

Research Article

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The importance of landscape heterogeneity and vegetation structure for the conservation of the Ortolan Bunting *Emberiza hortulana*

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Summary

Over the last decades, European farmland birds have strongly declined, mainly driven by agricultural intensification. The Ortolan Bunting *Emberiza hortulana* has suffered one of the most severe declines among farmland specialists. In order to maintain viable populations of the species in the long run, there is a vital need for evidence-based conservation measures. The main goal of this study was to detect the key drivers of breeding-territory selection and mating success of the species in an agricultural landscape in central Europe. We found that the landscape structure within the territories of Ortolan Bunting breeding pairs strongly varied from the overall habitat availability in the study area on both the territory and home-range scales. However, the environmental conditions also differed between the territories of breeding pairs and those of unpaired males. While landscape structure played an important role in breeding-territory selection, it had only weak effects on mating success. In contrast, crop type and vegetation height at potential nesting sites were important drivers of mating success. Overall, our study revealed that Ortolan Bunting has very complex breeding-habitat requirements. Only heterogeneous agricultural landscapes where (1) suitable song posts, (2) appropriate nesting sites, and (3) sufficient foraging habitats occur in close proximity are suitable for breeding. According to the findings of our study, agri-environmental schemes should primarily facilitate low-intensity farming practices that promote landscape heterogeneity, provide suitable nesting sites, and sustain a high abundance of invertebrate prey in farmlands.

Introduction

Over the last decades, terrestrial ecosystems all over the world have suffered an unprecedented decline of biodiversity (Foley *et al.* 2005, Stoate *et al.* 2009, Cardoso *et al.* 2020). Habitat loss due to land-use change is the most relevant driver behind this dramatic development. Since large parts of Europe's terrestrial surface are used for agriculture (CLC 2012), agro-ecosystems play an important role in biodiversity conservation (e.g. Henle *et al.* 2008, Sutcliffe *et al.* 2015). However, since the introduction of the European Common Agricultural Policies, land use in farmlands has been strongly intensified, especially in regions with productive soils (e.g. Donald *et al.* 2006, Reif and Vermouzek 2019). Agricultural intensification is particularly reflected by an increasing level of mechanisation and use of agro-chemicals, a simplification of crop rotation, and a large-scale expansion of monocultures such as maize (Benton *et al.* 2002, Robinson and Sutherland 2002, Sauerbrei *et al.* 2014, Fartmann *et al.* 2021a). Moreover, the aggregation of many small fields into a few larger ones has frequently caused a loss of landscape heterogeneity (Robinson and Sutherland 2002, Vickery and Arlettaz 2012, Šalek *et al.* 2021).

As a consequence, recent studies have revealed rapid declines of farmland specialists across various taxa (e.g. Newton 2004, Donald *et al.* 2006, Meyer *et al.* 2013, Bubová *et al.* 2015). Birds are well-established indicators of overall farmland biodiversity and the ecological health of agro-ecosystems (Donald *et al.* 2001, Morelli *et al.* 2014). Among birds, farmland dwellers have experienced the steepest losses (Donald *et al.* 2006, Busch *et al.* 2020, Burns *et al.* 2021). The main reasons for their steep decline have been structural changes in breeding habitats and a reduction in food availability and accessibility, which is especially true for insectivorous species (Vickery *et al.* 2001, Benton *et al.* 2002, Schaub *et al.* 2010). Moreover, long-distant migrants among farmland birds are particularly threatened as they are also subject to further threats outside their breeding ranges (e.g. Bairlein 2016, Gremion *et al.* 2022).

The Ortolan Bunting *Emberiza hortulana* is a long-distance migratory bird that breeds on the ground of arable fields throughout the vast majority of its European breeding range (Cramp and Perrins 1994, Glutz von Blotzheim 2011, Menz and Arlettaz 2011). In Europe, the species has undergone a significant population decline during the last decades, mainly driven by agricultural intensification in its breeding habitats together with illegal hunting during the autumn migration

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and environmental changes in their wintering grounds (Menz and Arlettaz 2011, Brambilla *et al.* 2017, Jiguet *et al.* 2019, BirdLife International 2021, Gremion *et al.* 2022). As a consequence, the Ortolan Bunting is listed as a species of European conservation concern (SPEC 2) and in Annex I of the European Birds Directive (BirdLife International 2017, 2021).

Previous studies aimed to identify habitat parameters which determine the occurrence of Ortolan Buntings in agricultural landscapes (e.g. Berg 2008, Menz *et al.* 2009, Vepsäläinen *et al.* 2005). Since habitat selection can vary strongly between different regions (Glutz von Blotzheim 2011), the habitat requirements of the Ortolan Bunting are still not fully understood (Menz and Arlettaz 2011). Male Ortolan Buntings exhibit high territory fidelity (Conrads 1969) and, in contrast to females, often remain in formerly used territories, even if they have deteriorated (Dale 2001). As a result, Europe's Ortolan Bunting populations are often characterised by a strongly male-biased sex ratio, which leads to reduced reproduction in fragmented populations (Dale 2001, Steifetten and Dale 2006, Jiguet *et al.* 2016). However, still little is known about the environmental factors affecting mating success.

The main goal of this study was to detect the key drivers of (1) breeding-territory selection and (2) mating success of the Ortolan Bunting in one of its last central European breeding strongholds (Prignitz region, north-eastern Germany). To address this issue, we compared the landscape structure between territories of breeding pairs (hereinafter referred to as BP), territories of unpaired territorial males (hereinafter referred to as UM), and randomly selected control samples (hereinafter referred to as CONTROL) on two different spatial scales: territory and home range. Furthermore, we assessed the impact of crop type and vegetation structure at potential nesting sites on the mating success of territorial males. Based on the findings of our study, we derived evidence-based recommendations for farmland management that will contribute to the long-term maintenance of the strongly declining bird species in agricultural landscapes.

Methods

Study species

The Ortolan Bunting is a passerine bird species with a western Palearctic breeding range (Menz and Arlettaz 2011, BirdLife International 2021). In Europe, breeding occurs in the southern part of the boreal zone, the temperate zone, and the Mediterranean Basin (Glutz von Blotzheim 2011, Keller *et al.* 2020, Jiguet *et al.* 2016). There is usually only one brood per season. However, replacement broods were reported from some areas of Europe (Conrads 1969, Menz and Arlettaz *et al.* 2011). The wintering grounds of the long-distance migrant are located in sub-Saharan Africa (Glutz von Blotzheim 2011, Jiguet *et al.* 2016). The population trend across its breeding range is negative (BirdLife International 2021).

The Ortolan Bunting is a ground-nesting bird that typically breeds in open habitats. The European populations are largely restricted to dry regions with well-drained soils (Conrads 1969, Menz and Arlettaz *et al.* 2011). In northern and temperate Europe, the vast majority of Ortolan Buntings breed in arable fields (Glutz von Blotzheim 2011, Menz and Arlettaz 2011).

On average, territories of Ortolan Buntings are ~3 ha in size (Conrads 1969, Berg 2008, Glutz von Blotzheim 2011). However, for foraging, the birds also often use larger home ranges up to 30 ha (Dale and Olsen 2002, Šalek *et al.* 2019). While adult Ortolan Buntings are mainly granivorous, nestlings strongly depend on

invertebrate prey (mainly Lepidoptera larvae, Coleoptera, and Orthoptera) (Conrads 1969, Glutz von Blotzheim 2011, Menz and Arlettaz 2011).

Study area

The study area comprises the north-western part of the Prignitz region, which is located in north-eastern Germany along the border between the federal states of Mecklenburg-Western Pomerania and Brandenburg (53°09'N, 11°46'E and 53°20'N, 11°73'E) (Figure 1). Compared with the central European average, the climate in the study area is dry and warm, with a mean annual precipitation of 615 mm and a temperature of 9.3°C (1981–2010, Station Lenzen [Elbe], 53°06'N, 11°29'E) (German Meteorological Service 2021). The landscape is characterised by a flat undulating relief on sandy soils of the Weichsel ice age (Marcinek and Nitz 1973). Arable land is the dominating land-cover type in the study area (CLC 2012). At the time of the study maize (30%) and winter rye (25%) were the predominant crop types in the study area, together covering more than half of the arable land. The remaining area of arable land was covered in equal parts by winter wheat (12%), potato (11%), winter barley (10%), and winter rape (9%). The agricultural landscape is interrupted by pine forests. Fields are frequently bordered by woody boundaries such as avenues, copses, hedgerows, tree rows, and single trees with old oaks being the dominant tree species (Bellenhaus and Fartmann 2009). The study area belongs to the EU Special Protection Area (SPA) Lower Elbe Valley. Along with

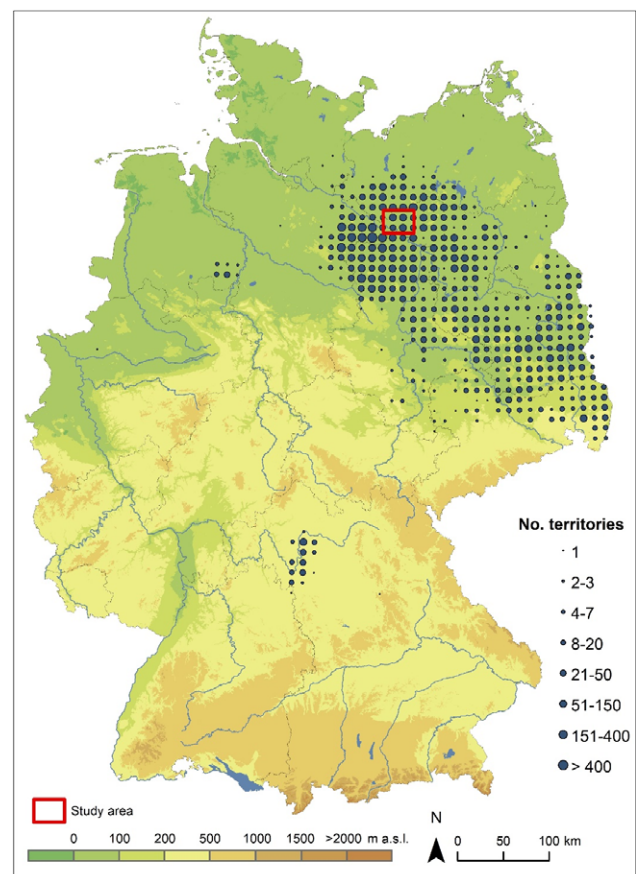


Figure 1. Breeding distribution and number of territories of the Ortolan Bunting in Germany according to Gedeon *et al.* (2014) and the location of the study area (Prignitz region).

the adjacent Wendland region, Prignitz represents the most important breeding stronghold of the Ortolan Bunting in central Europe (Gedeon *et al.* 2014) (Figure 1).

Bird surveys

Birds were sampled May–June 2012 using standardised territory mapping in five distinct subareas with a mean size (\pm SE) of 408 \pm 67 ha (range: 162–525 ha). Each subarea was visited five times between 05h00 and 10h00 with a time interval of at least seven days between each visit (Fischer *et al.* 2005). In accordance with Bibby *et al.* (2000), all observations of territorial behaviour, such as singing males, were recorded on a map (scale: 1:1,500). Simultaneous observations of territorial behaviour were used to separate territories of different birds in spatial proximity. Following the guideline provided by Andretzke *et al.* (2005), territory establishment was assumed if there were at least two observations of territorial birds at a minimum interval of seven days, one of which was in the period after 20 May.

Territories were classified into (1) those occupied by BP and (2) those of UM. Territories with birds giving prolonged alarm calls and territories with other evidence for breeding (i.e. adults carrying nesting material or feeding adults) were considered BP. Territorial males that were continuously singing throughout the breeding season but did not show any signs of mating were classified as UM (Andretzke *et al.* 2005, Steifetten and Dale 2006). To assess habitat preferences of the Ortolan Bunting, we compared BP with UM and CONTROL. The control samples were randomly selected using the tool “create random points” in ArcGIS 10.3. Altogether 55 control samples were analysed, which corresponded to the mean of the numbers of BP and UM. To make sure that the environmental conditions in the study area were adequately represented, we used stratified random sampling for the selection of the control samples (i.e. the number of control samples in the subareas was proportional to their area size).

Environmental parameters

Landscape structure

In June 2012, we recorded habitat types based on the German habitat classification scheme (Riecken *et al.* 2003) (see Appendix). According to the area requirements of the Ortolan Bunting (see above), the cover of habitat types was mapped on two spatial scales, i.e. territory (100 m radius, 3.1 ha) and home range (300 m radius, 28.3 ha), around the centres of all territories and control samples (Berg 2008, Šalek *et al.* 2019). Since previous studies detected an effect of crop type on the territory selection of the Ortolan Bunting (e.g. Conrads 1969, Berg 2008), arable fields were additionally classified according to their crop. Furthermore, the variable “woody boundary” was classified into “avenue”, “copse”, “hedgerow”, “tree row”, and “single tree”. Moreover, the habitat data were used to calculate landscape heterogeneity (H') within territories (BP and UM) and CONTROL samples using the Shannon Index (Morelli *et al.* 2013, Fartmann *et al.* 2018, Schwarz *et al.* 2018, Brüggeshemke *et al.* 2022):

$$H' = \sum_i p_i \ln p_i \text{ with } p_i = \frac{n_i}{N}$$

where N is the overall area of the territory or home range and n_i is the area of each habitat type within the two spatial levels. To avoid

overfitting, habitat types covering an area of less than 1% either within territories or home ranges were excluded from all following analyses.

Vegetation structure

We investigated the vegetation structure of potential nesting sites during the time of territory establishment (i.e. first observation date) for both BP and UM (see Appendix). In particular, we recorded crop type, vegetation cover (%), and height (cm) in the fields bordering the main song post of territorial males. Within these fields, vegetation cover and height were determined as the average value of three randomly chosen plots (2 m \times 2 m) per field. Since nesting sites of Ortolan Buntings are usually situated close to their song posts (Conrads 1968), these plots were situated within a distance of 5–20 m from the field edge (hereinafter referred to as potential nesting sites). The data of crop type at potential nesting sites were additionally used to calculate the Jacobs Index (Jacobs 1974): $D = (r - p) / (r + p - 2rp)$, where r is the proportion of a crop type used by BP and UM, respectively, and p the overall proportion of the crop type in the study area.

Statistical analysis

All statistical analyses were performed using R 3.4.1. (R Development Core Team 2021). In order to account for possible spatial autocorrelation, “subarea” was set as a random factor in all models. We additionally calculated Moran’s I statistics to test for spatial autocorrelation in model residuals using the R package *lctools* (Kalogirou 2020). To avoid multicollinearity, strongly intercorrelated variables were excluded prior to all multivariable analyses (Spearman rank correlations $|rs| > 0.6$) (see Appendix) (Dormann *et al.* 2013).

In all multivariable analyses, we applied model averaging based on an information–theoretic approach (Grueber *et al.* 2011). To identify the most important predictors of territory selection and mating success, all possible combinations of environmental parameters were tested resulting in a set of different candidate models. These candidate models were ranked based on Akaike’s information criterion corrected for small sample sizes (AIC_C) using the “dredge” function (R package *MuMIn*) (Bartón 2020). Only top-ranked models within $\Delta AIC_C < 3$ were used for model averaging (Grueber *et al.* 2011). Uninformative parameters were excluded from the model-averaging procedure (Arnold 2010). Model validation was performed using diagnostic plots (normality of residuals [Normal Q-Q] and non-linear patterns of residuals [residuals vs. fitted values]).

Differences in the area of habitat types and landscape heterogeneity between BP, UM, and CONTROL were assessed using univariate Linear Mixed-effects Models (LMMs) for each of the two spatial scales (territory and home range) (R package: *lme4*) (Bates *et al.* 2021). The respective environmental parameter was used as response variable, and territory type (i.e. BP, UM, and CONTROL, respectively) was included as a categorical predictor. The overall statistical significance of each model was assessed by likelihood ratio tests (type III test). Pairwise comparisons of territory types were carried out using Tukey contrasts as a post-hoc test (R package *multcomp*) (Hothorn *et al.* 2021).

To analyse the effects of landscape structure on breeding-territory selection (BP vs. CONTROL) and mating success (BP vs. UM), we applied multivariable Generalised Linear Mixed-effects Models

(GLMMs) with a binomial error distribution (R package: *lme4*) (Bates *et al.* 2021) (results based on top-ranked models within $\Delta AIC_C < 3$). In these analyses, we ran three different model sets for each of the two spatial scales (territory and home range): (1) a habitat-type model including the area of each of the 10 major habitat types (e.g. arable land, woody boundary, improved grassland, etc.); (2) a song-post model containing the area of potential song posts (i.e. area of each of the five subtypes of woody boundary); (3) a crop-type model including the area of each of the seven crop types (Table 1).

To assess the impact of vegetation structure (i.e. crop type and vegetation height, which was strongly correlated with vegetation cover, see Table 1) at potential nesting sites on mating success (BP vs. UM), we applied a multivariable GLMM with a binomial error distribution (R package: *lme4*) (Bates *et al.* 2021); results based on top-ranked models within $\Delta AIC_C < 3$. Winter rye served as the baseline in the categorical predictor variable “crop type”. As explorative data analysis suggested a hump-shaped relationship between mating success and vegetation height, the predictor variable “vegetation height” was centred and squared prior to the GLMM analyses. Furthermore, differences in absolute frequencies of crop types at potential nesting sites of BP and UM were compared using Fisher’s exact test.

Results

Abundance of the Ortolan Bunting

In total, we recorded 111 Ortolan Bunting territories in the five subareas, which corresponded to an abundance of 0.54 territories/10 ha. However, BP ($N = 60$) accounted for only 55% of the territories detected. The remaining 45% were occupied by UM ($N = 51$).

Differences in environmental conditions between territories and control

Environmental conditions strongly differed between BP, UM, and CONTROL, both on the territory and home-range scales (Table 1, Figure 2). Overall, territories of both BP and UM were characterised by a higher landscape heterogeneity on the territory but not the home-range scale in comparison with CONTROL (Figure 2). Arable land, with maize, winter rye, and winter wheat as the prevailing crops, was the dominant habitat type in BP, UM, and CONTROL on both spatial scales (Table 1). While the overall area of arable land did not differ on the territory scale, the home ranges of both BP and UM were characterised by larger areas of arable land compared with CONTROL. Our study also revealed distinct

Table 1. Differences in the area of habitat types (mean \pm SE, ha) in territories of breeding pairs (BP), unpaired males (UM), and control samples (CONTROL) on the territory and home-range scales. Differences between the groups were tested using univariable Linear Mixed-effects Models (LMM) with the habitat type as a response variable, territory type as a predictor, and subarea as a random factor. Significant differences are highlighted in bold type (** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. = not significant). Results of pairwise comparisons are indicated by different letters ($P < 0.05$).

Parameter	Territory				Home range			
	BP ($N = 60$)	UM ($N = 51$)	CONTROL ($N = 55$)	P	BP ($N = 60$)	UM ($N = 51$)	CONTROL ($N = 55$)	P
Arable land	2.58 \pm 0.06	2.53 \pm 0.07	2.36 \pm 0.14	n.s.	23.1 \pm 0.62^a	22.6 \pm 0.59^a	19.7 \pm 0.91^b	**
Maize	0.43 \pm 0.09	0.57 \pm 0.13	0.68 \pm 0.15	n.s.	4.87 \pm 0.81	5.90 \pm 1.02	4.51 \pm 0.70	n.s.
Winter barley	0.35 \pm 0.10	0.18 \pm 0.07	0.15 \pm 0.08	n.s.	2.98 \pm 0.75^a	1.48 \pm 0.53^{ab}	1.09 \pm 0.27^b	**
Winter rye	0.66 \pm 0.12	0.69 \pm 0.14	0.54 \pm 0.14	n.s.	6.24 \pm 1.03	6.57 \pm 1.21	5.38 \pm 0.98	n.s.
Winter wheat	0.55 \pm 0.11	0.35 \pm 0.10	0.30 \pm 0.11	n.s.	4.18 \pm 0.79^a	2.71 \pm 0.69^a	1.45 \pm 0.35^b	***
Potato	0.42 \pm 0.10^{ab}	0.58 \pm 0.15^a	0.29 \pm 0.13^b	*	3.61 \pm 0.72^{ab}	4.41 \pm 1.06^a	2.07 \pm 0.71^b	**
Winter rape	0.08 \pm 0.04	0.16 \pm 0.06	0.25 \pm 0.11	n.s.	0.99 \pm 0.36	1.38 \pm 0.52	2.19 \pm 0.89	n.s.
Set-aside	0.05 \pm 0.03	0.00 \pm 0.00	0.00 \pm 0.00	n.s.	0.12 \pm 0.05	0.04 \pm 0.03	0.03 \pm 0.03	n.s.
Woody boundary	0.24 \pm 0.02^a	0.21 \pm 0.02^a	0.05 \pm 0.01^b	***	1.10 \pm 0.10^a	0.93 \pm 0.08^a	0.62 \pm 0.07^b	***
Avenue	0.12 \pm 0.02^a	0.07 \pm 0.02^b	0.01 \pm 0.01^b	***	0.39 \pm 0.05^a	0.33 \pm 0.05^a	0.14 \pm 0.03^b	***
Copse	0.06 \pm 0.02^a	0.08 \pm 0.02^a	0.01 \pm 0.01^b	**	0.44 \pm 0.09^a	0.33 \pm 0.07^{ab}	0.11 \pm 0.04^b	**
Hedgerow	0.00 \pm 0.00	0.01 \pm 0.00	0.00 \pm 0.00	n.s.	0.03 \pm 0.01	0.06 \pm 0.02	0.04 \pm 0.02	n.s.
Single tree	0.01 \pm 0.00^a	0.00 \pm 0.00^{ab}	0.00 \pm 0.00^b	*	0.02 \pm 0.00	0.02 \pm 0.00	0.01 \pm 0.00	n.s.
Tree row	0.03 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	n.s.	0.17 \pm 0.04	0.19 \pm 0.05	0.27 \pm 0.05	n.s.
Improved grassland	0.13 \pm 0.04	0.12 \pm 0.04	0.32 \pm 0.10	n.s.	1.93 \pm 0.52	1.45 \pm 0.36	2.65 \pm 0.53	n.s.
Semi-natural grassland	0.00 \pm 0.00^a	0.00 \pm 0.00^a	0.21 \pm 0.10^b	*	0.19 \pm 0.12^a	0.06 \pm 0.05^a	2.01 \pm 0.66^b	***
Ditch	0.01 \pm 0.00	0.01 \pm 0.00	0.01 \pm 0.00	n.s.	0.08 \pm 0.14	0.06 \pm 0.13	0.08 \pm 0.14	n.s.
Field margin	0.18 \pm 0.02^a	0.13 \pm 0.01^b	0.05 \pm 0.01^c	***	0.66 \pm 0.05^a	0.55 \pm 0.04^{ab}	0.48 \pm 0.05^b	*
Path/road	0.10 \pm 0.01^a	0.08 \pm 0.01^a	0.03 \pm 0.01^b	***	0.44 \pm 0.03	0.41 \pm 0.03	0.35 \pm 0.03	n.s.
Coniferous forest	0.01 \pm 0.04	0.03 \pm 0.02	0.06 \pm 0.04	n.s.	1.62 \pm 0.21	3.21 \pm 0.45	1.64 \pm 0.49	n.s.
Deciduous forest	0.05 \pm 0.02	0.12 \pm 0.05	0.10 \pm 0.05	n.s.	0.60 \pm 0.21	0.87 \pm 0.24	0.78 \pm 0.28	n.s.
Settlement	0.01 \pm 0.01	0.02 \pm 0.01	0.00 \pm 0.00	n.s.	0.12 \pm 0.05	0.29 \pm 0.11	0.33 \pm 0.18	n.s.

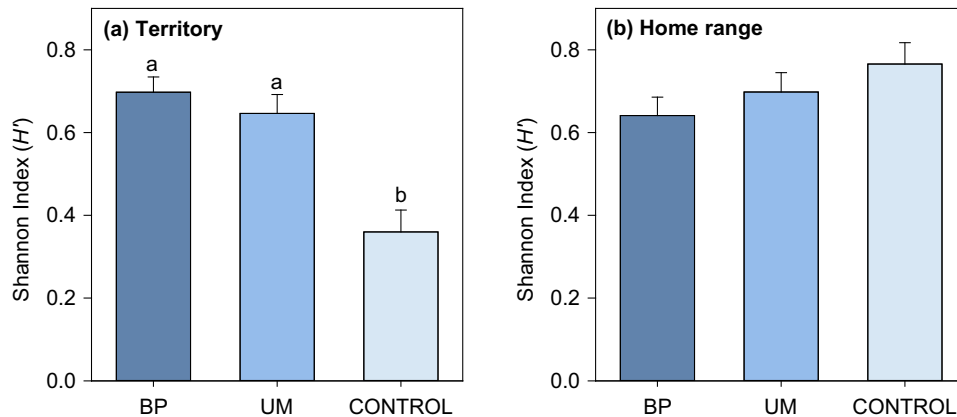


Figure 2. Differences in landscape heterogeneity (Shannon Index H') on the (a) territory and (b) home-range scales. Significant differences between the groups ($P < 0.05$) are indicated by different letters.

differences in the cover of several crop types, especially on the home-range scale (for more details see Table 1). Apart from that, we generally found similar patterns concerning the other parameters of landscape structure on the two spatial scales. In particular, the overall area of woody boundaries was larger in BP and UM than in CONTROL, both on the territory and home-range scales. These differences were also reflected in the consideration of landscape elements representing suitable song posts (e.g. avenues, copses, and solitary trees, for more details see Table 1). While the area of field margins clearly increased from CONTROL to UM to BP, the area of semi-natural grasslands was smaller in BP and UM compared with CONTROL. In addition, we detected a larger area of paths/roads on the territory scale in BP and UM compared with CONTROL.

Effects of landscape structure on breeding-territory selection (BP vs. CONTROL)

There were some similarities but also some differences in the environmental parameters determining breeding-territory selection on the territory and home-range scales (Table 2, Figure 3). On both scales the likelihood of territory establishment increased with area of woody boundaries and field margins (habitat-type model), the area of avenues and copses (song-post model), and the area of winter barley and winter wheat (crop-type model). On the territory scale, the likelihood of territory establishment additionally increased with the area of tree rows, single trees, and hedgerows, which represent other potential song posts (song-post model). On the home-range scale, we also found a positive relationship between breeding-territory selection and the area of arable land (habitat model) and the area of winter rye and potatoes (crop-type model). Even though model accuracy (i.e. marginal and conditional R^2) was generally high (Nakagawa *et al.* 2017), models performed better on the territory scale.

Effects of landscape and vegetation structure on mating success (BP vs. UM)

In contrast to the territory selection of BP (see above), we observed only weak effects of landscape structure on mating success (Table 3). On the territory scale, the likelihood of mating increased with the area of field margins (habitat-type model) and avenues (song-post model). We found no effects of landscape structure on the home-range scale.

Crop type and vegetation height at potential nesting sites (field bordering the main song post of a territorial male, see above) had clear effects on mating success (Figure 4, Table 4). Almost one-third of BP was found in winter rye and one-third in winter wheat (Figure 4a). The remaining third of BP mainly occurred in winter-barley and potato fields. While the proportion of UM was similar in winter rye and potato, they were found at a significantly higher frequency in maize and winter rape and a lower frequency in winter wheat. Compared with the overall availability in the study area, BP showed a preference for winter wheat while maize and rape were clearly underrepresented in territories of BP (Figure 4b). The GLMM analysis revealed that occurrence of winter wheat and maize as well as crop height were the main predictors of mating success (Table 4). The occurrence of winter wheat and an intermediate vegetation height at potential nesting sites, which was strongly intercorrelated with vegetation cover ($P < 0.05$, $r_s = 0.76$), fostered the likelihood of mating. In contrast, the occurrence of maize had a negative effect on mating success. Overall, the model had a very high explanatory power.

Discussion

Our study revealed that the landscape structure within territories of Ortolan Bunting BP strongly varied from the overall habitat availability in the study area on both the territory and home-range scales. However, the environmental conditions also differed between BP and UM. All territories were located in the agricultural landscape. Arable land was the prevailing habitat type in territories and positively affected the habitat selection of BP on the home-range scale. Moreover, the likelihood of BP occurrence increased with a larger area of woody boundaries and field margins on both spatial scales. While landscape structure strongly affected the selection of breeding territories, it had only weak effects on mating success. However, mating success strongly depended on crop type and vegetation height at potential nesting sites.

The Ortolan Bunting has very complex breeding-habitat requirements, in particular on the territory scale. Only heterogeneous agricultural landscapes where suitable song posts, appropriate nesting sites, and sufficient foraging habitats are available in close proximity are suitable for breeding (e.g. Berg 2008, Glutz von Blotzheim 2011, Menz and Arlettaz 2011, Brambilla *et al.* 2016). In line with these studies, we found that territories of BP and UM had a higher landscape heterogeneity on the territory scale. Since we

Table 2. Relationship between breeding-territory selection ($N_{BP} = 60$ vs. $N_{CONTROL} = 55$, multivariable Generalised Linear Mixed-effects Models [GLMMs] with binomial error structure) and landscape structure on the territory and home-range scales. “Subarea” was set as a random factor in all models. Model-averaged coefficients were derived from the top-ranked models ($\Delta AIC_C < 3$). R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa *et al.* 2017). Moran’s I statistics were based on global models (Kalogirou 2020). Significance levels are indicated as **** $P < 0.001$, *** $P < 0.01$, * $P < 0.05$.

Parameter	Territory				Home range			
	Estimate	SE	Z	P	Estimate	SE	Z	P
a) Habitat-type model								
(Intercept)	-2.95	1.53	1.92	n.s.	-4.15	1.22	3.41	***
Woody boundary	13.53	3.47	3.86	***	1.06	0.43	2.47	*
Field margin	6.87	2.87	2.37	*	1.38	0.61	2.23	*
Arable land	0.12	0.04	2.67	**
$R^2_m = 0.57-0.61/R^2_c = 0.72-0.74$					$R^2_m = 0.29-0.32/R^2_c = 0.29-0.32$			
Moran’s I: -0.06 (n.s.)					Moran’s I: 0.04 (n.s.)			
b) Song-post model								
(Intercept)	-1.94	0.68	2.81	**	-1.10	0.33	3.25	**
Avenue	16.83	3.71	4.48	***	2.66	0.67	3.96	***
Copse	13.31	4.20	3.17	**	2.07	0.62	3.29	**
Tree row	10.65	4.18	2.52	*
Single tree	125.11	46.80	2.64	**
Hedgerow	28.37	13.81	2.03	*
$R^2_m = 0.57-0.59/R^2_c = 0.68-0.69$					$R^2_m = 0.38-0.40/R^2_c = 0.38-0.40$			
Moran’s I: 0.02 (n.s.)					Moran’s I: 0.05 (n.s.)			
c) Crop-type model								
(Intercept)	-0.52	0.43	1.20	n.s.	-2.25	0.72	3.10	**
Winter barley	0.72	0.38	1.91	*	0.31	0.10	3.20	**
Winter wheat	0.63	0.32	1.93	*	0.25	0.07	3.54	***
Winter rye	0.11	0.04	2.80	**
Potato	0.11	0.05	2.05	*
$R^2_m = 0.44-0.47/R^2_c = 0.44-0.49$					$R^2_m = 0.43-0.45/R^2_c = 0.46-0.53$			
Moran’s I: -0.01 (n.s.)					Moran’s I: 0.01 (n.s.)			

found no differences in landscape heterogeneity and much lower explanatory power of the habitat-type and song-post models on the home-range scale, it seems that the species’ habitat requirements are generally less complex at this spatial level.

In our study, the likelihood of breeding-territory establishment increased with the availability of woody boundaries on both the territory and home-range scales. In the song-post model, the area of all five subtypes of woody boundaries had a positive effect on territory establishment on the territory scale. On the home-range scale, however, only the area of avenues and copses fostered territory establishment. Prominent trees providing an all-round view are the preferred song posts of Ortolan Bunting males (Conrads 1969, Berg 2008, Menz and Arlettaz 2011, Vepsäläinen *et al.* 2005). Consequently, the strong relationship between breeding-territory selection and the area of several types of woody boundaries on the territory scale can mainly be explained by the role woody boundaries play as song posts. In the study area, oaks are among the most dominant trees within the woody boundaries and are also most frequently used as song posts (Bellenhaus and Fartmann 2009). However, oak-rich woody

boundaries may also serve as important foraging habitats for the Ortolan Bunting on both spatial scales. In central Europe, oaks are among the trees with the highest diversity of phytophagous insects and provide a high abundance of prey during the breeding season (Conrads 1969, Brändle and Brandl 2001). The diet of young nestlings of Ortolan Buntings mainly consists of Lepidoptera caterpillars (Conrads 1969, Glutz von Blotzheim 2011). These are known to be an abundant and high-quality food source during the hatching period of nestlings, especially the larvae of the Green Oak Tortrix (*Tortrix viridana*) (Conrads 1969).

In the habitat-type models, the area of field margins additionally fostered breeding-territory establishment on both spatial scales. This is likely due to their importance as foraging habitats. For older chicks of the Ortolan Bunting, Coleoptera and Orthoptera are of more importance as food sources (Glutz von Blotzheim 2011). Within agricultural landscapes, field margins foster the abundance of both insect groups and generally increase the availability of arthropod prey for insectivorous farmland birds (e.g. Kuiper *et al.* 2013). This is especially true for nutrient-poor field margins with a

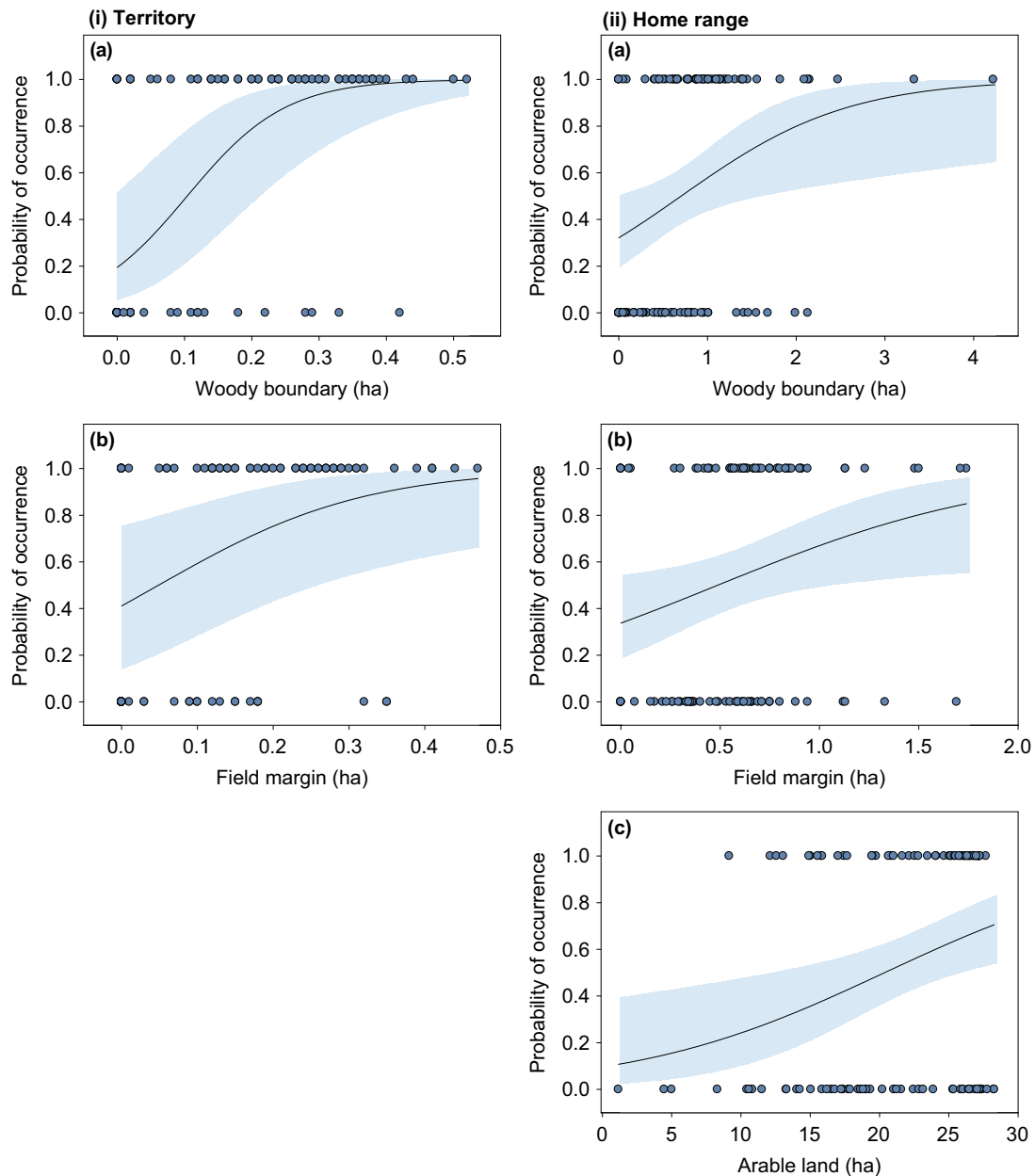


Figure 3. Probability of breeding-territory selection ($N_{BP} = 60$ vs. $N_{CONTROL} = 55$, multivariable Generalised Linear Mixed-effects Models [GLMMs] with binomial error structure) in relation to significant habitat types on the territory and home-range scales (see Table 2 for detailed GLMM statistics).

high phytodiversity, which are still widespread in the study area (Bellenhaus and Fartmann 2009).

Moreover, the likelihood of breeding-territory establishment increased with the overall area of arable land on the home-range scale. Since the home range is mainly used for foraging (Dale and Olsen 2002), we assumed that the predictors on this spatial scale mainly reflect preferences for potential foraging habitats. When foraging on the ground, Ortolan Buntings prefer habitats rich in bare ground such as arable fields with sparse vegetation cover (Menz *et al.* 2009). However, their suitability as foraging habitat differs depending on the crop type. Accordingly, we also found effects of the area of various crops in the crop-type models. The likelihood of territory establishment increased with the area of winter barley and winter wheat on both spatial scales. Larger areas of winter rye and potatoes additionally fostered territory

establishment on the home-range scale. Due to their open vegetation structure at the beginning of the breeding season, these crops appear generally suitable for foraging (Menz *et al.* 2009). However, the preferences for larger areas of winter barley and winter wheat fields on the territory scale also reflect the breeding requirements of the species (see below, Bellenhaus and Fartmann 2009).

It should be noted that the analyses considering landscape structure may be subject to some statistical issues. Since territories of farmland birds are often clustered along linear landscape elements such as woody boundaries, spatial autocorrelations between territories should be carefully checked to ensure statistical independence of bird territories in studies such as ours (Dormann *et al.* 2007). Given the lack of spatial autocorrelation in our study, we think that it is appropriate to tolerate certain spatial overlaps between territories in favour of a larger sample size (Zuckerberg

Table 3. Relationship between mating success ($N_{BP} = 60$ vs. $N_{UM} = 51$, multivariable Generalised Linear Mixed-effects Models [GLMMs] with binomial error structure) and landscape structure on the territory and home-range scales. “Subarea” was set as a random factor in all models. Model-averaged coefficients were derived from the top-ranked models ($\Delta AIC_c < 3$). R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa *et al.* 2017). Moran’s I statistics were based on global models (Kalogirou 2020). Significance levels are indicated as *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. = not significant.

Predictor	Territory				Home range			
	Estimate	SE	Z	P	Estimate	SE	Z	P
a) Habitat-type model								
(Intercept)	-0.73	0.75	0.97	n.s.	0.06	0.65	0.10	n.s.
Field margin	4.43	1.81	2.42	*
$R^2_m = 0.08-0.09/R^2_c = 0.08-0.09$					-			
Moran’s I: -0.02 (n.s.)					Moran’s I: -0.01 (n.s.)			
b) Song-post model								
(Intercept)	-0.27	0.35	0.77	n.s.	-0.36	0.33	1.06	n.s.
Avenue	3.77	1.76	2.12	*
$R^2_m = 0.11-0.16/R^2_c = 0.13-0.20$					-			
Moran’s I: -0.02 (n.s.)					Moran’s I: -0.02 (n.s.)			
c) Crop-type model								
(Intercept)	0.10	0.31	0.31	n.s.	-0.01	0.32	0.01	n.s.
-					-			
Moran’s I: -0.04 (n.s.)					Moran’s I: -0.03 (n.s.)			

et al. 2020). Although the analyses considering the two spatial scales revealed different results in our study, it is obvious that the factors on the territory and home range are not independently affecting Ortolan Bunting occurrence. Nevertheless, they were considered separately to avoid multicollinearity among predictors and to reflect the different habitat requirements of the Ortolan Bunting on the territory and home-range scales, respectively.

While mating success was weakly affected by landscape structure, it was strongly driven by crop type and vegetation height at potential nesting sites. Almost two-thirds of BP occurred in winter rye or winter wheat. In contrast, maize and winter rape at potential nesting sites were almost completely avoided. While UM were less frequently found in winter wheat, their proportion was clearly higher in maize and winter rape. In the GLMM analysis, an intermediate crop height and winter wheat at potential nesting sites increased the likelihood of mating, while maize reduced it. Our findings corroborate results of previous studies showing that an arable field’s suitability for breeding of the Ortolan Bunting depends on vegetation structure, which is closely related to crop type (Berg 2008, Morelli *et al.* 2012, Šalek *et al.* 2019). On the one hand, a warm microclimate is of crucial importance for the successful development of Ortolan Bunting chicks under the cool climatic conditions of central Europe (Vepsäläinen *et al.* 2005, Glutz von Blotzheim 2011). On the other hand, the vegetation has to provide sufficient shelter against predators and adverse weather conditions (Conrads 1969). Conrads (1968) pointed out that the vegetation height within fields should not exceed 30 cm during the period of territory establishment. Moreover, Šalek *et al.* (2019) found that an intermediate cover of bare ground was preferred by Ortolan Buntings. Accordingly, the negative effect of maize is due to its very sparse vegetation during the time of territory establishment in the study area (Bellenhaus and Fartmann 2009, Menz and Arlettaz 2011). However, winter cereals in general and winter wheat with its lower vegetation height in particular generally

provide suitable nesting sites (Bernardy 2008, Bellenhaus and Fartmann 2009). In addition to winter cereals, potato fields were colonised by BP, although to a lesser extent. Although they hardly provide vegetation cover at the beginning of the breeding season, their structure appears suitable for breeding from the end of May onwards (Bellenhaus and Fartmann 2009). Therefore, it can be assumed that they are especially suitable for late broods (e.g. replacement broods, second broods) (Glutz von Blotzheim 2011).

The main goal of this study was to detect key drivers of territory selection and mating success of the Ortolan Bunting in agricultural landscapes. In conclusion, our study has shown that only heterogeneous agricultural landscapes where suitable song posts, appropriate nesting sites, and sufficient foraging habitats occur in close proximity are suitable for breeding. In particular, the presence of oak-rich woody boundaries, field margins, and winter-cereal fields with an intermediate vegetation height promoted breeding territory establishment in the study area. Woody boundaries are important song posts, and cereal fields provide potential nesting habitats for the Ortolan Bunting (Bellenhaus and Fartmann 2009, Glutz von Blotzheim 2011). In addition, all three habitat types are likely used for foraging during the breeding period (Menz and Arlettaz 2011).

Implications for conservation

Ortolan Bunting males generally arrive earlier on the breeding grounds than females (Conrads 1969, Yosef and Tryanowski 2002). Additionally, they have much higher territory fidelity and their territory selection is primarily driven by the availability of song posts (Conrads 1969, Keusch 1991, Yosef and Tryanowski 2002, see also above). On the contrary, nesting-site selection is carried out by the females and mainly depends on crop type and its vegetation structure (Keusch 1991, Menz and Arlettaz 2011). The high territory fidelity of the males makes the Ortolan Bunting very sensitive to environmental alterations, especially structural

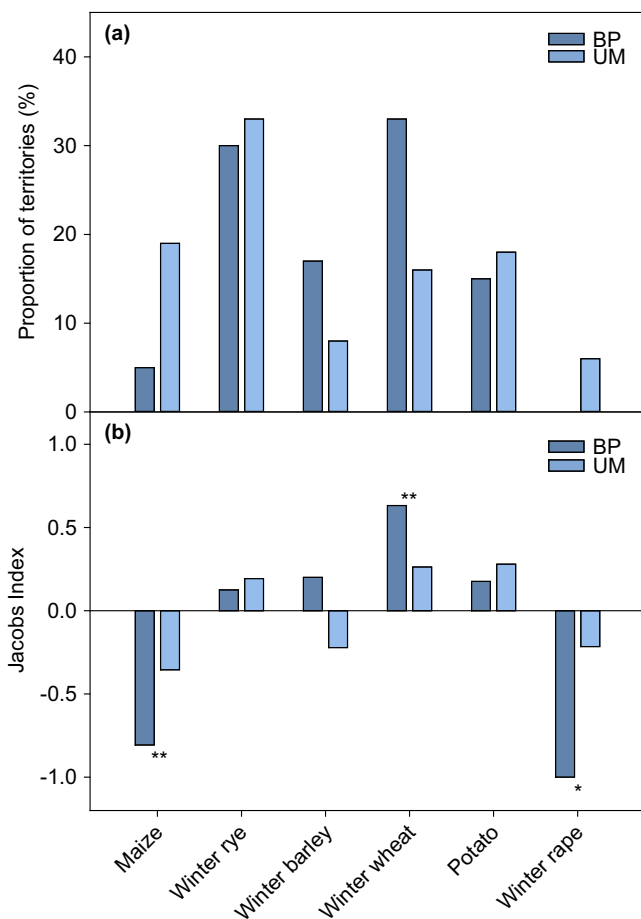


Figure 4. (a) Proportion of territories and (b) Jacobs Index indicating preferences for crop types at potential nesting sites within territories of breeding pairs (BP) ($N = 60$), and unpaired males (UM) ($N = 51$), in relation to the overall availability within the study area (zero line). Differences in the frequencies between BP and UM were tested using Fisher’s exact test. Significance levels are indicated as ** $P < 0.01$, * $P < 0.05$.

Table 4. Relationship between mating success ($N_{BP} = 60$ vs. $N_{UM} = 51$, multivariable Generalised Linear Mixed-effects Models [GLMMs] with binomial error structure) and vegetation structure and crop type at potential nesting sites (field bordering the main song post). “Subarea” was set as a random factor. Model-averaged coefficients were derived from the top-ranked models ($\Delta AIC_c < 3$). R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa *et al.* 2017). Moran’s I statistics were based on global models (Kalogirou 2020). λ^2 = variable was centred and squared. Significance levels are indicated as * $P < 0.05$, n.s. = not significant.

Predictor	Estimate	SE	Z	P
(Intercept)	-0.40	0.49	0.81	n.s.
Vegetation height (cm) λ^2	0.61	0.33	1.83	*
Winter wheat	1.22	0.61	1.99	*
Maize	-1.86	0.92	2.00	*
$R^2_m = 0.88-0.89/R^2_c = 0.88-0.89$				
Moran’s I: -0.02 (n.s.)				

changes at potential nesting sites (e.g. large-scale changes in cultivated crops). As in previous studies (Dale 2001, Steifetten and Dale *et al.* 2006), the population in the study area was characterised by a strongly male-biased sex ratio. UM accounted for 45% of the

territories, which indicates that reproduction is reduced and the population could decline further in the future (Jiguet *et al.* 2016).

During recent years, the large-scale expansion of energy crops such as maize and rape have contributed to rapid agricultural intensification in central European agricultural landscapes including the study area (Sauerbrei *et al.* 2014, LfU Brandenburg 2018, Fartmann *et al.* 2021a,b). This results in landscape homogenisation, a loss of nesting sites, and a reduction of food supply for the Ortolan Bunting (Menz and Arlettaz 2011). Since, the bird surveys underlying our study were conducted in 2012, it can be expected that the situation has further worsened further during the last 10 years. In most parts of central Europe, the species still exhibits a strong decline. Accordingly, the threat status of the Ortolan Bunting in Germany changed from “Vulnerable” to “Endangered” in the most recent Red List assessment (Ryslavý *et al.* 2020). Therefore, measures are urgently needed to promote suitable breeding conditions and increase food availability in agricultural landscapes. Agri-environmental schemes should primarily facilitate low-intensity farming practices that promote landscape heterogeneity and sustain a high abundance of invertebrate prey in farmland habitats (e.g. Birrer *et al.* 2007, Brambilla *et al.* 2017, Ponce *et al.* 2014). Increasing crop diversity towards larger areas of summer cereals, the reduction of fertiliser application, and wider spaces between sowing rows in winter cereals may increase the availability of suitable nesting and foraging sites within arable fields (Conrads 1969, Vepsäläinen *et al.* 2005, Menz and Arlettaz 2011). Additionally, we recommend reducing the use of pesticides to increase invertebrate abundance, which very likely would have broad benefits for the Ortolan Bunting and overall farmland biodiversity. Moreover, field margins cultivated with legume–cereal mixes provide well-suited refuges for breeding birds (Bernardy *et al.* 2008). Since they can also provide suitable breeding conditions for the species in otherwise unsuitable crops (e.g. maize and rape), such measures should be increasingly part of agri-environmental schemes. It has been shown that the implementation of conservation measures locally contributed to a stabilisation of the Ortolan Bunting populations (Jiguet *et al.* 2016). Since the current Common Agricultural Policies of the EU largely fail to bring benefits for farmland biodiversity, large-scale conservation actions which may help to maintain viable populations of the Ortolan Bunting in the long run are still lacking.

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