Habitat preferences of the Ortolan Bunting (*Emberiza hortulana*) in its prime wintering grounds, the cereal-dominated Ethiopian Highlands

JÉRÉMY GREMION,[1] GABRIEL MARCACCI,[2,3] (iD) JULIEN MAZENAUER,[2] TOLERA SORI,[4] FANUEL KEBEDE,[4] MIHRET EWNETU,[4] PHILIPPE CHRISTE,[1] (iD) RAPHAËL ARLETTAZ[2] (iD) & ALAIN JACOT*[2,5] (iD)

[1]*Department of Ecology and Evolution, University of Lausanne, Lausanne, CH-1015, Switzerland*
[2]*Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, CH-3012, Switzerland*
[3]*Functional Agrobiodiversity, University of Göttingen, Göttingen, D-37077, Germany*
[4]*Ethiopian Wildlife Conservation Authority, Head Office, Mexico Square, Addis Ababa, 386, Ethiopia*
[5]*Swiss Ornithological Institute, Valais Field Station, Sion, CH-1950, Switzerland*

Agricultural intensification and land-use changes are major factors impacting farmland biodiversity. The Ortolan Bunting *Emberiza hortulana* is the long-distance trans-Saharan migratory passerine that has undergone the most dramatic decline among all European farmland birds. The factors responsible for this decline may originate from the breeding grounds, migration stopovers and/or overwintering quarters. Very little is known about conditions on the species' wintering grounds, but a recent study has highlighted the utmost importance of the traditionally managed agroecosystems in the Ethiopian Highlands as a key wintering area, apparently harbouring as much as 90% of the world's Ortolan Bunting population. Using radiotracking and line transect surveys, this study aimed to provide fine-grained information about species–habitat relationships in the Ortolan Bunting overwintering quarters. Our results showed the importance, at the landscape scale, of small-scale agriculture, notably of traditionally managed, cereal-dominated fields interspersed with semi-natural structures. At a foraging-site scale, on the other hand, patches of bare ground in combination with large areas of post-harvesting stubble represented key habitat features. Stubbles provide an essential food resource and bare ground promotes ground foraging by enhancing food accessibility. The maintenance of a traditional agricultural economy will be essential to maintain the habitat potential for the Ortolan Buntings overwintering in the Ethiopian Highlands and will be instrumental in preserving its world population from further decline.

Keywords: agricultural intensification, Ethiopia, food security, migratory landbirds.

The increasing human population weighs on ecosystems and causes habitat loss and degradation (Cardinale *et al.* 2012). One driver of habitat destruction is agriculture, which has rapidly intensified since the Second World War (Garder 1996, Krebs *et al.* 1999). Intensification of agriculture and changes in land use are major factors impacting farmland biodiversity (Krebs *et al.* 1999, Benton *et al.* 2003) and European farmland bird species are no exception (Donald *et al.* 2001, Newton 2004). The main mechanisms affecting farmland species are multiple, ranging from the loss of heterogeneity at multiple scales, thereby decreasing essential breeding and feeding resources (Benton *et al.* 2003), to the use of pesticides that negatively impact food abundance and/or availability (Newton 2004, Chiron *et al.* 2014, Hallmann *et al.* 2014, Glemnitz *et al.* 2015), as well as the degradation of habitats due to the shift in crop species and agricultural techniques (i.e. mechanized machinery; Newton 2004, Eggers *et al.* 2011).

*Corresponding author.
Email: alain.jacot@vogelwarte.ch

Among declining avian species, there are many long-distance migrant birds. Conservation of migratory species is complex because of their dependency on suitable breeding grounds, multiple stopover sites along their migratory routes and optimal wintering sites (Benton *et al.* 2003, Vickery *et al.* 2014). Despite the potential importance of these different habitats, much of the current knowledge about the ecology and threats to Afro-Palaearctic migrants is restricted to factors acting on their European breeding grounds (Vickery *et al.* 2014). Thus, adding new information on non-breeding areas is key to a year-round understanding of a species' ecology and hence is crucial for its conservation. The most important factors in the non-breeding areas appear to be habitat changes through human activities, partly interacting with highly variable and unpredictable climatic conditions that can affect food abundance and availability (Vickery *et al.* 2014). Changes in agricultural practices are known to not only decrease food abundance, but also affect the phenology of peaks in seed abundance due to shifts in cultivated species and farming regimens (Glemnitz *et al.* 2015). Conservation issues may herewith also arise in the case of phenological mismatch between peaks in food supplies and the migratory cycle (Both *et al.* 2006, Douglas *et al.* 2010, Vickery *et al.* 2014). However, identifying factors causing population declines is a challenging task as multiple drivers interact, and they can operate at breeding, staging and wintering sites.

The Ortolan Bunting *Emberiza hortulana* is the only long-distance migrant among the Old World buntings (Emberizidae, Cramp & Perrins 1994) that migrates to sub-Saharan Africa and is exhibiting a strong decline, estimated at 89% between 1980 and 2014 (Keller *et al.* 2020). Recent studies using ring recoveries (Thoma & Menz 2014), light loggers, and genetic and isotope data (Jiguet *et al.* 2019) have demonstrated a migratory divide, with two distinct flyways separating the western from the eastern breeding population. The western flyway is used by approximately 10% of birds, which breed in western and northern Europe and winter in western Africa (Olsson *et al.* 2015). The strongest population declines are recorded in this western population (Jiguet *et al.* 2016), and several European countries have already lost the Ortolan Bunting as a breeding species (Keller *et al.* 2020): Belgium, the Netherlands (van Noorden 1999, Vieuxtemps & Jacob 2002, van Dijk *et al.* 2005)

and Switzerland (Knaus *et al.* 2018). Most of the causes of this decline have been attributed to land-use changes and agricultural intensification at the breeding sites, including the large-scale degradation of habitats (Menz & Arlettaz 2012), the transformation from traditional agriculture to monoculture by removing natural structures such as isolated treelines or hedges (Vepsäläinen *et al.* 2005, Brambilla *et al.* 2016, 2017), and the change of cultivation from summer to winter cereals (Eggers *et al.* 2011, Menz & Arlettaz 2012). The eastern flyway is used by birds breeding in a vast area ranging from Belarus over southern Russia, including the Balkan countries and down to Turkey until western Kazakhstan (Jiguet *et al.* 2019). These birds represent 90% of the global Ortolan Bunting population and overwinter in the cereal-dominated highlands of Eritrea and Ethiopia (Jiguet *et al.* 2019). The restricted size of the wintering area compared with the breeding grounds suggests that multiple breeding populations overwinter in the same region, making the species highly vulnerable to any deterioration in the wintering habitats. Therefore, studying habitat preferences in this rather small wintering agro-ecosystem is of utmost importance to the conservation of the Ortolan Bunting.

There is a long history of agriculture in the Ethiopian Highlands due to prime environmental and soil conditions that have led to human population expansion in recent decades (Holden & Yohannes 2002, Pender & Gebremedhin 2008, Headey *et al.* 2014). The Ethiopian Highlands today represent one of the most densely populated regions of Africa (Headey *et al.* 2014), where most arable lands are cultivated in a traditional way (Holden & Yohannes 2002, Pender & Gebremedhin 2008). Recent studies, however, indicate an increased use of fertilizers and pesticides (Josephson *et al.* 2014), especially so in intensively managed large-scale fields. This landscape homogenization has led to dichotomous landscapes composed of small-scale, traditional and extensive vs. large-scale, mechanized and intensive agroecosystems. Additionally, policy-induced agricultural intensification has strengthened this trend (Davis *et al.* 2009, Headey *et al.* 2014) with concomitant negative effects on biodiversity. In a recent study it has been demonstrated that only a few bird species benefit from those newly established open landscapes created by large-scale farming, and that avian abundance and diversity are

significantly higher in traditionally managed small-scale fields (Marcacci *et al.* 2020).

Here, we investigated the species–habitat associations of Ortolan Bunting in traditionally managed and industrialized cereal cultures in the Ethiopian Highlands at different spatial scales (landscape and field scale). The two contrasting farming systems are nearly binary (traditional vs. industrialized or small- vs. large fields), allowing us to investigate the effects of the operated farming practices and semi-natural habitats at a landscape scale. To understand habitat preferences on a field and foraging-site scale, we additionally conducted a radiotracking study. Using a combination of analyses of habitat preferences at these different spatial scales, this study provides the first quantitative assessment of the Ortolan Bunting's wintering habitat preferences and provides management recommendations for its conservation.

METHODS

Study area

We used geolocation data from Jiguet *et al.* (2019) to delineate the main study area. We focused on two large areas located in Central Ethiopia (Oromia Region; Fig. 1). Elevation of the study sites ranged from 2340 to 2670 m above sea level. The first large study area was situated on the Ethiopian plateau (west of the Rift Valley), between Chancho (9°18'45.0756"N, 38°45'24.843"E) and Debre Libanos (9°42'59.5188"N, 38°49'16.1508"E). Forty line-transects were placed between these two locations. This first study area comprised only small-scale traditional agriculture. We performed radiotracking at three sub-sites: Duber (9°27'44.28"N, 38°52'49.7994"E), Guto (9°19'40.0794"N, 38°45'34.2"E) and Lemi (9°48'12.9594"N, 38°54'29.1594"E). The second large study area was located on the plateau east of the Rift Valley, north of Bale Mountain National Park (Fig. 1). Here, the agricultural landscape was composed of two contrasting farming systems coexisting next to each other: small-scale traditional farming and large commercial farms (mostly cereal monocultures) using modern machinery (Marcacci *et al.* 2020). In the second study area, some small-holders also used mechanized methods for harvesting, a technique we never observed west of the Rift Valley. Eighty line-transects were distributed between Adamogne (7°2'17.0118"N, 39°0'

3.5532"E) and Sinana (7°4'3.2196"N, 40°12'46.5294"E). Our main radiotracking area was situated north of Washa (7°2'22.8078"N, 39°29'17.6784"E). Our main radiotracking area was situated north of Washa (7.039669°N, 39.488244°E). Research permits and authorizations were obtained from the Ethiopian Wildlife Conservation Authority (EWCA), the governmental organization responsible for conservation and utilization of Ethiopian wildlife.

Local-scale habitat preferences using radiotracking

To understand fully the field-scale species–habitat associations of Ortolan Buntings, a radiotracking study using miniaturized radio-transmitters was conducted over a 2-month period between December 2017 and January 2018 (Menz *et al.* 2009, Schaub *et al.* 2010). Ortolan Buntings were captured with mist-nets in combination with tape luring, and aged and sexed. We could determine the sex only for eight birds, all of them males. Buntings ($n = 12$) were equipped with radio-transmitters (Holohil BD-2, 6- to 10-week battery lives, 1.2 g, Holohil Systems Ltd, Carp, Ontario, Canada) using the leg-loop harness technique (55 mm according to Naef-Daenzer 2007, Menz *et al.* 2009). If necessary, loop size was individually adjusted according to individual body size.

We used the homing-in technique to locate tagged individuals (Menz *et al.* 2009, Schaub *et al.* 2010). The localizations are more precise using hand-held antennas for birds regularly sitting on the ground compared with other radiotracking techniques (Naef-Daenzer 2007). We used a three-element antenna and radioreceivers (Australis 26K Tracking Receiver, Titley Electronics, Australia) to track the birds. We tracked the birds twice a day to avoid the period of inactivity during the hottest hours (pers. obs. of J.G., G.M., J.M. and T.S.): a first daily session lasted from dawn to 10:00 h, and a second from 15:00 h until dusk. Each time a radiotracked bird was observed foraging or was detected on the ground, we considered this location a presence point of a foraging event (Cramp & Perrins 1994, Menz *et al.* 2009). Birds were radiotracked over 2–4 days to obtain at least 20 foraging occurrence points per individual. Between two localizations, we waited for a minimum of 15 min to avoid temporal correlations (Aebischer *et al.* 1993) and to be sure that the
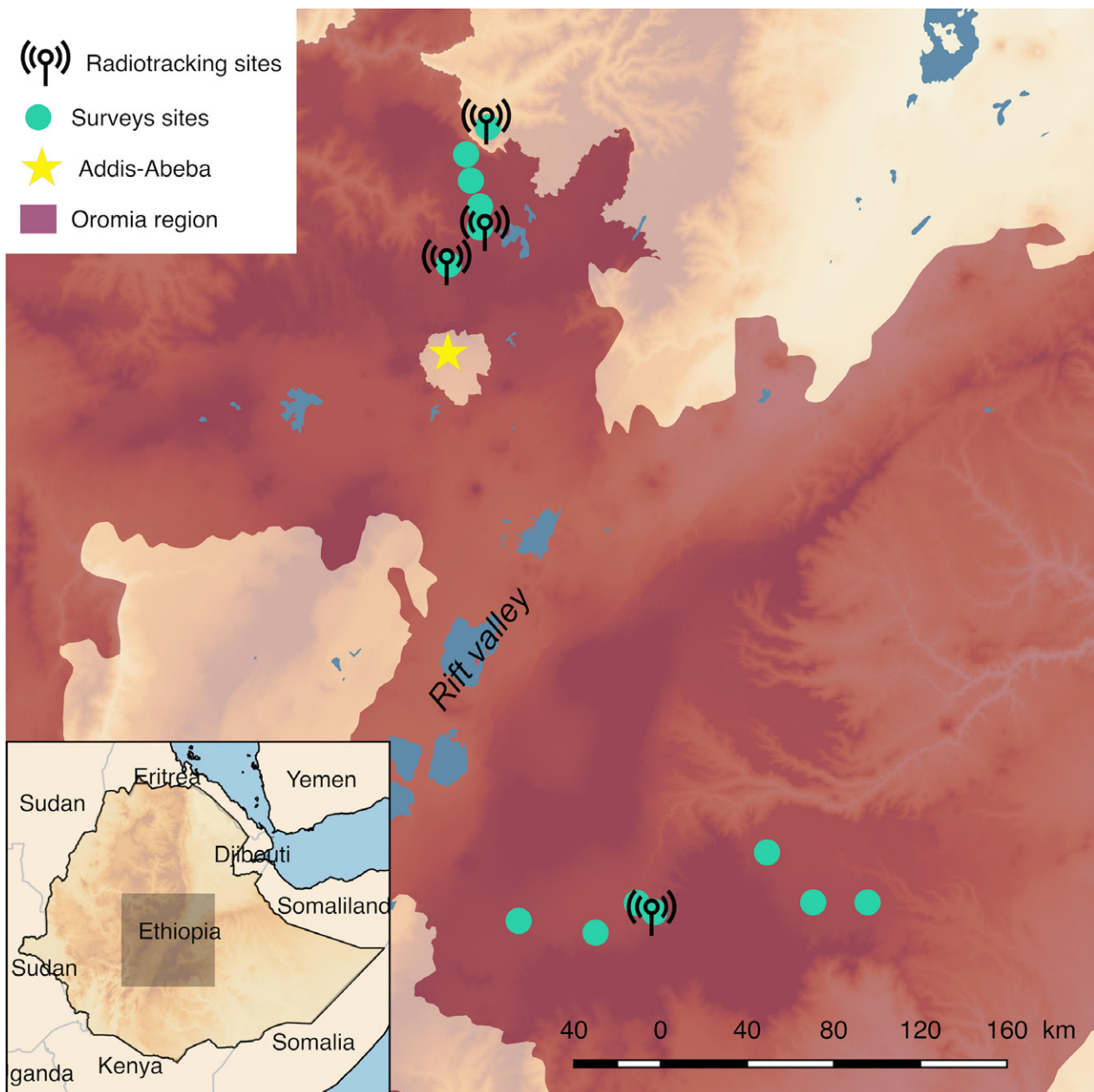
Figure 1. Study sites in the Ethiopian Highlands: one site west of the Rift Valley and another site east of the Rift Valley. Sub-sites of radiotracking are represented by emitting antennas and survey sub-sites by green circles (Quantum GIS Development Team 2012). [Colour figure can be viewed at wileyonlinelibrary.com]

new homing-in point was not an artefact of flushing the bird away from the previous point. Each homing-in localization was mapped precisely (± 3 m) with a Geographical Positioning System (Garmin e-Trex, Garmin Switzerland Distribution GmbH, Neuhausen am Rheinfall, Switzerland). For each recorded position of a tagged bird, home-ranges (note that we use 'home-range' for the habitat used by overwintering individuals) were estimated with the 100% minimum convex polygon (MCP) method (Buckland *et al.* 1991) using all locations (mean ± se = 36.75 ± 15.05) with a 50-m buffer around each location.

To analyse local-scale habitat preferences, we performed logistic regressions on a binary response variable (presence/pseudo-absence). Each time a

radiotracked bird was observed foraging or was detected on the ground, we mapped variables at the foraging location and at a randomly generated pseudo-absence point. Habitat variables (crop type, natural and cultivated ground vegetation cover, bare-ground cover, litter cover, mineral coverage, cultivated and natural vegetation height, field management variables; Table S1) were measured at two different scales: field scale (averaging at the scale of the field) and foraging-site scale (within a 2×2 m plot if the tracked bird was located precisely). An adjacent field was selected as a pseudo-absence for the field-scale habitat selection, and a pseudo-absence point $(2 \times 2$ m) situated 10 ± 1 m away from the foraging location was selected for the foraging-site scale habitat selection. In both cases, a list of randomized angles gave the directions for obtaining an associated pseudo-absence point/field. If the random pseudo-absence point was not in a field, it was discarded and a new random direction was generated for the selection of a new pseudo-absence point. The presence points and their unique pseudo-absence points were considered the stratum for statistical analysis.

We recorded several habitat variables including crop type (categories: barley/wheat, bean, labour/pasture (non-cultivated parcels), teff and other), natural and cultivated ground vegetation cover, bare-ground cover, litter cover (defined as the area covered by dead vegetal material including stubble, which was used as a proxy to estimate the amount of seeds), mineral cover, cultivated and natural vegetation height, and field management variables (including crop stage, grazing and the use of machines). Descriptions of variables are presented in Table S1. Data from 12 radiotracked Ortolan Buntings (field scale: 216 presence–absence pairs, mean $\pm$ se = 18 $\pm$ 6.4; foraging-site scale: 151 presence–absence pairs, mean $\pm$ se = 12.6 $\pm$ 6.8) were used for modelling habitat preferences. Radiotracking was performed by four observers (J.G., G.M., J.M., T.S.) working mostly in teams of two.

Landscape-scale habitat preferences using line transect surveys

The aim of this second part of the study was to understand the effects of landscape characteristics (e.g. natural or semi-natural habitats) on the Ortolan Bunting using the line-transect method inspired by Bibby *et al.* (2000) and successfully applied in several similar studies (e.g. Guyot *et al.*

2017, Rime *et al.* 2020). This method consists of following a predefined path called a transect across the study area and annotating each observed bird precisely on a map. A total of 120 transects (length 400 m, mean $\pm$ se = 399.33 $\pm$ 0.48 m) with a 50-m buffer plotted around them were selected according to a gradient ranging from complex to simplified landscapes (i.e. low to high amount of semi-natural habitats) and to the farming system (i.e. small-scale traditional farming vs. large commercial farms using modern machinery). We aimed to obtain a balanced ratio of landscape complexity along the continuum of agricultural intensification. The surveys were conducted between November 2017 and February 2018.

Before performing the bird surveys, each transect was mapped on a printed satellite picture (satellite picture of 1 : 1300) and then digitized in QGIS (Quantum GIS Development Team 2012). Different crop species were identified, and delineations of every field were precisely plotted. Semi-natural habitats were divided into five categories: grove, which represented every vertical vegetal structure taller than 30 cm (isolated trees, hedges, bushes, corrals, etc.), natural grassland (field margins, savannah-like habitats), rocks, rivers (including riverbed) and human settlements (houses, dirt roads). Variables such as mean field size, crop richness and crop diversity (Shannon index) were computed directly in QGIS 2.10 (Quantum GIS Development Team 2012) and R (version 3.6.1, R Core Team 2020).

Secondly, the exact locations of all individuals of every bird species seen or heard were recorded along the transect within a 50-m buffer from the transect line. All surveys took place during the first 4 h after dawn under favourable weather conditions (no rain and no strong wind) and lasted on average ($\pm$ se) 25 $\pm$ 5 min per transect, which allowed four to five transects to be surveyed per day and per observer. Each transect was surveyed twice by the same observer on two consecutive days and the order of surveyed transects was reversed for the surveys of the following day. Although the three observers (J.G., J.M., G.M.) have similar experience, surveys were carefully planned to balance the different transect categories (landscape complexity and farming system) between them equally. In this study, only data on the presence (yes/no) of Ortolan Buntings were considered (see Marcacci *et al.* 2020 for more details about the entire farmland bird community). Birds flying over the transect were excluded from the analyses.

Statistical analyses

All analyses were computed in R (version 3.6.1, R Core Team 2020). To analyse local-scale habitat preferences we performed generalized linear mixed models (GLMMs; package *lme4*, Bates *et al.*, 2014) on a binary response (presence vs. pseudo-absence) with ground cover and management variables as explanatory variables (cultivated vegetation cover, litter cover, bare ground cover, mineral cover, natural and cultivated vegetation height, crop stage, presence of grazing and harvesting method; see Table S1). Note that crop management variables (harvested or not, grazed or not and the use of machines) were not implemented in foraging-site-scale model selection. Individual and stratum were set as random effects to avoid pseudoreplication (Bolker *et al.* 2009). We also considered site (four levels: three sites west and one east of the Rift valley) as a random factor. Spearman's correlation coefficients between explanatory variables were checked. Where $|r_s| > 0.7$, the biologically most meaningful variable was kept for building models to avoid collinearity between variables. Cultivated vegetation and natural vegetation cover were highly correlated ($|r_s|_\text{field-scale} = -0.92$, $|r_s|_\text{foraging-site scale} = -0.96$). We decided to keep cultivated vegetation cover, as one aim of this study was to quantify the effect of agriculture on Ortolan Buntings. Proportional cover variables were *arcsin* square root-transformed to stretch small proportion values (Guyot *et al.* 2017). We also considered quadratic functions of all variables to detect an optimum in the foraging preferences.

The best models were selected based on Akaike's information criterion corrected for small sample size (AIC$_c$, Burnham & Anderson 2002). An automated selection approach using the function *dredge* from the package *MuMIn* (Bartoń 2016) was used to sort and select the best-ranked, competitive models (including quadratic effects) within ΔAIC$_c$ < 2 (Burnham & Anderson 2002).

For foraging-site-scale habitat preference models, we did not consider crop types because of a lack of convergence for this variable. We measured foraging selection in the different crop types using a contingency table analysis (Table S3). Assumptions for classical Pearson's chi-square tests were not met. Thus, *P*-values were computed using Monte-Carlo simulations with 10 000 replicates (Hope 1968).

At a landscape scale, transect data were analysed using GLMMs with a binomial error distribution (logit function), with the binary Ortolan Bunting occurrence (presence vs. absence) as the dependent variable and habitat variables as explanatory variables (proportions of grove, natural grassland, rocks, rivers, human settlements, crop richness and crop diversity). The presence of Ortolan Buntings was defined whenever at least one bird was recorded during each transect survey. In total, we surveyed 120 transects twice, making a total of 240 presences/absences. Crop diversity was highly correlated with the mean field size ($|r_s| = -0.783$) and we retained crop diversity for modelling. Proportional cover variables were *arcsin* square root-transformed. Quadratic functions of all numerical variables were also considered to detect an optimum. We set transect-id (i.e. to account for repeated counts) and date as random intercepts because we expected day-to-day changes (i.e. due to the migratory biology of overwintering Ortolan Buntings), which could affect bird counts over the field season. The model selection procedure was the same as for the selection of foraging-site-scale habitat preference models. All explanatory variables were *arcsin* square root-transformed and additionally standardized to better achieve model convergence and to enable a comparison of effect sizes. Model assumptions were fulfilled in all cases and were assessed from the underlying standard residual plots using the package *DHARMa* (Hartig 2021). With the same package, we further checked for overdispersion of all models.

To draw effect plots, we described the range of plausible parameter values using 95% Bayesian credible intervals (noted as CI95) of the model parameters (Korner-Nievergelt *et al.* 2015). We used the *sim()* function of the package *arm* (Gelman & Hill 2006) to calculate the posterior distribution assuming flat prior distributions (Gelman & Hill 2006). Credible intervals of regression lines were obtained from the joint posterior distribution of the model parameters (Zuur *et al.* 2009).

RESULTS

Local-scale habitat preference using radiotracking

The obtained wintering home ranges (MCP) ranged from 17.8 to 163.26 ha with a mean ± se of 81.04 ± 13.22 ha per individual. The most parsimonious field-scale model contained the

percentages of bare ground, litter, cultivated vegetation and whether the field was harvested or not (Table 1). These explanatory variables were considered the main determinants of habitat preference at the field scale. Bare ground had a linear and positive effect (Fig. 2a), whereas the percentage of litter represented mostly by the post-harvested stubble exhibited a quadratic effect with an optimum at 55% of litter cover (Fig. 2b). Non-harvested fields decreased the probability of a foraging event drastically: 0.054 (CI95 = 0.010–0.16) in an unharvested field and 0.43 (CI95 = 0.30–0.56) in a harvested field (Fig. 2c). As we did not detect machine harvesting west of the Rift Valley, the field-scale model selection was repeated only within eastern sites, with machine as an additional explanatory variable. The analysis yielded the same explanatory variables with or without the use of machinery as a covariate. Ortolan Buntings foraged significantly more often in traditional, manually harvested, fields (0.32, CI95 = 0.19–0.47) compared with fields harvested with machines (0.06, CI95 = 0.0082–0.22; Fig. 2d).

Two competitive models ($\Delta AIC_c < 2$) were selected for the foraging-site scaled habitat selection (Table 1). In line with the field-scale analysis, both models included a positive linear effect of bare ground, and foraging seemed optimal at intermediate amounts of litter (quadratic effect). In addition, high amounts of a mineral substrate seem to be important when foraging, as seen in the most competitive model (Table 1).

Comparisons between crop types of presence and pseudo-absence points computed by randomized contingency tables suggested that Ortolan Buntings selected a specific type of crop when foraging (Table S3). More specifically, radiotracked birds from the Ethiopian Highlands showed a preference for barley and wheat cultures and were never detected on uncultivated ground (pasture or labour), whereas bean (*Vicia* sp.) fields were largely preferred by eastern birds. The Ortolan Buntings from this eastern area also avoided uncultivated ground (only one occurrence) and were never detected in teff (*Eragrostis tef*) fields.

Landscape-scale habitat preferences of Ortolan Buntings

In total, we recorded 151 bird species and 14 496 individuals (Marcacci *et al.* 2020). With 1070 individuals detected across 42 of 120 transects (35%),

the Ortolan Bunting was the fifth most abundant bird species at our study sites. The occurrence probability of an Ortolan Bunting was best explained by a high crop diversity (Shannon diversity index) and the proportion of grove structures within the transects' buffer (Table 1). In landscapes without groves, the probability of occurrence was only 0.006 (CI95 = 0.0002–0.035), whereas a 15% fraction of groves increased this probability to 0.46 (CI95 = 0.08–0.89, Fig. 3a). The highest recorded grove coverage was 32.25%, where the occurrence probability levelled up to 0.87 (CI95 = 0.42–0.99). Low crop diversity ($H_{crop\ types} = 0$) had an occurrence probability of 0.004 (CI95 = 0.00002–0.03), whereas when crop diversity was high ($H_{crop\ types} = 1.81$; Fig. 3b), the probability increased up to 0.64 (CI95 = 0.12–0.97).

DISCUSSION

Our results demonstrate that the Ortolan Bunting is one of the most common bird species in the Ethiopian Highlands in winter (Jiguet *et al.* 2019) and highlight the importance of traditional agriculture for the conservation of this species. Habitat preferences differed depending on the scale considered. At foraging-site scale, our results showed striking similarities with observed preferences on the breeding sites (Menz & Arlettaz 2012): the relevance of patches of bare ground when foraging and the importance of a high amount of litter (e.g. food availability). At a broader landscape scale, traditionally managed fields that are interspersed with natural or semi-natural structures positively affected the occurrence probability of Ortolan Buntings, underlining the importance of structured, extensively managed agricultural landscapes (Brambilla *et al.* 2017).

The proportion of bare ground combined with intermediate amounts of litter, in particular stubble, seemed to be the main driver affecting the foraging behaviour of Ortolan Buntings in their wintering grounds, as observed in their breeding sites (Nævra 2002, Berg 2008, Menz *et al.* 2009, Morelli 2012, Brambilla *et al.* 2016, 2017). The preference for high amounts of bare ground could be explained by several non-mutually exclusive hypotheses. First, foraging in areas with patches of bare ground might increase mobility, thereby decreasing the physiological costs entailed in searching for food; this is because dense vegetation

Table 1. (A) Summary of the most parsimonious selected generalized linear mixed models for the field- and foraging-site-scale approach on 12 radiotracked Ortolan Buntings. (B) Summary of the selected models of landscape-scale habitat preference obtained from transect data.

(A) Local-scale habitat preference models (telemetry data)

	No. of model	Intercept Estimate	se	P-value	Bare ground Estimate	se	P-value	Litter Estimate	se	P-value	Litter^2 Estimate	se	P-value	Harvest Estimate	se	P-value	Mineral Estimate	se	P-value	df	AICc	Δi	wi
Field-scale	124	−3.103	0.758	< 0.001	1.390	0.231	< 0.001	1.930	0.359	< 0.001	−1.457	0.248	< 0.001	2.796	0.799	< 0.001				8	312.6	0.00	1.00
Foraging site-scale with 10-m pseudo-absence	30	−0.201	0.164	0.221	1.067	0.187	< 0.001	1.246	0.224	< 0.001	−1.220	0.226	< 0.001				0.240	0.153	0.224	8	308.4	0.00	0.55
	14	−0.157	0.260	0.546	1.054	0.197	< 0.001	1.215	0.248	< 0.001	−1.293	0.221	< 0.001							7	308.8	0.37	0.45

	No. of model	Intercept Ortolan Bunting Estimate	se	P-value	Bare ground Ortolan Bunting Estimate	se	P-value	Litter Ortolan Bunting Estimate	se	P-value	Litter^2 Ortolan Bunting Estimate	se	P-value	Use of machine Ortolan Bunting Estimate	se	P-value	df	AICc	Δi	wi
Field-scale – South only	62	−0.775	0.336	0.021	2.141	0.388	< 0.001	2.836	0.515	< 0.001	1.855	0.343	< 0.001	−2.236	0.892	0.012	7	145.0	0	1

(B) Landscape-scale preference models (transect data)

	No. of model	Intercept Ortolan Bunting Estimate	se	P-value	Grove cover (%) Ortolan Bunting Estimate	se	P-value	Shannon's diversity index of crop types Ortolan Bunting Estimate	se	P-value	Grassland cover (%) Ortolan Bunting Estimate	se	P-value	River cover (%) Ortolan Bunting Estimate	se	P-value	df	AICc	Δi	wi
Landscape-scale	133	−3.555	1.616	0.028	2.6380	1.023	0.010	2.399	0.987	0.015							5	185.5	0.00	0.55
	54	−3.616	2.111	0.087	2.905	1.161	0.011				0.889	0.695	0.201	1.073	0.578	0.063	6	187.2	1.70	0.23
	22	−3.497	2.131	0.101	3.033	1.192	0.011										6	187.4	1.84	0.22

All proportional explanatory variables were arcsin square-root transformed and all continuous variables were standardized. Each variable is shown with its associated coefficient (Estimate), standard error (se) and *P*-value. For each model, the number of degrees of freedom (df), Akaike's Information Criterion corrected for small sample size (AICc), the change in AICc (Δi) and the Akaike weight (wi) are presented.
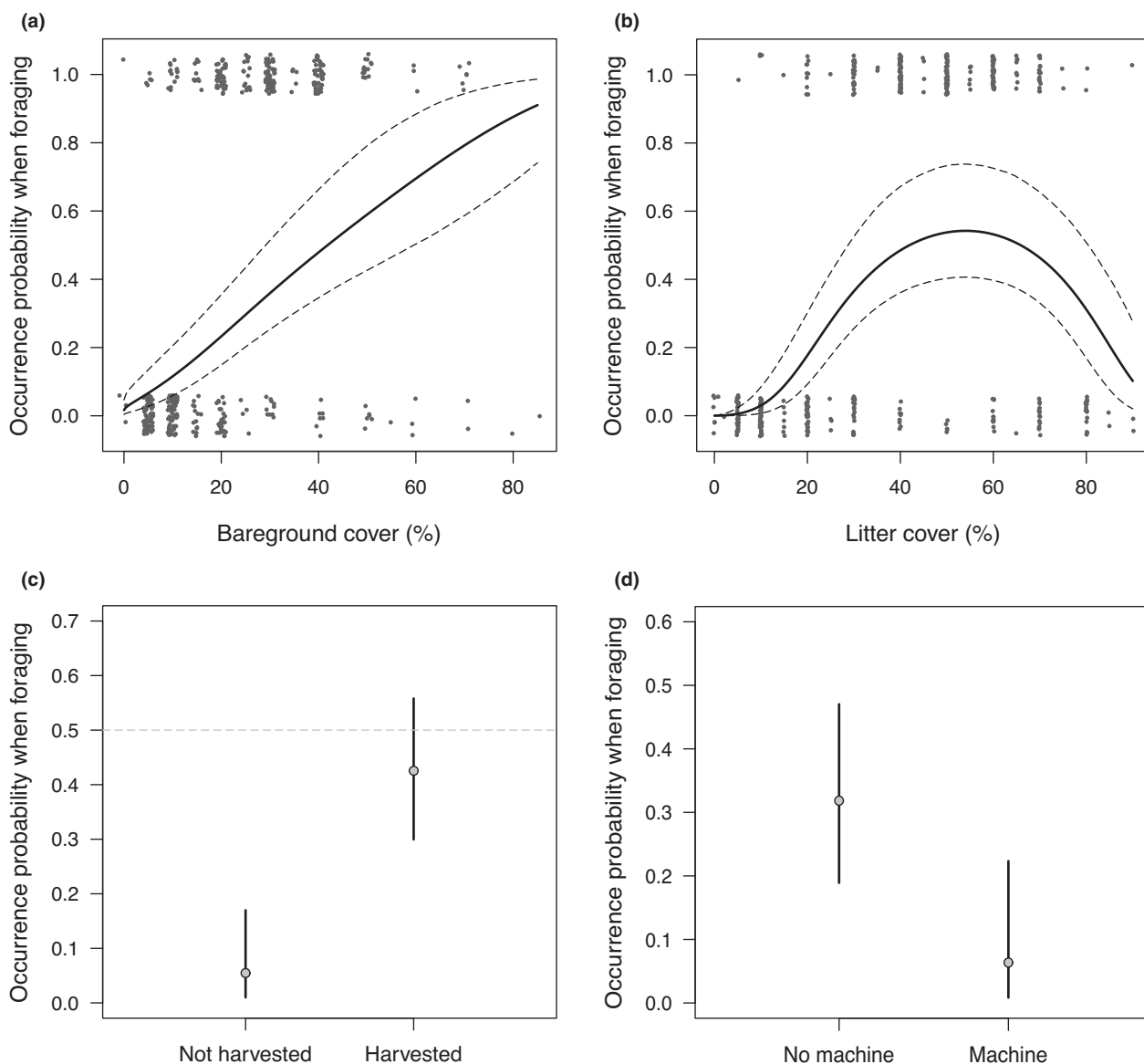
Figure 2. Local-scale habitat selection: relationships between bare ground (a), litter cover (b) and state of the field (harvested vs. not harvested) (c) on Ortolan Bunting foraging occurrence probabilities at the field scale drawn from a generalized linear mixed model. The 95% Bayesian credible intervals are indicated by dashed lines on (a) and (b), and by the bars in (c). (a, b) Points depict raw data. (d) Effect of harvesting method (manually vs. combine harvester) on the probability of foraging occurrence. Probabilities are drawn from a generalized linear mixed model. Because combine harvesters were only used in the eastern sites, only eastern birds were used to compute the model ($n = 6$). The dot represents the fit of the model and the line the range of the 95% Bayesian credible intervals.

impairs movements of ground-feeding farmland birds such as the Ortolan Bunting (Leal *et al.* 2019). Secondly, peripheral vision due to the lack of vegetation cover improves the detection of predators (Grzybowski 1983, Metcalfe 1984, Moorcroft *et al.* 2002), thus reducing mortality risk. Thirdly, on their breeding grounds, Ortolan

Buntings were associated with a high amount of bare ground, as this microstructure increases arthropod prey availability, abundance being modified by accessibility (Menz & Arlettaz 2012). This finding is congruent with other studies that found that prey detectability, whether insects or seeds, is enhanced by large amounts of bare ground (e.g.
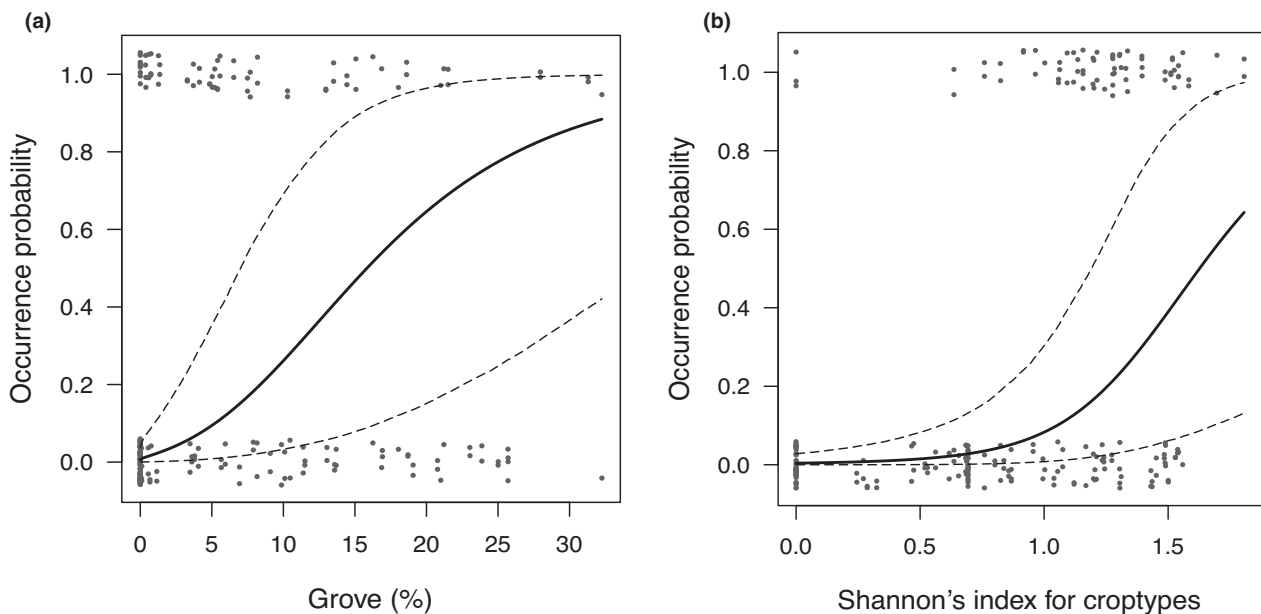
Figure 3. Landscape-scale habitat selection: effects of grove cover (a) and crop diversity (b) on Ortolan Bunting occurrence probability predicted from generalized linear mixed models. The 95% Bayesian credible intervals are delimited by the dashed lines on (a) and (b). Dots depict raw data.

Whitehead *et al.* 1995, Robinson & Sutherland 1999, Moorcroft *et al.* 2002, Menz *et al.* 2009) or a very short grass layer (Leal *et al.* 2019).

The detection/availability hypothesis is in line with the finding that Ortolan Buntings prefer an intermediate litter cover. Litter in cereal fields was mainly composed of stubble. In crops such as wheat and barley, stubble remains on the surface of the ground as long as the soil has not been ploughed. Here, compared with a tilling system where the stubble is ploughed after harvesting, the amount of available waste seeds is larger and remains available as a food source for much longer periods of time, which has proven essential for the survival of seed-eating birds wintering in farmland (Moorcroft *et al.* 2002, Gillings *et al.* 2005). Low amounts of stubble were associated with a low probability of a foraging event, most probably due to a lack of food resource. Foraging conditions above the observed optimum at around 50% of litter cover were less optimal, probably due to too dense a litter cover in combination with a lack of bare ground, which limits food availability. Ethiopia has a long history of traditional agriculture where cereal crops are mostly harvested manually (Logan 2014). Our results demonstrate that Ortolan Buntings benefit from

this traditional method with a low probability of foraging in mechanically harvested fields. The loss of grain in traditional harvesting is significantly higher (up to 57%) compared with combine harvesting (Hassena *et al.* 2000). This potential loss of grain associated with manual harvesting therefore constitutes a key foraging resource for seed-eating species.

When foraging, Ortolan Buntings showed a clear preference for cultivated fields, indicating their dependence on traditional agriculture to access food resources. The preferences for specific crop types differed between the western (preference for barley and/or wheat) and eastern (preference for beans) sites. This discrepancy may be explained by inter-site variation in crop composition, the phenology of the crops and their harvesting time. The preference in the eastern site for bean cultures is potentially comprehensible, as inter-cropping is a common practice in Ethiopia, resulting in within-field associations with cereals and wild weeds (Logan 2014). This enhanced heterogeneity in crop type and vegetation structure within these fields may explain the foraging preference of Ortolan Buntings for this crop. In contrast, teff leftovers after harvest were often neglected and probably avoided by the birds. The

low proportion of bare ground and the minute size of teff grains probably lead to an absence of this cereal in the Ortolan Bunting diet. Although Ortolan Buntings were seemingly not associated with unproductive fields such as pastures, they still seemed to rely on natural or semi-natural elements in this agro-ecosystem.

At a landscape scale, the Ortolan Bunting was dependent on the amount of groves (shrubs, trees, hedges, etc.), which may serve as refuges to escape predators or as roosting sites. This preference is in line with studies conducted on the breeding grounds, where these structures are important for singing, resting and nesting (Berg 2008, Menz *et al.* 2009, Brambilla *et al.* 2016, 2017, Šálek *et al.* 2018). However, given the expansion of smallholders in Ethiopia (Central Statistical Agency (Ethiopia) and ICF International 2016) and their need for fire wood and timber (Fentie *et al.* 2013, Logan 2014), tree cover has decreased dramatically in recent decades, leading to landscape simplification. Moreover, the remaining grove structures are often composed of only a few tree species (mainly eucalyptus and *Juniperus* sp.) serving anthropogenic needs (timber, firewood). These trends underline the need for large-scale projects of small-scale reforestation, contributing at the same time to socio-economic development of the local population and biodiversity. Ortolan Buntings also preferred heterogeneous landscapes with a high crop diversity. This may be due partly to an increase in field margins, where demarcation lines between fields can support semi-natural habitats such as field margins or shrub hedges (Benton *et al.* 2003, Vickery *et al.* 2009). A high crop and structural diversity may additionally be favoured due to prolonged or multiple food peaks. This is in contrast to monocultures, which offer a single food peak and thus concentrate available food resources in a shorter time window.

Here, we have demonstrated the importance of traditional extensive agriculture and semi-natural elements for this species, which suggest that it is sensitive to agricultural intensification. The combination of an agriculture sector still representing 85% of employment in Ethiopia (Central Intelligence Agency 2012, Josephson *et al.* 2014) and unprecedented human demographic growth will hence shape the future of this species, and biodiversity in general, in this agro-ecosystem. With restricted potential for irrigation and few opportunities to extend cultivated area in highlands,

agricultural intensification seems inescapable (Headey *et al.* 2014). Ongoing and future governmental plans to develop and extend new crops and cultivars (i.e. enhanced varieties), chemical fertilizers and new management practices (Spielman *et al.* 2010, Headey *et al.* 2014) urgently need to integrate biodiversity elements to guarantee the long-term persistence of this unique agro-ecosystem.

Under the scenario of agricultural intensification towards large-scale industrialized faming, we predict a degradation and loss of wintering habitat for the eastern Ortolan Bunting populations. This may have significant consequences for this emblematic species, as the overwintering population in the Ethiopian highlands represents about 90% of the global population (Jiguet *et al.* 2019) and acts as an important source of gene flow for the declining western population (Moussy *et al.* 2018). However, coexistence of the Ortolan Bunting's needs with agriculture that fulfils the growing population's demands seems possible. Multi-functional agricultural landscapes are needed (Fischer *et al.* 2008, 2014) that promote agricultural yield, biodiversity and ecosystem services (Tscharntke *et al.* 2012, Baudron *et al.* 2019). In the context of the Ethiopian Highlands, this will probably be best achieved in the context of small-scale farming with multiple crops (but see Marcacci *et al.* 2020) where new agricultural practices (e.g. new crop varieties, intercropping) will lead to a significant increase in yield, thereby ensuring food security without marked negative impacts on seed-eating bird species. Moreover, multifunctionality can be improved by favouring native trees and bushes in reforestation projects, as in the Humbo Community-based Natural Regeneration Project in Ethiopia (Brown *et al.* 2011). These structures seem crucial for Ortolan Buntings at a landscape scale, and smallholders would benefit from increased timber, firewood and a decrease in soil erosion (Pender & Gebremedhin 2008). However, to understand fully how ongoing and future intensification processes will affect small holders and biodiversity, it seems essential to conduct further studies setting scientific bases for a sustainable, wildlife-friendly farming intensification system.

AUTHOR CONTRIBUTION

Jérémy Gremion: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing-original draft (lead); Writing-review & editing (equal). **Gabriel Marcacci:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Julien Mazenauer:** Data curation (equal); Investigation (equal); Methodology (equal); Writing-review & editing (equal). **Tolera Sori:** Investigation (equal). **Fanuel Kebede:** Conceptualization (supporting); Project administration (equal); Writing-review & editing (supporting). **Mirhet Ewnetu:** Conceptualization (supporting); Project administration (equal); Writing-review & editing (supporting). **Philippe Christe:** Conceptualization (supporting); Resources (equal); Writing-review & editing (equal). **Raphael Arlettaz:** Conceptualization (supporting); Resources (equal); Writing-review & editing (equal). **Alain Jacot:** Conceptualization (lead); Investigation (supporting); Methodology (lead); Supervision (lead); Writing-review & editing (equal).

Data Availability Statement

The data that support the findings of this study are openly available at http://doi.org/10.5281/ze nodo.4912327

REFERENCES

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking gata. *Ecology* **75**: 1313–1325.

Bartoń, K. 2016. *MuMIn: Multi-model inference. R package version 1.15.6. Version 1*: 18.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2014. Fitting linear lixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

Baudron, F., Schultner, J., Duriaux, J.Y., Gergel, S.E. & Sunderland, T. 2019. Agriculturally productive yet biodiverse: human benefits and conservation values along a forest-agriculture gradient in Southern Ethiopia. *Landsc. Ecol.* **34**: 341–365.

Benton, T.G., Vickery, J.A. & Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**: 182–188.

Berg, Å. 2008. Habitat selection and reproductive success of Ortolan Buntings *Emberiza hortulana* on farmland in central Sweden – the importance of habitat heterogeneity. *Ibis* **150**: 565–573.

Bibby, C., Burgess, N., Hill, D. & Mustoe, S. 2000. *Bird Count Techniques*. London: Academic Press.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**: 127–135.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81–83.

Brambilla, M., Gustin, M., Vitulano, S., Falco, R., Bergero, V., Negri, I., Bogliani, G. & Celada, C. 2017. Sixty years of habitat decline: impact of land-cover changes in northern Italy on the decreasing Ortolan Bunting *Emberiza hortulana*. *Reg. Environ. Change* **17**: 323–333.

Brambilla, M., Gustin, M., Vitulano, S., Negri, I. & Celada, C. 2016. A territory scale analysis of habitat preferences of the declining Ortolan Bunting *Emberiza hortulana*. *Bird Study* **63**: 52–57.

Brown, D.R., Dettmann, P., Rinaudo, T., Tefera, H. & Tofu, A. 2011. Poverty alleviation and environmental restoration using the clean development mechanism: a case study from Humbo, Ethiopia. *Environ. Manage.* **48**: 322–333.

Buckland, S.T., White, G.C. & Garrott, R.A. 1991. Analysis of wildlife radio-tracking data. *Biometrics* **47**: 353.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd ed. New York: Springer.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A. & Kinzig, A.P. 2012. Biodiversity loss and its impact on humanity. *Nature* **486**: 59–67.

Central Intelligence Agency 2012. *World Factbook 2012*. Washington, DC: Central Intelligence Agency, Office of Public Affairs.

Central Statistical Agency (Ethiopia) and ICF International. 2016. Federal Democratic Republic of Ethiopia Demographic and Health Survey 2016 Key Indicators Report. *Ethiopians Water Sector Development Program*, 1–49.

Chiron, F., Chargé, R., Julliard, R., Jiguet, F. & Muratet, A. 2014. Pesticide doses, landscape structure and their relative effects on farmland birds. *Agric. Ecosyst. Environ.* **185**: 153–160.

Cramp, S. & Perrins, C.M. (eds) 1994. *The Birds of the Western Palearctic*, Vol. **IX**. Oxford: Oxford University Press.

Davis, K., Swanson, B. & Amudavi, D. 2009. *Review and Recommendations for Strengthening the Agricultural Extension system in Ethiopia*. Washington, DC: IFPRI.

Donald, P.F., Green, R.E. & Heath, M.F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**: 25–29.

Douglas, D.J.T., Newson, S.E., Leech, D.I., Noble, D.G. & Robinson, R.A. 2010. How important are climate-induced changes in host availability for population processes in an obligate brood parasite, the European Cuckoo? *Oikos* **119**: 1834–1840.

Eggers, S., Unell, M. & Pärt, T. 2011. Autumn-sowing of cereals reduces breeding bird numbers in a heterogeneous agricultural landscape. *Biol. Conserv.* **144**: 1137–1144.

Fentie, D., Fufa, B. & Bekele, W. 2013. Determinants of the use of soil conservation technologies by smallholder farmers: the case of Hulet Eju Enesie District, East Gojjam Zone, Ethiopia. *AJAFS* 01: 2321–1571.

Fischer, J., Abson, D.J., van Butsic, M., Chappell, J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G. & von Wehrden, H. 2014. Land sparing versus land sharing: moving forward. *Conserv. Lett.* **7**: 149–157.

Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L. & Ranganathan, J. 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? *Front. Ecol. Environ.* **6**: 380–385.

Garder, B. 1996. *European Agriculture: Policies, Production, and Trade*. London: Routledge.

Gelman, A. & Hill, J. 2006. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge: Cambridge University Press.

Gillings, S., Newson, S.E., Noble, D.G. & Vickery, J.A. 2005. Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. *Proc. R. Soc. Lond. B.* **272**: 733–739.

Glemnitz, M., Zander, P. & Stachow, U. 2015. Regionalizing land use impacts on farmland birds. *Environ. Monit. Assess.* **187**: 1–21.

Grzybowski, J.A. 1983. Sociality of grassland birds during winter. *Behav. Ecol. Sociobiol.* **13**: 211–219.

Guyot, C., Arlettaz, R., Korner, P. & Jacot, A. 2017. Temporal and spatial scales matter: circannual habitat selection by bird communities in vineyards. *PLoS One* **12**: e0170176.

Hallmann, C.A., Foppen, R.P.B., Van Turnhout, C.A.M., De Kroon, H. & Jongejans, E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* **511**: 341–343.

Hartig, F. 2021. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.1.* Available at: https://CRAN.R-project.org/package= DHARMa. Accessed 15 May 2021.

Hassena, M., Regassa, E., Mwangi, W.M. & Verkuijl, H. 2000. *A Comparative Assessment of Combine Harvesting Vis-A-Vis Conventional Harvesting and Threshing in Arsi Region*. Mexico City: CIMMYT.

Headey, D., Dereje, M. & Taffesse, A.S. 2014. Land constraints and agricultural intensification in Ethiopia: a village-level analysis of high-potential areas. *Food Policy* **48**: 129–141.

Holden, S. & Yohannes, H. 2002. Land redistribution, tenure insecurity, and intensity of production: a study of farm households in Southern Ethiopia. *Land Econ.* **78**: 573–590.

Hope, A.C.A. 1968. A simplified Monte Carlo significance test procedure. *J. R. Stat. Soc. Series B* **30**: 582–598.

Jiguet, F., Arlettaz, R., Bauer, H.-G., Belik, V., Copete, J.L., Couzi, L., Czajkowski, M.A., Dale, S., Dombrovski, V., Elts, J. & Ferrand, J. 2016. An update of the European breeding population sizes and trends of the Ortolan Bunting (*Emberiza hortulana*). *Ornis Fenn.* **93**: 186–196.

Jiguet, F., Robert, A., Lorrillière, R., Hobson, K.A., Kardynal, K.J., Arlettaz, R., Bairlein, F., Belik, V., Bernardy, P., Copete, J.L. & Czajkowski, M.A. 2019. Unravelling migration connectivity reveals unsustainable hunting of the declining Ortolan Bunting. *Sci. Adv.* **5**: eaau2642.

Josephson, A.L., Ricker-Gilbert, J. & Florax, R.J.G.M. 2014. How does population density influence agricultural intensification and productivity? Evidence from Ethiopia. *Food Policy* **48**: 142–152.

Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Marti, D., Anton, M., Klvanová, A., Kalyakin, M.V. & Bauer, H.G. 2020. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Barcelona: Lynx Edicions.

Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kéry, M., Strebel, N. & Sattler, T. 2018. *Distribution and Population Trends of Birds in Switzerland and Liechtenstein*. Sempach: Schweizerische Vogelwarte.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guélat, J., Almasi, B. & Korner-Nievergelt, P. 2015. *Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS, and Stan*. Cambridge: Academic Press.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. 1999. The second silent spring? *Nature* **400**: 611–612.

Leal, A.I., Acácio, M., Meyer, C.F.J., Rainho, A. & Palmeirim, J.M. 2019. Grazing improves habitat suitability for many ground foraging birds in Mediterranean wooded grasslands. *Agric. Ecosyst. Environ.* **270**: 1–8.

Logan, C. 2014. Agricultural intensification in Ethiopia: review of recent research. *Afr. J. Agric. Res.* **9**: 2377–2390.

Marcacci, G., Gremion, J., Mazenauer, J., Sori, T., Kebede, F., Ewnetu, M., Christe, P., Arlettaz, R. & Jacot, A. 2020. Large-scale versus small-scale agriculture: disentangling the relative effects of the farming system and semi-natural habitats on birds' habitat preferences in the Ethiopian highlands. *Agric. Ecosyst. Environ.* **289**: 106737.

Menz, M.H.M. & Arlettaz, R. 2012. The precipitous decline of the Ortolan Bunting *Emberiza hortulana*: time to build on scientific evidence to inform conservation management. *Oryx* **46**: 122–129.

Menz, M.H.M., Mosimann-Kampe, P. & Arlettaz, R. 2009. Foraging habitat selection in the last Ortolan Bunting *Emberiza hortulana* population in Switzerland: final lessons before extinction. *Ardea* **97**: 323–333.

Metcalfe, N.B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim. Behav.* **32**: 981–985.

Moorcroft, D., Whittingham, M.J., Bradbury, R.B. & Wilson, J.D. 2002. The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *J. Appl. Ecol.* **39**: 535–547.

Morelli, F. 2012. Correlations between landscape features and crop type and the occurrence of the Ortolan Bunting *Emberiza hortulana* in farmlands of Central Italy. *Ornis Fenn.* **89**: 264–272.

Moussy, C., Arlettaz, R., Copete, J.L., Dale, S., Dombrovski, V., Elts, J., Lorrilière, R., Marja, R., Pasquet, E., Piha, M. & Seimola, T. 2018. The genetic structure of the European breeding populations of a declining farmland bird, the Ortolan Bunting (*Emberiza*

hortulana), reveals conservation priorities. *Conserv. Genet.* **19**: 909–922.

Naef-Daenzer, B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *J. Avian Biol.* **38**: 404–407.

Nævra, A. 2002. Hortulanens skjebnetime. *Vår Fuglefauna* **25**: 62–81.

Newton, I. 2004. The recent declines of farmland bird populations in Britian: an appraisal of causal factors and conservation actions. *Ibis* **146**: 579–600.

Olsson, P., Selstam, G., Sondell, J.A.N. & Olsson, P. 2015. Wintering area and migration routes for Ortolan Buntings *Emberiza hortulana* from Sweden determined with light-geologgers. *Ornis Svec.* **25**: 3–14.

Pender, J. & Gebremedhin, B. 2008. Determinants of agricultural and land management practices and impacts on crop production and household income in the highlands of Tigray, Ethiopia. *J. Afr. Econ.* **17**: 395–450.

Quantum GIS Development Team 2012. Quantum GIS Geographic Information System. *Open Source Geospatial Foundation Project*. Beaverton: OSGeo.

R Core Team 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rime, Y., Luisier, C., Arlettaz, R. & Jacot, A. 2020. Landscape heterogeneity and management practices drive habitat preferences of wintering and breeding birds in intensively-managed fruit-tree plantations. *Agric. Ecosyst. Environ.* **295**: 106890.

Robinson, R.A. & Sutherland, W.J. 1999. The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. *Ecography* **22**: 447–454.

Šálek, M., Zeman, V. & Václav, R. 2018. Habitat selection of an endangered European farmland bird, the Ortolan Bunting *Emberiza hortulana*, in two contrasting landscapes: implications for management. *Bird Conserv. Int.* **29**: 144–158.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L. & Arlettaz, R. 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLoS One* **5**: e13115.

Spielman, D.J., Byerlee, D., Alemu, D. & Kelemework, D. 2010. Policies to promote cereal intensification in Ethiopia: a review of evidence and experience. *Food Policy* **35**: 185–194.

Thoma, M. & Menz, M.H.M. 2014. The Ortolan Bunting *Emberiza hortulana* wintering in West Africa, and its status as a passage migrant in Mauritania. *Malimbus* **36**: 13–31.

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* **151**: 53–59.

van Dijk, A.-J., Hustings, F., Koffijberg, K., van der Weide, M., Deuzeman, S., Dijksen, L., Zoetebier, D. & Plate, C. 2005. Kolonievogels en zeldzame broedvogels in Nederland in 2000–02. *Limosa* **78**: 45–64.

van Noorden, B. 1999. De Ortolaan *Emberiza hortulana*, een plattelandsdrama. *Limosa* **72**: 55–63.

Vepsäläinen, V., Pakkala, T., Piha, M. & Tiainen, J. 2005. Population crash of the Ortolan Bunting *Emberiza hortulana* in agricultural landscapes of southern Finland. *Ann. Zool. Fenn.* **42**: 91–107.

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis* **156**: 1–22.

Vickery, J.A., Feber, R.E. & Fuller, R.J. 2009. Arable field margins managed for biodiversity conservation: a review of food resource provision for farmland birds. *Agric. Ecosyst. Environ.* **133**: 1–13.

Vieuxtemps, D. & Jacob, J.-P. 2002. Des bruants ortolans (*Emberiza hortulana*) en période de nidification au Luxembourg belge en 2002. *Aves* **39**: 123–138.

Whitehead, S.C., Wright, J. & Cotton, P.A. 1995. Winter field use by the European Starling *Sturnus vulgaris*: habitat preferences and the availability of prey. *J. Avian Biol.* **26**: 193–202.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Berlin: Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Variables measured on the field at two different scales: field-scale and foraging-site scale.

Table S2. Area (ha) of Minimal Convex Polygons (MCP) and the number of points (homing-in points) used to build them presented for each radio-tracked Ortolan Bunting.

Table S3. Overview of the collected data on different crop types.