

Article

Impact of Environmental and Human Factors on the Populations of the Lesser Kestrel (*Falco naumanni*) at National and Local Scales

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Abstract

The global decline in biodiversity, mainly caused by human activities such as land use change, agricultural intensification, habitat degradation, and climate change, is impacting many species, including raptors. The lesser kestrel (*Falco naumanni*), a threatened colonial raptor strongly associated with traditional agricultural landscapes, has experienced marked distributional and demographic changes across Spain. Understanding the environmental and anthropogenic factors shaping its occurrence is essential for guiding effective conservation actions. In this study, we combined national-scale presence data with local breeding information to identify the main drivers influencing the species' spatial patterns and potential causes of local population change. Nationally, the lesser kestrel showed positive associations with prey availability, grasslands, and non-irrigated croplands, while urban areas, water bodies, and higher altitudes negatively affected its occurrence. Climatic variables, particularly precipitation during the warmest quarter and temperature seasonality, were also significant predictors. At the local scale (Córdoba province), colony abundance increased in non-irrigated agricultural areas and certain human-modified habitats, but declined in woodlands, open natural areas, and landscapes characterised by larger patch sizes. Overall, our findings highlight the relevance of preserving heterogeneous, traditional agricultural mosaics and maintaining prey-rich open habitats. By integrating national and local perspectives, this study identifies priority areas for conservation and provides actionable insights to support efforts aimed at halting the decline of the lesser kestrel in Spain.

Keywords: *Falco naumanni*; habitat suitability; land use; spatial distribution; species distribution model



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1. Introduction

Biodiversity is declining rapidly worldwide as a result of human activities [1]. Factors such as land use change, climate change, habitat fragmentation and degradation, pollution and the introduction of alien species have been identified as the main causes of this phenomenon [1,2]. This loss is manifested in the extinction of species, the disappearance of local populations, and the drastic reduction in the abundance of organisms across multiple ecosystems [3]. This crisis represents a direct threat to human well-being, as biodiversity not only provides essential resources such as food, medicines, and materials but also

sustains essential ecological processes that support species persistence and ecosystem functioning [4].

Not all biological groups have been equally affected by this process of biodiversity loss. While some taxa have shown a certain degree of resilience, others, such as insects, amphibians and especially birds of prey, have experienced significant population declines [5,6]. Because of their position at the top of food webs and their specific ecological requirements, birds of prey are particularly vulnerable to habitat loss and fragmentation, pollution, prey decline and, in some cases, direct persecution [7,8]. The conservation status of the lesser kestrel (*Falco naumanni*) not only reflects the pressures faced by small colonial raptors but also serves as an indicator of the ecological integrity of the open agro-pastoral landscapes it inhabits. This species may nest either solitarily or in colonies, although studies suggest that coloniality does not consistently yield reproductive or conservation advantages, as its benefits depend on factors such as reproductive synchrony, nest proximity, and breeder abundance [9,10]. Colonies are typically located on rocky cliffs or human constructions—such as occupied or abandoned country houses—where individuals use cavities in walls or roofs [11,12]. Their habitat consists of open areas associated with traditional agricultural landscapes such as the cereal steppes of the Iberian Peninsula [12]. Previous studies have stated that the presence of lesser kestrels in the Iberian Peninsula is associated with rural areas containing human constructions or unirrigated cereal and sunflower crops, with low scrub or forest cover and low precipitation rates [13]. Populations associated with agricultural areas rely heavily on dry cereal crops and grasslands, which provide essential foraging grounds [9,14,15]. However, the species has undergone significant population decline primarily due to habitat transformation linked to land use changes in agricultural environments [16]. Agricultural intensification—marked by a reduction in non-irrigated crops ($\approx 13\%$), an expansion of irrigated fields, and the spread of permanent woody crops such as olive groves—has progressively eroded suitable habitats for the lesser kestrel [17]. The disappearance of traditional fallow systems and the increased use of biocides have further reduced reproductive productivity [18]. Additional threats include the loss of grasslands, unplanned reforestation in historically open landscapes [13], and expanding urban development, which constrains hunting territories in peri-urban zones and restricts access to key foraging areas [17,19].

Besides its specific habitat requirements, the lesser kestrel plays a fundamental ecological role as a biological pest controller. This small raptor primarily feeds on invertebrates, mainly orthopterans, although it can also feed on small vertebrates such as reptiles, small mammals, and birds [14].

Despite its ecological and functional importance in agroecosystems, the lesser kestrel faces a major conservation challenge. Listed as a vulnerable species since 1995 in the Red Book of the Birds of Spain, due to a severe decline in its populations over the last 50 years and the increasing risk of extinction in the wild if current threats persist [20]. Breeding populations can be found in the southwestern half of the Iberian Peninsula, concentrated mainly in Extremadura, Andalusia, Castile and León, and Castile-La Mancha [12]. This context highlights the need to continue generating knowledge about the factors that affect its distribution and abundance, especially in agricultural and semi-natural landscapes. Regional censuses show an average annual decline of 6% since 2012 [16], representing a cumulative loss of 43% between 2012 and 2019 [11]. Of the 36 provinces with breeding populations, a decline has been documented in at least 14 of them, being particularly severe in regions that have historically had the highest population densities, such as Ciudad Real, Toledo, Badajoz, Cáceres, Seville, Cadiz, and Valladolid [11]. The sharp decline experienced by this species has been attributed mainly to its high sensitivity to alterations in breeding habitats [12,16], such as the loss of traditional buildings or agricultural intensification [13],

and to the decline in the density of large orthopterans [16]. In Andalusia, monitoring data since 2005 show pronounced declines of 60–70% in provinces such as Málaga, Almería and Jaén, and around 40% in Córdoba and Sevilla, with the countryside around Córdoba, the eastern areas of Jaén, northern Málaga, and the central and eastern regions of Sevilla being the most affected [21].

Another significant threat to the conservation of the lesser kestrel is the loss of nesting sites, mainly “*mechinales*”—holes in walls or under tiles of traditional buildings—which the species commonly uses for breeding [16]. This loss is often associated with the abandonment or restoration of rural buildings, in which these holes are frequently removed or sealed, or traditional tiles are replaced with modern models that prevent access [12]. However, it has been shown that this situation can be mitigated through conservation-oriented interventions, such as restoration actions that preserve existing cavities or the installation of artificial nesting boxes. On the other hand, possible interspecific competition with feral pigeon or jackdaw populations [16] has been suggested as a limiting factor in the availability of nesting sites. However, previous research has shown that the presence of other species does not appear to significantly restrict the use of cavities by lesser kestrels [21].

Within this ecological context, we hypothesise that the spatial distribution of the lesser kestrel in Spain, as well as the recent local population declines, are primarily driven by environmental and anthropogenic factors related to habitat structure, land use patterns and prey availability. To this end, two complementary approaches are proposed: first, the development of a national-scale ecological model to identify the main predictors of its distribution and project its potential habitat under current conditions; and second, the construction of a local-scale model to analyse the factors potentially responsible for the decline in the abundance of the species in areas where it has historically been present.

2. Materials and Methods

2.1. Study Area

The nationwide study was conducted in Spain, a country in south-western Europe characterised by pronounced climatic and geographical variability. The Spanish climate is predominantly Mediterranean, with hot, dry summers and mild winters [22]. The territory comprises extensive plains and cereal-growing landscapes interspersed with areas of scrubland, pastureland, and traditional woody crops such as olive groves and vineyards. This mosaic of land uses creates a heterogeneous agricultural matrix that provides suitable habitats for the lesser kestrel, including non-irrigated cereal fields, fallow land, and extensively managed grasslands [23]. The species benefits from this agroecosystem structure, which offers both foraging areas and opportunities in rural buildings and colonies distributed across open farmland.

The local-scale analysis focuses on the province of Cordoba, located in the Guadalquivir valley in southern Spain, where the climate is predominantly continental Mediterranean [24]. The landscape is shaped by gentle hills and broad plains, dominated by agricultural land uses such as olive, cereal and citrus crops, with areas of pastureland and patches of Mediterranean scrubland also present [25].

2.2. Biological Data of Lesser Kestrel

For the national-scale model, data on the presence of lesser kestrels were obtained from the Spanish Terrestrial Species Inventory [26] (Figure A1). The dataset consists of georeferenced presence-only records on a 10 × 10 km UTM grid, corresponding to the standard resolution used in national biodiversity atlases. Importantly, these presence records originate from the two official Spanish Breeding Bird Atlases compiled during the periods 1985–1997 and 1998–2002, which constitute the most recent validated national-

scale distribution data available for this species within the IEET. A total of 1081 validated presence records were obtained from the official repository of the Ministry for the Ecological Transition and Demographic Challenge (MITECO) <https://www.miteco.gob.es> (accessed on 12 April 2025).

For the local-scale analysis, abundance data were obtained from systematic breeding censuses conducted between 2012 and 2023 in the province of Córdoba by Bioterra Andalucía and the Regional Delegation of Agriculture, Fisheries, Water and Rural Development (<https://bioterraandalucia.com/>) (Figure A2). These censuses follow a standardised protocol carried out in April, before the kestrels lay their eggs, which allows a reliable estimation of the number of breeding pairs per colony. During this period, kestrel pairs tend to stay close to their nests and sometimes enter the nesting holes, which facilitates their detection and allows for a more accurate count of breeding pairs within each colony. The surveys are conducted before 11:00 h or after 17:00 h. Two or three observers carefully inspect each colony with telescopes for 1 or 2 h, depending on the activity of the kestrels and the size of the building, to evaluate reproductive activity. A census session is concluded when no new pairs are detected in the colony after 30–40 min. This procedure is repeated two or three times on different days [27].

Because the national atlas data represent presence-only information collected at irregular intervals, whereas the Córdoba dataset provides annual abundance estimates based on a standardised protocol, both datasets are methodologically different. Therefore, results are not directly comparable in terms of population trends, but they are complementary for identifying environmental drivers at national and local scales.

From the census points, buffers with a 10 km radius were generated around each site to establish their area of influence, serving as the unit of landscape analysis for the models. This distance was chosen based on the species' average home range during the breeding season [28], ensuring that the environmental factors relevant to its presence were adequately captured. At the same time, pseudo-absence buffers were generated in areas where the species is not currently present, in order to compare the environmental conditions between both groups (Figure A3). To create the pseudo-absence buffers, the same number of random points as population centres was generated.

2.3. Explanatory Variables

2.3.1. Explanatory Variables of the National-Scale Model

Environmental data used in this study were obtained from the official WorldClim database <https://www.worldclim.org/data/worldclim21.html> (accessed on 9 April 2025). To characterise environmental conditions across the study area (Table 1), we included in the model the 19 bioclimatic variables from WorldClim [28]. These variables represent long-term climatic averages (1970 to 2000) at ~1 km² spatial resolution and describe major gradients of temperature and precipitation that influence species distribution and habitat suitability.

Although the WorldClim v2.1 climate layers represent long-term averages for the period 1970–2000, their use is standard in macroecology and species distribution modelling. Climatological baselines are defined using 30-year reference periods, and the 1970–2000 interval is considered a stable and widely adopted benchmark for characterising average climatic conditions. For this reason, these data remain appropriate for broad-scale environmental modelling despite not overlapping fully with the temporal range of the species' atlas records.

Additionally, altitude (height above sea level) was extracted from the 20 m spatial resolution Digital Elevation Model (DEM) available from the download centre of Instituto Geográfico Nacional-IGN [29].

Table 1. List of variables and factors included in the national-scale model.

Factor	Variable	Spatial Resolution
Environmental	Bio 1 ¹ : Annual Mean Temperature ²	1 Km
	Bio 2 ¹ : Mean Diurnal Range ²	
	Bio 3 ¹ : Isothermality ²	
	Bio 4 ¹ : Temperature Seasonality ²	
	Bio 5 ¹ : Max Temperature of Warmest Month ²	
	Bio 6 ¹ : Min Temperature of Coldest Month ²	
	Bio 7: Temperature Annual Range ²	
	Bio 8: Mean Temperature of Wettest Quarter ²	
	Bio 9 ¹ : Mean Temperature of driest Quarter ²	
	Bio 10 ¹ : Mean Temperature of Warmest Quarter ²	
	Bio 11 ¹ : Mean Temperature of Coldest Quarter ²	
	Bio 12 ¹ : Annual Precipitation ²	
	Bio 13 ¹ : Precipitation of Wettest Month ²	
	Bio 14 ¹ : Precipitation of Driest Month ²	
	Bio 15 ¹ : Precipitation Seasonality ²	
	Bio 16 ¹ : Precipitation of Wettest Quarter ²	
	Bio 17 ¹ : Precipitation of Driest Quarter ²	
	Bio 18: Precipitation of Warmest Quarter ²	
	Bio 19 ¹ : Precipitation of Coldest Quarter ²	
Anthropogenic Land Cover	Altitude ³	20 m
	Human footprint ⁴	1 Km
	Heterogeneous crops ⁵	500 m
	Annual crops ⁵	
	Forest ^{1,5}	
	Scrubland ⁵	
	Grassland ⁵	
	Irrigated crops ^{1,5}	
	Non-irrigated crops ⁵	
	Urban areas ⁵	
	Water bodies ⁵	
Biological	Others ⁵	
	Presence of lesser kestrel ⁶	10 Km
	Presence of common kestrel ⁶	10 Km
	N° of prey species ⁶	10 Km

¹ Collinear variables excluded from the model due to having a Spearman correlation coefficient > 0.8. ² WordClim. ³ National Geographic Institute. ⁴ Wildlife Conservation Society. ⁵ Corine (Corine Land Cover). ⁶ Spanish Inventory of Terrestrial Species.

With regard to anthropogenic variables, the national-scale model included the Human Footprint Index [30] and land use [31] (Table 1). Human Footprint Index data were obtained from the Last of the Wild Project, Version 3 (2009), developed by the Socioeconomic Data and Applications Center (SEDAC), NASA. This dataset provides a globally consistent measure of human pressure on the environment, combining eight layers of human influence (population density, built-up areas, land transformation, night-time lights, accessibility, etc.), at a spatial resolution of 1 × 1 km.

Land use and land cover information used in the national-scale model was obtained from the CORINE Land Cover (CLC) 2018 map (the most recent available), available from the National Geographic Institute (IGN, Government of Spain). This database, developed within the framework of the European Copernicus Land Monitoring Service programme, provides harmonised mapping of land cover across Europe with a spatial resolution of 100 m and a three-level hierarchical classification, enabling consistent and comparable characterisation of land use on a large scale.

Data on the presence of common kestrels (*Falco tinnunculus*) were also obtained from the Spanish Terrestrial Species Inventory, in order to account for potential interspecific competition given the overlap in ecological niches and nesting sites with the lesser kestrel [32,33]. Additionally, presence data for seven species of small mammal prey such as the wood mouse (*Apodemus sylvaticus*), the common vole (*Microtus arvalis*), and shrews (*Crocidura* spp.), were included as proxies for prey availability [26,34]. All predictor datasets were available for the entire 10 × 10 km national UTM grid (5424 cells), ensuring full spatial coverage across Spain. Only the response variable (presence of *Falco naumanni*) was restricted to the 1081 cells containing validated records, while predictors were extracted for all grid cells, allowing an unbiased comparison between presence and absence cells (Table 1).

2.3.2. Explanatory Variables of the Local-Scale Model

For anthropogenic variables, the local-scale model includes the distance from population centres to the nearest country house (Figure A2) [35] and land use within the province of Cordoba [36] (Table 2).

Table 2. List of variables and factors included in the local-scale model.

Factor	Variable	Spatial Resolution
Anthropogenic Land Cover	Distance to the nearest country house ¹	50 m
	Heterogeneous crops ²	
	Annual crops ²	
	Forest ²	
	Scrubland ²	
	Grassland ²	
	Non-irrigated crops ²	
	Urban areas ²	
	Water bodies ²	
	Other ²	
Biological	Lesser kestrel population nuclei ³	10 km (buffers)
	Pseudo-absences	
Diversity metrics	Shannon's Diversity Index	50 m
	Simpson's Diversity Index	
	Mean Patch Area	
	Number of Patches	
Fragmentation and structure metrics	Patch Density	
	Edge Density	
	Landscape Cohesion Index	

¹ Developed by the authors based on Cortijos, haciendas y lagares. Province of Cordoba. Volume I–Volume II.

² Reclassified SIOSE. ³ Bioterra Andalucía.

For the local-scale model, the most recent “Sistema de Información de Ocupación del Suelo de España” (SIOSE-<https://www.siose.es/descripcion-ar>) database available from 2017 was used, also developed by the IGN in collaboration with the autonomous communities. This source integrates information from various official maps using advanced remote sensing, photointerpretation and multi-source analysis techniques, providing a spatial resolution of 25 m and a higher level of thematic detail with regard to mixed and transitional land cover types.

Subsequently, the original CLC (national-scale model) and SIOSE (local-scale model) classes were reclassified according to ecological and functional criteria, in order to group the cover types into more homogeneous categories that were more relevant for the analysis of species and ecological models (Table A1). The reclassification considered the following main cover classes: heterogeneous agricultural crops, homogeneous agricultural crops, water

bodies, woodland, open areas, non-irrigated herbaceous crops, non-irrigated woody crops, scrubland, grassland, urban areas, and others. This harmonisation ensured consistency between scales and facilitated the comparison of land use patterns and landscape diversity between the two models. In addition, zonal statistics were calculated from the same raster layer of coverage, with the aim of quantifying the area occupied by each land use class (reclassified SIOSE) within each spatial unit. The extraction of values from the raster was performed using the `terra::extract()` function, assigning each pixel to its corresponding class and linking it to the identifier of the container polygon.

For the local-scale model, landscape diversity, fragmentation, and cohesion metrics were calculated from the land cover layer (SIOSE), which had been previously reclassified and converted to raster format (50 m spatial resolution), in order to quantify the spatial structure and composition of the landscape around the analysis units corresponding to lesser kestrel observations (10 km radius buffers). The complete procedure was carried out in R version 4.4.1. (R Core Team, 2024) [37] using the `terra`, `landscapemetrics`, and `dplyr` (version 1.1.4) packages, enabling a reproducible, flexible, and fully automated workflow for all spatial units.

Each analysis polygon (spatial unit) was individually intersected with the land cover raster using a specific function that cropped and masked the raster to the polygon geometry. Global landscape metrics were calculated on the resulting raster using the `calculate_lsm()` function from the `landscapemetrics` package (version 0.2.1.5), which allows the spatial heterogeneity of land uses within each unit to be quantified. Seven representative metrics of landscape diversity and configuration were selected (Table 2).

Finally, the landscape metrics and zonal statistics were integrated into a unified database, linked through each buffer identifier. Spatial consistency and correspondence between layers were verified by comparing coordinate reference systems (CRS) and visually inspecting the results in a GIS environment (Supplementary Material File S1).

2.4. Statistical Analysis

The analytical workflow consisted of three main stages: (i) variable preparation and collinearity assessment, (ii) model fitting and selection, and (iii) model validation and evaluation. All statistical analyses were performed in R version 4.4.1. (R Core Team, 2024) [37], using the `dplyr` (version 1.1.4), `car` (version 3.1-3), `ggcorrplot` (version 0.1.4.1), `MASS` (version 7.3-65), `caret` (version 7.0-1), and `ggplot2` (version 4.0.1) packages. Two different models were developed to evaluate the factors that influence the distribution and abundance of the lesser kestrel:

At the national scale (Spain), a binomial model was fitted using the presence/absence of lesser kestrels in each 10×10 km grid cell as the response variable. The predictor variables included 19 bioclimatic variables, altitude, land use, human footprint, the presence of the common kestrel (*Falco tinnunculus*) as a potential competitor, and the number of prey species present in each grid square (ranging from 0 to 7 prey species).

At the local scale, in Cordoba province, abundance data (expressed as the number of breeding pairs per colony) were modelled using a Generalised Linear Model (GLM) with a negative binomial distribution. The explanatory variables included landscape diversity metrics, statistics on the occupation of different land covers, and the distance to the nearest country house or potential nesting structures (Table 2). Dispersion diagnostics confirmed that the local-scale model was not affected by overdispersion (DHARMA $p = 0.722$), validating the choice of error distribution.

Before modelling, all predictor variables were standardised and assessed for multicollinearity. Pairwise correlations between predictors were calculated using Pearson's coefficient to identify redundant variables. Variables with high collinearity ($|r| > 0.8$)

were excluded from further analyses to retain only independent predictors. In addition, multicollinearity between variables was assessed using the Variance Inflation Factor (VIF) with the *car* (version 3.1-3) package applying an iterative procedure in which the variable with the highest VIF was sequentially eliminated until all remaining predictors had a $VIF \leq 3$ [38].

For model calibration and validation, the dataset was partitioned into training (70%) and validation (30%) subsets using a stratified sampling procedure implemented with the *caret* package, ensuring similar distributions of abundance values in both sets (training $n = 232$; validation $n = 98$). The full negative binomial model, including all predictors retained after the collinearity screening, was fitted to the training subset using the *glm.nb* function from the MASS (version 7.3-65) package. Model selection followed an information-theoretic approach [39] and was implemented using a backward stepwise procedure based on the Akaike Information Criterion (AIC) through stepAIC. This approach allowed us to evaluate alternative model structures and select the most parsimonious model. Starting from the full model containing all predictors retained after the collinearity analysis, each nested model was compared through its AIC value, and the model with the lowest AIC was selected as the most parsimonious and best supported. This approach allowed us to evaluate alternative model structures and retain only the combination of predictors that optimised model fit while avoiding overparameterisation.

Based on the adjusted models, predicted values were projected onto the territory, which made it possible to identify areas of special interest for conservation—areas with confirmed presence of the species and low favourability (predicted value < 0.1)—as well as areas with potential for reintroduction—areas without current presence, but with a high probability of suitability (predicted value > 0.5).

The model calibrated with the training data was used to predict the values in the validation set, and its performance was evaluated using the Root Mean Square Error (RMSE) between the observed and predicted values. Model adequacy and predictive accuracy were visualised using scatterplots of observed versus predicted values and diagnostic plots of residuals.

Finally, once validated, the final negative binomial model was spatially projected across the entire province of Córdoba by applying it to a raster stack containing all land-cover and landscape metric layers used as predictors. This spatial projection produced a continuous prediction surface of breeding-pair abundance across the territory, allowing the identification of areas with high suitability or conservation interest.

3. Results

3.1. National-Scale Model

According to the Spanish Inventory of Terrestrial Species, we identified 1081 UTM grid cells with the presence of lesser kestrels out of the 5424 that comprise mainland Spain and the Balearic Islands (our territorial unit of analysis).

The results of the national-scale model identified the main factors that determine the presence of lesser kestrels in Spain. The model reveals a significant combination of climatic, anthropogenic, and land use variables consistent with the ecology of the species (Table 3).

At the national scale, the model identified both biotic and environmental variables as significant predictors of the presence of the lesser kestrel across Spain. Among the biotic factors, the presence of the common kestrel (*Falco tinnunculus*) showed a positive relationship ($p < 0.0001$), which may be explained by the shared habitat preferences of both species rather than a causal effect, and prey availability was also positively associated with the occurrence of the species ($p < 0.0001$).

Table 3. National-scale model with the best fit (AIC) to explain the presence of lesser kestrels.

	Estimate	Standard Error	z-Value	p-Value
Intercept	−7.39	6.8×10^{-1}	−10.82	<0.0001
Presence of Common Kestrel	6.1×10^{-1}	1.5×10^{-1}	4.16	<0.0001
Bio 7	2×10^{-2}	2.1×10^{-3}	10.79	<0.0001
Bio 18	-2×10^{-2}	2.0×10^{-3}	−11.51	<0.0001
Heterogeneous Crops	3.0×10^{-6}	1.9×10^{-6}	1.58	>0.05
Annual Crops	5.3×10^{-6}	3.6×10^{-6}	1.48	>0.05
Grassland	8.1×10^{-5}	3.2×10^{-5}	2.54	<0.05
Non-irrigated Crops	2.8×10^{-6}	6.4×10^{-7}	4.32	<0.0001
Urban Areas	-1.4×10^{-4}	4.8×10^{-5}	−2.83	<0.01
Water Bodies	-1.7×10^{-5}	3.6×10^{-6}	−4.80	<0.0001
Altitude	-8.3×10^{-4}	2.0×10^{-4}	−4.21	<0.0001
Human Footprint	6×10^{-2}	1×10^{-2}	8.49	<0.0001
N° of Prey Species	1.6×10^{-1}	3×10^{-2}	4.73	<0.0001
Bio 8	-3.0×10^{-3}	1.8×10^{-3}	−1.67	>0.05
Scrubland	-6.2×10^{-6}	4.0×10^{-6}	−1.54	>0.05

Climatic variables were also relevant. Temperature Annual Range (*Bio 7*) had a significant positive effect ($p < 0.0001$), whereas Precipitation of the Warmest Quarter (*Bio 18*) showed a significant negative relationship ($p < 0.0001$), indicating that the species tends to occur in warmer and drier regions (Figure 1).

In terms of land use, non-irrigated crops ($p < 0.0001$) and grasslands ($p < 0.05$) were positively related to the presence of the species, while urban areas ($p < 0.01$) and water bodies ($p < 0.0001$) had negative effects. Other land use categories, including scrubland, heterogeneous and annual crops, showed no significant association ($p > 0.05$). By contrast, scrubland, heterogeneous crops and annual crops showed no significant association ($p > 0.05$), suggesting that these cover types were not related to kestrel presence at the national scale.

Finally, the remaining significant predictors were altitude and human footprint. Altitude had a negative effect ($p < 0.0001$), whereas human footprint showed a positive effect ($p < 0.0001$), suggesting that the species is more frequent in lowland areas with moderate levels of human activity.

The national-scale model estimated the probability of presence of the lesser kestrel in the Iberian Peninsula, using a total of 5424 UTM cells of 10×10 km. The results are showed in Figure 2, where a high probability of occurrence (values greater than 0.39) can be observed in large areas of the south-west of the peninsula, especially in areas with large cereal-growing areas in Andalusia, Extremadura, Castile-La Mancha and part of Castile and León. In contrast, mountainous, forested or densely populated areas, such as the north of the peninsula or the Mediterranean coast, show very low probabilities of occurrence (≤ 0.02).

It is important to clarify that the value 0.39 does not represent a biological presence/absence threshold. The probability map was classified into five equal-frequency intervals (quintiles) to ensure an even representation of the probability gradient across Spain. Therefore, the upper limit of the fourth class (0.39) corresponds to the statistical boundaries of the quantile-based classification, not to a predefined ecological threshold such as 0.5. This approach is widely used to improve visual interpretation in species distribution maps.

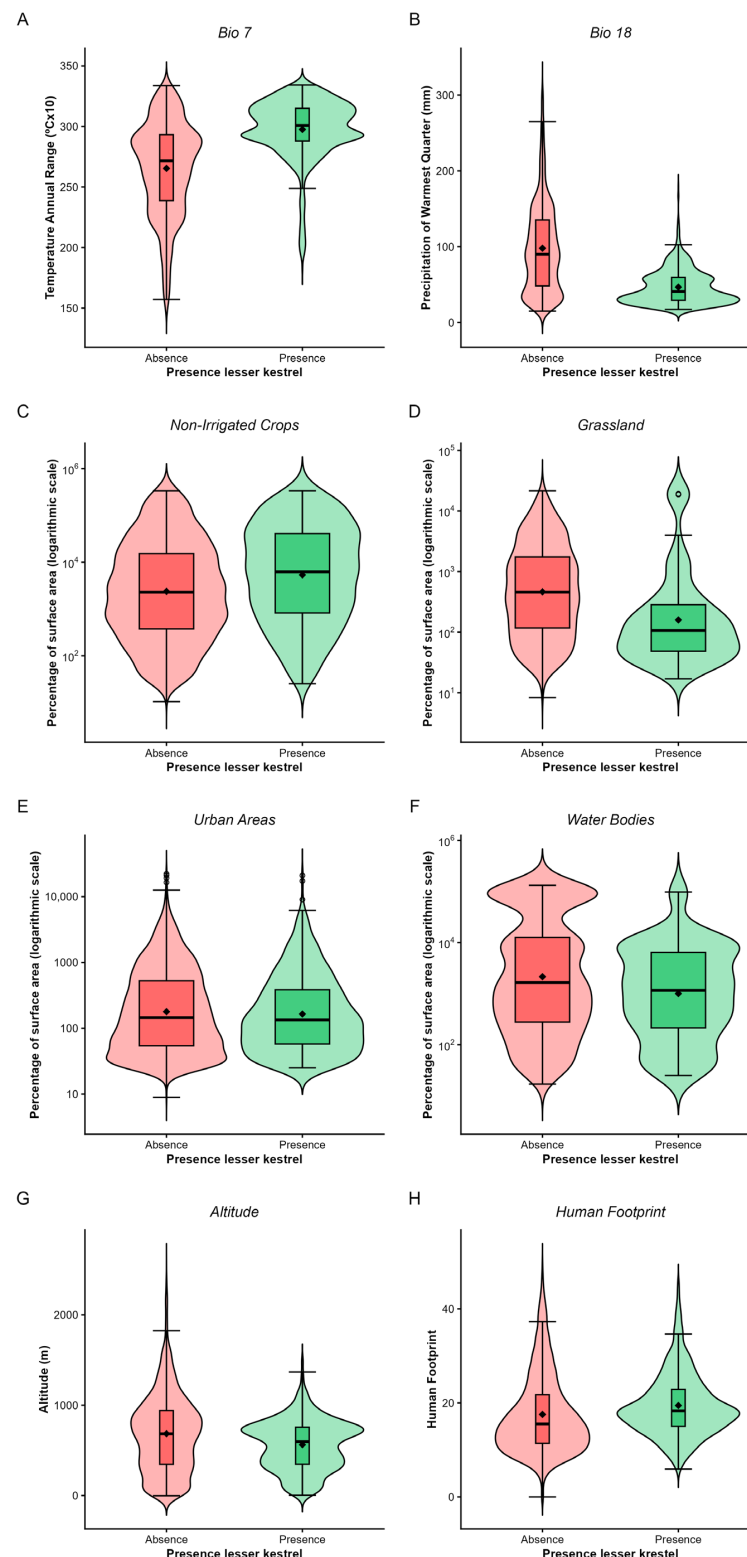


Figure 1. Comparison of environmental and anthropogenic variables between 10×10 km cells with presence (green) and absence (red) of lesser kestrels in the Iberian Peninsula. Violin plots show the distribution of each variable. The internal box represents the interquartile range (IQR), with the horizontal line indicating the median. Whiskers extend to $1.5 \times$ IQR, and the black dot denotes the mean value for each group. (A) Bio 7 (Temperature Annual Range); (B) Bio 18 (Precipitation of Warmest Quarter); (C) Non-Irrigated Crops; (D) Grassland; (E) Urban Areas; (F) Water Bodies; (G) Altitude; (H) Human Footprint Index.

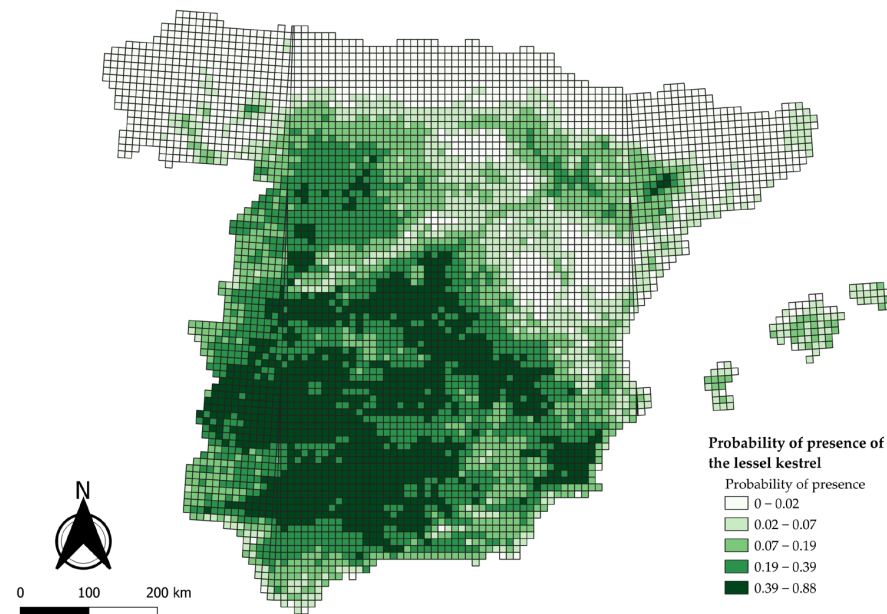


Figure 2. Model of the probability of presence of the lesser kestrel (*Falco naumanni*) in the Iberian Peninsula.

Based on the spatial projection of the values predicted by the lesser kestrel presence model, two types of key areas were identified (Figure 3). On the one hand, areas of special conservation interest were delimited, corresponding to grids cells with confirmed current presence of the species, but with low environmental favourability (predicted value < 0.1). On the other hand, potential reintroduction areas were detected, defined as grid cells where the species is not currently present, but which exhibit a high probability of suitability according to the model (predicted value > 0.5).

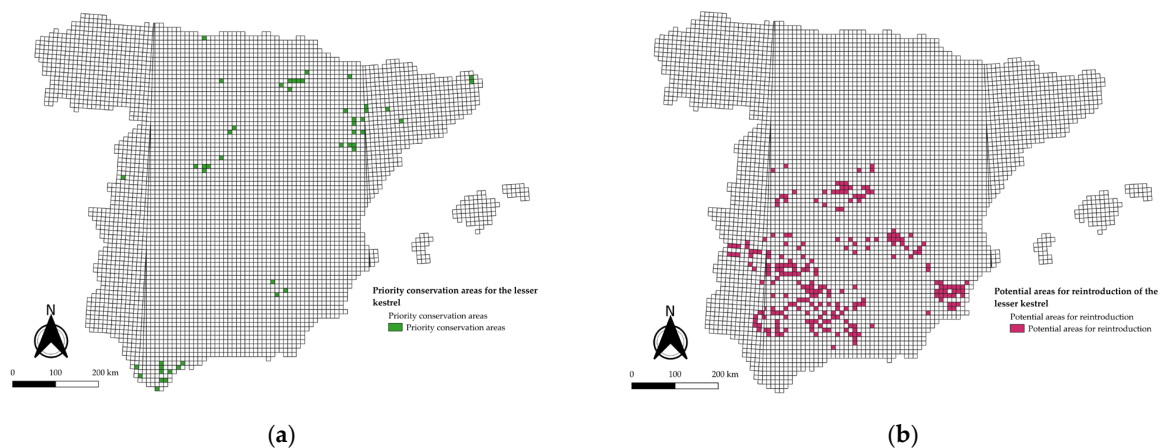


Figure 3. (a) Priority conservation areas for the lesser kestrel in the Iberian Peninsula, identified using the probability presence model. The green cells represent areas identified as priority for conservation; (b) Potential areas for reintroducing the lesser kestrel in the Iberian Peninsula. The magenta cells indicate areas with high suitability for establishing new colonies, according to the distribution model.

3.2. Local-Scale Model

A total of 164 population nuclei were monitored for the period 2012–2023 (Figure A2). In this second approximation, the variables retained in the most parsimonious model to explain kestrel abundance are shown in Table 4. In the case of land use, the following variables were included in the best model: urban areas, water bodies, non-irrigated crops, woodland, grassland, and open areas. Mean patch area and distance to country houses were

also included. The backward stepwise selection substantially improved model fit, reducing the AIC from 657.11 in the full model to 652.95 in the final selected model. This model was therefore retained as the most parsimonious structure explaining kestrel abundance.

Table 4. Local-scale model with the best fit (AIC) to explain the presence of lesser kestrels.

	Estimate	Standard Error	z-Value	p-Value
Intercept	1.268	8.167×10^{-1}	1.552	>0.05
Urban areas	2.248×10^{-4}	8.491×10^{-5}	2.647	<0.01
Water bodies	-9.562×10^{-4}	4.395×10^{-4}	-2.176	<0.05
Non-irrigated Crops	7.031×10^{-5}	1.775×10^{-5}	3.960	<0.0001
Woodland	-2.493×10^{-4}	7.084×10^{-5}	-3.519	<0.01
Grassland	2.561×10^{-4}	1.498×10^{-4}	1.709	>0.05
Open areas	-1.529×10^{-3}	4.569×10^{-4}	-3.347	<0.01
Mean Patch Area	-4.819×10^{-2}	2.071×10^{-2}	-2.326	<0.05
Distance country house	7.745×10^{-11}	4.850×10^{-11}	1.597	>0.05

At the local scale, the Generalised Linear Model (negative binomial) identified several variables with significant effects on kestrel abundance (Table 4). Among the land use variables, non-irrigated crops ($p < 0.001$) and urban areas ($p < 0.01$) showed significant positive effects, while woodland ($p < 0.001$), water bodies ($p < 0.05$), and open areas ($p < 0.001$) had significant negative effects. Grassland showed a positive but non-significant relationship with kestrel abundance ($p = 0.087$).

Regarding landscape metrics, mean patch area exhibited a significant negative effect ($p < 0.05$), indicating that kestrel abundance decreases with increasing patch size. Distance to the nearest country house showed a weak, non-significant positive relationship ($p > 0.1$). Model calibration and validation were performed using a stratified 70/30 training–validation split ($n = 232$ and $n = 98$, respectively). After model selection, predicted values were obtained for the independent validation subset, yielding an RMSE of 4.70. The predicted values of the local-scale model (Figure 4) show a clear spatial aggregation of lesser kestrel population centres in areas of south-central and south-eastern Cordoba province, where the largest breeding pairs' populations are located. On the other hand, the centre-north and south of the province, presents a lower population density, with scattered population centres and few breeding pairs.

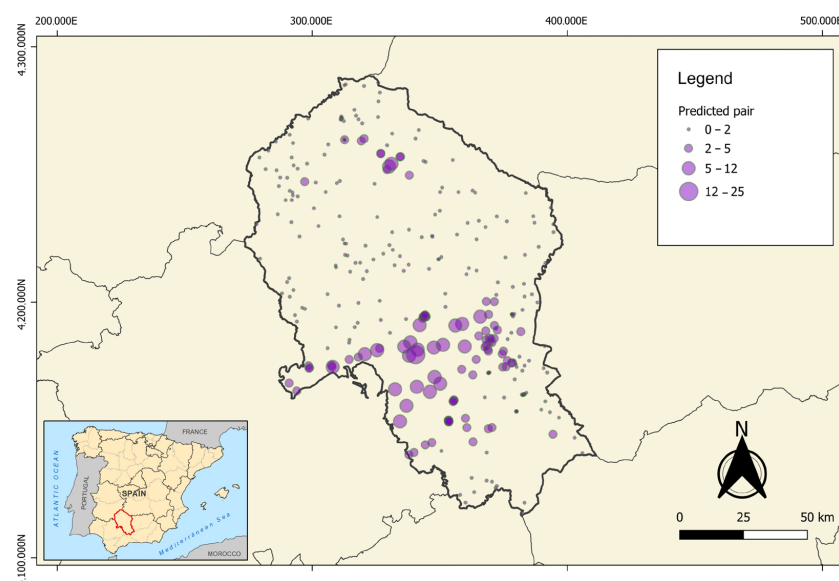


Figure 4. Prediction map of the number of breeding pairs of lesser kestrels (*Falco naumanni*) based on the local-scale model.

4. Discussion

This study provides an integrated assessment of the environmental and anthropogenic factors influencing the distribution and abundance of the lesser kestrel across spatial scales. By combining a national-scale presence–absence model with a local-scale abundance model, we were able to identify both large-scale drivers shaping the species' overall range and local-scale processes affecting population persistence. The results highlight the importance of traditional agricultural landscapes and prey availability as key determinants of kestrel occurrence, while also revealing the negative effects of urbanisation, water bodies, and forested areas. Together, these findings contribute to a more comprehensive understanding of the ecological requirements of the species and offer valuable guidance for conservation planning and habitat management.

4.1. Drivers of National-Scale Patterns

The strong relevance of prey availability in the model confirms that the presence of the kestrel is highly dependent on the abundance of food resources, as previously reported in other studies [40,41]. Although the diet of this species is mainly based on orthopterans (a variable that could not be included in the model due to lack of data), small mammals are considered its main prey during the breeding season, where they can account for up to 50% of the biomass consumed [34]. Likewise, the presence of the common kestrel (*Falco tinnunculus*) shows a positive relationship, which could reflect a selection of similar habitats rather than direct interspecific competition [42].

Regarding climatic variables, Temperature Annual Range (Bio 7) showed a positive association with the presence of the lesser kestrel, indicating a preference for areas with high annual temperature variability typical of continental and semi-arid Mediterranean regions. In contrast, Precipitation of the Warmest Quarter (Bio 18) exhibited a negative effect, suggesting that the species tends to avoid humid areas with intense summer rainfall. Overall, these results highlight the adaptation of the lesser kestrel to dry environments with marked thermal contrasts and limited summer precipitation, conditions that characterise the cereal steppe landscapes of the Iberian Peninsula [13].

With respect to land use, the positive relationship with non-irrigated crops highlights the importance of traditional agricultural landscapes for the conservation of the species. Several studies have shown that colonies tend to be located in extensive agricultural areas with fallow land and grasslands, where prey density is higher [41]. In contrast, urban environments and water bodies showed negative relationships, probably due to habitat fragmentation or the limited availability of prey in these environments (Figure 1). The negative effect of urban areas in the national-scale model could be due to the deterioration or restoration of historical buildings, which represents a major threat to the species' nesting habitats [16]. However, urban areas may also play a secondary role in supporting breeding populations, as previous studies have shown evidence that the availability of artificial nesting sites can boost colony growth [43]. This factor may explain the positive relationship observed for urban areas in the local-scale model. Although the fact that other land uses, such as heterogeneous or permanent crops, were not statistically significant could be due to their overlap with other variables already included in the model or to their limited spatial representation.

Finally, altitude and human footprint together reflect the species' preference for low-land areas, particularly cereal-growing farmlands, where abundant food resources and suitable nesting structures are available [44]. The positive association with moderate levels of human footprint suggests that the lesser kestrel benefits from landscapes characterised by traditional agricultural practices and a certain degree of anthropogenic transformation, typically associated with extensive agroecosystems. These environments also provide

artificial structures, such as telegraph poles and buildings, which are frequently used by the species for perching and nesting [45] (Figure 1).

These results support the notion that the lesser kestrel is highly sensitive to both landscape structure and climatic conditions, particularly to land use changes involving the replacement of cereal crops by intensive olive plantations. Such transformations reduce the extent of suitable habitat and the abundance of prey available to the species [14], with important implications for its long-term conservation [32]. As land use and climate continue to change, it will be essential to incorporate these factors into predictive modelling and the design of management strategies at both regional and national scales.

The modelled spatial distribution reflects a strong association of the lesser kestrel with open agricultural landscapes and continental climatic conditions characterised by high thermal variability and low summer precipitation [13,15,46]. This pattern coincides with the distribution observed in actual presence data [11], mainly concentrated in the semi-arid cereal steppes of central and southern Spain. In addition, anthropogenic variables such as human footprint and land use contributed significantly to defining the species' potential distribution, highlighting its tolerance to moderately transformed agricultural environments where nesting structures and prey resources remain available [16,21,27].

With regard to the areas of special conservation interest (Figure 3a), their low favourability may result from anthropogenic pressures or land use changes that threaten the persistence of existing populations [13,15,18,33]. In contrast, the potential reintroduction areas (Figure 3b) show favourable environmental and territorial conditions for supporting new colonies and provide a sound scientific basis for the planning of restoration and range-expansion strategies for the species [5,15,47].

While the national-scale model provides a broad understanding of the environmental and anthropogenic factors shaping the distribution of the lesser kestrel across Spain [13,17], the local-scale analysis offers a more detailed perspective on the processes influencing population abundance within specific territories. The province of Cordoba, selected as a representative area of the species' core range, allowed us to explore how landscape configuration and land use composition affect breeding colony density and persistence at a finer spatial resolution [13,40,41,48].

4.2. Ecological Interpretation of Local-Scale Patterns

Based on the results of the local-scale model, the abundance of breeding pairs of kestrels is primarily determined by land use and landscape variables such as non-irrigated crops, urban areas, woodland, water bodies, and open areas. Non-irrigated crops and urban areas showed significant positive effects, confirming the species' preference for traditional agricultural landscapes and the use of human structures as nesting sites. In contrast, woodland, water bodies, and open areas exhibited significant negative effects, suggesting that habitats dominated by woody vegetation or lacking vegetation cover may represent suboptimal environments for the species. These conditions likely reduce prey availability or limit access to open ground for foraging [9,15]. Grassland showed a weak positive but non-significant relationship with kestrel abundance ($p = 0.087$), indicating that although such habitats may offer suitable foraging conditions, they are not the main predictors of local population density in the study area.

The negative effect of mean patch area may be explained by the species' preference for fragmented landscapes, as reported in previous studies [47]. The lesser kestrel tends to occupy heterogeneous agricultural mosaics composed of small and diverse patches, which generate a greater edge effect and a variety of foraging opportunities. Such fine-grained landscapes are favourable for this species because they reduce searching and hunting time, increasing foraging efficiency [18,48].

The lack of statistical significance for the distance to country houses may be related to issues of spatial scale. Most buffers, both with and without the presence of the species, showed average distances to country houses shorter than the typical foraging range of the lesser kestrel. Consequently, this variable did not represent a sufficiently wide gradient to detect meaningful differences in the model. In other words, proximity to country houses does not represent a limiting factor in the study area, as it is almost always within the bird's functional range of movement. This lack of significance could also be due to the suitability of each country house for the species, as the condition of the country houses was not taken into account, requiring it to have gaps under the roof or in the building so that it can be used for nesting [49].

Based on the spatial projection of predicted values for breeding pairs (Figure 4), the highest concentrations are found in agricultural areas dominated by cereal crops and extensive herbaceous crops, coinciding with the actual distribution patterns of the species [11]. In contrast, mountainous or hilly areas, characterised by a lower proportion of herbaceous habitats and greater forest cover, show very low or zero estimated abundance values. This coincidence between high prediction values and the actual presence of colonies reinforces the validity of the model for identifying favourable habitats at the local scale, especially in heterogeneous agricultural landscapes with an abundance of buildings (e.g., country houses and warehouses) that can serve as nesting sites.

Taken together, the national- and local-scale models provide complementary perspectives on the factors influencing the distribution and abundance of the lesser kestrel in Spain. The integration of climatic, land use, and landscape variables allowed the identification of both broad-scale environmental gradients and local habitat features that determine the suitability of territories for breeding colonies. These findings underscore the relevance of adopting multiscale approaches to understand species–environment relationships, as processes acting at different spatial levels often interact to shape population dynamics. Moreover, the combined use of ecological modelling and field data offers a powerful framework for detecting priority areas for conservation and for anticipating potential shifts in the species' range under future land use and climate change scenarios.

5. Conclusions

This study has identified the main environmental and anthropogenic factors that influence the distribution of the lesser kestrel in Spain, integrating both national- and local-scale analyses. At the national scale, the results revealed that the presence of the species is positively associated with non-irrigated crops, grasslands, prey availability, and moderate levels of human footprint, whereas urban areas, water bodies, and higher altitudes have negative effects. These findings confirm the species' preference for extensive open agricultural landscapes with low summer rainfall and high thermal variability, where both trophic resources and nesting opportunities are abundant.

At the local scale, the models highlighted the importance of non-irrigated crops and urban areas as positive predictors of abundance, while woodland, water bodies, open areas, and mean patch area showed negative effects. The lack of significance of other factors, such as distance to country houses or grassland cover, may be related to the spatial resolution of the analysis or the limited variability of these variables within the study area. Interestingly, the variable urban areas had contrasting roles depending on the spatial scale, illustrating how the same factor can have different ecological implications at regional and local scales.

The spatial projection of the models allowed the identification of key areas for conservation, especially those with existing populations but low suitability—potentially indicating vulnerability or population decline—and currently unoccupied areas with high suitability, which could be considered for reintroduction or population reinforcement actions.

Overall, these findings provide useful tools for the conservation planning of the lesser kestrel, enabling the prioritisation of areas for active management. They also emphasise the importance of traditional agricultural landscapes as key elements in the conservation of steppe birds and underscore the need for sustainable agricultural policies that integrate biodiversity objectives.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/conservation6010002/s1>.

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Abbreviations

The following abbreviations are used in this manuscript:

GLM	Generalised Linear Model
UTM	Universal Transverse Mercator
MITECO	Ministry for the Ecological Transition and Demographic Challenge
DEM	Digital Elevation Model
IGN	Instituto Geográfico Nacional
SEDAC	Socioeconomic Data and Applications Center
NASA	National Aeronautics and Space Administration
CLC	CORINE Land Cover
SIOSE	Sistema de Información de Ocupación del Suelo de España
CRS	Coordinate Reference Systems
GIS	Geographic Information System
AIC	Akaike Information Criterion
RMSE	Root Mean Square Error

Appendix A. Impact of Environmental and Human Factors on the Populations of the Lesser Kestrel (*Falco naumanni*) at State and Local Scales

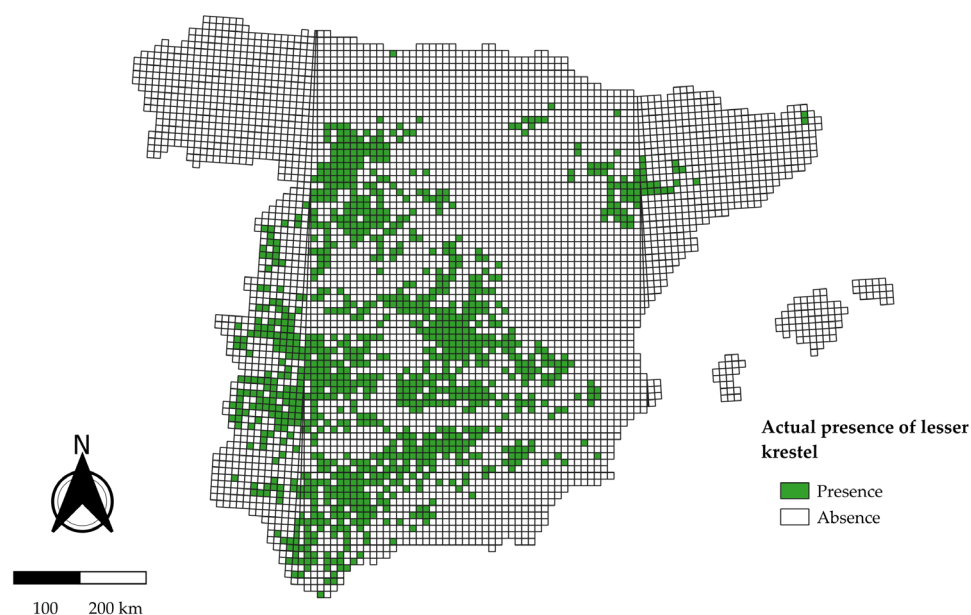


Figure A1. Recorded presence of lesser kestrels (*Falco naumanni*) in the Iberian Peninsula according to 10 × 10 km UTM grids. Green indicates grids with presence and white indicates those without records. Source: Spanish Terrestrial Species Inventories.

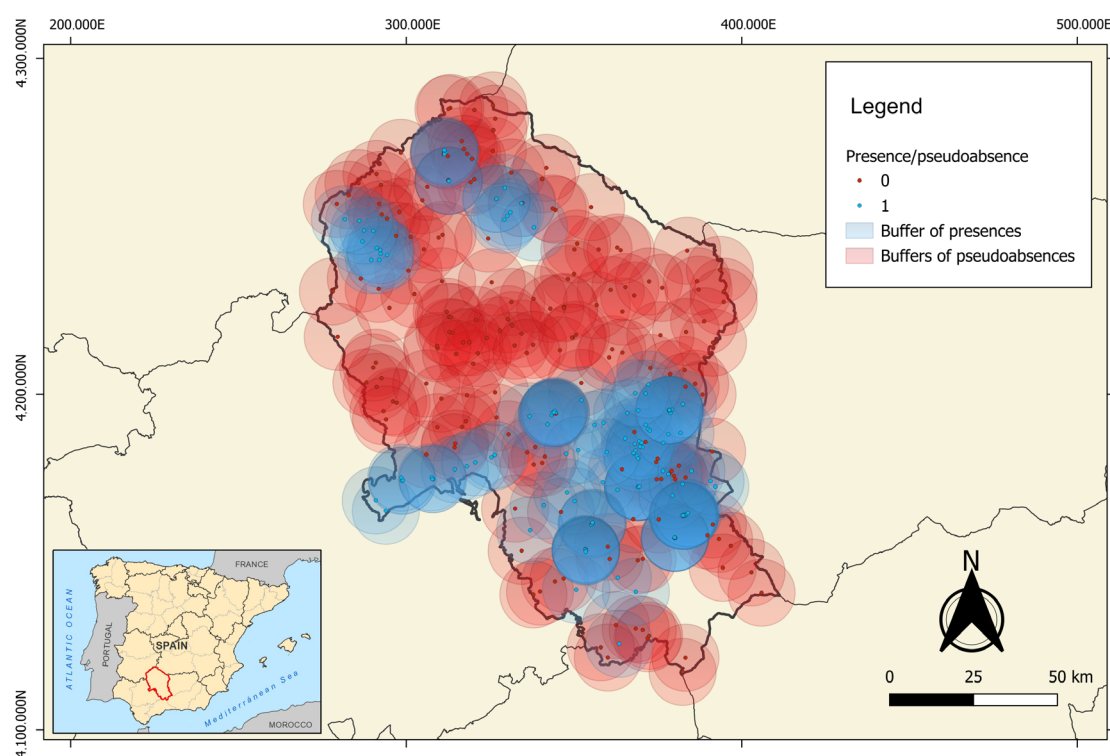


Figure A2. Distribution and size of lesser kestrel (*Falco naumanni*) population centres in the province of Cordoba. The size of the circles represents the estimated number of breeding pairs in each centre. Source: Author's own work based on censuses (2012–2023).

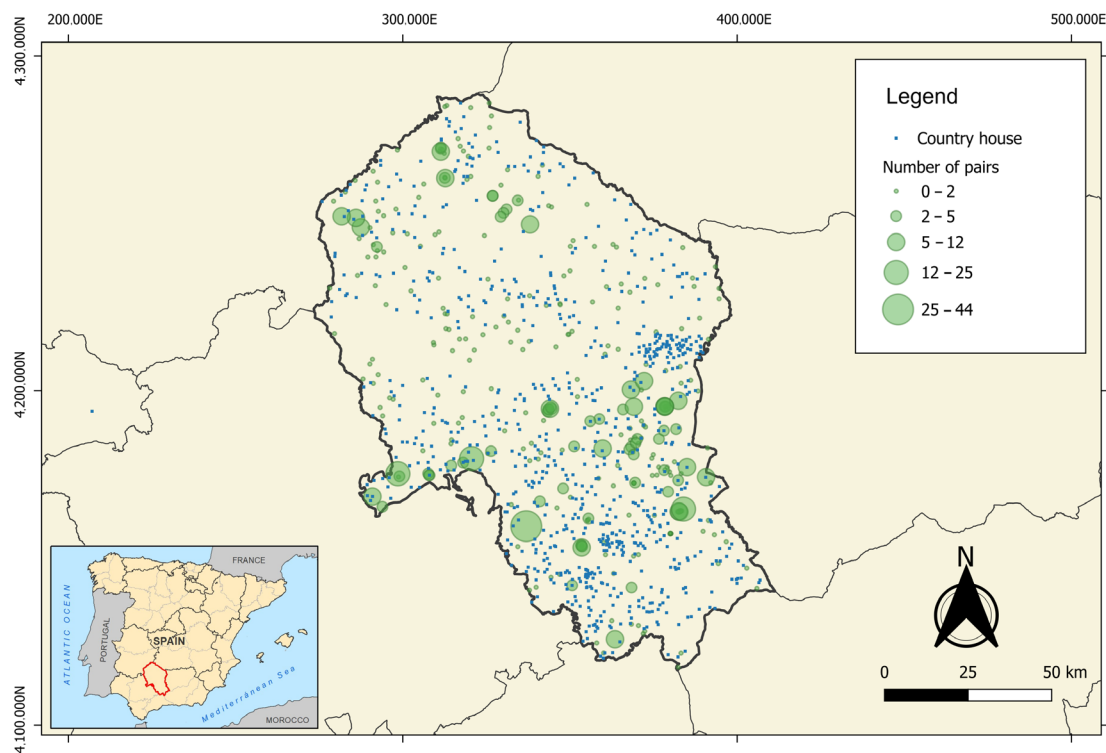


Figure A3. Spatial distribution of lesser kestrel (*Falco naumanni*) population centres and pseudo-absence points in the province of Cordoba. The 10 km buffers are represented around each centre (blue) and each pseudo-absence point (red), used for analysis at the local scale. Source: Authors' own work based on censuses and the generation of random pseudo-absences.

Table A1. Reclassification and grouping of land cover classes for CORINE and SIOSE information.

Reclassification	CORINE	SIOSE
Urban areas	111—Continuous urban fabric	111—Urban area
	112—Discontinuous urban fabric	112—Suburb
	121—Industrial or commercial units	113—Discontinuous urban area
	122—Road and rail networks and associated land	114—Urban green area
	123—Port areas	121—Agricultural and/or livestock facility
	124—Airports	122—Forestry facility
	131—Mineral extraction sites	123—Mining extraction
	132—Dump sites	130—Industrial
	133—Construction sites	140—Public service facility
	141—Green urban areas	150—Agricultural settlement and orchard
	142—Sport and leisure facilities	160—Road or rail network
		162—Puerto
		163—Aeropuerto
		171—Supply infrastructure
Water bodies	411—Inland marshes	172—Waste infrastructure
	412—Peatbogs	220—Greenhouse
	421—Salt marshes	411—Wet and marshy area
	422—Salines	412—Peat bog
	423—Intertidal flats	413—Salt marsh
	511—Water courses	414—Salt pan
	512—Water bodies	514—Artificial water body
	521—Coastal lagoons	511—Watercourses
	522—Estuaries	513—Reservoir
	523—Sea and ocean	515—Sea
		516—Glacier and/or perpetual snow

Table A1. Cont.

Reclassification	CORINE	SIOSE
Non-irrigated crops	211—Non-irrigated arable land	210—herbaceous crop
Annual crops	221—Vineyards 222—Fruit trees and berry plantations 223—Olive groves	231—Citrus fruit trees 232—Non-citrus fruit trees 233—Vineyards 234—Olive trees 235—Other woody crops 236—Combination of woody crops
Irrigated crops	212—Permanently irrigated land 213—Rice fields	
Heterogeneous crop	241—Annual crops associated with permanent crops 242—Complex cultivation patterns 243—Land principally occupied by agriculture 244—Agro-forestry areas	250—Crop mix 260—Crop mix with vegetation 340—Vegetation mix
Forest	311—Broad-leaved forest 312—Coniferous forest 313—Mixed forest	311—Deciduous forest 313—Mixed forest 312—Coniferous forest
Scrubland	321—Natural grassland 322—Moors and heathland 323—Sclerophyllous vegetation 324—Transitional woodland shrub	330—Scrubland
Grassland	231—Pastures	320—Grassland or Herbaceous vegetation 240—Pasture
Other	331—Beaches, dunes, and sand plains 332—Bare rock 333—Sparsely vegetated areas 334—Burnt areas 335—Glaciers and perpetual snow	351—Beach, dune or sandy area 352—Rocky area 353—Temporarily deforested due to fires 354—Bare soil

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