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Farmland composition and farming practices explain spatio-temporal variations in red-legged partridge density in central Spain



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- Red-legged partridge density depends on land-use and farmland management.
 Density increases with the availability of
- pastures and rain-fed vineyards.
- Lower density is related to increasing irrigated vineyards, modulated by nitrate regulation.
- Red-legged partridge density declined by 51% from 2010 to 2017.
- Steeper declines are linked with the loss of pastures and the spread of tree crops.

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ABSTRACT

Many farmland bird populations are declining, and their negative trends are often associated with changes in land-use or farming practices, including the use of agrochemicals. The red-legged partridge (RLP) is a Mediterranean farmland game species of high socio-economic importance whose populations are thought to have declined sharply since the mid-20th century associated with farmland changes. However, no large-scale studies have tested whether abundance or trends of RLP are related to farmland composition or management.

We used hierarchical distance sampling models to estimate RLP abundance in 2010 in central Spain (Castilla-La Mancha), a main European population stronghold of this species. We studied associations between RLP density and land-uses (including variation in management: irrigated crops or organic farming). We also assessed regional abundance variation over seven years (2010–2017) and its relationship with changes in land-use.

Our results show that RLP abundance increased with the availability of natural vegetation and traditional rain-fed vineyards, but decreased with increasing proportions of tree crops and irrigated vineyards; the latter association was less pronounced in areas sensitive to nitrate contamination in water, where the amount of fertilizers applied in farmland and use of certain farming practices is more strictly regulated. These results support the idea that increases in intensive vineyards are detrimental to the RLP. We also report a strong population decline of RLP in the region, with a 51% abundance reduction in seven years. This decline was steeper in areas where more natural vegetation had been lost and where ecological tree crops had increased.

Overall, our results indicate that changes in land-use (type of crop, or the destruction of natural vegetation in farmland) and farming practices (e.g. use of irrigation in certain crops, use of nitrates) have important impacts on this farmland bird, affecting both spatial distribution and population dynamics.

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1. Introduction

After millennia of slow agricultural expansion, a large part of the European landscape is currently dedicated to agriculture (Krebs et al., 1999; European Environmental Agency, 2017). Many terrestrial bird species have adapted and rely on this semi-natural environment, finding suitable breeding or wintering habitats in it (Tucker and Heath, 1994; Tucker and Evans, 1997; Robinson et al., 2001). However, the Common Agricultural Policy (CAP), a milestone for European agriculture, has been a turning point for farmland biodiversity (Donald et al., 2002; Reif and Vermouzek, 2019; Traba and Morales, 2019). The deep and quick modernization of European farming practices after the CAP, with a marked agricultural intensification in a short time (Matson et al., 1997; Pain and Pienkowski, 1997; Reif and Vermouzek, 2019), has driven strong declines of many farmland bird species (Donald et al., 2001; Benton et al., 2002; Donald et al., 2002; Storkey et al., 2012). Agricultural intensification has led to landscape-level changes (landscape composition and configuration through changes in land use and plot size), but also to changes in agricultural practices within land-uses (e.g. mechanization, use of pesticides, fertilizers or irrigation), all of which have had direct or indirect effects on wildlife (Matson et al., 1997; Pain and Pienkowski, 1997; Reif and Vermouzek, 2019; Traba and Morales, 2019).

Land-use changes (the promotion of some crops over others, in some cases changing from annual to permanent crops, the loss of crop rotations, or the abandonment of low productive farmland) and other landscape-level changes (the increase in field size for allowing more efficient mechanization, the disappearance of field margins, or the increased monoculture) alter the extent of suitable areas for birds because of changes in the vegetation structure or food abundance (Benton et al., 2002; Wilson et al., 2005; Storkey et al., 2012). Within farmland, landscape heterogeneity usually increases habitat suitability for birds, as this increases the likelihood of finding adequate resources for a wide range of species throughout the year (Benton et al., 2003; Siriwardena et al., 2012). Additionally, the importance of non-cropped habitats (which often consist of natural vegetation, either shrubs or natural grasslands) and fallow lands within the farmland matrix has also been highlighted for many birds, providing foraging, mating, and nesting habitats (Vickery et al., 2002; Vickery et al., 2009; Mcmahon et al., 2010; Tarjuelo et al., 2020).

Farming practices, such as mechanization, change in harvest schedules, or use of chemical inputs, may also have important effects on wildlife (Fry, 1995; Matson et al., 1997; Mineau and Whiteside, 2013; Stanton et al., 2018), even when land-use does not change. Examples of this are the comparison of traditional (goblet-shaped) vs trellis irrigated vineyards in Spain (Cabodevilla et al., 2021), organic vs conventional crops (Solomou and Sfougaris, 2011; Myers et al., 2019), or the use of coated seeds in annual crops (Prosser and Hart, 2005; Lopez-Antia et al., 2016, 2021). Farmland practices may also have impacts on the quality of the environment. For example, excessive use of nitrates as fertilizers may alter the quality of surface and underground waters, subsequently impacting vegetation or fauna using those areas (Rodríguez-Estival et al., 2010; Britton et al., 2017; Chen et al., 2019; Paredes et al., 2020).

The red-legged partridge (*Alectoris rufa*; hereafter RLP) is a common species of rain-fed farmland of south-western Europe, whose natural populations inhabit mainly the Iberian Peninsula (Arroyo et al., 2020). The species has a strong socio-economic and ecological importance: it is a main small gamebird species (Andueza et al., 2018), and an important trophic resource for many Iberian predators (Calderón, 1977), including threatened species such as Bonelli's eagle (*Aquila fasciata*) and Imperial eagle (*Aquila adalberti*). It is a habitat generalist, which inhabits natural environments as well as farmland mosaics, but in Spain it is more abundant in areas dominated by arable land (Blanco-Aguiar, 2007). Habitat changes over time have strongly affected how RLP use different habitats (Delibes-Mateos et al., 2012). In the mid-twentieth

century the areas favorable to RLP in Andalusia, southern Spain, were strongly associated with natural vegetation (mostly scattered Mediterranean scrubland) and open evergreen oak forests with underlying grasslands in low altitude mountain ranges (400-1300 m). However, in recent decades, the habitats in those mountain ranges have been abandoned or modified, and turned into dense scrublands or wood-lands, which are unsuitable to partridges. Nowadays, the most favorable areas for RLP are dominated by croplands (Delibes-Mateos et al., 2012), making them much more likely to be affected by agricultural intensification.

RLP populations in Spain strongly declined in the second half of the 20th century (Blanco-Aguiar, 2007), and the decline may have continued in recent decades (BirdLife International, 2018). Population declines have also been detected in France and less markedly in Portugal (Arroyo et al., 2020). Declines have been suggested to be associated with changes in farmland, including loss of habitat heterogeneity, earlier cereal harvest, and use of agrochemicals. Accordingly, abundance and survival are lower in more homogeneous farmland areas with fewer field margins (Buenestado et al., 2009), high nest losses are observed due to earlier harvest of cereal (Casas and Vinuela, 2010), and coated seeds have been shown to have negative effects on the species (Lopez-Antia et al., 2016, 2021; Lennon et al., 2020). Nitrates absorbed through drinking water have also been shown to have negative effects on the species (Rodríguez-Estival et al., 2010), so areas where fertigation in vineyards is widespread can potentially be negative for RLP. Many studies conducted on captive partridges have shown that agrochemicals currently used in modern agriculture adversely affect survival and reproduction (e.g. Fernández-Vizcaíno et al., 2020; Ortiz-Santaliestra et al., 2020), although fewer studies have quantified exposure levels in wild RLPs (e.g. Lopez-Antia et al., 2016; Fernández-Vizcaino_et_al. submitted) or whether population trends are linked to proxies of agrochemical exposure. In fact, the magnitude of the population decline (at least in recent years) has been questioned from hunting sectors (RFEC, 2020) and no large-scale study has assessed whether abundance or trends of RLP are related to farmland composition or management, which could have important implications when designing management measures to promote the species conservation status.

Here we used hierarchical distance sampling models to estimate RLP density variation in space and time over 7 years (2010–2017) in Castilla-La Mancha, a large and important Spanish region for the species (Blanco-Aguiar et al., 2003; Blanco-Aguiar et al., 2004). First, we assessed the relationship between land-use composition in the farm-land environment and spatial variations in abundance, based on bird and habitat data from a single year (2010). In particular, we tested whether RLP abundance varied with the availability of natural (non-cropped) vegetation or with farming practices (e.g. irrigated vs non-irrigated crops, organic farming, or limitations to the use of fertilizers in areas sensitive to nitrate contamination in water). Second, we assessed abundance trends over 7 years and investigated if population changes can also be explained by habitat changes. We discuss the implications of our results for the species' conservation, management, and hunting sustainability.

2. Material and methods

2.1. Study area

We conducted this study in Castilla-La Mancha (Appendix A, Fig. A1), a region that holds one of the population strongholds of the RLP in Spain and Europe (Blanco-Aguiar et al., 2003; Blanco-Aguiar et al., 2004). It is also one of the Spanish regions in which RLP hunting is most important (Blanco-Aguiar et al., 2003). Castilla-La Mancha (79,463 km²) is administratively divided into five provinces and is sparsely populated (25.74 per/km²). This region is mostly a plateau, with a mean elevation of 696 m.a.s.l. (meters above sea level) and around 80% of its surface is below 1000 m.a.s.l., although there are

also some important mountainous areas reaching 1800 m.a.s.l. (Pons-Giner, 2011). Regarding agriculture, farmland covers 46% of the surface (around 37,000 km²), with rain-fed cereal (11,759 km²), vineyards (4652 km²), and olive trees (4437 km²) being the most important crops (ESYRCE, 2020). 23.5% of the farmland (8724 km²) is kept as fallow annually, as part of the farming cycle (ESYRCE, 2020). Other crops (irrigated cereal, legumes, orchards, industrial crops, fodder crops or vegetable plots) cover each less than 3% of the farmland area. Regarding non-agricultural habitats, forests cover 38% of the region's surface (30,049 km²) and grasslands 6.5% (ESYRCE, 2020).

2.2. Partridge data

Field data was collected by regional wardens as part of a monitoring program of RLP breeding phenology (Arroyo and Guzman, 2017). Observations took place from 2010 to 2017. A large number of transects were sampled the first year throughout the region (n = 170, Appendix A, Fig. A1a), although 49 of them had to be discarded due to a lack of information on transect length or observation distances. In subsequent years, a much smaller number of transects was monitored (28–36 transects per year). Transects sampled in 2011–2017 were not necessarily the same each year. For the study of trends, we only considered those transects sampled at least twice between 2010 and 2017 (n = 48, Appendix A, Fig. A1b).

The transects (ca. 14.5 km in length, range 3.2 km to 39.8 km) were driven by car at slow speed (<30 km/h), stopping each time that a partridge or a group of partridges was observed. For each sampling in each transect, date, start, and finishing time were noted. For each observation, the number of partridges, the age group (i.e. adult or chick) of each individual, and the perpendicular distance to the transect line (estimated visually) were noted. Samplings in each transect each year were aimed to be repeated weekly or every 10 days from mid-April to late-July, although variations occurred among transects due to logistic constraints (with an average of 10 visits per transect and year, range 1 to 16). Samplings occurred throughout the day (between sunrise and sunset), although most frequently during early morning or early evening. In this study, we only considered counts of adult RLPs.

2.3. Land-use and environmental data

We used the Spanish Land Cover Information System (SIOSE, 2011) to describe land-use composition in each transect in 2010. The SIOSE database is spatially very accurate and provides detailed information about the distributions of various types of land cover, including information on whether crops are irrigated or not. There are four available versions of SIOSE, and we used SIOSE, 2011 as the closest temporally to partridge data obtained in 2010.

We calculated for each transect the proportion of each land-use as follows. SIOSE data was set on a polygon layer. A polygon might have a unique value (e.g. herbaceous crops) or be a combination of habitats with their respective percentages into the polygon (e.g. 75% herbaceous crops, 25% olive groves). We obtained a polygon layer for each of the habitats of interest for the RLP (shrubland; pastures; forests; urban areas; irrigated and rain-fed vineyards, irrigated and rain-fed arable lands, and irrigated and rain-fed tree crops, see Table 1). We created a buffer of 200 m on each side of the transect line (200 m being the distance above which partridges were not detected according to our data). We obtained the proportion of each habitat type into the buffered transects applying the corresponding correction related to the percentage (i.e. if a polygon of 100 ha had 75% of herbaceous crops, we considered 75 ha of herbaceous crops in that polygon).

As RLP uses field margins for breeding and refuge (Casas and Vinuela, 2010), we also calculated an index of field margins for each transect, as the sum of perimeters of fields within the transect buffer divided by the area of the transect buffer. All these spatial analyses were

performed in R (R Core Team, 2018) with the packages *raster* (Hijmans, 2017) and *dplyr* (Wickham et al., 2018).

Additionally, we used QGIS software (QGIS Development Team, 2018) to calculate for each transect the proportion of organic vineyards, organic fallows/pastures, organic annual crops, and organic tree crops. These were estimated based on geographic information on crops with organic certification in the year 2011, provided by the regional government (Junta de Comunidades de Castilla-La Mancha, JCCM).

Each transect was also categorized as being within or outside an area sensitive to nitrate contamination in water (hereafter nitrate sensitivity), based on the distribution of vulnerable zones to nitrate contamination for the years 2008–2011 (MITECO, 2013). We considered each transect as "nitrate sensitive" if it was partially or totally inside a nitrate-contamination risk area; and "non-sensitive" if it was entirely outside a nitrate-contamination risk area. Nitrate sensitive areas (i.e. declared as vulnerable to nitrate contamination in water) have additional restrictions regarding the amount of nitrate that can be applied in farmland (e.g. in vineyards it is restricted to a maximum of 70–90 N kg/ha per year, depending on soil properties), as well as the type of farming practices that can be implemented (e.g. when manure is applied, it is encouraged to be buried) (Order of 07/02/2011, JCCM).

Furthermore, we calculated climatic variables and altitude for each transect (Table 1). These variables were raster layers with an original resolution of ~1 km² (Agencia Estatal de Meteorología, 2011; US Geological Survey, 1996). From these, we created raster layers with higher resolution (100 m × 100 m) maintaining the original values and obtained a mean value in each of the transect buffers.

For assessing habitat changes for the analyses of partridge trends (see below), the only available update of SIOSE was for 2014. We considered three years as a too short temporal window to identify changes. For assessing changes in land-use, therefore, we used Corine Land Cover, which has less information (e.g. it does not allow separating between irrigated and non-irrigated crops, and it provides a single landuse type for each polygon, which may underestimate the availability of certain land-uses in areas with a combination of habitats), but was available for 2006, 2012 and 2018. We used the Accounting Layers (https://www.eea.europa.eu/data-and-maps/data/corine-land-coveraccounting-layers), which allow direct comparison of land-use estimation across years, and thus calculation of changes. We calculated (using the R software) the proportional difference in each land-use between 2006 and 2018 to maximize the identification of land-use changes with time. We estimated changes in the following land-uses: arable land (CLC code 211), heterogeneous agricultural areas (areas covered by a diversity of crops in small plots, CLC code 242, or areas of farmland interspersed with small patches of natural vegetation, CLC code 243), vineyards (CLC code 221), tree crops (olive trees and fruit trees, CLC codes 222 or 223), pastures (grasslands or grazed pastures, CLC codes 321 or 231), shrubs (transitional woodland-shrub, CLC code 324, and sclerophyllous vegetation, CLC code 323) and urban areas (CLC code 11; see Appendix E). We also estimated changes in organic crops (organic vineyard, organic fallow and pastures, organic annual crops, organic tree crops) using data from plots with organic accreditation in 2011 and 2015 (provided by JCCM). We created shapefiles of distribution of organic crops as described above, although for data of the year 2015 we used the SIGPAC database from 2018 (as it was closest to 2015). We estimated changes in the proportion covered by those organic crops within each transect buffer using QGIS software (QGIS Development Team, 2018).

2.4. Analyses of RLP abundance and habitat

For analyses of correlates of spatial variation in abundance, we only used the 2010 data, when the sample size was largest (n = 121 transects; Appendix A, Fig. A1a). We performed a hierarchical distance-sampling model to estimate partridge abundance in each transect. Hierarchical models (based on repeated surveys) simultaneously account

Table 1

Climatic, topographic, and habitat variables considered in the abundance model.

Type of variable	Variable name	Code	SIOSE	VIF
Final set selected	Rain-fed tree crops (Olive groves and other woody crops)	RfTreeC	223 + 232 + 241	2.790
(climate ² and habitat ^{1,4,5} variables)	Days with maximum temperature \geq 25 °C in summer	DTx25Sum		2.667
	Annual temperature range (=TJul - TJan) (°C)	TRan		2.340
	Shrubland	Shrub	320	2.162
	Organic tree crops	OrgTree		2.012
	Pastures	Past	300	1.882
	Forests	Forest	312 + 313 + 316	1.872
	Organic annual crops	OrgAnnu		1.746
	Field margin density	FMargin		1.718
	Total precipitation in autumn	PAut		1.710
	Organic fallow and pastures	OrgPast		1.700
	Rain-fed Vineyard	RfVine	231	1.686
	Minimum temperature in winter (°C)	TnWin		1.682
	Irrigated Vineyard	IVine	231	1.604
	Irrigated Arable land	IArable	212	1.401
	Buildings	Build	101	1.222
	Irrigated tree crops (Olive groves and other tree crops;	ITreeC	223 + 232 + 241	1.168
	almond or pistachio)			
	Nitrate sensitivity	Nitrate		
Habitat ^{1,4}	Rain-fed Herbaceous crops	RfArable	212	55.451
	Organic vineyard	OrgVine		3.163
Climate ² and Topography ³	Mean temperature in winter	TWin		3634.764
	Maximum temperature in summer	TxSum		1182.713
	Mean temperature in summer	TSum		906.843
	Mean temperature in spring	TSpr		585.491
	Mean temperature in autumn	TAut		420.909
	Maximum temperature in autumn	TxAut		131.365
	Maximum temperature in spring	TxSpr		67.053
	Maximum temperature in July	TxJul		42.213
	Days with maximum temperature ≥ 25 °C	DTx25		35.708
	Total precipitation in winter	PWin		13.449
	Maximum temperature in winter	TxWin		12.603
	Days with maximum temperature ≥ 25 °C in autumn	DTx25Aut		10.041
	Total precipitation in spring	PSpr		8.338
	Total precipitation in summer	PSum		6.636
	Days with maximum temperature \geq 25 °C in spring	DTx25Spr		5.447
	Mean annual actual evapotranspiration (mm)	AET		4.320
	Mean altitude (m)	Alt		3.515

Highlighted in bold are those variables with VIF < 3 that were included in the initial abundance model, as stated in Methods. Variables are sorted according to the VIF value. The VIF procedure was performed separately for environmental (climate and topography) and habitat variables. VIF values of excluded variables are those of the variable before removed it from the set of variables. VIF values in bold are those obtained with the final set of selected variables. VIF values were calculated with standardized variables. The variable "Nitrate sensitivity" was not considered in VIF analysis because it is categorical. The column "SIOSE" denotes the SIOSE code of the variable. Beyond SIOSE categories, we also used SIOSE attributes to distinguish between rain-fed (attribute 31) and irrigated (attributes 32 and 33) land uses.

Sources: 1 SIOSE (2011), 2 Agencia Estatal de Meteorología (2011), 3 US Geological Survey (1996), 4 JCCM, 5 MITECO.

for both spatial variations in abundance and heterogeneity in detection probability (Sillett et al., 2012; Kéry and Royle, 2015). Thus, parameters are hierarchically structured, and variations at each level (i.e. abundance and detection) can be directly modeled as functions of covariates (Chandler et al., 2011). Using the replicas we can also estimate the probability phi of the individuals being available for detection, relaxing the distance sampling assumption that at distance 0 of the transect line, all individuals are detected (g(0) = 1). Specifically, we fitted the generalized distance sampling model of Chandler et al. (2011) using the function gdistsamp from the R package unmarked (Fiske and Chandler, 2011) that extends the distance sampling model of Royle et al. (2004) to estimate the probability of being available for detection, and also allows the use of the negative binomial distribution to model abundance. We assumed closure within each sampling period (i.e. no change in adult abundance within transects from mid-April to late-July). We truncated our data by observation distances (maximum of 150 m) to favor a proper fit of distance sampling models. By doing so, we excluded 0.34% of the observations.

We performed three steps in the model selection process, adding more complexity at each step: 1) null models to select between Poisson or the negative binomial distribution and to estimate the detection function, in which a negative binomial distribution and a Hazard rate detection function were selected and thus maintained in successive models; 2) to the best model identified in the previous step, we added explanatory variables to the detection parameter; 3) to the best detection model identified in the previous step, we added explanatory variables potentially affecting abundance and selected the best models. In all cases, the best models were selected using AIC comparisons. Combinations of tested models are provided in Appendix B. In the third step, we obtained 10 models that had AIC values within 2 points of the best model, so we considered all these 11 models as equally adequate (Bozdogan, 1987). We used a parametric bootstrap to test the goodness of fit (GoF) of the best model. We simulated 1000 data sets from this model and used error sums-of-squares, chi-square, and Freeman-Tukey fit statistics to quantify the fit of the model to the data sets (Kéry and Royle, 2015). We report the estimates of these models in Appendix C.

Variables included in the detection model were the following: hour (categorical variable; morning, midday/afternoon, evening), date (continuous variable starting at April 1st), quadratic term of date (to allow for non-linear seasonal detection variation), habitat structure (open, close and intermediate), and the interactions between hour and date and between hour and quadratic term of date (see Appendix B). Hour categories were defined as follows: morning was considered before 12:00, midday/afternoon was considered between 12:00 and 18:00, and evening was considered after 18:00. Habitat structure was derived from the above-mentioned habitat variables as follows: open = proportion of closed habitats (forest, scrub and buildings) < 10%, intermediate = proportion of closed habitats between 10 and 30%, close = proportion of closed habitats >30%. Variables affecting detection were selected based on previous work on the study species (Jakob et al., 2014).

Candidate variables affecting abundance included a pool of 37 climatic, topographic, and habitat variables that theoretically could affect partridge abundance (Table 1), as well as nitrate sensitivity (risk of nitrate contamination in water). Variables were standardized for analyses. We performed a variance inflation factor (VIF) with all the variables to check for collinearity, removing sequentially the variable with the highest VIF until the set of variables had a VIF lower than 3 (Zuur et al., 2010). We performed this procedure separately for environmental (climate and topography) and habitat variables, as they give information of different predictor sets. Afterward, we checked the VIF of the remaining variables altogether (Table 1). The whole set of environmental variables is detailed in Table 1, as well as the final set selected for modeling. VIF values were calculated with the function *multicol* from R package *fuzzySim* (Barbosa, 2015).

We computed the predicted effect of each variable on detection and abundance based on model averaging, using the *predict* function of *unmarked* R package on a *fitList* object containing the 11 best models (Appendix B). In addition, we used the function *ranef* of *unmarked* R package to estimate posterior abundances from the best model, i.e., the one with the lowest AIC value. This function uses empirical Bayes methods. We then used these posterior abundances to calculate the density of partridges in each transect (RLP/ha per transect) and plotted them in a map to show the spatial distribution of RLP densities (RLP/ ha) in the study region.

2.5. Analyses for partridge trends and habitat changes

These analyses were carried out using only those transects that had been monitored at least two years between 2010 and 2017 (n = 48transects, totalling 258 transect-year observations). We first estimated the RLP abundance in each transect and year with hierarchical distance-sampling models (one model per sampling year) using the function gdistsamp from the R package unmarked (Fiske and Chandler, 2011). We applied the same model selected above, maintaining the same model parameters selected in previous analyses, with same explanatory variables affecting detection probability, but excluding the explanatory variables affecting abundance. We also truncated our data by observation distances (maximum of 150 m) to favor a proper fit of distance sampling models. As we had not found temporary migration in the abundance model (2010 full model, phi = 1), i.e. no variation in population sizes between the beginning and the end of the temporary replications, here we assumed no temporary migration. We used a parametric bootstrap to test the GoF of the model for each year. We simulated 1000 data sets from each of our models and used error sums-ofsquares, chi-square, and Freeman-Tukey fit statistics to quantify the fit of each model to the data sets (Kéry and Royle, 2015). All models had quite good fits to the data (Appendix F), with a c-hat between 1.2 and 1.9. We used the function ranef of unmarked R package to estimate posterior distributions of the abundance. As above, these posterior abundances were used to calculate the density of partridges in each transect (RLP/ha per transect).

To assess population abundance change during our study period we initially carried out a Generalized Linear Mixed Model (GLMM, R package *lme4*; Bates et al., 2015), with ln(density) in each transect and year as a response variable (gaussian distribution), year as a categorical covariate, and "transect identity" as a random term affecting the intercept. We used year as a categorical rather than continuous variable as we did not have a priori indications of whether trends had occurred, or whether these (if existing) had occurred in particular years or throughout the period. We used a Tukey HSD post hoc test for comparisons between 2010 and 2017 abundances (*lsmeans* R package; Russell, 2016).

Subsequently, we built GLMMs to assess whether habitat change affected temporal trends in density, with ln(density) as the response variable, "transect identity" as a random term, year and year² (to account for the non-linear trends found, see results) as continuous variables, and two-term interactions between year and each habitat-change variable (changes in arable land, mosaic farmland areas, tree crops, vineyards, shrubland, pastures, urban areas, organic annual crops, organic tree crops, organic fallow and pastures, and organic vineyard) to test whether the slope of the trend had varied in relation to the degree of habitat change. As above, we first assessed whether habitat-change variables were collinear by performing the VIF with all the habitatchange variables, removing sequentially the variable with the highest VIF until the set of variables had a VIF lower than 3 (Zuur et al., 2010). In this process, we removed "change in arable land" and "change in mosaic farmland areas". All other habitat-change variables were retained (Appendix E). Models, therefore, included changes in tree crops, vineyards, shrubland, pastures, urban areas, organic annual crops, organic tree crops, organic fallow and pastures, and organic vineyard. We used the *dredge* function of the *MuMIn* R package (Barton, 2020) to identify the best model (within the subset that included year and $year^2$ as explanatory terms) according to AIC values.

3. Results

3.1. Partridge abundance and habitat

Detectability of RLP varied quadratically throughout the season (Table 2; Appendix C, Table C1), being higher at the beginning of the survey period (April) and in summer (July), but lowest in late May and June (Fig. 1c). Time of day had also an effect on detectability (Table 2; Appendix C, Table C1), which seemed to be overall higher during morning and evening than during midday and early afternoon (Fig. 1a; Fig. 1b). Moreover, as shown by the statistical significance of their interaction, the effect of time of day varied throughout the season: at the beginning of the sampling season (April and early May), detectability was higher in the morning whereas from June onwards detectability was higher in the evening (Fig. 1a; b; c). Finally, detectability varied with habitat structure and was higher in open habitats (Fig. 1b; Table 2; Appendix C, Table C1).

Density in transects ranged from 0.001 to 0.606 partridges per ha (mean = $0.118 \text{ RLP/ha} \pm 0.12 \text{ SD}$), being heterogeneously distributed throughout the region (Fig. 2). The best model explaining variations in RLP abundance included seven explanatory variables (Table 2): abundance was higher in areas with higher winter temperature and lower autumn rainfall, was higher where the proportion of pastures and the proportion of traditional rain-fed vineyards was higher, but where the proportion of irrigated vineyards and rain-fed tree crops was lower (Fig. 3). This model also included the interaction between the proportion of irrigated vineyards and the nitrate sensitivity category (Fig. 3h). The latter showed that the negative association between RLP abundance and the proportion of irrigated vineyards was less pronounced in nitrate sensitive areas, where the use of nitrates is more restricted (Fig. 3h). This model had a good fit to the data (Appendix D), with a c-hat of 1.31, providing accurate abundance estimations. Ten other models had AIC values within 2 points of the best model (Appendix C, Table C2). The climatic variables entered in all of them, as well as rain-fed and irrigated vineyards, pastures were included in 8 of the models and the interaction between irrigated vines and nitrates in 7 of them. Other differences with the best model included a replacement of rain-fed tree crops by organic tree crops (similar negative relationships) in certain models, the (non-significant) inclusion of shrubland in some models, or the (non-significant) inclusion of irrigated arable land in one model (Appendix C, Table C2). Modelaveraged results for all variables included in the 11 models are shown in Fig. 3.



Fig. 1. Red-legged partridge's detectability (based on models average of best models in Appendix C, Table C1) in relation to the time of day (a and b), date (c), and habitat openness (d). See estimates and statistical significance of the best 11 models with an AIC value within 2 points in Appendix C, Table C1. The effects of hour and date are represented for open habitat and the effect of habitat is represented for morning and considering mean values for date. Dark line/dots represent the mean effect and the shaded area and whiskers the 95% confidence intervals.

3.2. Partridge abundance trends

RLP density significantly differed between years (GLMM with year included as the only explanatory variable; $F_{7,210} = 18.95$, P < 0.001). Overall, RLP density decreased throughout the study period (Fig. 4), with a mean density in 2017 that was 51% lower than that of 2010 (Tukey HSD test $t_{210} = 5.21$, P < 0.001; considering the extremes from the 95% CI, this decline ranged from -8% to -74%). This decline occurred mainly in the middle of the study period, between 2012 and 2014 (Fig. 4).

The best model explaining RLP trend variations included year (as a continuous variable), its quadratic term (to account for the non-linear effects visually found in Fig. 4), and the interaction between year and two explanatory habitat-change variables: change in pastures and change in organic tree crops (Table 3). The interactions showed that the decline of partridge abundance over years was more pronounced where more pastures had been lost, and where organic tree crops had increased most (Fig. 5). It is worth noting that, within the study region and sampling period, when changes in the surface area of pastures were observed, these were always losses (Fig. 5).

4. Discussion

Our study showed that both low winter temperatures and high autumn precipitation explained variation in RLP abundance and seem to be important limiting factors. Moreover, variation in RLP abundance was strongly dependent on farmland composition and management after taking climate effects into account. Specifically, it showed that density was positively related to the extent of natural vegetation (particularly pastures) and traditional rain-fed vineyards, but negatively related to the extent of irrigated vineyards and tree crops. In addition, our results confirmed that wild RLP populations in Castilla-La Mancha, one of the most important regions for the species, have markedly declined (-51%) between 2010 and 2017. We further showed that these negative trends were modulated by land-use changes.

Consistent with previous works (Buenestado et al., 2008; Casas and Vinuela, 2010; Diaz-Fernandez et al., 2013), we found that agrosystems that include a higher proportion of natural vegetation (particularly pastures) support higher RLP abundance. This emphasizes the necessity of maintaining natural vegetation patches within farmland landscapes, which provide a suitable habitat for nesting, feeding, and protection, and for the conservation of farmland biodiversity more generally (Perkins et al., 2002; Vickery et al., 2002; Casas and Vinuela, 2010; Mcmahon et al., 2010; Tarjuelo et al., 2020). Additionally, certain elements of agrosystems were also associated with higher RLP abundance, such as traditional rain-fed vineyards. Vineyards have great importance for RLP populations, since they provide shade and protective cover, especially after cereal harvest (that takes place between late May and mid-June in this region) when cereal crops (stubbles) do not offer any cover (Buenestado et al., 2008; Sumozas, 2009). GPS-tracking studies have indeed recently shown that RLP uses vineyards more often in summer and during midday, the hottest hours (Mougeot et al., unpublished results), looking for shade, cover for protection from predators or water. On the opposite, tree crops (including olive groves) do not seem to be suitable habitats for RLPs in the region. This result is in line with findings by Buenestado et al. (2008) in southern and central Spain, but contrasts with other studies from southern Spain and Portugal, where RLP seemed to benefit from olive grove availability (Borralho et al., 1999, 2000; Delibes-Mateos et al., 2012). These differences may be related to the ground management of those tree crops, as within the study region olive groves are often intensively managed, with mechanical



Fig. 2. Spatial distribution of Red-legged partridge's densities (RLP/ha) in the study region. Densities obtained from the best model (mod20) using the *ranef* function. Darker colors and larger circles indicate higher densities. The Province names are indicated in grey.

tillage, leaving the ground bare between trees, and with the use of fertigation in irrigated groves (Moncunill, 2013). Moreover, an agricultural landscape dominated by tree crops could be detrimental to the species. In any case, these inconsistencies should be addressed and clarified in future studies, but we suggest they might be mostly due to management differences.

In line with the above, and beyond the importance of specific landuses, we found that RLP abundance was conditioned by the way some crops were managed. Thus, even if RLP abundance increased with the availability of traditional rain-fed vineyards, the relationship was the opposite if considering irrigated vineyards. Irrigated vineyards in Spain are almost always trellis-vineyards (Cabodevilla et al., 2021), and thus their physiognomy and structure are different from that of traditional vineyards. The greater height and wider open space between rows of trellis-vineyards may provide less vegetation cover for RLP under the vines, but more shade. A study at the plot level showed that the probability of RLP occurrence, over the summer, was higher in trellis vineyards than in traditional vineyards (Cabodevilla et al., 2021). Thus, the variation in abundance in areas with higher availability of trellis vineyards may not be directly related to the different structure of these crops, but to other factors, for example the provision of water. RLP depends on water resources during the summer and might be attracted to irrigated vineyards to drink (Borralho et al., 1998; Cabodevilla et al., 2021). The application of fertilizers through the irrigation water is a common practice (fertigation is applied in at least a third of modern, irrigated vineyards; Cabodevilla et al., 2021). Irrigation by dripping allows to provide water straight to the vines and therefore to save water in arid farmland. When fertilizers (mostly nitrates) are applied via the irrigation systems their concentration in water is very high, exceeding by 10 times the recommended limit for public safety

(Rodríguez-Estival et al., 2010) and may expose birds like RLP to a toxic dose of nitrates, with associated adverse effects on health (Ley, 1986; Rodríguez-Estival et al., 2010). Our results showed that a greater proportion of irrigated vineyards was associated with reduced RLP abundance at the landscape level and that this association was stronger in non-sensitive areas to nitrate contamination, where there are no limitations regarding the amount of fertilizer that can be applied to irrigation water (Order of 07/02/2011, JCCM). These patterns are consistent with a negative effect of nitrate exposure in intensive vineyards on RLP populations, and with experimental studies that showed adverse effects of nitrate water consumption on bird physiology and health (Rodríguez-Estival et al., 2010). Therefore, if this water source does actually attract birds during the summer months, fertigation could be an important ecological trap for this and other species.

Other types of management did not seem to affect RLP abundance. For example, we found no evidence that the availability of organicallygrown arable crops was associated with higher RLP densities. However, the relative importance of these organic crops, in terms of percentage of agricultural surface, was very small (2.2% on average), and may not have been sufficient for us to detect significant associations. These results should be verified in future studies focused on the effect of organic crops (e.g. Moreau et al. 2021). The negative relationship between organically-grown tree crops may simply reflect the negative relationship found with rain-fed tree crops (as both of these variables were included mostly as alternates in the selected models).

Beyond the spatial relationships with land-use observed in 2010, we also found a marked temporal variation in abundance, with a 51% decline of RLP abundance between 2010 and 2017 (8%–74% considering best-case and worst-case scenarios). This is of particular concern given that this region holds one of the largest wild populations of RLP in the



Fig. 3. RLP densities (RLP/ha) in relation to climate and land-use variables based on model averaging of best models presented in Appendix C, Table C2. The effect of each variable is represented considering mean values for the other variables and for non-sensitive nitrate areas. Dark lines represent the mean effect and the shaded areas their 95% confidence intervals.

world (Blanco-Aguiar et al., 2003; Blanco-Aguiar et al., 2004) and is likely to be a good indicator of the RLP populations status globally. Our results also showed that the RLP population decline was not linear throughout the study period, but mainly occurred in two years (2013 and 2014) with periods of relative stability before and after. This suggests that environmental or demographic conditions might prevent

Table 2

Estimates (\pm SE) and parameter statistics of the best model (mod20) on variations in RLP abundance. Variable codes as in Table 1.

	Estimate	SE	Z-ratio	Р
Detection				
Intercept	2.365	± 0.03	78.02	<0.001
Hour Midday	-0.028	± 0.17	-0.17	0.87
Hour Evening	0.144	± 0.05	3.03	<0.01
Date	-0.134	± 0.01	-10.83	<0.001
Date2	0.135	± 0.01	11.69	<0.001
Habitat_I	-0.117	± 0.03	-3.48	<0.001
Habitat_C	-0.141	± 0.06	-2.32	<0.05
Midday:Date	0.142	± 0.12	1.2	0.23
Evening:Date	0.168	± 0.03	4.84	<0.001
Midday:Date2	-0.226	± 0.13	-1.77	0.08
Evening:Date2	-0.072	± 0.03	-2.41	<0.05
Abundance				
Intercept	-2.442	± 0.13	-19	<0.001
PAut	-0.555	± 0.10	-5.41	<0.001
TnWin	0.359	± 0.09	3.92	<0.001
RfVine	0.178	± 0.09	1.96	<0.05
IVine	-0.429	± 0.17	-2.48	<0.05
Past	0.189	± 0.10	1.87	0.06
RfTreeC	-0.177	± 0.09	-2.03	<0.05
Nitrate	0.159	± 0.17	0.93	0.35
IVine:nitrate	0.334	± 0.19	1.77	0.08

the population to recover from stochastic events leading to a few consecutive bad years in terms of poor survival or bad reproduction.

In line with the results on abundance, RLP trends were modulated by land-use changes: declines were more marked where the proportion of pastures (natural vegetation) had declined most, and where organic tree crops had increased most. As mentioned above, natural vegetation within the farmland landscape is extremely important for RLP and its reduction was associated with steeper declines. RLP is a groundnesting species that mainly feeds on seeds and green plants, but also consumes arthropods during the nestling period (Jiménez et al.,



Fig. 4. RLP density (RLP/ha) variation over the studied period: density estimation by year (dots) and its confidence intervals (whiskers) according to a GLMM model with year as a categorical explanatory variable.

Table 3

Estimates (\pm SE) and statistic parameters of the best model on the effect of habitat on RLP abundance trends. YR:OrgTreeChg = interaction between year and change in organic tree crop surface; YR:PastChg = interaction between year and change in pasture surface. Variable codes as in Appendix E.

Model	AIC		Intercept	year	Year ²	Yr:OrgTreeChg	Yr:pastChg
mod140	576.1	Estimate (±SE) Df F P	-2.304 (±0.15) 1, 69 245.7 <0.001	-0.221 (±0.05) 1, 217 17.4 <0.001	0.015 (±0.01) 1, 217 3.8 0.05	-0.023(±0.01) 1, 254 16.2 <0.001	0.025(±0.01) 1, 245 18.4 < 0.001

1991). The decrease in pastures probably implies a reduction of trophic resources and suitable breeding habitat for this species (Vickery et al., 2002: Vickery et al., 2009; Casas and Vinuela, 2010; Mcmahon et al., 2010). Regarding the effect of organic tree crops, and as mentioned above, this could be indicative of the availability of tree crops at large. The negative relationship could reflect the loss of suitable habitat for the species, as areas dominated by tree crops seem to be negative for the species. A limitation on the amount of tree crops has been identified as a conservation measure within protected farmland areas for steppe birds (JCCM, 2017), and these results support this measure. Exposure to agrochemicals might have also contributed to the observed decline, in particular the triazole fungicides that are routinely applied as cereal seed treatment during sowing in central Spain (Lopez-Antia et al., 2016; Fernández-Vizcaíno et al., submitted). Exposure to these fungicides during late winter has been shown by experiments with captive partridges to disrupt reproduction and reduce RLP productivity by half (Fernández-Vizcaíno et al., 2020; Lopez-Antia et al., 2021) and therefore have the potential to cause rapid population declines like those reported in this study (-51% in 7 years).

The observed population decline of RLP confirms the delicate situation of this game bird species (BirdLife International, 2020) and has strong implications for its management. In Spain, millions of RLPs (including both wild and farm-reared ones) are hunted each year (Andueza et al., 2018) and RLP hunting generates a large economic turnover, of more than a billion euros annually (Garrido, 2012). Thus, the observed population trend is not only a conservation issue for RLP but also a socio-economic issue. Even if hunting may not be the main cause of the decline, the observed decline highlights the need to carefully adjust hunting pressure to the species abundance and dynamics in order to prevent additive effects. Currently, many hunting estates invest important efforts trying to increase the RLP populations in their estates for hunting purposes (Arroyo et al., 2012). They implement some measures potentially useful for wild RLP population recovery, such as predator control, the provision of supplementary food, water, and game crops (crops planted specifically for game that are not harvested), which might also be beneficial to other threatened species (Smith et al., 2010; Estrada et al., 2015; Cabodevilla et al., 2020). But many of these estates also conduct releases of farm-reared RLPs (Caro et al., 2014;



Fig. 5. Effect of changes on the surface covered by (a) pasture and (b) organic tree crops on RLP trends (from the model in Table 3). Predicted densities are given in RLP/ha. Change values are given as a proportional (%) decrease or increase within the transect band (400 m buffer area). This change ranged from -10.1 to +0.3 in case of pastures and from -8.7 to +8.9 in case of organic tree crops. The lines represent the mean effect and the shaded area the 95% confidence intervals.

Cabodevilla et al., 2020), which do not help wild breeding population recovery (Diaz-Fernandez et al., 2013) because most released birds die before spring (Gortázar et al., 2000). In addition, these releases may be detrimental to wild populations due to the dissemination of pathogens or genetic introgression (Villanúa et al., 2008; Casas et al., 2012; Díaz-Sánchez et al., 2012) or increased hunting pressure on the wild stocks (Casas et al., 2016).

The observed marked population decline, which has been sometimes questioned (e.g. RFEC, 2020), highlights the need for a continued monitoring of this species. In that respect, our results regarding the species detectability also provided useful information to optimize future monitoring programs. Our results indicate that the best time to perform RLP surveys (within the time frame of our study) is in late April/early May or in July. The low detectability observed from mid-May to early July is probably due to both incubation behavior and the higher vegetation in crops at that time. In any case, this period should be avoided for assessing abundance (although it may be an important time to assess breeding phenology, Guzmán et al., 2020). Regarding the sampling hour, morning monitoring seemed to be more efficient in early spring (Jakob et al., 2014), whereas detectability was higher in the hours before sunset in July, perhaps because of a higher activity of birds after the very hot afternoons. This should be taken into account when designing monitoring programs. One way or another, it will always be advisable to use repeated surveys to account for detectability during the modeling process (Jakob et al., 2014; Kellner and Swihart, 2014), e.g. using hierarchical distance models, in order to obtain more reliable information on RLP abundance.

In conclusion, this study showed that farmland composition and farming practices explain variation in the abundance and trends of the RLP, an important farmland bird species. The results highlight the value of mosaic agricultural landscapes for generalist farmland birds like RLPs, including herbaceous vegetation layers such as pastures and crops with abundant leafy cover such as traditional rain-fed vineyards, thus offering foraging and shelter sites to avoid predators and high summer temperatures. Besides, population trend results (with a marked population decline observed but occurring mainly over a few years) suggests that current environmental conditions may not allow RLPs to recover from negative effects of stochastic events (e.g. poor weather-related productivity). These results reflect the delicate situation of this species of strong socioeconomic and ecological importance. Scientists, public institutions, farmers, and hunting federations should work together to solve the RLP conservation issue, rethink agricultural management, avoiding intensification and an excessive use of agrochemicals, restricting the expansion of tree crops, and promoting patches of natural or semi-natural vegetation whilst ensuring that hunting is carried out sustainably.

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CRediT authorship contribution statement

Xabier Cabodevilla: Data curation, Formal analysis, Writing – original draft. Alba Estrada: Data curation, Formal analysis, Writing – review & editing. François Mougeot: Conceptualization, Writing – review & editing. José Jimenez: Formal analysis, Writing – review & editing. Beatriz Arroyo: Conceptualization, Data curation, Formal analysis, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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