European Journal of Wildlife Research (2026) 72:64
https://doi.org/10.1007/s10344-026-02094-8

RESEARCH

Linking landscapes: analyzing corridors for bearded vultures in the Iberian Peninsula

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Received: 8 May 2025 / Revised: 28 March 2026 / Accepted: 11 April 2026

Abstract

The Bearded Vulture (*Gypaetus barbatus*) is listed in the Spanish Catalogue of Threatened Species as "Endangered." Historically, it occupied mountainous regions across Asia, Europe, and Africa, and had a wide distribution throughout the Iberian Peninsula. However, its current presence in Spain is now limited to specific mountain ranges. The decline is due to various threats, including habitat loss, human disturbance, and poisoning, which necessitate targeted conservation efforts such as reintroduction and conservation programs. This study focuses on identifying potential ecological corridors and evaluating landscape connectivity for Bearded Vultures across key regions in Spain. Using environmental favourability models and a resistance-based approach (1/favourability) at a 10 × 10 km resolution, we generated maps of landscape connectivity and identified high- and low-connectivity areas. Corridors were delineated from areas of high connectivity and validated using GPS tracking data from tagged individuals. Our results reveal critical connectivity pathways in northern Spain, particularly linking Picos de Europa and the Pyrenees, influenced by topography, food availability, and distance to anthropogenic features. These findings emphasize the importance of maintaining functional corridors for the species and provide spatially explicit guidance for conservation planning to ensure long-term population viability.

Keywords Connectivity · Conservation · Ecological corridors · Favourability · *Gypaetus barbatus* · Modelling · Movements · Scavenger bird

Introduction

The Bearded Vulture (*Gypaetus barbatus*) is one of the most endangered birds of prey in Europe (subsp. *G. b. barbatus*), listed in Annex I of the EU Birds Directive (79/409/EEC and 2009/147/EEC), Appendix II of the Bern Convention, the Bonn Convention, and CITES. In North Africa (subsp. *G. b. barbatus*), it is classified as Critically Endangered based on IUCN criteria, due to its rarity and small population size (Allaoui and Cherkaoui 2018). In Europe, its conservation status was updated to Vulnerable in 2019 according to the IUCN, while in Spain it is classified as Endangered in the Spanish Catalogue of Threatened Species (RDL 139/2011, February 4). Historically, the species occupied all major mountain ranges of the Iberian Peninsula (Hiraldo et al. 1979; Orta et al. 2020). However, persecution, poisoning and habitat alteration caused a severe population decline, leading to its extinction in several regions (Margalida et al. 2008). At present, the species persists mainly through a relict breeding population in the Pyrenees, comprising approximately 126 reproductive units (RUs), according to the latest census conducted in 2018, which represent more than 70% of the European population (Margalida and Martínez 2020).

Conservation actions over recent decades have focused on population recovery through reintroduction, supplementary feeding, and mitigation of non-natural mortality. One of the most successful reintroduction programs took place in the Alps, where a stable population has been re-established (Schaub et al. 2024). In Spain, reintroductions have restored small populations in the Cantabrian Mountains (Picos de Europa) and Sierra de Cazorla, where the species had disappeared for decades (Hiraldo et al. 1979; Margalida

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and Martínez 2020). Additionally, natural recolonization has been documented in the Vasco-Navarra mountains and the Moncayo Massif (Margalida and Martínez 2020). More recently, the reintroduction of Bearded Vultures in the Sierra de Gredos represents a key effort to re-establish the species in the Central System, contributing to range expansion and increasing the potential for demographic and genetic exchange between populations (Margalida et al. 2013).

Despite these advances, the species remains highly fragmented in Spain. Bearded Vultures show a strong degree of philopatry, especially individuals born in the wild (Tréhin et al. 2024), with individuals tending to remain close to their natal areas, a behavior that can limit dispersal and slow colonization of new suitable habitats (López-López et al. 2013). This trait and conspecific attraction can hinder dispersal and limit geographic expansion, potentially affecting genetic diversity and breeding output (Carrete et al. 2006a, b a, 2006 b, Margalida et al. 2013; López-López et al. 2013). Therefore, enhancing habitat connectivity is crucial to promote dispersal and improve resilience to environmental changes (Tréhin et al. 2024).

The importance of landscape connectivity for the conservation of the Bearded Vulture has been explicitly highlighted in the Spanish National Strategy for the Conservation of the Bearded Vulture (2025), which identifies connectivity as a critical milestone for ensuring population viability and facilitating natural dispersal between reintroduced and relict populations. However, despite its recognized relevance, no connectivity model has yet been developed for the species within the context of Iberian populations.

The Bearded Vulture is a specialized osteophagous scavenger (Margalida 2008; Margalida et al. 2009) strongly associated with mountain systems characterized by steep terrain, rocky nesting sites, and open landscapes that facilitate food detection (Ferguson-Lees and Christie 2001; Orta et al. 2020). Its diet relies largely on carcasses of medium-size domestic ungulates (*Ovis* and *Capra*) and wild ungulates (*Rupicapra* and *Capra*), linking its spatial ecology to extensive livestock farming systems (Margalida et al. 2007a, b, 2018; Arrondo et al. 2023). Extensive livestock farming is critical to the conservation of mountain ecosystems in developed countries (Pătru-Stupariu et al. 2020; Muñoz et al. 2021), contributing significant economic, social, and ecological value (Reiné 2017).

Technology has been instrumental in the conservation of the Bearded Vultures, providing essential data through the use of GPS transmitters (Silva et al. 2017; García-Jiménez et al. 2020). These devices have allowed researchers to monitor flight paths (Gil et al. 2014; García-Jiménez et al. 2018), identify key feeding areas (Margalida et al. 2016) and map juvenile dispersal zones (Margalida et al. 2013). GPS data are essential for detecting threats, such as poisoning and collisions with human infrastructure (Vignali et al. 2021), and assessing the effectiveness of supplementary feeding sites (Moreno-Opo et al. 2015; Margalida et al. 2016, 2017). Additionally, it aids in monitoring individuals released during reintroduction programmes to ensure their survival (Gil et al. 2014). However, although recent advances in movement ecology (e.g. semi-mechanistic approaches such as iSSA) allow robust modelling of animal movement and corridor identification, telemetry-based approaches may still be limited by spatial biases related to the distribution of tracked individuals and monitored areas. This can restrict their application for large-scale connectivity assessments, particularly in regions where populations are small or recently reintroduced.

In this context, landscape-based connectivity modelling provides a complementary approach to movement data, allowing the identification of areas that facilitate or constrain movement based on environmental favourability (Torres et al. 2017; Pulido-Pastor et al. 2021). Favourability models integrate ecological factors influencing species presence while minimizing the effect of prevalence, making them especially suitable for species with fragmented or expanding populations (Real et al. 2006; Marchetto et al. 2023). When translated into resistance surfaces, favourability-based approaches allow the identification of areas with lower movement cost, without implying absolute barriers to movement, but rather gradients of connectivity that reflect landscape permeability (Torres et al. 2017; Pulido-Pastor et al. 2021).

The aim of this study is to develop the first large-scale connectivity model for the Bearded Vulture in the Iberian Peninsula, identifying potential ecological corridors and priority areas for conservation. By integrating favourability-based resistance surfaces with connectivity analyses, we aim to provide a spatial framework that supports current conservation actions, guides future reintroductions, and contributes to the implementation of national and international conservation strategies for this species.

Methods

Study area

This study was conducted across the main mountain systems of mainland Spain, located in southwestern Europe (Fig. 1A), which currently host breeding or reintroduced populations of the Bearded Vulture: the Central System, the Cantabrian Mountains, the Baetic Mountains and the Pyrenees. These mountain ranges represent key regions for the conservation and expansion of the species and encompass a wide environmental gradient relevant for connectivity

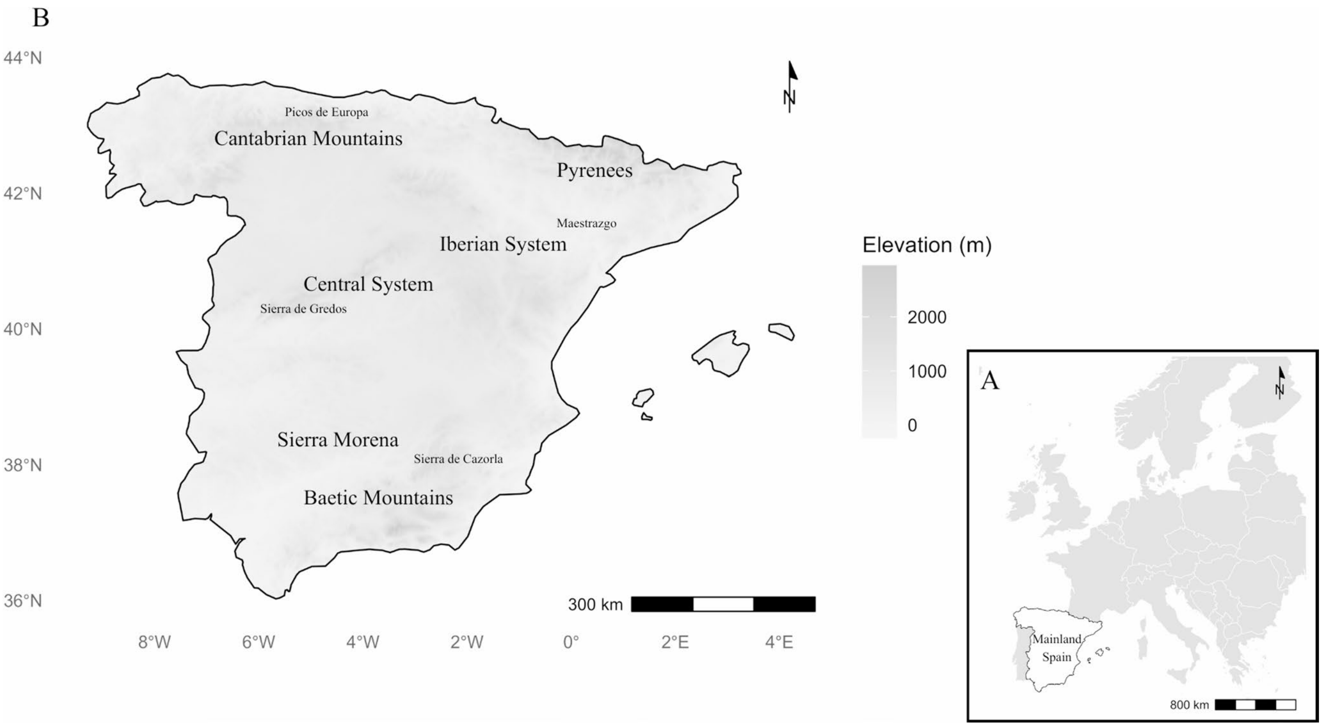

Fig. 1 Location of mainland Spain on the European continent (**A**) and the main mountain ranges in peninsular Spain (**B**)

analyses (Fig. 1B). All these regions offer unique ecological settings that shape the habitat requirements and environmental conditions for the Bearded Vulture (Margalida and Bertran 2000; Margalida et al. 2008, 2013; Estrada et al. 2025).

The Central System divides the Iberian Meseta into northern and southern sub-plateaus and is characterized by a heterogeneous topography with extensive high-altitude areas. Sierra de Gredos constitutes its highest sector, reaching 2,592 m a.s.l., and hosts one of the most recent reintroduction initiatives for the Bearded Vulture in Spain. The Cantabrian Mountains extend along the northern coast of the Iberian Peninsula and include the Picos de Europa massif, which reaches elevations of up to 2,648 m a.s.l. This region is characterized by steep relief, limestone formations, and a humid Atlantic climate. The Baetic Mountains, located in southern Spain, comprise the highest mountain range of the Iberian Peninsula, reaching 3,479 m a.s.l. The Baetic system hosts one of the main reintroduced populations of the species in Spain, particularly in Sierra de Cazorla Natural Park, and plays a key role in large-scale connectivity across the peninsula. Finally, the Pyrenees form a major biogeographic barrier between the Iberian Peninsula and continental Europe, extending from the Bay of Biscay to the Mediterranean Sea and reaching a maximum elevation of 3,404 m a.s.l. They currently support the only long-established breeding population of the species in the Iberian Peninsula.

These mountain systems differ in climate, topography, land use, and degree of human influence, but all provide suitable conditions for the Bearded Vulture, including rugged terrain for nesting, open landscapes for foraging, and the presence of wild and domestic ungulates (Aguilera-Alcalá et al. 2022; Estrada et al. 2025). Extensive livestock farming remains a key socio-ecological feature across these regions and plays an important indirect role in the conservation of scavenger communities by maintaining carrion availability (García-Ruiz and Lasanta-Martínez 1993; Aguilera-Alcalá et al. 2022; Estrada et al. 2025).

Data collection

Movement data were obtained from Bearded Vultures equipped with solar-powered GPS transmitters. Devices included 50 g GPS/GSM Ornitrack transmitters (Ornitela, Lithuania) and 90 g GPS/GPRS Bird Solar transmitters (e-obs, Germany), attached using a teflon thoracic harness following established protocols (Tomkiewicz et al. 2010).

A total of 57 individuals were tracked across three regions. Five individuals were monitored in Sierra de Gredos, 39 in Picos de Europa, and 13 in the Aragonese Pyrenees. Tracking periods differed among regions, reflecting the timing of reintroduction and monitoring programmes: 2006–2023 in the Pyrenees, 2010–2023 in Picos de Europa, and 2022–2023 in Sierra de Gredos. GPS data were used exclusively for the validation and ecological interpretation of connectivity patterns and not for the construction of the connectivity model itself. Although a total of 57 individuals were tracked, only a small subset performed long-distance movements between distinct mountain systems. These rare inter-population movements were considered the most appropriate for validating large-scale connectivity patterns, as resident movements within home ranges do not reflect dispersal processes across the landscape. Therefore, validation analyses were restricted to individuals exhibiting such long-distance movements.

Distribution modelling

To model large-scale ecological connectivity, we first developed an environmental favourability model describing the breeding distribution of the Bearded Vulture across the Iberian Peninsula. This approach is based on the favourability function proposed by Real et al. (2006), which allows disentangling the effect of species prevalence from the influence of environmental predictors and is particularly suitable for comparative and spatial analyses at broad scales.

Favourability (F) was calculated as:

$$F = \frac{\frac{P}{1-P}}{\frac{n_1}{n_0} + \frac{P}{1-P}}$$

where P is the probability of breeding presence obtained through logistic regression, and n_1 and n_0 represent the number of occupied and unoccupied operational geographic units (OGUs), respectively. OGUs consisted of UTM grid cells of 10 × 10 km, a spatial resolution commonly used in large-scale distribution studies and appropriate for wide-ranging soaring birds such as the Bearded Vulture (Vignali 2021; Del Moral 2022).

Favourability values range from 0 (completely unfavourable conditions) to 1 (highly favourable conditions). A value of 0.5 indicates that the local probability of breeding presence equals the overall prevalence of the species across the study area. In other words, environmental conditions at this value are neither particularly favourable nor unfavourable relative to the average conditions available for the species. Values above 0.5 indicate areas where environmental conditions are more favourable than expected given the species prevalence, whereas values below 0.5 indicate less favourable conditions (Acevedo and Real 2012). Importantly, favourability is independent of prevalence, meaning that it reflects how suitable environmental conditions are for the species regardless of whether the species is currently present or absent in a given cell. This property makes favourability particularly useful for identifying environmentally suitable areas independently of current occupancy patterns, which is especially relevant for species with fragmented or expanding distributions. All modelling procedures were conducted in R (R Core Team 2024).

Model evaluation

The performance of the favourability model was assessed in terms of discrimination and classification capacity. Discrimination ability was evaluated using the area under the receiver operating characteristic curve (AUC; Lobo et al. 2008). Classification performance was assessed using a favourability threshold of F = 0.5, which represents the point at which environmental conditions are equally favourable and unfavourable relative to species prevalence (Real et al. 2006). This threshold is commonly used in favourability modelling as a biologically meaningful reference value. In addition, the following metrics were calculated: sensitivity (proportion of OGUs with reported breeding correctly classified as favourable), specificity (proportion of OGUs without reported breeding correctly classified as unfavourable), correct classification rate (CCR), over-prediction rate (OPR; proportion of OGUs without reported breeding classified as favourable), and under-prediction rate (UPR; proportion of OGUs with reported breeding classified as unfavourable). These metrics range from 0 to 1 and are widely used in species distribution modelling (Fielding and Bell 1997; Barbosa et al. 2013). In addition, Cohen's Kappa index (Cohen 1960) was calculated to quantify agreement between observed and predicted breeding presence beyond chance.

Predictor selection and model construction

The favourability model was constructed following the methodology described by Acevedo and Real (2012), using environmental predictors related to topography, climate, human activity, food availability, and land use (Supplementary Material, Table S1). These variables are known to influence key demographic and ecological processes of the Bearded Vulture (Donázar et al. 1993; Margalida et al. 2007a, b; Estrada et al. 2025).

To reduce multicollinearity, Spearman correlation coefficients were calculated between all pairs of predictor variables. When correlations exceeded $p = 0.8$ within each environmental factor, only the variable with the highest individual predictive power was retained (López-Ramírez et al. 2024). To control for the inclusion of predictors by chance (García 2003), a False Discovery Rate (FDR) correction was applied following Benjamini and Hochberg (1995). Only variables with a score test significance below an FDR threshold of 0.05 were retained for subsequent modelling steps (Benjamini and Yekutieli 2001).

A multivariate forward–backward stepwise logistic regression was then applied to model the breeding distribution of the species (Fig. 2). The modelling process started from a null model assigning a constant breeding probability to each OGU based on overall species prevalence. In each forward step, the variable most strongly associated with breeding presence, as identified by Rao's score test, was added to the model. In subsequent steps, variables explaining the residual variation were incorporated iteratively. The backward procedure allowed for the removal of previously included variables if they ceased to contribute significantly to model performance, ensuring an optimal balance between explanatory power and model parsimony (Legendre and Legendre 1998).

The final model thus represents a simplified but ecologically meaningful combination of predictors explaining the observed breeding distribution of the Bearded Vulture. Model coefficients were estimated using a likelihood ascent gradient algorithm, and the relative contribution of each predictor was assessed using the Wald test (Wald 1943).

Because favourability explicitly accounts for species prevalence, the model is robust to spatial gaps in current breeding records and does not aim to reproduce the exact current distribution of breeding territories (Real et al. 2006; Marchetto et al. 2023). Instead, it identifies environmentally suitable areas across the landscape, providing an appropriate and unbiased foundation for subsequent connectivity and corridor analyses (Torres et al. 2017; Pulido-Pastor et al. 2021).

Corridor analysis

To identify potential ecological corridors, environmental favourability values were transformed into a cost surface representing movement resistance across the landscape. Movement cost was defined as the inverse of favourability:

$$COST = \frac{1}{FAVOURABILITY}$$

This transformation assigns low movement costs to environmentally favourable areas and higher costs to less favourable areas, reflecting reduced suitability for movement. Unlike binary habitat classifications, this approach allows for gradual transitions between low- and high-quality areas, providing greater flexibility in modelling movement through heterogeneous landscapes. Importantly, areas of low favourability are not treated as absolute barriers but as zones where movement is more energetically or ecologically costly. This assumption is particularly appropriate for a highly mobile soaring species such as the Bearded Vulture, which can traverse suboptimal areas but is expected to preferentially move through landscapes that maximize flight efficiency and resource availability.

This approach follows well-established principles in landscape connectivity modelling based on habitat quality or resistance surfaces (Adriaensen et al. 2003; Zeller et al. 2012; Torres et al. 2017; Pulido-Pastor et al. 2021). By using environmental favourability rather than simple

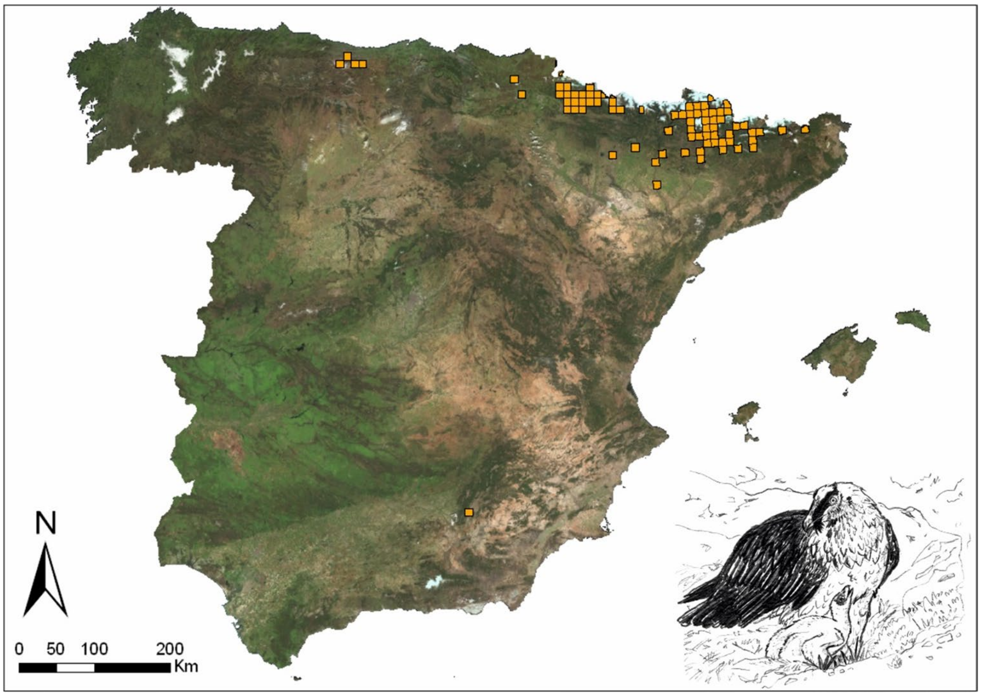

Fig. 2 Bearded Vulture breeding presences used for the model based on UTM 10 × 10 km grid cells of the study area (Margalida 2022; Fundación para la Conservación del Quebrantahuesos 2024)

habitat presence or absence, the cost surface integrates multiple ecological drivers of movement, including topography, food availability, land use, and human disturbance, all of which are known to influence Bearded Vulture mobility and spatial behaviour (Margalida et al. 2016; Vignali et al. 2021; Estrada et al. 2025).

Connectivity analyses were conducted entirely within the R environment (R Core Team 2024) to ensure methodological transparency and reproducibility. Raster processing was performed using the terra package (Hijmans et al. 2023), and movement modelling was implemented using the gdistance package (Van Etten 2017). The cost raster was used to build a transition matrix that quantified the ease of movement between adjacent grid cells based on cumulative movement cost. Least-cost paths and corridor surfaces were then calculated between core areas representing wild and reintroduced Bearded Vulture populations. Connectivity values were classified into four categories (low, medium, high, very high) based on quantiles. This classification was used to facilitate interpretation of spatial patterns and does not affect the underlying continuous connectivity values.

The resulting corridors represent areas of relatively low cumulative movement cost and highlight priority zones for maintaining or enhancing landscape connectivity between populations. These corridors are not interpreted as fixed routes but as probabilistic movement zones where environmental conditions are more favourable for dispersal. By basing the analysis on favourability-derived costs, the identified corridors reflect the ecological preferences of the species while allowing sufficient flexibility to account for occasional movement through less suitable areas.

Results

Environmental favourability model

The environmental favourability model (Fig. 3) shows areas with high potential for breeding presence across the Iberian Peninsula, forming the basis for subsequent connectivity analyses. The model for the breeding distribution of the Bearded Vulture included ten predictor variables: one

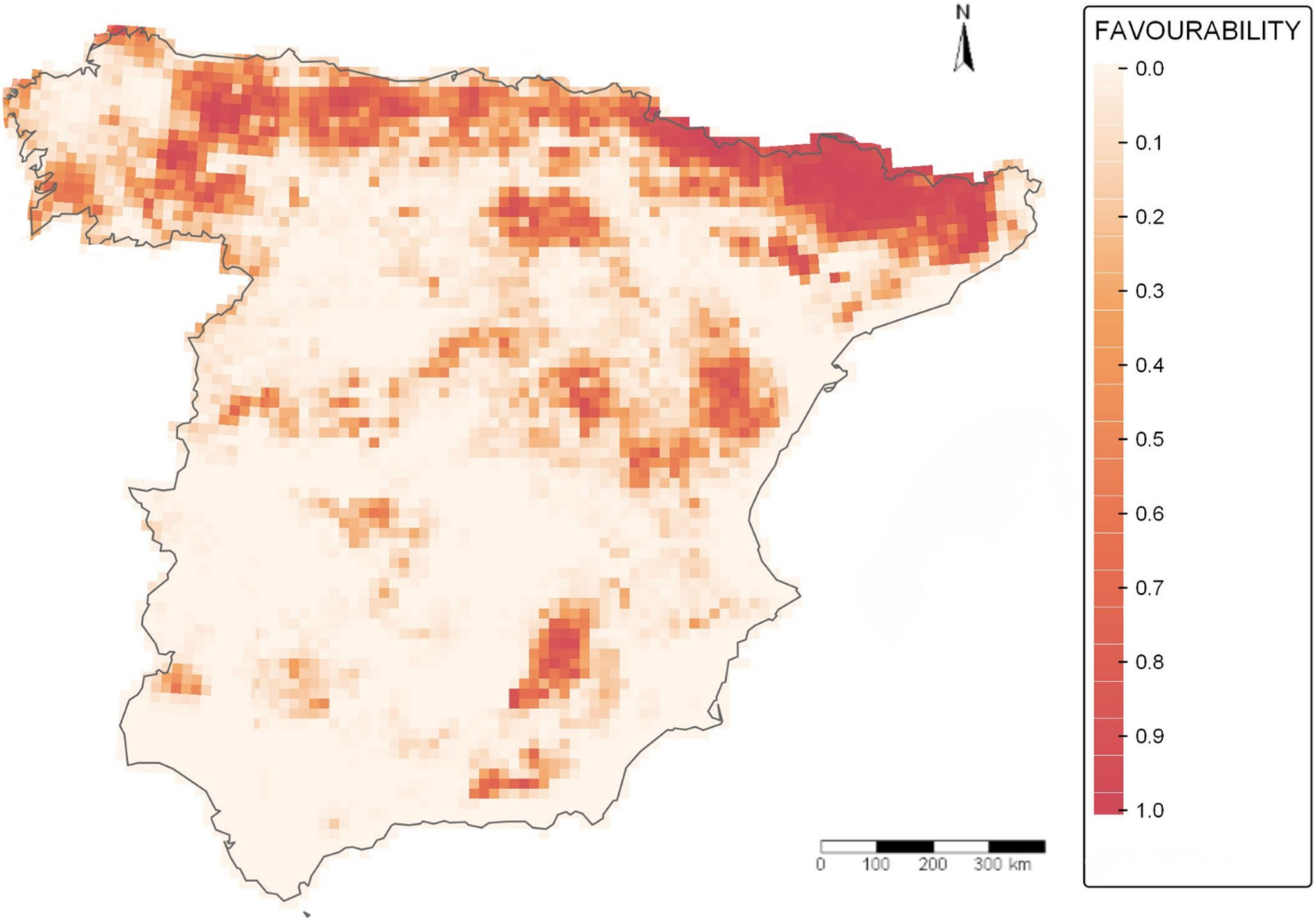

Fig. 3 Environmental favourability for Bearded Vulture (*Gypaetus barbatus*) breeding across mainland Spain. Favourability values were calculated using the favourability function (Real et al. 2006) applied to UTM 10 × 10 km grid cells. Values range from 0 (unfavourable conditions) to 1 (highly favourable conditions)

Table 1 Variables included in the logistic regression model via a forward–backward stepwise selection process, ranked by their order of addition. *β* are the coefficients in the logit function, SE is the standard error of these coefficients, Wald is the value of Wald's statistic, representing the relative importance of each variable in the model, and *p* is the significance of the coefficients according to the Wald test

Variable	β	S.E.	Wald	*p*
Favourability for the Iberian Wild Goat	2.204	0.557	15.614	<0.001
Mean number of days with precipitation ≥ 10 mm in spring	0.658	0.163	16.225	0.014
Mean number of days with precipitation ≥ 1 mm in winter	−0.257	0.031	67.099	<0.001
Mean number of days with precipitation ≥ 30 mm in autumn	0.689	0.285	5.854	0.016
Mean number of days with precipitation ≥ 30 mm in spring	−1.810	0.453	15.915	<0.001
Mean number of days with minimum temperature ≤ 0 °C in summer	−1.059	0.347	9.313	0.002
Mean annual number of days with minimum temperature ≥ 20 °C	−0.145	0.044	10.433	0.001
Distance to the nearest highway (km)	0.001	0.002	27.922	<0.001
Topographic Wetness Index	−2.294	0.319	51.853	<0.001
Irrigated crops	0.078	0.017	21.674	<0.001
Constant	35.835	5.528	42.026	<0.001

related to topography, six to climate, one to food availability, one to human activity, and one to land use (Table 1). Climatic variables accounted for a substantial proportion of the explanatory power of the model. In particular, the mean number of days with precipitation ≥ 1 mm in winter showed the highest contribution according to the Wald statistic.

Variables positively associated with breeding favourability included the favourability for Iberian wild goat (*Capra pyrenaica*), the mean number of days with precipitation ≥ 10 mm in spring, the mean number of days with precipitation ≥ 30 mm in autumn, distance to the nearest highway, and the presence of irrigated crops. In contrast, the mean number of days with precipitation ≥ 1 mm in winter, the mean number of days with precipitation ≥ 30 mm in spring, the mean number of days with minimum temperature ≤ 0 °C in summer, and the Topographic Wetness Index negatively influenced breeding favourability (Table 1).

The model showed excellent discrimination capacity (AUC = 0.963) and strong classification performance (Table 2). Sensitivity, specificity, and correct classification rate all exceeded 0.85, indicating a high ability to correctly identify both favourable and unfavourable operational geographic units (OGUs). The under-prediction rate was very low (UPR = 0.002), whereas the over-prediction rate was high (OPR = 0.827), reflecting the existence of extensive environmentally suitable areas that remain unoccupied.

Table 2 Assessment of the discrimination and classification capabilities of the favourability model. The indices evaluated include AUC, sensitivity, specificity, correct classification rate, over-prediction rate, under-prediction rate, and Cohen's Kappa index

Measure	Values
Area Under the Curve	0.963
Sensitivity	0.850
Specificity	0.937
Correct Classification Rate (CCR)	0.936
Over-prediction rate (OPR)	0.827
Under-prediction rate (UPR)	0.002
Cohen´s Kappa Index	0.268

Connectivity analysis

Environmental favourability values were transformed into a continuous cost surface by applying the inverse function (1/favourability), generating a gradient of movement resistance across the Iberian Peninsula. This cost surface reflects increasing ecological resistance in areas of lower favourability while allowing movement through all areas, rather than defining strict barriers.

The resulting connectivity map identified potential ecological corridors linking wild and reintroduced Bearded Vulture populations, including the Pyrenees, Picos de Europa, Maestrazgo, Sierra de Gredos and Sierra de Cazorla (Fig. 4). Areas of very high connectivity were primarily associated with mountain systems and regions characterized by favourable topography, food availability (ungulates), and lower human disturbance, forming continuous pathways between core population areas.

Corridor validation

The spatial analysis revealed that both Eva and Monica, two female Bearded Vultures (released in Picos de Europa in 2018 and originally from Pyrenees), exhibited significant movement between these regions during different seasons. These individuals were the only tracked vultures that performed inter-population movements between major mountain systems, whereas all other individuals remained within their respective home ranges and did not exhibit long-distance displacement.

- Eva made two round trips between Picos de Europa and the Pyrenees: one during the winter of 2022–2023 (*Supplementary Material*, Figure S1A) and another during the summer of 2022 (Supplementary Material, Figure S1B).

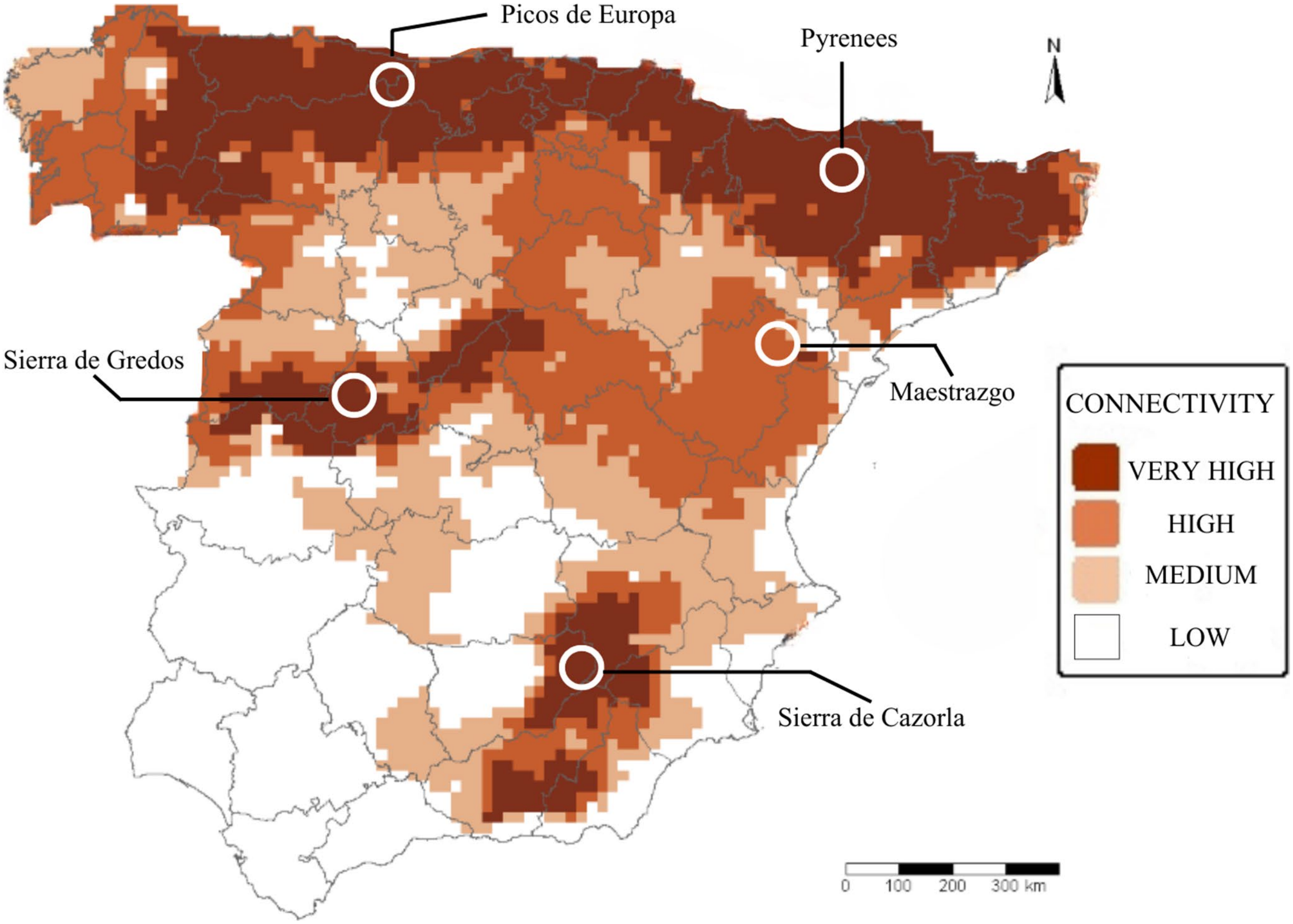

Fig. 4 Connectivity map for Bearded Vultures in Mainland Spain. Black lines represent administrative boundaries (provinces), while circles denote Bearded Vulture population centres

Table 3 Proportion of points classified into different connectivity categories for each individual (Eva (summer 2022), Eva (winter 2022-23), and Monica (spring 2023). The categories reflect the level of connectivity based on the corridor analysis, ranging from *Very High* to *Low*. Percentages indicate the distribution of GPS locations across these categories; N refers to the total number of GPS locations

ID	*N*	Very high	High	Medium	Low
Eva (2022)	7753	95.8%	4.2%	0%	0%
Eva (2023)	727	95.79%	4.21%	0%	0%
Monica (2023)	2863	95.40%	4.4%	0.2%	0%

– Monica also completed a round trip, traveling from Picos de Europa to the Pyrenees and back during the spring of 2023 (Supplementary Material,Figure S2). Unfortunately, this individual was found dead in France in 2024.

For both Bearded Vultures, movements occurred more frequently in grid cells with very high connectivity, avoiding territories of lower connectivity (Table 3; Fig. 5).

Discussion

The conservation of the Bearded Vulture in Spain faces complex challenges that require integrated approaches combining habitat suitability, landscape connectivity, and mitigation of human pressures (Margalida et al. 2013). Among these, maintaining and restoring ecological connectivity between isolated and reintroduced populations has been identified as a key priority, both at the scientific level and within current conservation policies.

In this context, the present study provides the first large-scale connectivity model for the Bearded Vulture in the Iberian Peninsula, addressing a critical knowledge gap. Notably, connectivity has been explicitly recognised as a strategic objective in the Spanish National Strategy for the Conservation of the Bearded Vulture (Ministry for the Ecological Transition and the Demographic Challenge 2025), highlighting the relevance and timeliness of our results for applied conservation planning.

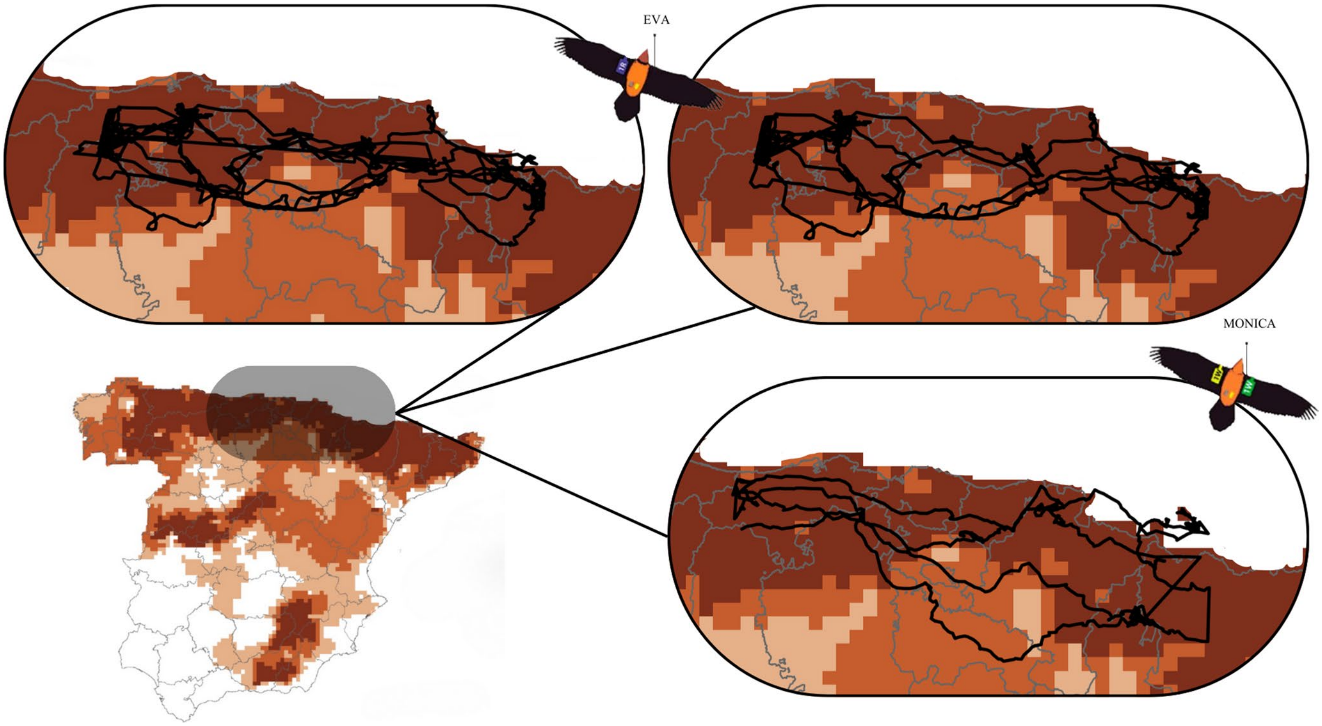

Fig. 5 Movement pattern of Eva and Monica during their travels between Picos de Europa and the Pyrenees and vice versa. Black lines represent movement paths, with stronger colour indicating better connectivity

Our corridor analysis using biogeographical methods reveals strong potential connectivity between several key population nuclei, particularly between Picos de Europa and the Pyrenees, but also between other key regions, particularly between Sierra de Gredos and Picos de Europa, as well as between Sierra de Cazorla and Gredos. These high-connectivity pathways may be critical for facilitating movement and genetic exchange between isolated populations. The corridor between Maestrazgo and nearby regions also exhibited strong connectivity, suggesting that these areas play a pivotal role in maintaining a functional network for the Bearded Vulture across the Iberian Peninsula. These results suggest the existence of a functional ecological network capable of facilitating dispersal and gene flow across the Iberian Peninsula, even in a species characterised by marked philopatry (López-López et al. 2013).

Validation using movement data

Importantly, the predicted corridors are not only theoretical outputs derived from biogeographical models, but are supported by empirical movement data. The long-distance movements performed by two reintroduced females (Eva and Monica) between Picos de Europa and the Pyrenees closely overlapped with areas classified as very high connectivity. Both individuals concentrated more than 95% of their GPS locations within the highest connectivity classes during these journeys, strongly supporting the ecological realism of the proposed corridors.

Although only a few individuals were used for validation, this reflects the inherent rarity of long-distance dispersal events in Bearded Vultures rather than a limitation of the dataset. Most tracked individuals exhibited resident behaviour within their home ranges and therefore do not provide information on functional connectivity between populations. Nevertheless, the observed agreement between independent movement data and the predicted corridors provides additional support for the plausibility of the proposed connectivity patterns. This convergence suggests that favourability-based connectivity modelling, when combined with telemetry data, can offer a useful framework for identifying potential movement pathways.

Ecological interpretation of corridors

The connectivity patterns identified are consistent with the ecological requirements of the species. By basing movement costs on environmental favourability, the corridors integrate multiple drivers of Bearded Vulture movement, including topography, food availability, climate, and human disturbance. Importantly, areas of low favourability are not treated as absolute barriers, but as zones of increased movement cost, allowing for realistic movement across heterogeneous landscapes (Torres et al. 2017). This approach is particularly appropriate for a highly mobile soaring species capable of traversing suboptimal areas when ecological conditions permit.

High-connectivity corridors frequently coincide with mountain systems characterised by extensive livestock farming, rugged terrain, and relatively low human disturbance, features known to favour Bearded Vultures (Donázar et al. 1993; Margalida et al. 2007a, b; Estrada et al. 2025). These corridors are therefore likely to represent not only movement pathways, but also areas of elevated conservation value more broadly. Overall, the strong agreement between independently observed dispersal movements and the predicted high-connectivity areas supports the ecological relevance of the model. While validation is necessarily limited to rare long-distance movements, these events represent the most informative processes for assessing functional connectivity at large spatial scales.

Conservation implications

The identification of priority connectivity zones has direct implications for conservation management. Protecting and managing these corridors should be a central component of future conservation actions (Crooks and Sanjayan 2006; Rudnick et al. 2012; Santangeli et al. 2019), ensuring that infrastructure development, tourism expansion, and land-use changes do not compromise landscape permeability for the species. Anthropogenic threats, particularly collisions with power lines, wind turbines, and other infrastructure, remain a major cause of mortality for Bearded Vultures (Margalida et al. 2008; Margalida 2016; Vignali et al. 2021). Mitigation measures should be prioritised within high-connectivity corridors, where dispersing individuals are most likely to concentrate their movements.

At the same time, extensive livestock farming remains a cornerstone of Bearded Vulture conservation (Estrada et al. 2025), providing a natural food source across mountain landscapes. Maintaining traditional grazing systems through appropriate economic incentives and agri-environmental policies will be essential for sustaining both habitat favourability and functional connectivity (Aguilera-Alcalá et al. 2022; Oliva-Vidal et al. 2022).

Policy relevance and future perspectives

By explicitly identifying priority corridors and validating them with real movement data, this study provides actionable information that can directly support the implementation of the Spanish National Strategy for the Conservation of the Bearded Vulture (Ministry for the Ecological Transition and the Demographic Challenge 2025). The results can inform Supplementary Feeding Stations (SFS) planning, environmental impact assessments, and the designation of areas where stricter protection or mitigation measures are required.

In conclusion, our findings show that the Iberian Peninsula retains a high potential for functional connectivity among Bearded Vulture populations. Strengthening and safeguarding this connectivity will be crucial for ensuring the long-term viability of both wild and reintroduced populations. Continued monitoring of dispersal movements, combined with adaptive corridor modelling, will further enhance the effectiveness of conservation strategies for this endangered vulture.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-026-02094-8.

Acknowledgements We would like to thank the reviewers for their work, which has greatly helped to improve this manuscript.

Author contributions I.N. Conceived the idea and design of the study, I.N., J.C.G. and J.A.G. Performed the experiments and collected data, I.N. Analyzed the data, I.N. Developed methods, I.N., A.R.M. and M.A.F. Wrote and edited the manuscript, J.C.G. and J.A.G. Contributed resources.

Funding Funding for open access publishing: Universidad de Málaga/CBUA. This research did not receive specific funding.

Data availability The data presented in this study are available in this article and from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

References

Acevedo P, Real R (2012) Favourability: concept, distinctive characteristics and potential usefulness. Naturwissenschaften 99:515–522. https://doi.org/10.1007/s00114-012-0926-0

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost'modelling as a functional landscape model. Landsc Urban Plann 64(4):233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Aemet IMP (2011) Atlas climático ibérico: Temperatura del aire y precipitación (1971–2000). Departamento de Producción de la Agencia Estatal de Meteorología de España - Departamento de Meteorologia e Clima. Instituto de Meteorologia de Portugal

Aguilera-Alcalá N, Arrondo E, Pascual-Rico R, Morales-Reyes Z, Gil-Sánchez JM, Donázar JA, Moleón M, Sánchez-Zapata JA (2022) The value of transhumance for biodiversity conservation: vulture foraging in relation to livestock movements. Ambio 51(5):1330–1342. https://doi.org/10.1007/s13280-021-01668-x

Allaoui I, Cherkaoui S (2018) New breeding record of Lammergeier (*Gypaetus barbatus barbatus*) in Morocco and proposals for its conservation. Go-South Bull 15:137–140

Arrondo E, Guido J, Oliva-Vidal P, Margalida A, Lambertucci S, Donázar JA, Anadón J, Cortés-Avizanda A, Sánchez-Zapata JA (2023) From Pyrenees to Andes: The relationship between transhumant livestock and vultures. Biol Conserv 283:110081. https://doi.org/10.1016/j.biocon.2023.110081

Barbosa AM, Real R, Muñoz AR, Brown JA (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers Distrib 19:1333–1338. https://doi.org/10.1111/ddi.12100

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J Roy Stat Soc: Ser B (Methodol) 57:289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency. Ann of stat 1165–1188. https://doi.org/10.1214/aos/1013699998

Carrete M, Donázar JA, Margalida A (2006a) Density-dependent productivity depression in pyrenean bearded vultures: implications for conservation. Ecol Appl 16(5):1674–1682

Carrete M, Donázar JA, Margalida A, Bertran J (2006b) Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? Biol Lett 2(4):624–627

Cohen J (1960) A coefficient of agreement for nominal scales. Educational Psychol Measurementy 20:37–46. https://doi.org/10.1177/001316446002000104

Corine Land Cover (2018) Copernicus Land Monitoring Service. https://land.copernicus.eu/en/products/corine-land-cover

Crooks KR, Sanjayan M (eds) (2006) Connectivity conservation, vol 14. Cambridge University Press

Del Moral JC (2022) Buitre negro *Aegypius monachus.* En, B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante y J. C. del Moral: *III Atlas de las aves en época de reproducción en España*. SEO/BirdLife. Madrid. https://atlasaves.seo.org/ave/buitre-negro/

DERA (2013) Datos espaciales de referencia de Andalucía. – Instituto de Estadística y Cartografía de Andalucía. Consejería de Economía y Conocimiento

Donázar JA, Hiraldo F, Bustamante J (1993) Factors influencing nest site selection, breeding density and breeding success in the bearded vulture (*Gypaetus barbatus*). J Appl Ecol. https://doi.org/10.2307/2404190

ESRI (2016) ArcGIS [software GIS], version 10.4.1. https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources

Estrada A, Martínez-Padilla J, Martínez JM, Anadón JD, de la Cruz L, Vicente-Serrano SM, Margalida A (2025) Linking favourability models with breeding output: a modelling approach to improve management and conservation actions for a threatened avian scavenger. Biol Conserv 307:111165

Farr TG, Kobrick M (2000) Shuttle radar topography mission produces a wealth of data. Eos Trans Am Geophys Union 81(48):583–585. https://doi.org/10.1029/EO081i048p00583

Ferguson-Lees J, Christie DA (2001) Raptors of the World. Christopher Helm, London

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49. https://doi.org/10.1017/S0376892997000088

Fundación para la Conservación del Quebrantahuesos (2024) Seguimiento de ejemplares. https://quebrantahuesos.org/seguimiento-de-ejemplares-vivos-list/

García LV (2003) Controlling the false discovery rate in ecological research. Trends Ecol Evol 18:553–554. https://doi.org/10.1016/j.tree.2003.08.011

García-Jiménez R, Pérez-García JM, Margalida A (2018) Drivers of daily movement patterns affecting an endangered vulture flight activity. BMC Ecol 18(1):39

García-Jiménez R, Margalida A, Pérez-García JM (2020) Influence of individual biological traits on GPS fix-loss errors in wild bird tracking. Sci Rep 10(1):19621

García-Ruiz JM, Lasanta-Martínez T (1993) Land-use conflicts as a result of land-use change in the Central Spanish Pyrenees: a review. Mount Res Dev. https://doi.org/10.2307/3673658

GBIF.org (2025) GBIF Occurrence. https://doi.org/10.15468/dl.vr23xm

Gil JA, Báguena G, Sánchez-Castilla E, Antor RJ, Alcántara M, López-López P (2014) Home ranges and movements of non-breeding Bearded Vultures tracked by satellite telemetry in the Pyrenees. Ardeola 61(2):379–387. https://doi.org/10.13157/arla.61.2.2014.379

Hijmans RJ, Bivand R, Dyba K, Pebesma E, Sumner MD (2023), November *Terra [R Package]*

Hiraldo F, Delibes M, Calderón J (1979) El quebrantahuesos (*Gypaetus barbatus*) (L.). Sistemática, taxonomía, biología, distribución y protección. Monografías 22, Ministerio de Agricultura, ICONA 114–121

IGME (2015) Mapa Geológico de la Península Ibérica, Baleares y Canarias a Escala 1/1.000.000. – Instituto Geológico y Minero de España (IGME), Laboratorio Nacional Portugués de Energía y Geología. LNEG)/Ministerio de Ciencia, Innovación y Universidades

INE (2025) *Censo agrario*. Instituto Nacional de Estadística. https://www.ine.es/jaxi/Tabla.htm?tpx=5207

Legendre P, Legendre L (1998) Numerical ecology (2nd English edition). Elsevier Science, Amsterdam, The Netherlands

Lobo JM, Jiménez-Valverde A, Real R (2008) Auc: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x

López-López P, Zuberogoitia Í, Alcántara M, Gil JA (2013) Philopatry, natal dispersal, first settlement and age of first breeding of Bearded Vultures *Gypaetus barbatus* in central Pyrenees. Bird Study 60(4):555–560. https://doi.org/10.1080/00063657.2013.842537

López-Ramírez S, Real R, Muñoz AR (2024) The northern wheatear is reducing its distribution in its southernmost European range and moving to higher altitudes. J Avian Biol 2024:e03217. https://doi.org/10.1111/jav.03217

Marchetto E, Da Re D, Tordoni E, Bazzichetto M, Zannini P, Celebrin S, Rocchini D (2023) Testing the effect of sample prevalence and sampling methods on probability-and favourability-based SDMs. Ecol Modell 477:110248

Margalida A (2008) Bearded vultures (*Gypaetus barbatus*) prefer fatty bones. Behav Ecol Sociobiol 63:187–193. https://doi.org/10.1007/s00265-008-0649-6

Margalida A (2016) Quebrantahuesos–*Gypaetus barbatus* (Linnaeus, 1758)

Margalida A (2022) Quebrantahuesos Gypaetus barbatus. In, B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante y J. C. del Moral: III Atlas de las aves en época de reproducción en España. SEO/BirdLife. Madrid. https://atlasaves.seo.org/ave/quebrantahuesos/

Margalida A, Bertran J (2000) Breeding behaviour of the bearded vulture (*Gypaetus barbatus*): minimal sexual differences in parental activities. Ibis 142(2):225–234

Margalida A, Martínez JM (2020) El Quebrantahuesos en España: Población reproductora en 2018 y método de censo. Instituto de Investigación de Recursos Cinegéticos (CSIC-UCLM-JCCM), Ciudad Real

Margalida A, García D, Cortés-Avizanda A (2007a) Factors influencing the breeding density of bearded vultures, Egyptian vultures and Eurasian griffon vultures in Catalonia (NE Spain): management implications. Anim Biodivers Conserv 30(2):189–200

Margalida A, Mañosa S, Bertran J, García D (2007b) Biases in studying the diet of the bearded vulture. J Wildl Manag 71(5):1621–1625

Margalida A, Heredia R, Razin M, Hernández M (2008) Sources of variation in mortality of the bearded vulture *Gypaetus barbatus* in Europe. Bird Conserv Int 18:1–10

Margalida A, Bertran J, Heredia R (2009) Diet and food preferences of the endangered bearded vulture *Gypaetus barbatus*: a basis for their conservation. Ibis 151:235–243. https://doi.org/10.1111/j.1474-919X.2008.00904.x

Margalida A, Carrete M, Hegglin D, Serrano D, Arenas R, Donazar JA (2013) Uneven large-scale movement patterns in wild and reintroduced pre-adult bearded vultures: conservation implications. PLoS One 8(6):e65857. https://doi.org/10.1371/journal.pone.0065857

Margalida A, Pérez-García JM, Afonso I, Moreno-Opo R (2016) Spatial and temporal movements in Pyrenean Bearded Vultures (*Gypaetus barbatus*): integrating movement ecology into conservation practice. Sci Rep 6(1):35746. https://doi.org/10.1038/srep35746

Margalida A, Pérez-García JM, Moreno-Opo R (2017) European policies on livestock carcasses management did not modify the foraging behavior of a threatened vulture. Ecol Ind 80:66–73

Margalida A, Oliva-Vidal P, Llamas A, Colomer MA (2018) Bioinspired models for assessing the importance of transboundaring management and transhumance in the conservation of avian scavengers. Biol Conserv 228:321–330. https://doi.org/10.1016/j.biocon.2018.11.004

Margalida A, Jiménez J, Martínez JM, Sesé JA, García-Ferré D, Llamas A, Razin M, Colomer M, Arroyo B (2020) An assessment of population size and demographic drivers of the Bearded Vulture using integrated population models. Ecol Monogr 90(3):e01414. https://doi.org/10.1002/ecm.1414

Ministry for the Ecological Transition and the Demographic Challenge (2025) National strategy for the conservation of the bearded vulture (*Gypaetus barbatus*) in Spain and Portugal. https://www.miteco.gob.es/es/biodiversidad/publicaciones/pbl-fauna-flora-estrategias-quebrantahuesos.html

Moreno-Opo R, Trujillano A, Margalida A (2015) Optimization of supplementary feeding programs for European vultures depend on environmental and management factors. Ecosphere 6:127

Muñoz E, Martín D, Tenza A, Casasús I, Bernués A, Villalba D (2021) Exploración preliminar del impacto del cambio climático sobre los sistemas ganaderos de montaña en el Pirineo aragonés, vol 11. XIX Jornadas sobre Producción Animal, p AIDA

Oliva-Vidal P, Sebastián-González E, Margalida A (2022) Scavenging in changing

ORNL (2001) LandScan 2000 global population database. Oak Ridge National Laboratory (ORNL), Oak Ridge, Tennessee

Orta J, de Juana E, Marks JS, Sharpe CJ, García EF (eds) (2020) Bearded Vulture (*Gypaetus barbatus*). Birds of the World. Cornell Lab of Ornithology, New Yor

Pătru-Stupariu I, Hossu CA, Grădinaru SR, Nita A, Stupariu MS, Huzui-Stoiculescu A, Gavrilidis AA (2020) A review of changes in mountain land use and ecosystem services: from theory to practice. Land 9(9):336. https://doi.org/10.3390/land9090336

Pulido-Pastor A, Márquez AL, Guerrero JC, García-Barros E, Real R (2021) Metapopulation patterns of Iberian butterflies revealed by fuzzy logic. Insects 12(5):392. https://doi.org/10.3390/insects12050392

R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Real R, Barbosa AM, Vargas JM (2006) Obtaining environmental favourability functions from logistic regression. Environ Ecol Stat 13:237–245. https://doi.org/10.1007/s10651-005-0003-3

Reiné RJ (2017) ¿Por qué investigar los pastos del Pirineo aragonés? Lucas Mallada: revista de ciencias 19:9–22

Rudnick D, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps C, Trombulack SC (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology

Santangeli A, Girardello M, Buechley E, Botha A, Minin ED, Moilanen A (2019) Priority areas for conservation of Old World vultures. Conserv Biol 33(5):1056–1065. https://doi.org/10.1111/cobi.13282

Schaub M, Loercher F, Hegglin D, Arlettaz R (2024) Demographic assessment of reintroduced Bearded Vultures in the Alps: success in the core, challenges in the periphery. Ecological Solutions and Evidence 5(2):e12347. https://doi.org/10.1002/2688-8319.12347

Silva R, Afán I, Gil JA, Bustamante J (2017) Seasonal and circadian biases in bird tracking with solar GPS-tags. PLoS One 12(10):e0185344

Tomkiewicz SM, Fuller MR, Kie JG, Bates KK (2010) Global positioning system and associated technologies in animal behaviour and ecological research. Philos Trans R Soc Lond B Biol Sci 365(1550):2163–2176. https://doi.org/10.1098/rstb.2010.0090

Torres RT, Carvalho J, Serrano E, Helmer W, Acevedo P, Fonseca C (2017) Favourableness and connectivity of a Western Iberian landscape for the reintroduction of the iconic Iberian ibex *Capra pyrenaica*. Oryx 51(4):709–717. https://doi.org/10.1017/S003060531600065X

Tréhin C, Duriez O, Sarrazin F, Betton B, Fonderflick J, Lörcher F, Marlé E, Seguin JF, Traversier J, Ziletti N, Mihoub JB (2024) Long-distance post-release movements challenge the metapopulation restoration of Bearded Vultures. Ecosphere 15(8):e4856. https://doi.org/10.1002/ecs2.4856

Van Etten J (2017) R package gdistance: distances and routes on geographical grids. J Stat Softw 76:1–21

Vignali S (2021) Predicting areas of potential conflicts between bearded vultures (*Gypaetus barbatus*) and wind turbines in the Swiss Alps. Doctoral Dissertation, University of Bern

Vignali S, Lörcher F, Hegglin D, Arlettaz R, Braunisch V (2021) Modelling the habitat selection of the Bearded Vulture to predict areas of potential conflict with wind energy development in the Swiss Alps. Glob Ecol Conserv 25:e01405. https://doi.org/10.1016/j.gecco.2020.e01405

Wald A (1943) Tests of statistical hypotheses concerning several parameters when the number of observations is large. Trans Am Math Soc 54:426–482

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797. https://doi.org/10.1007/s10980-012-9737-0