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Measuring difference in edge avoidance in grassland birds: the Corncrake is less sensitive to hedgerow proximity than passerines

Aurélien G. Besnard^{1,2} · Yoan Fourcade^{1,2} · Jean Secondi^{1,2}

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Abstract Edge avoidance is an important feature of habitat selection in grassland birds, as their density is usually reduced close to habitat boundaries. In many extensively managed European grasslands, fragmentation is caused by the presence of wooded hedgerows dividing meadows. Comparing the magnitude of hedgerow avoidance by co-occurring species is essential for the management of grassland areas and the implementation of efficient conservation schemes. We quantified hedgerow avoidance by the Corncrake and four grassland passerines in western France. As expected, all species avoided hedgerows, but the effect was less pronounced for the Corncrake. We hypothesize that this may reflect a lower predation risk towards the larger and most inconspicuous species. Alternatively, social communication in Corncrakes may be less impeded by wooded vegetation than in passerines. However, the mechanisms responsible for the observed pattern remain uncertain. Nevertheless, our study provides a general technique that can be applied to measure boundary avoidance. This information is important for policymakers

in their efforts to improve management guidelines, which often do not take edge effects into account.

Keywords Hay meadows · Ground-nesting birds · Whinchat · Yellow wagtail · Reed bunting · Corn bunting

Zusammenfassung

Unterschiede in der Meidung von Randstrukturen bei Grünlandarten: Wachtelkönige sind weniger empfindlich gegenüber der Nähe zu Hecken als Singvögel

Randeffekte sind ein wichtiges Merkmal bei der Habitatwahl von Grünlandarten, da sie in der Nähe von Habitatgrenzen normalerweise eine geringere Dichte aufweisen. In vielen extensiv bewirtschafteten Grünlandgebieten in Europa sind die Wiesen und Weiden durch Gebüsch- und Heckenstrukturen zerteilt, was in einer Fragmentierung dieser Flächen resultiert. Ein Vergleich des Umfangs der Heckenmeidung durch nebeneinander vorkommende Arten ist essentiell für das Management von Grünlandgebieten und die Implementierung effizienter Schutzkonzepte. Wir quantifizierten die Meidung von Hecken durch Wachtelkönige und vier weiteren Wiesensingvogelarten in Westfrankreich. Wie erwartet, mieden alle Arten Heckenstrukturen, wobei der Einfluss bei Wachtelkönigen weniger ausgeprägt war. Wir nehmen an, dass dies ein geringeres Prädationsrisiko zugunsten der größeren und unauffälligeren Art widerspiegeln könnte. Andererseits könnte durch Gebüschvegetation die soziale Kommunikation bei Wachtelkönigen weniger behindert sein als bei Singvögeln. Dennoch bleiben die Mechanismen, die für das beobachtete Muster verantwortlich sind, unklar. Gleichwohl bietet diese Studie eine allgemeine Technik, die zur Abschätzung der Meidung von Habitaträndern angewendet werden kann.

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A. G. Besnard and Y. Fourcade contributed equally to this work.

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✉ Yoan Fourcade
yoanfourcade@gmail.com

¹ GECCO, Université d'Angers, Angers, France

² UMR CNRS 6554 LETG, Université d'Angers, Angers, France

Diese wichtigen Informationen helfen Entscheidungsträgern Managementrichtlinien zu verbessern, die oftmals Randeffekte nicht mit einbeziehen.

Introduction

The fragmentation of ecosystems is one of the main drivers of biodiversity loss worldwide (Saunders and Hobbs 1991; Fischer and Lindenmayer 2007; Haddad et al. 2015). It often results from habitat destruction, which divides habitats into smaller and more isolated patches (Fahrig 2003). Fragmentation may also occur with the introduction of linear structures such as roads (Lesbarrères and Fahrig 2012) that reduce the size of continuous habitat patches. Fragmentation not only contributes to the disruption of connectivity within meta-populations (Baguette et al. 2013); it also alters the intrinsic characteristics of the remnant patches. Indeed, changes in the shape and size of habitat patches may lead to biodiversity loss due to the species–area relationship (Ryabicki and Hanski 2013)—the link between the number of species found in a habitat and its area—or through edge effects (Fischer and Lindenmayer 2007). Edge effects are changes in abiotic and biotic conditions at the border between two adjacent habitats (Murcia 1995) that can prevent the settlement of some species in areas close to the habitat boundary.

The edge effect phenomenon in birds has received considerable attention, particularly with respect to grassland birds, as this heterogeneous group faces a severe decline worldwide (Donald et al. 2001), largely caused by agriculture intensification and fragmentation by roads or urbanization. The habitats of grassland birds in many areas are subject to fragmentation by wooded patches and hedgerows that are otherwise considered beneficial for biodiversity. These landscape features contribute significantly to edge effects in many grassland bird species (Fonderflick et al. 2013). Because individuals tend to avoid settling near wooded hedges (Bollinger and Gavin 2004), local density is generally higher in large un-fragmented patches (Vickery et al. 1994). This pattern, extensively described in North American grassland birds (e.g., Imbeau and Desrochers 2002; Ribic et al. 2009; Sliwinski and Koper 2012), has often been attributed to higher parasitism and predation rates near hedges (Whittingham and Evans 2004). Empirical support of these hypotheses is scarce (Paton 1994; Davis et al. 2006; Benson et al. 2013; Perkins et al. 2013), and thus the process or combination of processes driving edge avoidance in grassland birds remains unclear. Regardless of the mechanism involved, studies have shown that patch size and hedgerow proximity are major predictors of distribution and breeding success for

grassland birds (Winter et al. 2006; Besnard and Secondi 2014). Therefore, the response of birds to the presence of hedges appears to be an important factor to consider in implementing conservation measures.

In most parts of the European Union, the management of grassland habitats of conservation interest is administered through agri-environmental schemes (AES), which were implemented to mitigate the effects of agricultural intensification (Kleijn and Sutherland 2003). Yet many grassland species continue to decline, and some habitats such as floodplain meadows are still threatened (Krause et al. 2011). Grassland-targeted AES usually favour extensive management through delayed mowing and banning or reducing the use of fertilization, with no consideration of the landscape context, which may strongly reduce their effectiveness. For instance, subsidizing extensive meadows in small parcels may fail to protect grassland birds that avoid the most fragmented areas (Besnard and Secondi 2014). AES would benefit, rather, from finer integration of habitat selection of target species and consideration of interspecific variation in that response as a means to optimize conservation measures.

In western France, the lower reaches of the Loire River catchment are covered by extensive hay meadows that host a number of bird populations, including the nationally endangered Corncrake (*Crex crex*), which is a species of conservation concern in western Europe (Crockford et al. 1997; Green et al. 1997). The decline of the Corncrake population caused by high mortality during mowing (Tyler et al. 1998) was the main reason for implementing AES on these floodplain grasslands. These measures were expected to benefit the entire grassland community (Wilkinson et al. 2012), including grassland passerines. While these species are known to be sensitive to patch size and hedgerow density (Besnard and Secondi 2014), responses to edge proximity—both among individual passerine species and in the Corncrake, the flagship species—have never been quantified. Since differences in landscape requirements among species remain unknown, it is difficult to determine whether the whole bird community is optimally protected by current conservation schemes. In the present study, therefore, we quantify and compare hedgerow avoidance by the Corncrake and the main passerine species of the study area, and we propose a new method for quantification of edge avoidance.

Materials and methods

Study area and species sampling

The study area covers ca. 50,000 ha of floodplains along the lower 200 km of the Loire River and its main

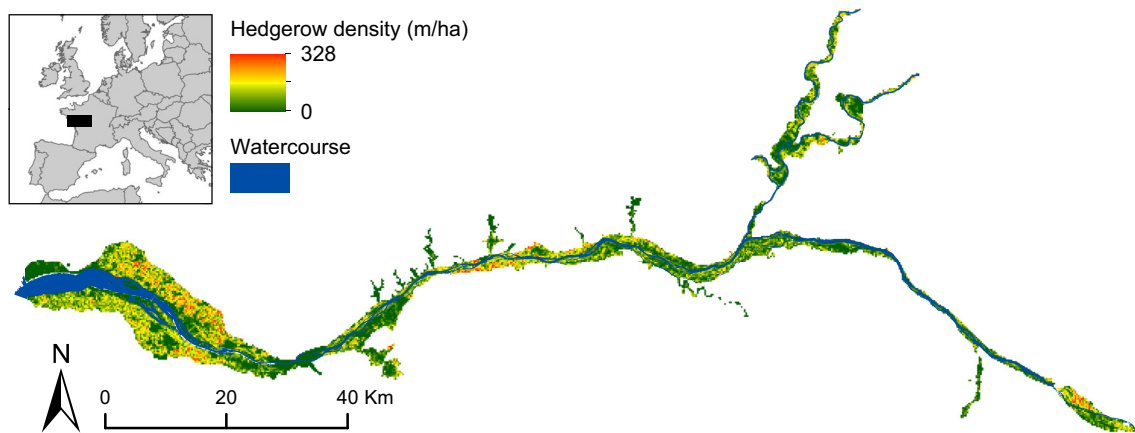


Fig. 1 Map of the study area showing the variation in hedgerow density (expressed in m/ha in each 250×250 m grid cell). The upper-left inset shows the location of the study area in western Europe

tributaries (Fig. 1). The primary habitat type is grassland, representing 76 % of the land use across the area (37,800 ha). Patches of crops and woodlands represent 7 % (3600 ha) and 16 % (8100 ha), respectively, of the entire study area. Traditional land use includes hedgerows, but their density varies greatly within the area, with patch size ranging from approximately 1 to 250 ha (Fig. 1). Five species dominate the grassland bird community: four passerines—the Whinchat (*Saxicola rubetra*), Corn bunting (*Emberiza calandra*), Yellow wagtail (*Motacilla flava*) and Reed bunting (*Emberiza schoeniclus*)—and a rail species, the Corncrake (*Crex crex*). Whinchat and Corncrake numbers have declined drastically over recent decades, in both the study area and most of western Europe, as a result of agriculture intensification (Fuller et al. 1995; Green et al. 1997). Delayed mowing has been implemented as part of agri-environmental schemes to mitigate the effects of grass cutting on Corncrake breeding, which has contributed to maintaining extensive practices. As a consequence, most grasslands within the study area are mown annually in June or July, with little to no fertilizer application.

Most of the grasslands were surveyed once during the 2009, 2010, 2011 or 2013 breeding seasons (April–June) to record passerine occurrences. Sites were visited during the peak of breeding activity, between sunrise and noon, in good weather conditions with low wind and no precipitation in order to ensure optimal detectability. Grasslands were travelled on foot, and all birds encountered by the observer and confirmed by visual contact (using binoculars and spotting scopes) were reported on IGN[®] 1/25,000 maps and then digitized on GIS [geographic information systems] software. This protocol allowed a nearly exhaustive survey of grassland sites, with constant sampling intensity. The Corncrake is nocturnal and remains hidden in vegetation, and could not be sampled using the same protocol as that used for passerines. The species is annually surveyed

by LPO Anjou, a local ornithological NGO [non-governmental organisation], but the most complete sampling of calling males is carried out only for national surveys, following a designated protocol. The most recent and complete national survey available was conducted in 2006, with the result that Corncrake data were a few years older than passerines and landscape data. However, land use can be considered constant in the area on this time scale, given the technical constraints due to flooding and AES incentives. Corncrakes were surveyed at night between 11 p.m. and 3 a.m. All meadows were visited at least twice during the breeding season (May–June). The location of each calling male was estimated by the observer from at least two distant points. All observations were compiled at the end of the season to remove duplicate individuals and to estimate territory centres. Because it is more difficult to determine the precise location of a Corncrake than of a passerine, we verified the robustness of our results to errors of location assignment in the field. Thus we created ten jittered datasets in which Corncrake occurrences were moved randomly within a 50-m buffer around their original locations, and the statistical models described below were also computed using these datasets.

GIS and statistical analyses

Land use was mapped by digitizing grassland, woodland and cropland patches using aerial photographs (BD Ortho[®] IGN, pictures taken in 2011) and ArcGIS 10 (Esri), and hedgerows, i.e., linear wooded structures, were similarly digitized. We assessed landscape characteristics around bird occurrences in buffers with a radius ranging from 10 to 1000 m, in increments of 10 m (400 buffer sizes in total). Two types of data were extracted from these buffers: (1) the proportion of grassland area in buffers compared to all habitat types (grassland, woodland and cropland in the

study area), and (2) hedgerow density, calculated as the total hedgerow length divided by the sum of the areas of grassland, woodland and cropland. In addition to bird locations, we extracted the same landscape data from a set of 1000 points randomly distributed in grasslands across the study area to determine the baseline if birds settled at random in habitat patches. All GIS analyses were performed using a Python routine under ArcGIS 10 (Esri).

In order to assess the response of each species to landscape at all scales, we computed statistical models linking grassland proportion and hedgerow density to buffer radius (log-transformed to linearize the relationship). For hedgerow density, we used a compound Poisson general linear mixed model with a Tweedie distribution of errors to account for the fact that our response variables contained an excess of null values. Grassland proportion was modelled with a linear mixed model after logit transformation of the response variable. Tweedie mixed models were computed using the “cplm” R package (Zhang 2014), while linear mixed models were computed using the “lme4” R package (Bates et al. 2014). We included spatial filters as co-variables in all statistical models to control for spatial autocorrelation. Spatial filters are eigenvectors extracted from the geographic coordinates of occurrences by a principal coordinate analysis on the distance matrix [spatial eigenvector mapping, Diniz-Filho and Bini (2005); Dormann et al. (2007)]. We selected eigenvectors based on the broken-stick method (Diniz-Filho et al. 1998), which assumes that eigenvectors whose observed eigenvalue exceeds the expected eigenvalue are adequate to describe spatial autocorrelation in the dataset. Spatial eigenvectors and their associated eigenvalues were calculated with the “codep” R package.

To test whether responses significantly differed among species, we first computed models using the full dataset with buffer radius, species and spatial filters (18 selected) included as fixed effects, while point IDs were included as random effects. For each response variable, we also computed models including only the spatial filters as fixed effect and point IDs as random effects, hereafter referred to as “spatial models,” thus describing only the spatial information regarding the distribution of points. We also computed an additional type of model excluding species identity from the fixed effects. We extracted the Akaike information criterion (AIC) from these models to highlight the most significant effects.

In a second step, to visualise the species-specific responses to landscape features, we computed the same types of statistical models for each species (and random points). Here, grassland proportion and hedgerow density were modelled as a function of buffer radius and spatial filters, with point IDs as random effect. Spatial filters were extracted for each dataset, resulting in the selection of two

filters for the Yellow wagtail and a single filter for the other species. Spatial autocorrelation in random points was best described by 17 filters. Again, a spatial null model was computed using only the spatial filters as fixed effect and was compared with the full model using AIC. Partial regression plots showing the relationship between the proportion of grassland or hedgerow density and the spatial scale (buffer radius) for each species were represented using the “visreg” R package (Breheny and Burchett 2015).

We then quantified the influence of hedgerow proximity on bird presence more precisely. For each bird occurrence and random point, we extracted the distance to the nearest hedgerow, and binned values in 20-m distance classes to obtain occurrence frequency as a function of distance to hedgerow. These raw data were transformed as a proportion of total occurrences across distances. Second, for each distance class and each species, we calculated the deviation between the observed proportion and the expected proportion of occurrences estimated by the random points. We then modelled the relationship between the deviation and the distance to hedgerow by nonlinear regression. Preliminary investigations showed that the most relevant function was a damped sine wave-shaped function with the following equation: $\text{difference vs. random} = A \times \exp(-\gamma \times \text{distance}) \times \cos(\omega \times \text{distance} + \varphi) - B$. The unknown coefficients were estimated using the nonlinear least squares estimate function implemented in R (R Development Core Team 2013). The distance under which the modelled proportion of bird occurrence was lower than the expected proportion was estimated using the “investr” R package (Greenwell and Schubert Kabban 2014).

Results

Overall, we recorded 1602 bird occurrences: 595 Whinchats, 182 Corn buntings, 273 Yellow wagtails, 212 Reed buntings and 340 Corncrakes. There was a significant species effect in the proportion of grassland area around occurrences, as shown by the difference in AIC values between the full model and the spatial model or the model that did not include species identity as explanatory variable (Table 1). Species models were all significantly more accurate than spatial models (Table 2, all $\Delta\text{AIC} > 12,000$), and revealed that all bird species tended to be preferentially found in areas where the proportion of grassland was larger than that observed at random locations (Fig. 2a). Corncrake response (intercept 5.65; buffer size coefficient -0.57) was in the same range as that of passerines (range: intercept 5.23–6.05; buffer size coefficient -0.64 to -0.47), and it is noteworthy that the Reed bunting was the

Table 1 Coefficients (\pm standard-error) and Akaike information criterion (AIC) for models predicting grassland proportion or hedgerow density around occurrences, using the full dataset of occurrences

| Models | Intercept | Log buffer radius | Corncrake | Whinchat | Corn bunting | Reed bunting | Yellow wagtail | AIC |
|--------------------------|---------------|-------------------|----------------|----------------|----------------|----------------|----------------|-----------|
| Grassland proportion | | | | | | | | |
| Spatial model | 2.271 (0.017) | | | | | | | 594,201.2 |
| Excluding species effect | 5.633 (0.019) | −0.565 (0.001) | | | | | | 442,034.2 |
| Full model | 5.922 (0.065) | −0.565 (0.001) | 0.213 (0.066) | 0.350 (0.052) | 0.549 (0.073) | 0.563 (0.073) | 0.631 (0.063) | 441,917.8 |
| Hedgerow density | | | | | | | | |
| Spatial model | 4.126 (0.012) | | | | | | | 2,402,263 |
| Excluding species effect | 2.256 (0.015) | 0.327 (0.002) | | | | | | 2,380,777 |
| Full model | 2.410 (0.028) | 0.328 (0.002) | −0.269 (0.057) | −0.677 (0.045) | −0.647 (0.062) | −0.971 (0.060) | −0.894 (0.053) | 2,373,925 |

All models include the 18 spatial filters that describe spatial autocorrelation. Random points are taken as reference for species effect

most sensitive species to grassland proportion while the Whinchat was the least sensitive.

With regard to grassland proportion, the density of hedgerows around occurrences was dependent on the species considered. The full model gave a much better fit than the spatial model and the model that did not take species into account, as revealed by AIC values (Table 1). Again, species models were significantly better than spatial models (Table 2, all Δ AIC > 1700). This was not true for models with random points, but as these include only random locations, we did not expect them to exhibit a response different from that of a simple spatial model. Interestingly, the responses of individual species highlighted that the Corncrake (intercept 2.85; buffer size coefficient 0.26) was less sensitive to hedgerow density than passerines (range: intercept −2.70–0.31; buffer size coefficient 0.56–1.08), especially at small scales, and its distribution was by far the closest to the distribution of random points (intercept 3.59; buffer size coefficient 0.19) (Fig. 2b). On the contrary, responses differed little between passerine species regardless of spatial scale considered. Although they departed slightly from the originals, the models computed using the jittered Corncrake datasets showed the same pattern, especially at small scales (supplementary Fig. S1), and had non-overlapping coefficients with passerines models (supplementary Table S1). We thus considered that our inferences were robust to the uncertainty related to Corncrake location.

All species had a lower proportion of occurrences close to hedgerows than expected by chance (Fig. 3). At 20 m, the proportion of Reed bunting and Yellow wagtail was 25.0 % lower than expected by chance, and a similar value was found for the Whinchat (−23.3 %). This deviation was less pronounced for the Corncrake (−11.0 %) and the Corn bunting (−15.6 %). The distance at which the proportion of birds crossed the random proportion of presence varied between 59 m (Corncrake) and 104 m (Reed bunting). The three other species had intermediate values (Whinchat 76 m, Corn bunting 85 m, Yellow wagtail 88 m).

Discussion

In this study, we compared the magnitude of hedgerow avoidance among four co-occurring bird species in western France. Although these four species were thought to rely on the same type of grassland habitat, our results provide evidence of interspecific variation in edge avoidance. We observed no clear evidence of differential habitat selection with regard to the proportion of meadow. In contrast, we found that all species exhibited a pattern of hedgerow avoidance, a response that had previously been suggested in these bird species (Besnard and Secondi 2014). We

Table 2 Coefficients (\pm standard error) for models predicting grassland proportion or hedgerow density around occurrences, for each dataset of occurrences (random points and five bird species)

| Models | Intercept | Log buffer radius | AIC | AIC sp |
|----------------------|----------------|-------------------|-------------|-------------|
| Grassland proportion | | | | |
| Random | 5.436 (0.033) | −0.546 (0.002) | 169,572.5 | 1,018,515.0 |
| Corncrake | 5.646 (0.050) | −0.565 (0.004) | 53,285.4 | 70,757.0 |
| Whinchat | 6.025 (0.040) | −0.641 (0.003) | 105,311.4 | 146,658.3 |
| Corn bunting | 6.046 (0.073) | −0.621 (0.005) | 30,240.9 | 43,162.1 |
| Reed bunting | 5.584 (0.061) | −0.506 (0.004) | 34,925.4 | 46,268.3 |
| Yellow wagtail | 5.230 (0.068) | −0.468 (0.004) | 46,836.9 | 58,857.8 |
| Hedgerow density | | | | |
| Random | 3.590 (0.020) | 0.194 (0.003) | 1,021,413.0 | 227,394.2 |
| Corncrake | 2.849 (0.039) | 0.261 (0.005) | 285,920.7 | 287,685.3 |
| Whinchat | 0.215 (0.030) | 0.650 (0.005) | 516,739.9 | 524,721.6 |
| Corn bunting | 0.307 (0.054) | 0.563 (0.010) | 159,178.9 | 163,252.5 |
| Reed bunting | −2.695 (0.061) | 1.079 (0.013) | 168,521.0 | 174,140.5 |
| Yellow wagtail | −1.750 (0.049) | 0.928 (0.010) | 226,751.8 | 236,333.3 |

The Akaike information criterion (AIC) is given for each model, as well as for spatial models including only spatial filters (AIC sp)

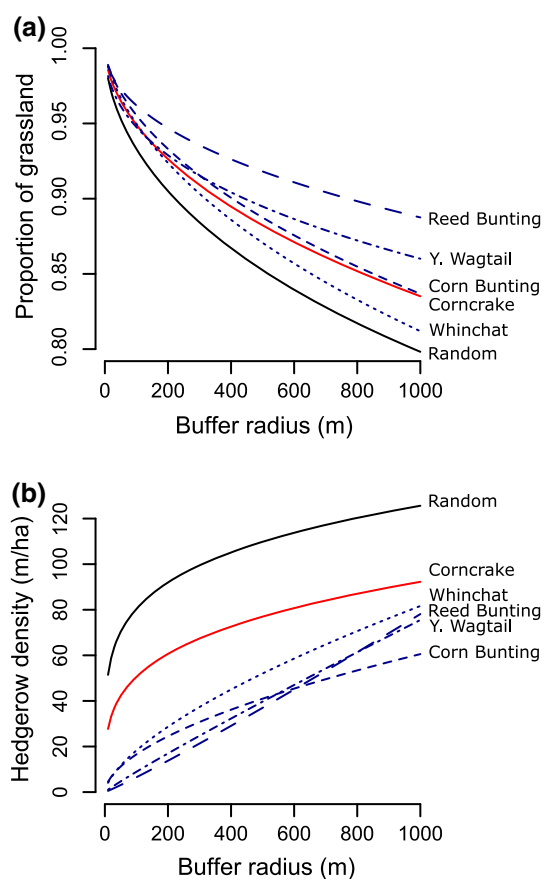


Fig. 2 Partial regression plot showing the response of the five species studied to **a** the proportion of grassland and **b** the density of hedgerows. The pattern resulting from 1000 random points is also plotted

quantified this pattern for the first time for each species, revealing that avoidance was weaker for the Corncrake than for passerines. Indeed, Corncrakes were observed in

areas with greater hedgerow density than passerines. Likewise, the distance to the nearest hedgerow below which fewer birds than expected were found was shorter for the Corncrake. These new results provide essential data for the management of grassland areas and the implementation of conservation schemes that can benefit the entire community of grassland birds.

The analysis of land use surrounding occurrences showed that birds settled in areas with a higher proportion of grassland than expected at random. This is congruent with several studies highlighting area sensitivity in grassland birds (Winter and Faaborg 1999; Johnson and Igl 2001; Ribic et al. 2009), i.e., they occur at higher densities in large patches of suitable habitats—grasslands in the present case—than in small and fragmented patches (Robbins 1979). The fact that the Reed bunting appeared to be the most sensitive species to the proportion of grassland is, at first glance, intriguing. Indeed, its main habitat is wetland rather than grassland per se (Brickle and Peach 2004). However, the maintenance of hay meadows in the area is often associated with high risk of flooding, which prevents the implementation of other agricultural activities. Therefore, large patches of grasslands are now frequently located within the wettest areas, flooded during several weeks or months per year, which could explain why Reed buntings are primarily found in such places rather than in more heterogeneous and drier areas. In general, area sensitivity might be explained by mechanisms involving patch size itself, such as higher food resources, microclimate, social attraction or vegetation structure (Ribic et al. 2009). However, this pattern is likely driven at least in part by edge avoidance, a phenomenon we highlighted with the apparent avoidance of hedgerows by our study species.

Historically, edge avoidance in grassland birds has been largely attributed to elevated predation risk close to parcel

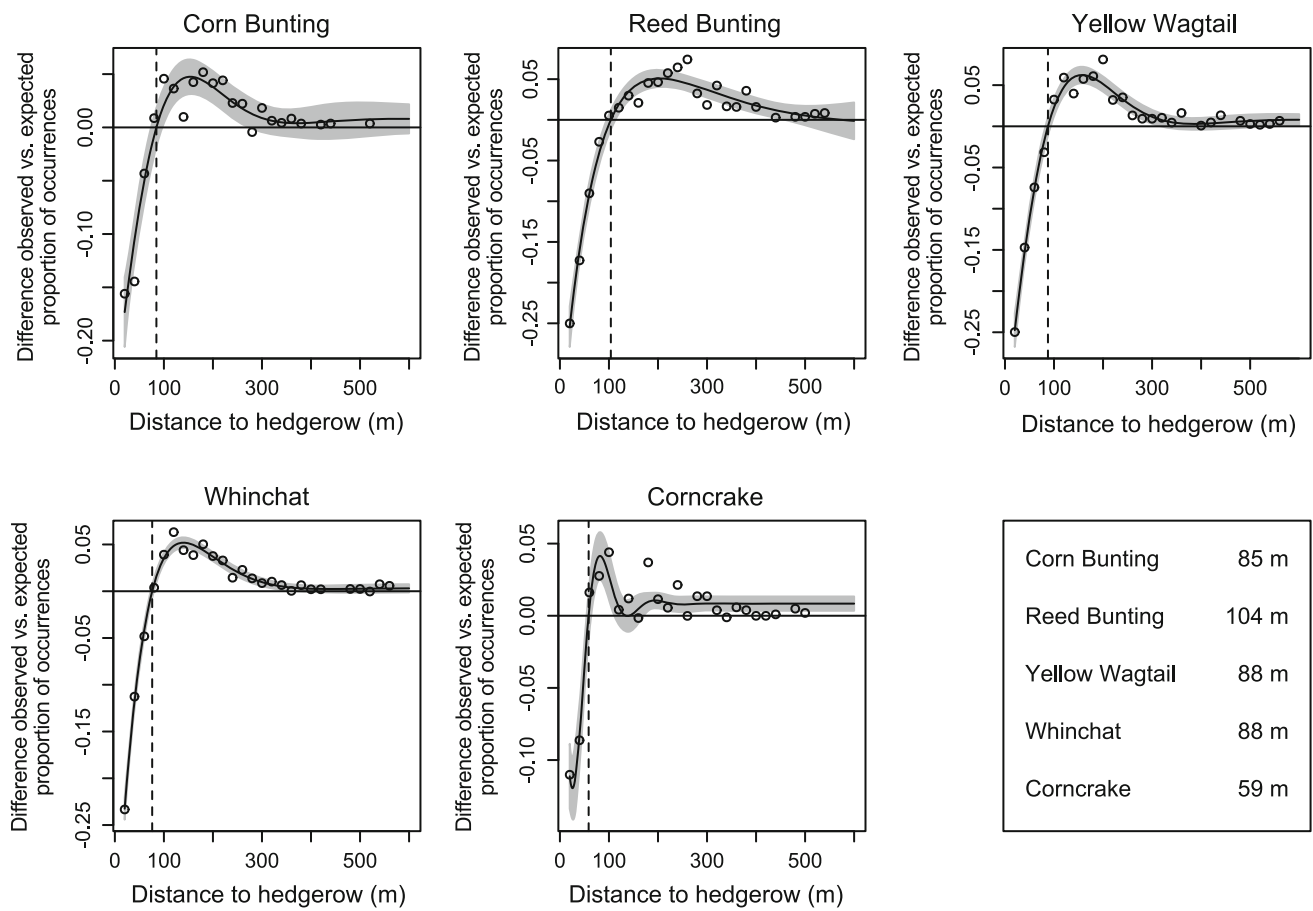


Fig. 3 Difference between the observed and expected proportions (based on 1000 random points laid in grassland patches) of bird occurrences plotted against the distance to the nearest hedgerow, for the five bird species. The shaded grey intervals show the fitted non-

linear regression and its 95 % confidence intervals. The dotted vertical line shows the distance at which bird occurrence proportion crosses the expected (horizontal line). The bottom-right box indicates this minimum distance to the nearest hedgerow for each species

boundaries, and especially wooded hedgerows (Whittingham and Evans 2004). However, most empirical studies have failed to demonstrate such a process (Lahti 2001; Renfrew et al. 2005). Nevertheless, this hypothesis may explain the differences observed between Corncrake and passerines. Although predation by feral cats or mustelids has been reported for adult Corncrakes (Green et al. 1997), their vulnerability to predators using hedgerows is likely lower than that for passerines. Indeed, passerine behaviour may increase the risk of predation by visual predators. While Corncrakes remain hidden in the vegetation and are essentially active at night (Schäffer and Koffijberg 2004), passerines are diurnal. They fly above the vegetation top and use the tallest swards as perching sites, which may aid in the detection of nest sites close to hedgerows (Ribic et al. 2009), or at least induce a higher perception of predation risk. Given their highly dissimilar body size (Corncrake 165 g; passerines 17–47 g), we might also assume a more limited susceptibility to small predators for Corncrakes than passerines.

An alternative and non-exclusive hypothesis is that differences in social behaviour could be responsible for the observed differences in hedgerow avoidance between Corncrake and passerines. Corncrake males emit loud broadband calls at night to attract mates (Tyler and Green 1996) and deter competitors (Budka and Osiejuk 2013). Such a signal propagating across dense vegetation (Ręk and Osiejuk 2011) and through hedgerows, thus enabling night surveys, allows for social communication even in highly fragmented areas. In this respect, although a strict grassland specialist, the Corncrake frequently makes use of isolated vertical structures like bushes as singing sites (Schäffer and Koffijberg 2004). In contrast, passerines rely on softer songs and visual displays (Odeen and Bjorklund 2003), which are partly or entirely blocked by vertical hedges. Moreover, conspecific attraction can be an important driver of habitat selection in grassland passerines (Ahlering et al. 2006), and thus the greater edge avoidance by passerine species may be a consequence of their tendency to cluster in large unfragmented patches to enhance social interaction.

In conclusion, we showed that the distribution pattern of co-occurring grassland birds differed according to the presence of hedgerows. Such vertical structures contribute to fragment habitat, rendering patches unsuitable when their shape or size does not allow settlement. The negative impact of hedgerows and wooded edges on habitat selection in grassland birds has been demonstrated in many species (Fletcher and Koford 2003; Renfrew and Ribic 2008). In response to these results, the removal of hedgerows in order to enhance the density of grassland passerine populations has been tested with success in North America (Ellison et al. 2013). However, this effect remains sometimes unrecognized, especially when hedgerows are traditional practices and have a high conservation value. Thus they are often encouraged in light of their positive impact on overall biodiversity (Batáry et al. 2010). Grassland birds, however, are highly specialized and need un-fragmented grassland patches in which to settle and breed. In this context, the conservation of hedgerows and grassland birds within the same area may result in conflicting effects that could be detrimental to the grassland bird community (Besnard and Secondi 2014). Moreover, in our study area, AES are strictly defined to match the requirements of the Corncrake phenology, and are implemented in its breeding areas. With the Corncrake considered here as an umbrella species, AES are expected to benefit other grassland birds as well. In view of our results, however, it appears that their habitat requirements differ, since some grassland patches hosting Corncrakes may be unsuitable for passerines because of the presence of hedgerows. Therefore, variation in edge avoidance should be better accounted for in the definition of protected areas. More broadly, a better integration of the landscape context would appear to be a valuable means of improving agri-environmental schemes.

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