	OSR	Yes	**0.25 ± 0.03**
		No	**0.40 ± 0.03**
	Field beans	Yes	**0.26 ± 0.04**
		No	**0.38 ± 0.03**
	No crop	Yes	**0.69 ± 0.05**
		No	**0.22 ± 0.02**
	Road	Yes	**0.53 ± 0.06**
		No	**0.33 ± 0.02**
	Edge	Yes	**0.39 ± 0.03**
		No	**0.33 ± 0.03**
	AES trials	Yes	**0.21 ± 0.02**
		No	**0.47 ± 0.03**
	Trees	Yes	**0.53 ± 0.04**
		No	**0.24 ± 0.02**