Key habitat factors of breeding birds in agricultural hedgerow landscapes in East-Fryslân, The Netherlands, in European perspective – ecological evaluation and relation to agri-environmental schemes

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Modern agricultural landscapes suffer heavily from biodiversity loss. To counter this loss, it is important to understand the key factors that affect biodiversity in these landscapes. We studied the relationships between breeding birds and the habitat characteristics of the small-scale hedgerow landscapes of East-Fryslân, The Netherlands, a typical agricultural landscape that is under pressure from upscaling and habitat degradation. We questioned whether our findings collaborate the results of hedgerow studies from other countries. We also analysed whether agri-environmental schemes were effective for breeding birds. In this study, breeding birds and fifteen habitat factors were surveyed along 170 transects in two different regions in East-Fryslân in 2018. 37 bird species were identified, of which 19 were woodland species, 18 shrub species and 7 hedgerow specialists. We found five habitat characteristics to be key factors for breeding bird numbers. Four of these factors were intrinsic factors of the hedges (i.e. shrub cover, cover of brambles and nettles, crown width, hedge width at the base) and one spatial factor (i.e. number of hedge corners within a 150-m radius, corresponding to hedge intersections). Four key factors were the same for the two regions, but effect sizes differed between factors and species groups. As proxies for habitat volume (amount of habitat), the intrinsic key factors for hedgerow breeding birds in East-Fryslân correspond to those found in Britain and Eastern Europe, despite considerable differences in botanical composition, structure and management of the hedges. In contrast to studies on British hedges, we found mainly quantitative key factors and only one qualitative factor (cover of brambles and nettles). We found one spatial key factor (hedge intersections) and no correlation of bird numbers with density of hedges in the vicinity. We discuss the ecology of the key factors with respect to food provisioning and breeding. We also conclude that agri-environmental schemes favour key habitat factors and through this shrub birds. Implications of our findings are that traditional management favours breeding birds, but also that management should partly be extensified.

Key words: hedgerows, hedgerow characteristics, agricultural landscape, breeding birds, shrub birds, woodland birds, habitat factors, hedgerow management

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Modern agricultural landscapes suffer heavily from biodiversity loss (e.g. Donald *et al.* 2001, Voriseck *et al.* 2010, Staley *et al.* 2020), for example through the disappearance and degradation of natural elements in the landscape, like hedges. However, hedges have not disappeared everywhere in the agricultural landscape. In two regions of East-Fryslân in the north of The Netherlands, small scale hedgerow landscapes have persisted. Farmers in these regions apply Agri-Environmental Schemes (AES) to manage the hedges and associated biodiversity, such as breeding songbirds and bats. In order to preserve this biodiversity and to reach the AES goals, habitat requirements of target species need to be determined and management possibly adjusted. In the UK, several studies have examined the relationship between hedge characteristics and occurrence of birds (Arnold 1983, Osborne 1984, O'Connor 1984, Green *et al.* 1994, Parish *et al.* 1994, 1995, MacDonald & Johnson 1995, Fuller *et al.* 1997, Hinsley & Bellamy 2000, Redhead *et al.* 2013). In mainland Europe, there have only been a few studies on birds in hedgerow landscapes, e.g. in Germany (Batary *et al.* 2010) and Poland (Szymánski & Antczak 2013, Kujawa *et al.* 2019). In this study, we investigate which habitat factors correlate with breeding bird abundance in hedges in two regions of East-Fryslân (Northeast and Southeast). And we investigate whether our findings agree with the findings of British and other mainland studies, as there are important differences in management, structure and species composition of the hedges between countries. We also discuss the ecology of the key habitat factors and the implications of our findings for conservation management.

We expect that factors related to the shrub layer (e.g. shrub cover) correlate best with shrub bird abundance, and factors related to the tree layer (e.g. width of the tree crown) correlate best with woodland bird abundance. We expect that both quantitative (related to habitat volume) and qualitative (e.g. certain species of shrubs or trees) factors play a role. We also expect that spatial factors (number of corners, hedge density in the vicinity) influence bird abundance and relate to both shrub and woodland species (Lack 1988, Hinsley & Bellamy 2000, Nemethova & Tirinda 2005).

METHODS

Study area and hedgerow types

The study has been carried out in the east of the province of Fryslân in the north of The Netherlands. In the area two regions are distinguished, Northeast (NE) and Southeast (SE), with the town of Drachten in the middle at 53.10°N, 6.08°E (Figure 1). Regions NE and SE have a surface area of 25,000 and 40,000 ha, respectively. The landscape in both regions is domi-

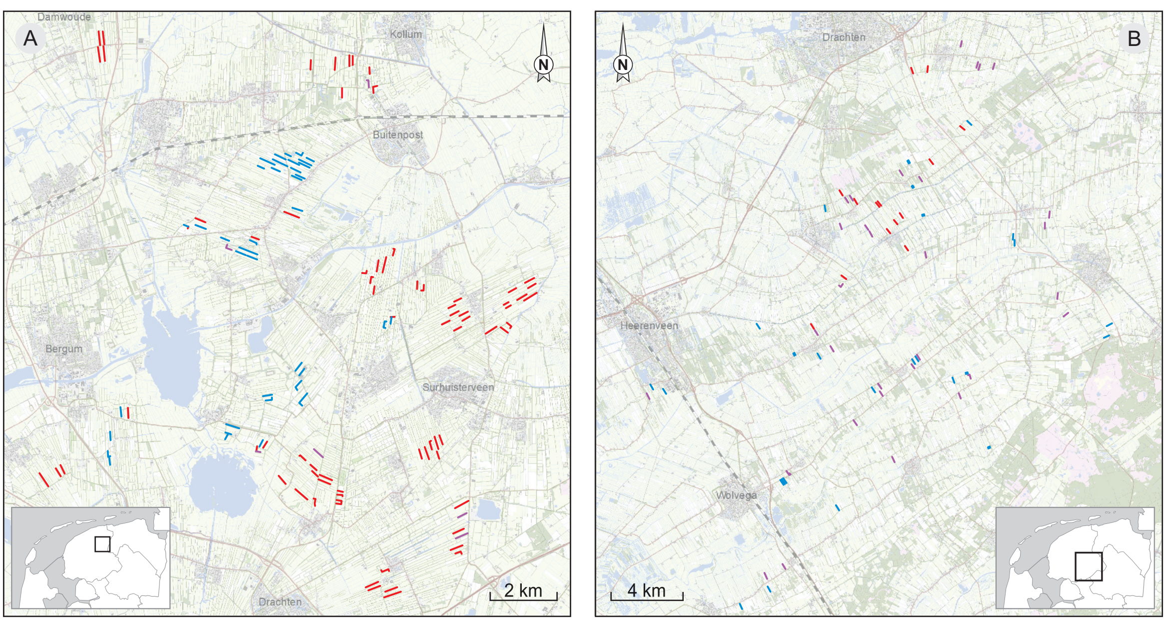

Figure 1. Location of the study regions, (A) Northeast NE and (B) Southeast SE, and the 170 transects along which data of breeding birds and habitat characteristics were collected. Orange lines are transects along alder hedges, blue lines are transects along banked hedges, purple lines are transects along wood strips.

nated by agricultural fields with hedgerows as linear boundaries between the grasslands.

The grasslands are utilised for dairy farming and the hedgerows were, until recently, managed for aesthetic and agricultural purposes. More recently, Agri-Environmental Schemes (AES) also aim to preserve biodiversity, especially breeding birds and bats. The hedges consist of three types: banked hedges, alder *Alnus* sp. hedges and wood strips (Figure 2). Banked hedges are formed by lines of trees and shrubs growing on an earth bank with a ditch at the base. The dominant tree species is Common Oak *Quercus robur*. Alder hedges are formed by lines of trees and shrubs dominated by Common Alder *Alnus glutinosa* trees. These hedges do not grow on banks, but along ditches, on one or both sides. Wood strips are strips, more than five meters wide, that have been planted with a mixture of shrubs and trees. Common Oak and Downy Birch *Betula pubescens* are the most abundant tree species.

The two regions are distinguished in this study because the landscape scale and hedge types are different. The landscape in NE has a smaller scale than in SE (Figure 1). In NE the proportion of hedge types in our study was 66% alder hedges, 31% banked hedges and 3% wood strips, whereas in SE it was 24% alder hedges, 31% banked hedges and 44% wood strips (Figure 1). Alder hedges are typical for Northeast-Fryslân; wood strips are typical for Southeast-Fryslân. Total length of alder hedges in NE is 2500 km and of banked hedges 300 km (in SE this is not known).

All hedge types in East-Fryslân are found on loamy, sandy soils. Alder hedges grow in moister conditions than banked hedges and wood strips. Well-developed hedges contain a herbaceous, shrub and tree layer and are suitable breeding habitat for many bird species. As a rule, the alder hedges are coppiced every 21 years, banked hedges every 25 years, with some trimming every seven years. Wood strips are irregularly cut. After coppicing, hedges have a shrubby structure during the first years of regrowth. Over the years the hedges grow tall, the trees allowed to grow until 21–25 years of age. Properly managed hedges also comprise individual standard trees: trees that are not cut at the end of the rotation but are allowed to grow distinctly older.

Frysian hedges differ from British hedges. Frysian hedges are coppiced every 21–25 years while British hedges are trimmed frequently (every few years) and kept short. The result is that the Frisian hedges are generally much higher (Green *et al.* 1994, MacDonald & Johnson 1995, Broughton *et al.* 2021). Hedges in lowland England are 1.9–3.2 m high on average, while Frysian hedges easily reach three to five times that height. British hedges are dominated by Common Hawthorn *Crataegus monogyna* (French & Cummins 2001), while in the Frysian hedges Oak or, in wetter habitats, Alder dominate. There are also differences in

Figure 2. Examples of (A) a banked hedge, (B) an alder hedge and (C) a wood strip with a track in the centre. A is an example of a hedge with large width at the base and large crown width, but moderate shrub cover and cover of brambles and nettles. B is an example of a hedge with relatively small crown width but large shrub cover and cover of brambles and nettles.

the species composition of the breeding bird community, as a consequence of different geographical regions (Oosterveld *et al.* 2017).

Survey methods

TRANSECTS

We collected data on breeding birds and on habitat characteristics in hedges in spring 2018 along 100 transects in NE and 70 transects in SE (Figure 1). Criteria for hedge selection were (1) homogenous structure, (2) located at least 200 m from another hedge that was monitored, (3) located at least 200 m from gardens, farm yards and woodlots, (4) evenly distributed over well managed and poorly managed hedges and (5) proportion of hedge types according to presence in the region. Mean length of the transects was 301 ± 150 m (±SD).

BIRDS

All bird species in the hedges were surveyed five times during the breeding season of 2018 using the breeding bird survey methodology of the Dutch National Common Bird Census (van Dijk & Boele 2011). In this methodology observations are collected that indicate territoriality, mostly song. For each species in each transect we did not calculate the number of territories, but we used the total number of territory indications across the five counts for analysis. The five counts were evenly distributed over the breeding period 1 April to 25 June, with approximately two weeks between each count.

HABITAT FACTORS

Habitat factors are defined as hedgerow characteristics that may govern the occurrence and abundance of breeding songbirds. Fifteen factors were identified as potentially affecting breeding bird abundance, based on literature and field experience (Table 1). We distinguished eleven 'intrinsic' factors and four 'spatial' factors. Intrinsic factors are characteristics of the hedges themselves, like cover of the shrub layer or of the tree crown. Spatial factors are characteristics of the landscape in the direct vicinity of a transect, like density of hedges within a certain radius. Habitat characteristics in NE were censused by a group of four persons, in SE by one person.

Data analysis

The relationship between bird numbers and habitat factors was analysed for three different groups of species (i.e. woodland species, shrub species, hedgerow species; Table 2) and not for individual species. We used groups to identify habitat characteristics that were of significant importance to songbird communities as a whole (guilds). Each species was classified as a woodland species, a shrub species or a hedgerow species, based on its nesting and habitat preference. Shrub birds prefer shrubby features in hedges, such as the young stages of regrowth after coppicing. Woodland birds prefer older growth for foraging in tree crowns and holes to breed in. Hedgerow species are species for which the hedgerow landscape of NE-Fryslân comprises a large part of the national population related to the area of the region (Oosterveld *et al.* 2017), so the region is of special significance for these species. This guild contains a selection of shrub and woodland species: five shrub species (Common Whitethroat *Sylvia communis*, Lesser Whitethroat *Sylvia curruca*, Icterine Warbler *Hippolais icterina*, Garden Warbler *Sylvia borin*, Song Thrush *Turdus philomelos*) and two woodland species (Common Redstart *Phoenicurus phoenicurus*, Mistle Thrush *Turdus viscivorus*). Two of the hedgerow species (Icterine Warbler and Mistle Thrush) are on the national Red List of threatened breeding birds (van Kleunen *et al.* 2017).

We used the total number of territory indications over the five surveys as a measure of breeding bird abundance. Relations between number of territory indications and habitat factors were analysed using a Poisson error distribution, which is suitable for count data. The regression analyses were done in the statistical software program R (R Core Team 2016), using the package 'stats'. Number of territory indications was modelled against the offset of log(transect length) to account for different transect lengths (i.e. number per km of transect). Poisson models used the default log link function. At the start, all independent factors were added into the model. Then, factors were sequentially removed from the model, after which the model fit was evaluated using Akaike's Information Criterion (AIC). This procedure aims to balance model fit against number of parameters in order to find the most parsimonious model. The backward method is the preferred method, because the forward method produces so-called suppressor effects. These suppressor effects occur when factors are only significant when another factor is held constant.

The resulting models were checked for the usual model assumptions, i.e. linearity, absence of multicollinearity and the absence of highly influential observations, following the guidelines given by Tabachnick & Fidell (2006) and Zuur *et al.* (2009). The first assumption was checked by QQ-plots of the residuals. Collinearity among variables was assessed using variance inflation factors (VIF; R package 'car'), where VIF values

Table 1. Habitat factors censused in this study.

Habitat factor	Description	Survey method	Ecological function
Intrinsic factors			
Type of element	banked hedge, alder hedge, wood strip	visual observation	
Under AES or not		information from the farmers' collective	AES would enhance bird numbers
Hedge width	width at the base of the hedge between fences	visually estimated in m (to the nearest half m)	amount of habitat
Shrub cover	% cover of the shrub layer up to four meter height, seen from aside	estimated visually in four classes 0–5%, 5–33%, 33–66%, 66–100%	cover breeding habitat feeding habitat
Cover of brambles and nettles	% combined cover of undergrowth of brambles *Rubus* spp. and nettles *Urtica* spp. seen from aside	visually estimated with 5% accuracy	cover breeding habitat, especially *Sylvia* warblers feeding habitat
Number of hawthorns, roses, mountain ash		counted in the field	cover breeding habitat
Number of tree and shrub species		counted in the field in four classes 1–2, 3–4, 5–10 and 10 or more species	habitat differentiation
Number of standard trees	a standard tree is a solitary tree that is left standing while coppicing the hedge. As a result it is older than the rest of the hedge	counted in the field	extra amount of habitat habitat differentiation
Length of vegetation of nutrient-poor conditions		visually estimated in four classes, 0–5%, 5–33%, 33–66%, 66–100% of total length of the transect	habitat differentiation
Length of species rich vegetation of moist conditions		visually estimated in four classes, 0–5%, 5–33%, 33–66%, 66–100% of total length of the transect	habitat differentiation
Tree crown width	measured as area of vertical projection of tree crown over full length of the transect, it is a measure of habitat volume	measured in m^2 from aerial photos from spring 2018 in a geografical information system (GIS)	amount of habitat
Spatial factors			
Use of adjacent fields	grassland, maize or other (for example potatoes)	registered in the field	feeding habitat influencing amount of insects in hedge
Presence or absence of a floristically diverse, adjacent field margin of at least 4 m wide	floristically diverse means a presence of a variety of grass species and a variety of herbs such as Cuckoo Flower *Cardamine pratense*, buttercup *Ranunculus* spp. and dock *Rumex* spp. over the majority of length of the transect	visually estimated	feeding habitat influencing amount of insects in hedge
Density of hedges in the vicinity	length of hedges in m within a radius of 150, 300 and 500 m around the transect	derived from aerial photos from spring 2018 in a geographical information system (GIS)	amount of habitat
Number of hedge corners in the vicinity	a measure of intersections between hedges: an intersection of two hedges has four corners, a T-junction has two. Number of corners within a radius of 150, 300 and 500 m	derived from aerial photos from spring 2018 in a geographical information system (GIS)	amount of habitat of extra quality

higher than 5 were considered to indicate collinearity and these variables were removed from the model. Observations with a particularly high influence on the model were identified by Cook's distance, using 0.5 as a threshold value.

We considered the significant factors selected by the models as the key habitat factors in predicting the number of bird territory indications.

For each model, pseudo R^2 values from the Poisson regression models (R package 'rsq') are given to indicate which percentage of the variance of the number of observations was explained by the model. The relative importance of each factor within the regression model is given by the level of significance and the incidence rate ratio (effect size), which is calculated as the exponent of the regression model coefficients. The values of the habitat factors were standardized (so that the mean = 0 and SD = 1) in order to compare effect sizes of different habitat factors. The effect size plots were made using the package 'jtools'.

Because of the differences in the hedges between NE and SE, we initially considered region as an interaction term in the analysis, but models appeared too complex. For that reason we analysed the regions separately.

The impact of agri-environmental schemes on both bird numbers and the most important habitat variables was tested using ANOVA analysis (aov function in R). This was done for the relevant species groups (woodland, shrub and hedgerow species) and the most important habitat variables (brambles *Rubus* sp. and nettles *Urtica* sp., shrub cover, crown width and hedge width). In addition, we tested for any interactions between AES and region.

RESULTS

Species diversity and abundance

Species diversity was higher in SE than in NE for woodland birds and shrub birds; diversity of hedgerow species was equal (Table 3). Average number of territory indications per km was in SE about two times higher than in NE for all three species groups.

Table 2. Breeding bird species observed during the transect surveys, with information on breeding habitat preferences and number of territory indications. Species groups are based on habitat preference and typical nest location following Cramp (1985, 1988, 1992, 1993), Cramp & Perrins (1994a,b), Cramp & Simmons (1980): t = tree breeding, g = ground breeding, b = breeding in buildings, c = cavity breeding, sc = scrub breeding, sh = shrub breeding, bold = hedgerow species in NE. Numbers of territory indications in the two regions are added between parentheses, for example (sh, 11, 4) means the species is a shrub breeder, there were 11 territory indications in NE-Fryslân and four territory indications in SE-Fryslân.

Shrub species	Woodland species
Lesser Whitethroat *Sylvia curruca* (sh, 11, 4)	Short-toed Treecreeper *Certhia brachydactyla* (c, 2, 7)
Willow Warbler *Phylloscopus trochilus* (g, 15, 6)	Eurasian Hobby *Falco subbuteo* (t, 1, 2)
Marsh Warbler *Acrocephalus palustris* (sc, sh, 1. 0)	Common Buzzard *Buteo buteo* (t, 0, 5)
Eurasian Bullfinch *Pyrrhula pyrrhula* (sh, t, 0, 1)	Eurasian Jay *Garrulus glandarius* (t, 11, 18)
Common Whitethroat *Sylvia communis* (g, sh, 41, 41)	Yellowhammer *Emberiza citrinella* (g, sh, 0, 48)
Dunnock *Prunella modularis* (sh, 10, 13)	**Common Redstart** *Phoenicurus phoenicurus* (c, 11, 5)
Willow Tit *Poecile montanus* (c, 0, 1)	Great Spotted Woodpecker *Dendrocopus major* (c, 2, 5)
Common Blackbird *Turdus merula* (sh, b, 42, 72)	**Mistle Thrush** *Turdus viscivorus* (t, 1, 1)
European Robin *Erithacus rubecula* (g, sh, b, 3, 31)	Wood Pigeon *Columba palumbus* (t, 5, 10)
European Goldfinch *Carduelis carduelis* (sh, t, 3, 1)	Great Tit *Parus major* (c, 70, 114)
European Greenfinch *Chloris chloris* (sh, t, 0, 2)	Blue Tit *Cyanistes caeruleus* (c, 14, 78)
European Stonechat *Saxicola rubicola* (g, 1, 8)	Spotted Flycatcher *Muscicapa striata* (t, c, b, 0, 1)
Icterine Warbler *Hippolais icterina* (sh, 9, 3)	Tree Sparrow *Passer montanus* (c, 7, 6)
Long tailed Tit *Aegithalos caudatus* (sh, 0, 3)	Common Starling *Sturnus vulgaris* (c, 2, 6)
Garden Warbler *Sylvia borin* (sh, 19, 69)	Chiffchaff *Phylloscopus collybita* (g, sc, sh, 80, 115)
European Wren *Troglodytes troglodytes* (sh, b, 84, 55)	Tree Pipit *Anthus trivialis* (g, 1, 7)
Song Thrush *Turdus philomelos* (sh, 11, 8)	European Pied Flycatcher *Ficedula hypoleuca* (c, 0, 3)
Blackcap *Sylvia atricapilla* (sh, 19, 104)	Common Chaffinch *Fringilla coelebs* (t, 2, 44)
	Carrion Crow *Corvus corvus* (t, 12, 11)

Key habitat factors

Goodness-of-fit for the most parsimonious regression models for the different species groups was reasonably good, with the exception of hedgerow birds in NE (R^2 = 0.04; Table 4). For the other species groups and regions R^2 ranged from 0.29 to 0.49.

The key habitat factor for woodland species in both regions was crown width. In NE, shrub cover and number of corners within a radius of 150 m from the transect were also key habitat factors. In SE, hedge width at the base of the elements was a key factor (all positive relationships; Table 4). In both regions, the effect size of crown width was largest compared to the other factors (Figure 3B,D). Selected models explained an equal amount of variance in numbers of territory indications for both regions (0.41 and 0.40).

Cover of brambles and nettles and hedge width at the base were key factors for shrub birds in both regions, and shrub cover additionally in SE (all positive relations; Table 4). Cover of brambles and nettles had by far the largest effect size in SE, but an equal effect size in the case of hedge width in NE (Figure 3A,C). The selected model for shrub birds in SE explained a larger amount of variance than in NE (0.49 vs. 0.29).

For the hedgerow birds in NE we were unable to find a fitting model; in SE there was a strong effect of cover of brambles and nettles on the number of territory indications of hedgerow birds (Table 4, Figure 3E).

Table 3. Average number of species (n) and territory indications per km (n/km) of the species groups per region (NE Northeast, SE Southeast).

	NE	SE
Woodland species (n)	14	18
Shrub species (n)	15	17
Hedgerow species (n)	7	7
Woodland birds (n/km)	10	21
Shrub birds (n/km)	13	20
Hedgerow species (n/km)	2.8	6.2

Effects of AES

Absence of AES in our final models is not because of collinearity with another habitat factor. Yet, AES may have an impact on bird densities because it correlates not just with one habitat factor but with multiple habitat factors. To study this potential multiple interaction effect we analysed the effects of AES on bird numbers and on habitat factors separately. This analysis showed that hedges under AES had higher densities of shrub birds ($F_{1,132}$ = 6.395, P = 0.0126), but not higher densities of woodland birds ($F_{1,132}$ = 1.19, P = 0.277) and of hedgerow birds ($F_{1,132}$ = 0.052, P = 0.821). In addition, hedges under AES had (although marginally significant) larger hedge width ($F_{1,128}$ = 3.746, P = 0.0551), higher shrub cover ($F_{1,132}$ = 3.143, P = 0.0785), higher cover of brambles and nettles ($F_{1,132}$ = 3.028, P = 0.0841), but not larger crown width ($F_{1,132}$ = 1.035, P = 0.311). Therefore, AES did indeed positively correlate with multiple habitat factors and via these with breeding densities of shrub birds. There were no significant interactions between AES and region for any of the bird groups or habitat factors.

Table 4. Habitat factors that correlate with territory indications of breeding birds in hedges in the regions of Northeast (NE)- and Southeast (SE)-Fryslân. Only significant factors from the most parsimonious models are presented. R^2 is proportion of variance explained by the model (goodness-of-fit). +: positive relation, +: P < 0.05, ++: P < 0.01, +++: P < 0.001. See Table 1 for an explanation of the factors.

Species group	R^2	Shrub cover	Cover of brambles/nettles	Crown width	Hedge width	Number of corners 150 m
Woodland species						
NE	0.41	+++		+++		++
SE	0.40			+++	+	
Shrub species						
NE	0.29		+++		++	
SE	0.49	+	+++		+++	
Hedgerow species						
NE	0.04					
SE	0.31		+++			

DISCUSSION

Habitat representation

The 15 potential habitat factors used in this study to explain bird numbers were selected based on local landscape characteristics favoured by breeding birds and on habitat studies from other countries (mainly Britain; e.g. Hinsley & Bellamy 2000). Our results demonstrate that indeed several of these factors are relevant for breeding songbirds in the hedgerows of East-Fryslân. The selected models explained variance in numbers of woodland birds reasonably well in both regions (R^2 = 0.40 and 0.41, respectively). For shrub birds this also accounted for SE (R^2 = 0.49), but to a lesser extent for NE (R^2 = 0.29). For hedgerow birds, explanation of variance of territory indications in NE was very poor (R^2 = 0.04); in SE explanation of the selected model was moderate (R^2 = 0.31). The poor model fit of hedgerow birds in NE may be explained by the fact that five of seven hedgerow species are shrub species and two are woodland species. The model for shrub species in NE had quite a low fit and in combination with different key factors for woodland birds this resulted in a very poor fit of the model.

Overall, we conclude that the selected habitat characteristics are relevant for the breeding songbirds of the hedgerows of East-Fryslân. In the next paragraph, we elaborate on the significant habitat key factors that were selected with our models for the three species groups.

Key factors and regional differences

Over all three species groups, five out of fifteen habitat factors were key factors, with three factors being important for two groups: shrub cover, cover of brambles and nettles, and hedge width at the base.

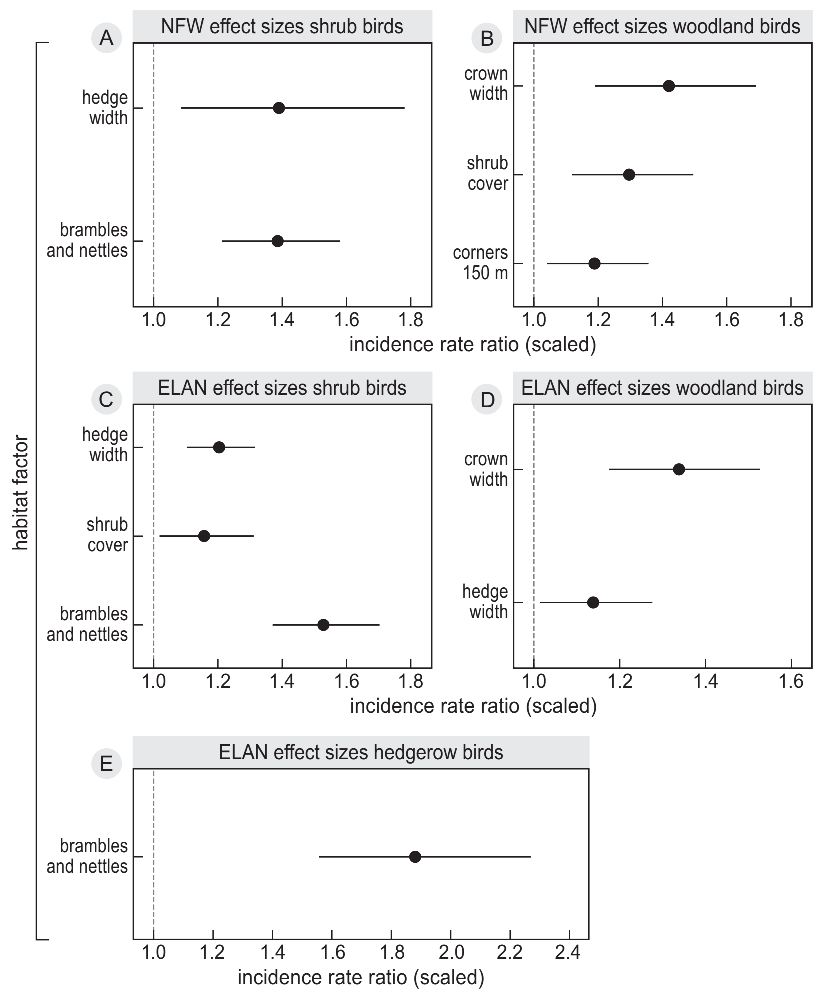

Figure 3. Effect sizes of key habitat factors for numbers of territory indications of (A) shrub birds and (B) woodland birds in Northeast-Fryslân, and territory indications of (C) shrub birds, (D) woodland birds and (E) hedgerow birds in Southeast-Fryslân.

For woodland birds, crown width had the largest effect size in both regions. In NE, shrub cover and number of hedge corners within a 150-m radius were additional key factors for woodland birds. In SE hedge width was an additional key factor. The effect of crown width is in accordance with our expectation that characteristics related to trees would be key factors for woodland birds. In that respect, shrub cover as an additional key factor for woodland birds (and not for shrub birds) in NE, and hedge width as an additional key factor in SE, is unexpected. This outcome may reflect that woodland species also use the shrub layer and lower parts of the hedges during breeding, e.g. for foraging. Number of corners was only found to be a key factor for woodland birds in NE and not in SE (see 'Relative importance of intrinsic and spatial factors' for further discussion).

For shrub birds, cover of brambles and nettles had the largest effect size in SE, and was a key factor in NE too. Hedge width was a key factor in both regions and shrub cover in SE. This outcome is in accordance with our expectation that key factors for shrub birds would be related to the shrub layer. That is to say, brambles and nettles in hedges usually grow in front of shrubs as a fringe vegetation. And a wider hedge at the base usually provides more space for shrubs to develop and for tree crowns to grow wider.

Larger average width of the transects in SE probably explains the higher numbers of birds in SE than in NE. In SE, 44% of the transects were wider than 5 m (the wood strips), while in NE 3% were wider than 5 m. Hedge width was important for both woodland birds (in SE) and shrub birds (in NE and SE).

The lack of significant key factors for hedgerow birds in NE may reflect the fact that the species meet relatively favourable breeding conditions in NE compared to other regions in The Netherlands, and that these favourable conditions may be a result of total landscape setting rather than individual habitat characteristics. On the other hand, cover of brambles and nettles is a specific key factor for hedgerow birds in SE.

Relative importance of intrinsic and spatial factors

Several studies found not only intrinsic factors of the hedges to be important for presence and abundance of breeding birds, but also spatial factors, such as presence in the vicinity of different crops, herb rich field margins, other hedges and wooded area (Green *et al.* 1994, Parish *et al.* 1994, MacDonald & Johnson 1995, Hinsley & Bellamy 2000, Stoate & Boatman 2002, Nemethova & Tirinda 2005, Vickery *et al.* 2009, Whittingham *et al.* 2009, Batary *et al.* 2010, Holt *et al.* 2010, Kujawa *et al.* 2019, Broughton *et al.* 2021). In our study four of the five key factors (shrub cover, cover of brambles and nettles, crown width and hedge width at the base) appeared to be intrinsic and one factor spatial (number of corners within 150-m radius). In other studies, relative importance is rarely analysed. Kujawa *et al.* (2019) found that in a Polish agricultural landscape shrub cover was by far the most important factor for breeding bird density and to a lesser extent spatial factors, such as an adjacent ditch and crops. In our study we also found that shrub cover was one of the key factors.

Only one spatial factor (number of corners) was important for woodland birds, in NE only, with a relatively small effect size compared to crown width and shrub cover. We found no effect of adjacent land use (grass, maize, other), adjacent herb rich field margins or density of hedges within a 150–500-m radius. An explanation of the absence of the effect of hedge density in the vicinity of the transects may be that the landscape in both regions is quite homogenous, so hedge density does not differentiate between transects. Absence of effects of adjacent land use and herb rich field margins are surprising because these effects are often found (review in Hinsley & Bellamy 2000) or sometimes even dominant, for example effects of land cover in Southwest England (Broughton *et al.* 2021)

Ecological evaluation of key factors

Shrub cover, cover of brambles and nettles, and hedge width at the base were key factors for two out of three species groups.

Shrub cover had a larger effect in NE (1.3 on woodland birds) than in SE (1.1 on shrub birds). This difference was not due to a higher cover in the hedges in NE (measured in the same transects in 2019; Oosterveld *et al.* 2020), but the presence of flowering shrubs such as hawthorn *Crataegus* sp. and roses *Rosa* sp. may explain this difference. Hawthorns were twice as abundant in NE-hedges and roses six times, compared to SE (Oosterveld *et al.* 2020). These flowering shrubs offer good feeding and nesting opportunities for songbirds (Moore *et al.*, 1967, Walker *et al.*, 2005, Staley *et al.* 2012). On the other hand, we included number of hawthorns and number of roses as separate habitat factors in the analyses, and they were not selected in the best models. Other factors may play a role too, for example dimensions of the hedge. In the narrower banked and alder hedges of NE, with less habitat volume than the wider wood strips, shrub cover possibly outweighs shrub cover in wood strips.

Cover of brambles and nettles was the key factor with the largest effect of all factors on shrub birds (in NE together with hedge width). Its significance presumably lies in its dense structure and thorny character (of bramble), which provide safe feeding and nesting locations. Its significance may also lie in the rich flowering of brambles that attracts many insects in the breeding season as food for the insectivorous bird species. This vegetation type was found to be important for nesting Common Whitethroats in several studies (Persson 1971, Mason 1976, Halupka *et al.* 2002, Szymańsky & Antczak 2013). Common Whitethroats were fairly common in our transects, contributing much to the number of territory indications of shrub species.

Hedge width at the base was a key factor for shrub birds (in both NE and SE) and for woodland birds (in SE; though of moderate effect size compared to other key factors). In NE, hedge width had a strong correlation with hedge type (variance inflation factor VIF >5). This is because banked hedges are wider than alder hedges and in NE banked hedges hold about two times higher bird densities than alder hedges (Oosterveld *et al.* 2017). In SE, the high proportion of wood strips in the transects may explain the effect of hedge width. The large width of wood strips (>5 m) per unit of length compared to banked and alder hedges (1–4 m on average) offers more habitat volume, and hence more space to live for both shrub birds and woodland birds. This relation between habitat volume and bird abundance has been found in many studies (Arnold 1983, Osborne 1984, Green *et al.* 1994, Parish *et al.* 1994, 1995, MacDonald & Johnson 1995, Hinsley & Bellamy 2000, Fennessy & Kelly 2006, Whittingham *et al.* 2009, Siriwardena *et al.* 2012, Redhead *et al.* 2013, Graham *et al.* 2018, Hall *et al.* 2018, Kujawa *et al.* 2019).

Crown width is the key factor with the largest effect size for woodland birds in both regions. It implies different features in the two regions. In SE it is related to the wood strips more than five meter wide that are characteristic for the region (44% of the transects). These wood strips are rare in NE (3% is more than five meters wide). In NE, banked and alder hedges dominate and a higher crown width implies an older age of the hedge. Both wide wood strips and older hedges represent more volume of habitat compared to smaller and younger elements, and hence, more space to live for the (woodland) birds. The importance of older hedges for woodland species is understandable since older trees have more cavities to breed in and add micro habitat to a stand. Additional micro habitat provides extra opportunities for food, shelter and nesting (Peterken 1996, Bengtsson *et al.* 2000, Humphrey 2005).

The number of hedge corners within a 150-m radius in the surrounding landscape was a key factor for woodland species in NE. Hedge corners are related to hedge intersections, with four corners for cross intersections and two for T-junctions. The effect of hedge corners for woodland birds in NE corresponds to the findings of Lack (1988) and Nemethova & Tirinda (2005). These authors found that more hedge intersections resulted in higher densities of many breeding birds. This effect is thought to be related to territories being more compact at intersections, facilitating more efficient foraging, territory defence and escape from predators (Lack 1988). Nemethova &Tirinda (2005) found the effect mainly for shrub species such as Blackcap *Sylvia atricapilla*, Common Whitethroat, Lesser Whitethroat, Common Nightingale *Luscinia megarhynchos* and Icterine Warbler, and in accordance with our results for one woodland species, the Great Tit *Parus major*. Of five species that Lack (1988) found to have significantly higher densities at hedge intersections, three were shrub species (Eurasian Wren *Troglodytes troglodytes*, European Robin *Erithacus rubecula* and Common Blackbird *Turdus merula*) and two were woodland species (Great Tit and Blue Tit *Cyanistes caeruleus*).

The reason for the absence of a corner effect in SE may be the high proportion of wood strips (>5 m) and the larger scale of the landscape in SE. Probably the wide wood strips, with a milder micro climate than hedges, allow for more compact territories, so that the effect of corners is not detectable in SE. Another reason might be that there are less corners in the vicinity because of the larger scale of the landscape in SE than in NE.

Comparison with other countries

To our knowledge, relationships between breeding birds and hedge characteristics have been extensively studied in Britain and to a lesser extent in Eastern Europe (Poland, Czech Republic).

Fuller *et al.* (2001) found six species of breeding birds to be hedgerow specialists in England and Wales: Dunnock *Prunella modularis*, Common Whitethroat, Lesser Whitethroat, Common Linnet *Carduelis cannabina*, European Goldfinch *C. carduelis*, European Greenfinch *C. chloris* and Yellowhammer *Emberiza citrinella*. Of these species, two were found to be hedgerow specialists in NE-Fryslân too, namely the Common and Lesser Whitethroat (Oosterveld *et al.* 2017). The other specialist species in the UK were also present in the Frisian hedges, but did not appear to prefer this landscape (on a national scale). These findings are in line with the idea that guilds of hedgerow specialist breeding birds differ in composition over countries and geographical regions.

The key habitat factors for bird abundance in the Frisian hedges are in fact proxies for habitat volume. In British studies these proxies were also often found to be important for bird diversity and abundance, such as hedge width, hedge height, shrub cover and crown width (Arnold 1983, Osborne 1984, Green *et al.* 1994, MacDonald & Johnson 1995, Parish *et al.* 1994, 1995, Hinsley & Bellamy 2000, Fennesy & Kelly 2006). In the Czech Republic and Poland, vegetation volume, hedge width (Némethová & Tirinda 2005) and shrub cover (Kujawa *et al.* 2019), respectively, were found as key factors for breeding bird diversity and abundance in hedges. In our study also hedge width, shrub cover and another proxy of habitat volume, crown width, were found. Cover of brambles and nettles has not regularly been mentioned in other studies, but is also found in Western Poland to be important for breeding *Sylvia* warblers (Szymánski & Antczak 2013).

The effect of cover of brambles and nettles on shrub birds in both Frisian regions and on hedgerow birds in SE, though partly also related to habitat volume, is in fact the only qualitative aspect of the hedges among the key factors. Other qualitative factors, such as diversity of shrub and wood species, number of hawthorns, roses and mountain ash, number of standard trees, length of vegetation of nutrient-poor conditions and length of species rich vegetation of moist conditions, did not appear to correlate with bird numbers of any species group in East-Fryslân despite the fact that they were widely present. In British studies, qualitative factors correlated more often with breeding bird numbers, such as the presence of trees in hedges, number of woody species and presence of short vegetation in the herb layer (Hinsley & Bellamy 2000, Fennessy & Kelly 2006, Whittingham *et al.* 2009, Siriwardena *et al.* 2012).

In Britain, hedge density in the surrounding landscape has also been identified as an important factor for breeding bird abundance in hedgerows (review in Hinsley & Bellamy 2000; Whittingham *et al.* 2009). In our study, we did not find this effect for the species groups, not within any radius of the transects.

A possible explanation for the stronger effect of both qualitative factors and hedge density in the vicinity in British hedges may be the higher frequency of coppicing in Britain. At higher coppicing frequency, hedges are on average in a younger stage, having less habitat volume and habitat differentiation compared to less frequently coppiced hedges like in East-Fryslân. This younger stage of the hedges offers less habitat for an individual bird to establish its territory. In this situation songbirds in a specific hedge location may be more dependant of qualitative aspects of the habitat and may need more hedge length nearby to have enough habitat volume to establish a territory.

Effects of AES

In Britain, AES are found to be effective in enhancing numbers of priority farmland birds (in field edges; Bright *et al.* 2015). In our analysis of AES we found a positive effect of AES on shrub birds and we found (although marginally significant) larger width, higher shrub cover and higher cover of brambles and nettles in hedges under AES-contract compared to hedges without contract. AES in Fryslân means maintaining a coppicing cycle of 20–25 years, accompanied with management advice on, for example, additional planting of shrubs and reducing mowing of brambles and nettles. Central to the AES is maintaining coppicing instead of abandoning management or removing the hedge. Traditional coppicing in East-Fryslân (with its long cycle) favours shrub cover, a key factor for breeding birds in both regions. The positive effect of this traditional coppicing on breeding birds is evident. On the other hand, this coppicing management under AES does not allow hedges to grow old and to grow a large crown width, a key habitat factor for Frisian woodland species. In a British study, Staley *et al.* (2012) concluded that there are positive effects of longer coppicing cycles on food provisioning in breeding birds. Given the strong positive effect of crown width on woodland birds in our study, the AES should be amended to support stopping coppicing in order to let hedges grow old. When mature hedges with a wide crown evidently lead to reduced productivity in the adjacent field, this lost revenue could be compensated via the AES.

Management implications

Our findings have a number of clear management implications. To gain high numbers of breeding shrub, woodland and hedgerow birds, one should have hedges with a high shrub cover, high cover of brambles and nettles, large crown width, a large hedge width at the base and many hedge corners (i.e. intersections) within a 150-m radius in the vicinity. The management implications differ slightly between the two regions. And a general reservation may be relevant here. Our finding that several key factors from our study also apply to British hedges, suggests a wide validity of management implications. However, local circumstances and histories may need specific modifications of the implications.

Shrub cover is enhanced by periodic coppicing. Coppicing removes most of the tree layer of a hedge and stimulates dense regrowth of shrubs and trees, resulting in much shrub cover. Coppicing every 21–25 years is standard management in East-Fryslân and appears to be effective for increasing woodland bird abundance in NE and to a lesser extent for increasing shrub bird numbers in SE. So, to preserve breeding bird abundance in the hedges, the standard coppicing regime should be continued in both regions. The effect of shrub cover on woodland birds in NE and not in SE, may be influenced by the two times higher density of hawthorns and six times higher density of roses in NE-hedges (as these shrubs attract insects when flowering). This suggests that woodland bird abundance in SE-hedges can be enhanced by additional planting of hawthorns and roses.

A further management implication is to reduce mowing of brambles and nettles that grow as a fringe vegetation at the base of the hedge (beneficial for shrub birds in both regions and hedgerow birds in SE). This mowing is often done yearly as brambles and nettles grow over the electric fence, thus decreasing electrical power and effectiveness of the fence. However, when dense undergrowth is present, with hawthorns, brambles and nettles, an electric fence is not necessary. Another reason for frequent mowing is to oppose expansion of the shrub into the field. By informing farmers about the biodiversity benefits of shrub habitats, it may be possible to persuade them to refrain from mowing entirely or restricting it as far as the fence.

Implications of a positive effect of crown width differ between regions. In SE, the effect is caused by the wide wood strips. For enhancing bird numbers these strips could be made wider. Or more new strips could be planted relative to banked and alder hedges. The effect of crown width was also strong in NE. In the small banked and alder hedges that dominate in NE, it is related to older age of the hedges. An implication of the positive effect of crown width would be in NE to let the hedges grow older. Traditionally, coppicing in NE is carried out every 21–25 years to prevent hedges from growing so tall that they reduce productivity of adjacent fields. As a consequence, farmers will likely only accept older hedges when income, generated from biodiversity gains, would equal or exceed production loss. The AES could be amended in this way.

To let hedges grow older is contradictory to coppicing in order to create dense shrub. As both factors are key factors for breeding bird abundance, the contradiction can be solved by spatial distribution of the two management types. Locations where productivity loss in adjacent habitat is extraneous, e.g. along a minor road or a residual field corner, could be priority locations for letting hedges grow old. Or hedges with a north-south orientation with the least of shade at noon.

One could also plant wood strips in NE instead of banked and alder hedges, but this is not in line with the regional landscape characteristics of small hedges. The same applies for widening the hedges. To widen hedges in NE, would also be against regional landscape characteristics. An improvement that better matches regional characteristics, is, in the case of single-sided alder hedges (on one side of a ditch), to plant an additional hedge on the other side of the ditch. Formerly, double sided alder hedges were common, but for ditch cleaning many were transformed into single-sided ones.

The positive effect of hedge corners on woodland birds in NE means that intersections between hedges should be preserved or restored. For efficiency in grassland management, many intersections have been removed over time. And there is pressure to remove more. This tendency may be reversed, when a farmer generates income from biodiversity benefits that equals or exceeds production loss.

Our findings do not indicate that there should be different management strategies for the typical hedgerow species compared to the shrub and woodland birds. All management strategies mentioned above are also supportive of hedgerow species.

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SAMENVATTING

Onze agrarische cultuurlandschappen hebben zwaar te lijden onder het verlies aan biodiversiteit. Om dit verlies tegen te gaan, is het belangrijk om de belangrijkste factoren te kennen die de biodiversiteit in deze landschappen beïnvloeden. Wij bestudeerden in 2018 de relaties tussen broedvogels en habitatkenmerken van de kleinschalige coulisselandschappen van Oost-Fryslân, Nederland, een typisch agrarisch landschap dat onder druk staat van schaalvergroting en habitatdegradatie. We vroegen ons af of onze bevindingen overeenkomen met resultaten van heggenstudies in andere landen. We analyseerden ook of de regeling voor agrarisch natuurbeheer effectief is voor broedvogels. Tijdens dit onderzoek werden broedvogels en vijftien habitatfactoren geïnventariseerd langs 170 transecten in twee verschillende regio's in Oost-Fryslân. Er werden 19 bosvogelsoorten en 18 struweelsoorten vastgesteld, waaronder 7 houtwalspecialisten, We vonden vijf habitatkenmerken als sleutelfactoren voor broedvogelaantallen. Vier van deze factoren waren intrinsieke factoren van de singels en wallen (struikbedekking, bedekking van bramen en brandnetels, kroonomvang, breedte aan de voet) en één ruimtelijke factor (aantal hoekpunten binnen een straal van 150 m, overeenkomend met dwarsverbindingen tussen singels en wallen). Vier sleutelfactoren waren dezelfde voor de twee regio's, maar de effectgroottes verschilden tussen de factoren en de soortgroepen. Als maat voor habitatvolume (hoeveelheid habitat) komen de intrinsieke sleutelfactoren voor broedvogels in singels en wallen in Oost-Fryslân overeen met die in Groot-Brittannië en Oost-Europa, ondanks aanzienlijke verschillen in botanische samenstelling, structuur en beheer van de singels en wallen. In tegenstelling tot studies aan Britse heggen vonden wij vooral kwantitatieve sleutelfactoren en slechts één kwalitatieve factor (bedekking van bramen en brandnetels). We vonden één ruimtelijke sleutelfactor (dwarsverbindingen) en geen correlatie van vogelaantallen met de dichtheid van singels en wallen in de omgeving. We bespreken de ecologie van de sleutelfactoren met betrekking tot voedselvoorziening en broeden. We concluderen ook dat de regeling voor agrarisch natuurbeheer de belangrijkste habitatfactoren en daarmee de struweelvogels bevorderen. Implicaties van onze bevindingen zijn dat traditioneel beheer broedvogels bevordert, maar ook dat het beheer ruimte zou moeten laten voor het oud worden van bomen.

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