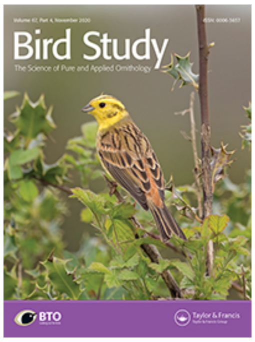

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# Ecological correlates of Golden Eagle *Aquila chrysaetos* breeding occurrence in Sardinia

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**ABSTRACT**

**Capsule:** Golden Eagles *Aquila chrysaetos* in Sardinia are clustered across the main mountain ranges of the island, with a preference for undisturbed and homogeneous inland habitats.

**Aims:** To analyse habitat preferences of the Golden Eagle in Sardinia, Italy, at the landscape and home range spatial scales.

**Methods:** Landscape scale habitat preferences were analysed using the 10 × 10 km Universal Transverse Mercator grid and the home range scale was based on the spatial distribution of breeding territories. Generalized linear models were fitted with three different sets of environmental predictors (topographic, bioclimatic and land use variables) to analyse the spatial distribution of Golden Eagles with a case–control design.

**Results:** Eagles showed a preference for rugged and elevated areas, characterized by a certain degree of humidity and surrounded by areas of forest. The distribution of Golden Eagles on this Mediterranean island was negatively affected by the occurrence of arable farmland and coastal areas, as well as by the effects of habitat fragmentation.

**Conclusions:** The results of this study could contribute to future management strategies and conservation projects aimed to protect this species, and may be used to identify the most suitable conservation areas for this and other competing species, such as the Bonelli's Eagle *Aquila fasciata*, which is currently the subject of a reintroduction project in Sardinia.

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The study of the relationship between the geographic distribution of a given species and the main features of its environment (e.g. topographic, landscape and climatic factors) is often quantified using predictive modelling (Guisan & Zimmermann 2000) and is essential to guide appropriate conservation decisions (Larson *et al.* 2004, Nams *et al.* 2006). In recent decades, species distribution modelling has been commonly used to identify suitable habitat and to predict a potential distribution of target taxa (Robertson *et al.* 2003, Rushton *et al.* 2004, Matyukhina *et al.* 2015), with particular emphasis on threatened species (Guisan & Zimmermann 2000).

The Golden Eagle *Aquila chrysaetos* is a raptor with a wide Holarctic distribution, that inhabits a large variety of habitats, especially mountain systems and uplands (Del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001). Although the species suffered heavy persecution in the nineteenth century, its populations now appear stable throughout Europe and the species is listed as 'Least Concern' by the International Union for Conservation of Nature (BirdLife International 2017).

The Golden Eagle population in Italy currently consists of at least 622 breeding pairs (Fasce & Fasce 2017). Although it shows a positive trend across the Italian peninsula (Brichetti & Fracasso 2003, Fasce & Fasce 2017), the species is listed as 'Near Threatened' on the Italian Red List (Rondinini *et al.* 2013). The Sardinian population has also increased, from an estimated population of 25–38 pairs in the 1970s (Schenk 1976) to

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40–50 pairs in the 1990s and 2000s (Schenk 1995, Asuni *et al.* 2003, Fasce & Fasce 2003), and is currently estimated at 57–70 breeding pairs (Ruiu 2017, Fasce & Fasce 2017, Sirigu *et al.* 2019). In Sardinia, unlike other Mediterranean populations, the Golden Eagle is demographically isolated and immigration from continental populations appears to be scarce and unlikely (authors' personal observations). Thus, knowledge of its ecological requirements at local level is essential for its conservation and useful to support the management of isolated populations in similar environments in other regions across the wide range of the species.

The aim of this paper is to analyse the habitat preferences of the Golden Eagle in Sardinia, with emphasis on investigating the environmental features that favour this important island population. Furthermore, the Golden Eagle is a potential competitor of the Bonelli's Eagle *Aquila fasciata* (Gil-Sánchez *et al.* 1994, 1996, Del Hoyo *et al.* 1994, Carrete *et al.* 2001, 2002, 2005, López-López *et al.* 2004, Martí & del Moral 2003, Real 2004, Martínez *et al.* 2007). Bonelli's Eagle disappeared from Sardinia at the end of the twentieth century, most likely due to illegal taking for the black market and direct persecution (Raganella-Pelliccioni *et al.* 2018). The results of this study may also be important to evaluate the potential niche segregation between these two species, which could be of particular interest for the reintroduction project of Bonelli's Eagle currently underway in Sardinia (AQUILA a-LIFE, LIFE16 NAT/ES/000235).

## Methods

A total of 56 breeding territories regularly occupied in 2019 by Golden Eagles was analysed, by using a case–control design (Hosmer & Lemeshow 2000, Keating & Cherry 2004) at two spatial scales: (i) Landscape scale, (10 × 10 km, Universal Transverse Mercator (UTM) cells where the species was present or absent); and (ii) Home range scale, based on the spatial distribution of breeding territories, in 5 km radius plots centred at nesting sites. This measure is a conservative but reliable approximation of the core home range of Golden Eagles (Sergio *et al.* 2006, Haworth *et al.* 2010), particularly taking into account the movements of breeding Golden Eagles tracked by telemetry in Mediterranean areas (López-López, P. unpublished data).

### *Measurement of habitat variables at the landscape scale*

For this analysis, we considered as occupied the 118 cells (UTM 10 × 10 km squares) intersecting the plots of 5 km radius centred on the 56 Golden Eagle nesting sites occupied by the species. The remaining 193 cells encompassing Sardinia territory were considered as unoccupied (*N* total = 311) (Figure 1). Both occupied and unoccupied cells were sampled to record information on 18 environmental variables using Geographic Information System (GIS) software (Table 1). The variables were related to topography, land use and bioclimate. Land use variables were obtained from the CORINE Land cover map (https://land.copernicus.eu/pan-european/corine-land-cover/clc2018) at 1:25000 scale. At this scale, CORINE Land cover classes (CLCs) have been considered at the first CORINE hierarchic level (EEA 2000). Topographic variables were obtained

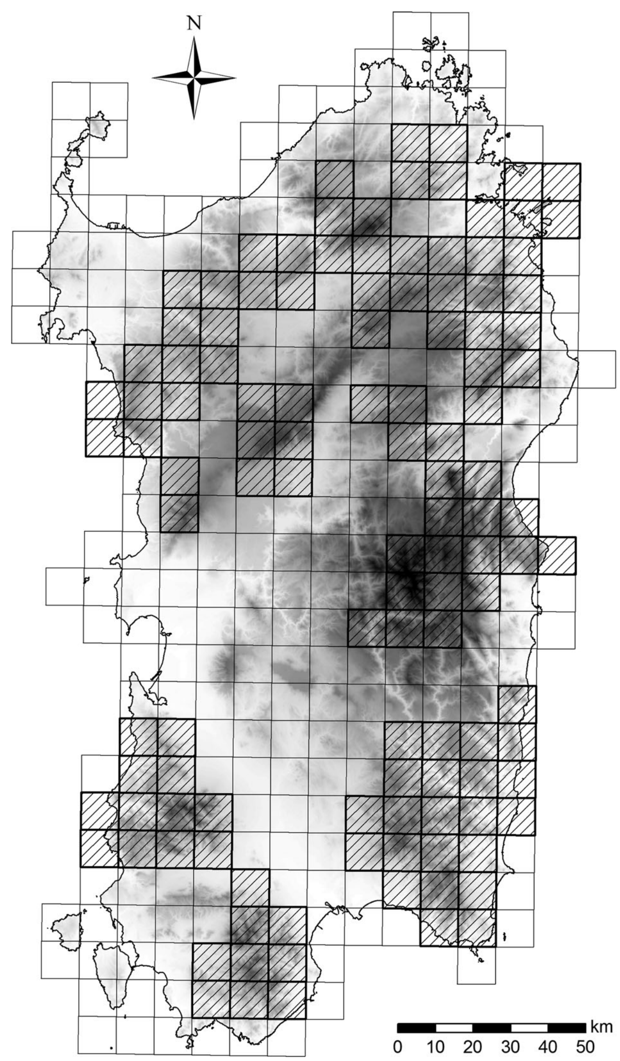


Figure 1. Distribution of the Golden Eagle in Sardinia, Italy, with the overlapping grid of Universal Transverse Mercator (UTM) 10 × 10 km squares. Occupied cells are shaded with dashed lines. Background: Digital Elevation Model at 25-m horizontal resolution (source: Copernicus European Environment Agency; https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1/view).

from a digital elevation model (DEM) with 10 m pixels of horizontal and vertical resolution. The bioclimatic ombrotype was obtained from the Annual Ombrothermic Index ($I_o$) (Canu *et al.* 2015). This index shows the average annual availability of water for plants by including the reduction in rainfall efficiency with increasing temperatures in its formula:

$$I_o = (P_p/T_p),$$

where $P_p$ is the total rainfall (mm) of all months with positive average temperature and $T_p$ is the sum of the monthly average temperature (°C) of all months with positive average temperature (Mesquita & Sousa 2009).

### Measurement of habitat variables at the home range scale

Nest sites and a subset of an equal number of randomly selected unoccupied points were geo-referenced on a GIS digital map. Circular plots with a radius equal to 5 km were then drawn around nest sites and unoccupied points to determine the minimum utilized home range (Sarà & Di Vittorio 2003). Then, both occupied ($n = 56$) and control ($n = 56$) points were independently sampled to collect information on 23 variables using GIS software. Environmental predictors included land use and other variables describing habitat composition (Table 1). At this scale, CLCs were used according to the second hierarchical level (EEA 2000) except for artificial areas and inland waters, which were considered at the first level. The count, perimeter, surface and CLC of singles patches of all plots were obtained from the same digital map. The mosaic patterns were redrawn following Forman (1995) using the numbers, perimeters, surfaces and boundaries of patches of CLCs defined in Table 1.

**Table 1.** Explanatory variables used to characterize the habitat preferences of Golden Eagles at landscape and home range scales in Sardinia. The corresponding CORINE Land cover class code at two levels is shown in brackets.

| Scale | Variables | |
|---|---|---|
| **Landscape** | **Topographic** | |
| | **Asl u** | Higher altitude |
| | **Asl m** | Mean altitude above sea level |
| | **Asl r** | Range of altitude (min-max) |
| | **Slo U** | Higher slope |
| | **Slo m** | Average slope |
| | **Slo r** | Range of slope (min-max) |
| | **Land use** | |
| | **Art** | Artificial (1) |
| | **Agr** | Agricultural (2) |
| | **For** | Forest and semi-natural areas (3) |
| | **Wet** | Wetlands and water bodies (4–5) |
| | **Ses** | Sea surface |
| | **(Bioclimatic) Ombrotypes** | |
| | **LD** | Lower Dry |
| | **UD** | Upper Dry |
| | **LSH** | Lower Sub-humid |
| | **USH** | Upper sub-humid |
| | **LH** | Lower humid |
| | **UH** | Upper humid |
| | **LHH** | Lower Hyper-humid |
| **Home range** | **Topographic** | |
| | **Asl u** | Higher altitude |
| | **Asl m** | Mean altitude above sea level |
| | **Asl r** | Range of altitude (min-max) |
| | **Slo U** | Higher slope |
| | **Slo m** | Average slope |
| | **Slo r** | Range of slope (min-max) |
| | **Land use** | |
| | **Art** | Artificial and infrastructures (11, 12, 13, 14) |
| | **Ara** | Arable land (21) |
| | **Per** | Permanent crops (22) |
| | **Pas** | Pastures (23) |
| | **Het** | Heterogeneous agricultural areas (24) |
| | **For** | Forests (31) |
| | **Shru** | Shrubs and/or herbaceous vegetation associations (32) |
| | **Ope** | Open spaces with little or no vegetation (33) |
| | **Wet** | Wetlands and Water bodies (41, 42, 51) |
| | **Sea** | Sea surface |
| | **Mosaic** | |
| | **s** | Number of different Land cover classes |
| | **NPA** | Number of habitat patches of any cover type |
| | **R** | Relative CLC richness = (s/smax) × 100 |
| | **LPA** | Surface of the largest patch/territory surface (x/5000 ha) |
| | **H′** | CLC Diversity = –Σ pi log pi |
| | **Do** | CLC dominance = log s + H′ |
| | **D** | Mean fractal dimension = (logP/logA) |

### Statistical analysis

In order to assess differences between habitat characteristics of Golden Eagle occupied and unoccupied cells at both landscape and home range scales, we compared the mean values of variables using univariate Mann–Whitney tests. To account for the effect of multiple comparisons we computed corrected *P*-values using the Benjamini–Hochberg multiple comparisons procedure for controlling the false discovery rate (Benjamini & Hochberg 1995). In addition, we also computed statistics of effect size and 95% confidence intervals for the Mann–Whitney tests, which, unlike *P*-values, are not affected by sample size.

We then fitted generalized linear models (GLMs) to model habitat features characterizing breeding sites of Golden Eagles. The dependent binomial variable (presence/absence of the species) was coded as 1/0 and, therefore, a logit-link function and a binomial distribution of error structure were used (McCullagh & Nelder 1989). Firstly, we ran a stepwise forward regression procedure to test the statistical significance of each variable in turn. This method has already been used to rank habitat preferences of raptors and to obtain predictive distribution models for conservation (Hosmer & Lemeshow 2000, López-López *et al.* 2006, 2007a, 2007b). In the regression procedure, we used every subset of variables described in Table 1 as independent predictors. Variables were excluded from each subset when they did not correlate significantly with the presence of Golden Eagles (Wald test $P >$ 0.05; Di Vittorio *et al.* 2012, 2014). We avoided performing a global model including all subsets because the introduction of such a large number of predictors could cause over-parameterization and over-fitting problems (Balbontín 2005, López-López *et al.* 2007a, Di Vittorio & López-López 2014). Environmental variables were standardized to eliminate the effect of differences in the original scale of measurement.

To prevent the bias in model parameters estimation due to spatial autocorrelation (Legendre & Legendre 1998), we corrected the models by including a spatial term using a third-degree polynomial equation of the central latitude ($x$) and longitude ($y$) of each cell as follows (Borcard & Legendre 2002):

$$b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$$

Then, to eliminate the non-significant spatial terms (Legendre & Legendre 1998), we ran a preliminary stepwise forward regression with the nine terms of the equation as predictor variables and the presence/absence of Golden Eagles as dependent variables. Subsequently, the significant spatial terms ($P < 0.05$) were included with other variables (i.e. topographic, land use and bioclimatic or mosaic) in each model to test if these accounted for a significant change in deviance. Finally, after running independent logistic regression models corrected for spatial autocorrelation, we built three additional models at each scale including only significant variables obtained in previous analyses by running the best subset regression option. At every subset of each scale, we selected the best model ranked by Akaike's information criterion corrected for small sample sizes (AICc; Akaike 1973, Burnham & Anderson 2002). To facilitate the interpretation of results, we plotted the predicted probability of each of the best models for each subset of environmental predictor at both scales (landscape and home range). Finally, we also tested the spatial distribution pattern of territories in Sardinia by means of the Moran's test for spatial autocorrelation (Moran 1950). Statistical significance was set in all analyses at $P < 0.05$, which were run in R (R Core Team 2020).

## Results

### Landscape scale

According to univariate tests, all variables except wetlands and water bodies (Wet), Lower- Hyper-humid (LHH) and Upper Dry Ombrotype (UD) showed significant differences between occupied and unoccupied UTM squares (Table 2). The highest effect sizes were observed for forest (For), higher altitude (Asl u) and range of altitude (Asl r), illustrating the preference of Golden Eagles for forest habitats at higher elevation above sea level (Table 2).

At the landscape scale, the GLMs results showed that the probability of occurrence of Golden Eagles increased with longitude ((Table 3). Regarding the topographic subset, the occurrence of Golden Eagles was positively correlated with slope (mean and range) and with the highest elevation above sea level, and negatively correlated with mean elevation (Table 3). In terms of land use, the probability of eagle occupation increased with the increase in forested areas. Regarding the bioclimatic subset, the distribution of Golden Eagles in Sardinia was significantly correlated with territories characterized by a moderate degree of humidity, in particular with the sub-humid ombrothermic profiles typical of the mountainous and elevated areas of the region (Canu *et al.* 2015). The relationship between the predicted probability of occurrence of the species and each set of environmental predictors showed a combination of linear and non-linear shapes, evidencing complex relationships between the presence of eagles and environmental characteristics (Figure 2).

### Home range scale

Moran's test for spatial autocorrelation showed that the distribution pattern of Golden Eagle territories in Sardinia was significantly clustered (Moran's Index = 0.35, $z$-score = 12.78, $P = 0.01$). At this scale, univariate tests comparing occupied territories and circular plots used as control showed significant differences in topographic variables, land use variables except for infrastructures (Art), permanent crops (Per), heterogeneous agricultural areas (Het), and wetlands (Wet), and all mosaic predictors (Table 4). The effect size was high for topographic predictors, moderate for forests (For), shrublands (Shru) and open spaces with little or no vegetation (Ope). The highest negative effect size was observed for arable farmland (Ara) (Table 4).

The GLMs results showed a complex effect of longitude on the distribution of the Golden Eagle at

**Table 2.** Comparisons of environmental predictor values (mean and standard deviation) in cells occupied (presence) and unoccupied (absence) by the Golden Eagle in Sardinia. Land use surface expressed in hectares. See variables abbreviations in Table 1. Abbreviations: BH = Benjamini & Hochberg method (1995).

| | | Occupied | | Unoccupied | | | | Effect size | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Group | Variable | Mean | sd | Mean | sd | W | *P* | r | Lower 95%CI | Upper 95% CI | *P*-corrected BH |
| Topographic | Asl u | 849.42 | 297.09 | 469.87 | 329.80 | 4502 | 0.000 | 0.508 | 0.424 | 0.584 | 0.000 |
| | Asl m | 398.33 | 240.05 | 205.42 | 212.29 | 5448 | 0.000 | 0.438 | 0.349 | 0.524 | 0.000 |
| | Asl r | 726.92 | 221.33 | 401.81 | 260.69 | 3926 | 0.000 | 0.550 | 0.471 | 0.624 | 0.000 |
| | Slo U | 69.12 | 7.66 | 57.91 | 13.98 | 5410 | 0.000 | 0.441 | 0.347 | 0.522 | 0.000 |
| | Slo m | 15.26 | 5.68 | 8.83 | 5.80 | 4650 | 0.000 | 0.497 | 0.411 | 0.573 | 0.000 |
| | Slo r | 69.12 | 7.66 | 57.89 | 13.97 | 5393 | 0.000 | 0.442 | 0.356 | 0.523 | 0.000 |
| Land use | Art | 175.75 | 281.03 | 268.81 | 439.25 | 13832 | 0.001 | −0.180 | −0.284 | −0.072 | 0.002 |
| | Agr | 2883.50 | 2367.34 | 4021.17 | 3156.27 | 13471 | 0.007 | −0.154 | −0.261 | −0.051 | 0.009 |
| | For | 5915.98 | 2736.45 | 2550.06 | 2303.79 | 4059 | 0.000 | 0.540 | 0.456 | 0.618 | 0.000 |
| | Wet | 45.99 | 140.18 | 122.03 | 374.64 | 12441 | 0.103 | −0.092 | −0.198 | 0.019 | 0.109 |
| | Ses | 978.77 | 2420.77 | 3037.93 | 3929.49 | 14793 | 0.000 | −0.285 | −0.382 | −0.194 | 0.000 |
| Bioclimatic | LD | 362.01 | 924.00 | 1333.45 | 2647.99 | 13498 | 0.003 | −0.169 | −0.274 | −0.063 | 0.004 |
| | UD | 3193.52 | 2658.71 | 3304.64 | 3185.32 | 11303 | 0.914 | 0.006 | −0.095 | 0.119 | 0.914 |
| | LSH | 3411.20 | 2538.48 | 1626.85 | 2452.48 | 5797 | 0.000 | 0.416 | 0.321 | 0.502 | 0.000 |
| | USH | 1332.10 | 1820.69 | 597.32 | 1544.54 | 6125 | 0.000 | 0.420 | 0.319 | 0.524 | 0.000 |
| | LH | 683.99 | 1742.59 | 113.49 | 594.33 | 8006 | 0.000 | 0.339 | 0.221 | 0.448 | 0.000 |
| | UH | 46.13 | 311.38 | 0.54 | 7.05 | 10826 | 0.012 | 0.142 | 0.023 | 0.238 | 0.014 |
| | LHH | 1.94 | 19.29 | 0.00 | 0.00 | 11194 | 0.071 | 0.103 | 0.067 | 0.168 | 0.079 |

the home range scale, with the probability of occurrence increasing moderately from west to east (Table 5). Moreover, the probability of a territory being occupied increased with increasing altitude above sea level and slope, and was negatively correlated with arable land extension (poorly represented in the areas occupied by the species and distributed in non-suitable areas) and with the proximity to the coastline (Table 5). Finally, the distribution of the Golden Eagle was negatively correlated with the fractal dimension which measures the degree of shape complexity, which is a good proxy of habitat fragmentation (Rutledge 2003). Similar to the landscape level, the relationship between the predicted probability of occurrence of the species and each set of environmental predictors showed a mixture of combinations of linear and non-linear shapes (Figure 3).

## Discussion

The island of Sardinia is a suitable area for Golden Eagles, based on its landscape characteristics, low human density (68 inhabitants per km$^2$, https://ugeo.urbistat.com) and landscape characteristics that favour relatively abundant prey availability. Indeed, with at least 56 pairs in 2020, this island hosts an important

**Table 3.** Generalized linear model (GLM) estimates and significance statistics of the Wald test for the probability of occurrence of Golden Eagles in Sardinia at landscape scale. Variable abbreviations available in Table 1. Abbreviations: AICc = Akaike Information Criterion corrected for small sample size; df = degrees of freedom; LR = likelihood ratio test.

| Variable | Estimate | Standard | Wald | *P* | AICc | df | LR $X^2$ | *P* |
|---|---|---|---|---|---|---|---|---|
| **Spatial** | | | | | | | | |
| Intercept | −0.523 | 0.121 | 18.624 | 0.000 | | | | |
| x | 0.510 | 0.125 | 16.747 | 0.000 | | | | |
| Explained deviance % | 94.40 | | | | | | | |
| **Topographic** | | | | | | | | |
| Intercept | −0.838 | 0.163 | 26.545 | 0.000 | 296.448 | 4 | 126.554 | 0.000 |
| Asl u | 1.656 | 0.397 | 17.418 | 0.000 | | | | |
| Asl m | −0.705 | 0.348 | 4.113 | 0.043 | | | | |
| Slo r | 0.658 | 0.272 | 5.847 | 0.016 | | | | |
| Slo m | 0.535 | 0.196 | 7.437 | 0.006 | | | | |
| Explained deviance % | 67.00 | | | | | | | |
| **Land use** | | | | | | | | |
| Intercept | −0.633 | 0.143 | 19.701 | 0.000 | | | | |
| For | 1.390 | 0.164 | 72.228 | 0.000 | | | | |
| Explained deviance % | 67.00 | | | | | | | |
| **Bioclimatic** | | | | | | | | |
| Intercept | −0.570 | 0.135 | 17.944 | 0.000 | 395.358 | 3 | 25.592 | 0.000 |
| UD | 0.316 | 0.141 | 5.002 | 0.025 | | | | |
| LSH | 0.850 | 0.137 | 38.255 | 0.000 | | | | |
| LH | 0.811 | 0.203 | 16.003 | 0.000 | | | | |
| Explained deviance % | 81.14 | | | | | | | |

population of this raptor (about 9% of the Italian population; Fasce & Fasce 2017, Ruiu 2017).

Our results showed that topographic, land use and bioclimatic factors could properly describe the habitat preferences of Golden Eagles in Sardinia. At both scales, our models showed a positive effect of longitude on the probability of occurrence of the species. This result can be explained by the distribution of the main mountain ranges in the island, which follow a positive west–east gradient.

In relation to topographic factors, the occurrence of Golden Eagles was correlated with more rugged areas, highlighting that the species selects cells with pronounced slope. The slope-linked variables were correlated with Golden Eagle occurrence at both scales, as already reported in other studies (Carrete *et al.* 2000, McIntyre *et al.* 2006, Tapia *et al.* 2007, Sergio *et al.* 2006, Katzner *et al.* 2012a, Di Vittorio & López-López 2014, Stefânescu & Bâlescu 2019, Fielding *et al.* 2020). The results regarding elevation support this idea, suggesting that the species prefers areas with single high-elevation places (positive correlation with higher elevation) above a lower-elevation background (negative correlation with mean elevation). The species seems to prefer territories characterized by a rugged topography that provides suitable places for nesting. As cliff availability is correlated to the ruggedness of the terrain (Carrete *et al.* 2000, Balbontín 2005, López-López *et al.* 2006), it is likely that the observed preference for rugged land is merely reflecting the availability of suitable nesting cliffs (López-López *et al.* 2004, 2007a).

Topography is also known to influence the flight behaviour of eagles, with the efficiency of movements across the territory being favoured by thermals and orographic uplifts (Bohrer *et al.* 2012, Katzner *et al.* 2012b, Singh *et al.* 2016, Fielding *et al.* 2020) that may facilitate displacement and eventually foraging (McGrady *et al.* 2002, McLeod *et al.* 2002). Since the wing morphology of Golden Eagles is adapted for soaring flight (McGrady 1997, Watson 1997), landscape features that support soaring flight may be preferred (Fielding *et al.* 2020). In addition, a rugged topography may imply a higher availability of three-

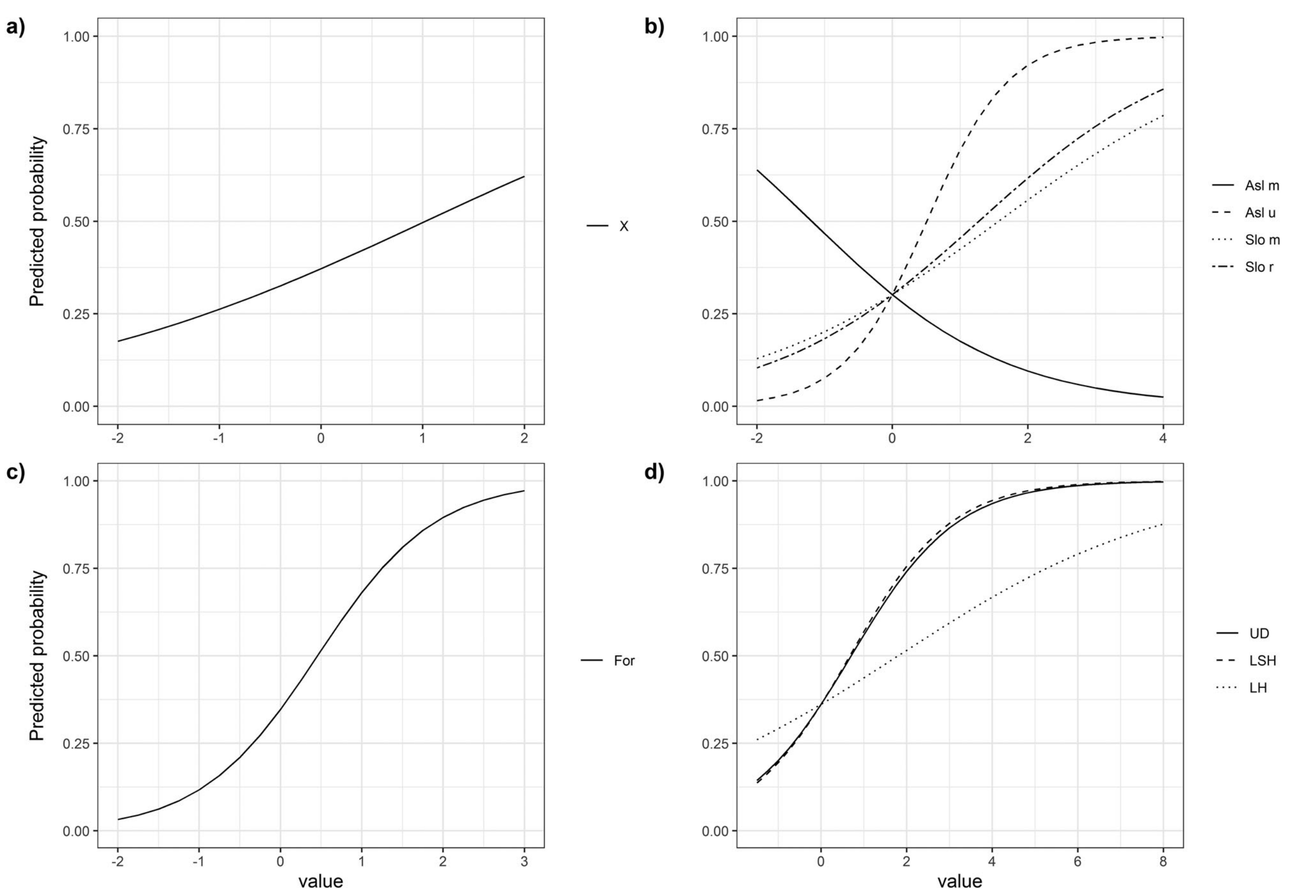


Figure 2. Predicted probability of occurrence of Golden Eagle in Sardinia according to the best GLM model for (a) spatial, (b) topographic, (c) land use, and (d) bioclimatic environmental predictors at landscape scale. See Table 1 for abbreviations of explanatory variables. Value in *x*-axis refers to standardized values of each independent predictor included in the best GLM.

**Table 4.** Comparisons of environmental predictors (mean and standard deviation) in occupied territories and a random set of unoccupied 5 km-radius plots by the Golden Eagle in Sardinia. Land use surface expressed in hectares. See variables abbreviations in Table 1. Abbreviations: BH = Benjamini & Hochberg method (1995).

| | | Territories | | Control | | | | Effect size | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Group | Variable | Mean | sd | Mean | sd | W | *P* | r | Lower 95%CI | Upper 95% CI | *P*-corrected BH |
| Topographic | Asl u | 917.66 | 279.36 | 517.48 | 237.22 | 424 | 0.000 | 0.629 | 0.503 | 0.716 | 0.000 |
| | Asl m | 498.00 | 227.04 | 232.93 | 180.94 | 523 | 0.000 | 0.575 | 0.437 | 0.700 | 0.000 |
| | Asl r | 756.19 | 197.31 | 436.77 | 183.21 | 346 | 0.000 | 0.672 | 0.562 | 0.759 | 0.000 |
| | Slo U | 69.66 | 7.33 | 58.59 | 10.02 | 533 | 0.000 | 0.569 | 0.436 | 0.690 | 0.000 |
| | Slo m | 17.32 | 4.69 | 8.35 | 4.01 | 209 | 0.000 | 0.747 | 0.661 | 0.812 | 0.000 |
| | Slo r | 69.66 | 7.33 | 58.59 | 10.02 | 533 | 0.000 | 0.569 | 0.434 | 0.682 | 0.000 |
| Land use | Art | 303.68 | 441.43 | 307.43 | 521.11 | 1722 | 0.371 | −0.085 | −0.276 | 0.101 | 0.473 |
| | Ara | 98.11 | 266.57 | 2260.06 | 1709.94 | 2999 | 0.000 | −0.810 | −0.866 | −0.733 | 0.000 |
| | Per | 208.03 | 443.92 | 291.83 | 599.89 | 1743 | 0.279 | −0.103 | −0.285 | 0.079 | 0.401 |
| | Pas | 4.59 | 24.69 | 81.86 | 174.61 | 2059 | 0.000 | −0.383 | −0.516 | −0.252 | 0.000 |
| | Het | 2146.48 | 1633.33 | 1667.99 | 1096.02 | 1324 | 0.156 | 0.134 | −0.062 | 0.327 | 0.239 |
| | For | 1467.86 | 1351.82 | 787.61 | 962.10 | 977 | 0.001 | 0.325 | 0.159 | 0.485 | 0.001 |
| | Shru | 3053.62 | 1619.19 | 1761.13 | 1247.06 | 858 | 0.000 | 0.390 | 0.215 | 0.534 | 0.000 |
| | Ope | 252.89 | 364.06 | 80.74 | 189.16 | 952 | 0.000 | 0.352 | 0.177 | 0.512 | 0.000 |
| | Wet | 202.57 | 955.39 | 91.11 | 327.40 | 1461 | 0.424 | 0.076 | −0.128 | 0.265 | 0.514 |
| | Sea | 113.75 | 556.03 | 524.00 | 1451.22 | 1793 | 0.023 | −0.214 | −0.355 | −0.049 | 0.045 |
| Mosaic | s | 9.64 | 2.33 | 10.39 | 2.44 | 1855 | 0.092 | −0.160 | −0.327 | 0.029 | 0.152 |
| | NPA | 35.20 | 12.44 | 37.27 | 12.78 | 1688 | 0.487 | −0.066 | −0.251 | 0.122 | 0.560 |
| | R | 25.38 | 6.13 | 27.35 | 6.42 | 1855 | 0.092 | −0.160 | −0.332 | 0.011 | 0.152 |
| | LPA | 0.46 | 0.16 | 0.46 | 0.15 | 1609 | 0.814 | −0.023 | −0.211 | 0.170 | 0.851 |
| | H′ | 1.54 | 0.38 | 1.55 | 0.33 | 1554 | 0.935 | 0.008 | −0.175 | 0.199 | 0.935 |
| | Do | 2.50 | 0.50 | 2.55 | 0.43 | 1616 | 0.782 | −0.026 | −0.202 | 0.155 | 0.851 |
| | D | 0.70 | 0.01 | 0.70 | 0.01 | 1735 | 0.333 | −0.092 | −0.293 | 0.116 | 0.450 |

dimensional space per unit of two-dimensional space. This favours the potential for undetected approach to prey (Watson 1991). Finally, in mountainous regions, more rugged territories often have lower levels of human disturbance, which in turn favours the presence of eagles (Watson 1997).

At the landscape scale, the occurrence of Golden Eagles increased with the surface area occupied by the forest. These areas are particularly widespread in the mountainous regions of Sardinia (Camarda *et al.* 2015) and have increased in recent decades as a result of land abandonment by farmers since the 1960s (Ruiu 2017). Although this preference for forest has already been reported in some studies (Tjernberg 1983, Bergo 1984, Watson 1992, Chaparro 1996, Watson 1997, Carrete *et al.* 2000, López-López *et al.* 2007a, Stefânescu & Bâlescu 2019), other studies analysing the relationship between Golden Eagle distribution and forest area revealed that the species prefers open habitats and usually avoids woodlands

**Table 5.** Generalized linear model (GLM) estimates and significance statistics of the Wald test of the probability of occurrence of Golden Eagle in Sardinia at home range scale. Abbreviations: AIC = Akaike Information Criterion corrected for small sample size; df = degrees of freedom; LR = likelihood ratio test.

| Variable | Estimate | Standard | Wald | *P* | AICc | df | LR $X^2$ | *P* |
|---|---|---|---|---|---|---|---|---|
| **Spatial** | | | | | | | | |
| Intercept | −0.002 | 0.191 | 0.000 | 0.990 | | | | |
| $x^3$ | 0.693 | 0.201 | 11.849 | 0.001 | | | | |
| Explained deviance % | 89.60 | | | | | | | |
| **Topographic** | | | | | | | | |
| Intercept | −0.273 | 0.344 | 0.631 | 0.427 | 74.314 | 3 | 103.036 | 0.000 |
| Asl m | 0.968 | 0.461 | 4.403 | 0.036 | | | | |
| Slo U | 1.435 | 0.615 | 5.448 | 0.020 | | | | |
| Slo m | 2.527 | 0.616 | 16.832 | 0.000 | | | | |
| Explained deviance % | 43.22 | | | | | | | |
| **Land use** | | | | | | | | |
| Intercept | −2.344 | 0.855 | 7.515 | 0.006 | 68.964 | 2 | 106.274 | 0.000 |
| Ara | −6.113 | 1.493 | 16.773 | 0.000 | | | | |
| Sea | −0.854 | 0.305 | 7.835 | 0.005 | | | | |
| Explained deviance % | 44.66 | | | | | | | |
| **Mosaic** | | | | | | | | |
| Intercept | −0.004 | 0.197 | 0.000 | 0.985 | 155.516 | 2 | 19.612 | 0.000 |
| $x^3$ | 0.826 | 0.216 | 14.552 | 0.000 | | | | |
| *D* | −0.515 | 0.210 | 6.007 | 0.014 | | | | |
| Explained deviance % | 84.86 | | | | | | | |

for hunting (Watson *et al.* 1987, McGrady *et al.* 1997, Pedrini & Sergio 2001, McGrady *et al.* 2002, Balbontín 2005, Ontiveros *et al.* 2005, Di Vittorio & López-López 2014, Watson 2010, Katzner *et al.* 2012a). Furthermore, forest cover could negatively influence the breeding success (Whitfield *et al.* 2001, 2007). However, the natural and semi-natural woodland structure of Sardinia is often full of open landscapes with widely spaced trees, facilitating prey capture by large raptors like the Golden Eagle (Watson 1992).

Our results showed that Golden Eagles tend to occupy areas characterized by relatively high levels of humidity, most likely to avoid excessive temperatures during the breeding season (Steenhof *et al.* 1997, López-López *et al.* 2007a), and confirming that the occurrence of the species can be influenced by climatic factors (Beecham & Kochert 1975, Watson *et al.* 2003, López-López *et al.* 2007a, Moreno-Rueda *et al.* 2009, McIntyre & Schmidt 2012, Di Vittorio & López-López 2014, Stefânescu & Bâlescu 2019).

At the home range scale, the area of arable farmland was negatively correlated with the presence of Golden Eagles. This avoidance of arable farmland, also reported in other studies (Marzluff *et al.* 1997, Watson 2010, Carrete *et al.* 2000, López-López *et al.* 2007a, Katzner *et al.* 2012a, Stefânescu & Bâlescu 2019), could be explained by different, non-mutually exclusive reasons: (i) the disturbance caused by a high number of people working on agricultural land (Carrete *et al.* 2000), (ii) the fact that this land use class is not very common within the altitude occupied by the species in Sardinia; or (iii) its poor prey-productivity due to the type of management (Stefânescu & Bâlescu 2019). However, in general, the relationship between Golden Eagles and agricultural areas should not be considered as necessarily negative, as shown by the traditional management of small agricultural areas in Spain (Tapia *et al.* 2007) or Sicily (Di Vittorio & López-López 2014), where the occurrence of Golden Eagles at the territory scale was positively related with the area of arable farmland.

At both spatial scales, we found a clear negative effect of sea surface extent (a good proxy of coastal environment). This is probably due to an interactive

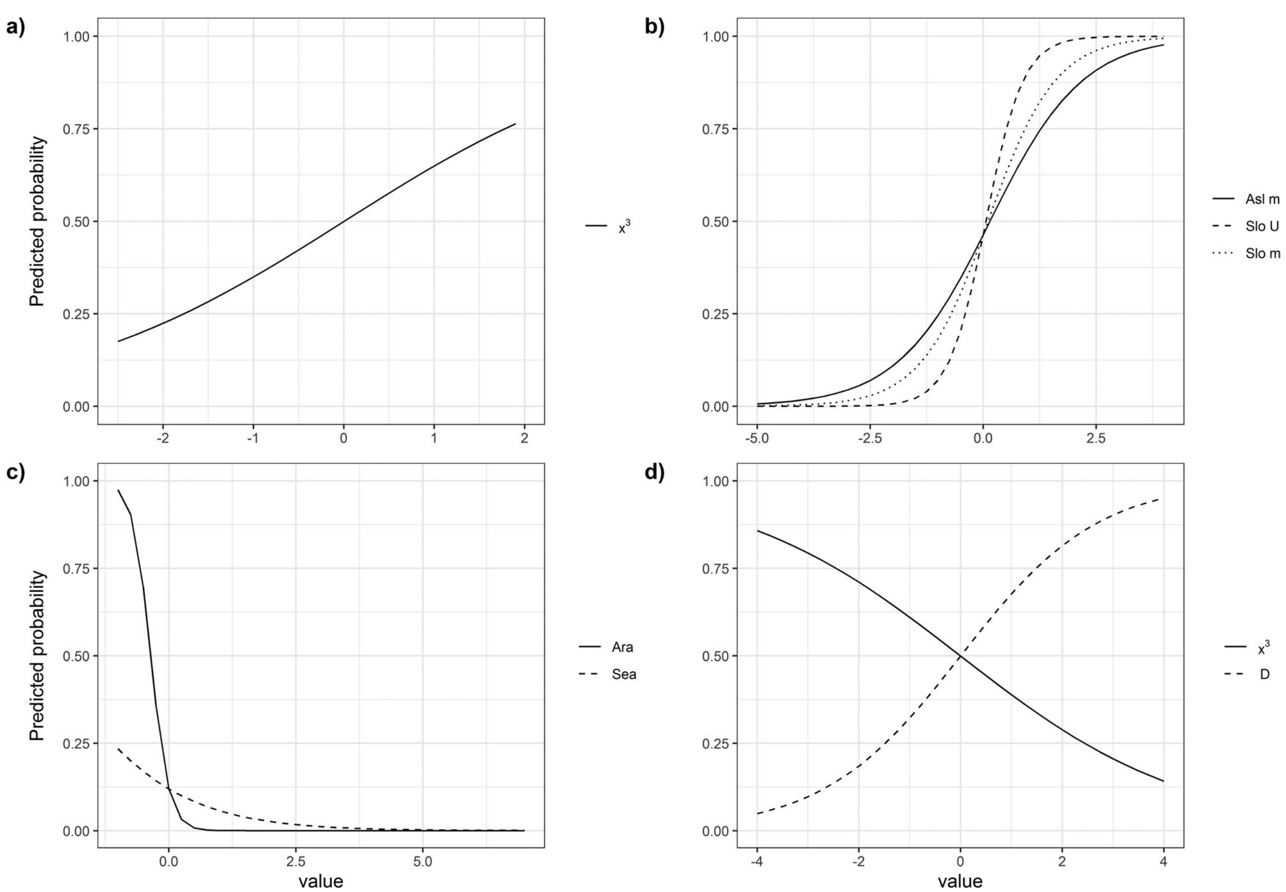


Figure 3. Predicted probability of occurrence of Golden Eagle in Sardinia according to the best GLM model for (a) spatial, (b) topographic, (c) land use, and (d) mosaic environmental predictors at home range scale. See Table 1 for abbreviations of explanatory variables. Value in *x*-axis refers to standardized values of each independent predictor included in the best GLM.

effect between higher human presence and less suitable habitat of these areas (López-López *et al.* 2007a). As other studies suggest, Golden Eagles could avoid coastal places with strong human presence for nesting because of their potential 'low quality' for breeding (Carrete *et al.* 2002, Whitfield *et al.* 2004, López-López *et al.* 2007a), as this raptor is rather intolerant of persistent human presence (Watson & Dennis 1992, Watson 1997, Brendel *et al.* 2002, McLeod *et al.* 2002, López-López *et al.* 2004, Kaisanlahti-Jokimäki *et al.* 2008, Martin *et al.* 2009, Watson 2010, Lado & Tapia 2012). Furthermore, marine habitats provide fewer updrafts and potentially poor prey densities for the species (Watson 1997).

Finally, the negative association of the species distribution with environmental complexity (as explained by the variable 'mean fractal dimension') could indicate the preference of Golden Eagles for large portions of continuous suitable habitat and, therefore, the threat produced by habitat fragmentation and shrinkage of suitable habitat patches (Watson 2010, Katzner *et al.* 2012a, D'Addario *et al.* 2019). This is particularly important in Sardinia, where very frequent summer arson (Nudda *et al.* 2015) and land abandonment can favour habitat fragmentation in many otherwise suitable areas of the island (PAF 2014).

### *Conservation implications*

The results of this study could contribute to future management strategies and conservation projects aimed at protecting Golden Eagles in Sardinia, and may be used to identify the most suitable conservation areas for this raptor. In order to maintain suitable areas for this population, we recommend that management should be focused on maintaining open and forested habitats, especially within the altitudinal range occupied by the species.

Finally, there is another implication with regards to potential competition with the Bonelli's Eagle, for which a reintroduction project is underway in Sardinia. Topographic, land use and bioclimatic factors are among the main factors determining the segregation between these two species (Gil-Sánchez *et al.* 1994, López-López *et al.* 2004, Román-Muňoz *et al.* 2005, Carrascal & Seoane 2009, Moreno-Rueda *et al.* 2009). Our results support the idea of partial niche segregation between the species, as areas occupied by Golden Eagle are usually higher in altitude and colder than those occupied by Bonelli's Eagle (Gil-Sánchez *et al.* 1994, López-López *et al.* 2004, Moreno-Rueda *et al.* 2009). Moreover, Bonelli's Eagle seems to be more tolerant to human presence than Golden Eagle (López-López *et al.* 2004, Moreno-Rueda *et al.* 2009), and the extensive non-irrigated agricultural areas are fundamental components of the landscapes favoured by Bonelli's Eagle (Ontiveros & Pleguezuelos 2003, Penteriani *et al.* 2003, Gil-Sánchez *et al.* 2004, López-López *et al.* 2007a, Carrascal & Seoane 2009, López-López & Urios 2010, Di Vittorio *et al.* 2012), especially if associated with high habitat complexity (López-López *et al.* 2011, Di Vittorio *et al.* 2012). Thus, our results highlight different patterns of habitat selection and niche segregation regarding land use, bioclimatic conditions and human pressure that should favour the coexistence of Golden and Bonelli's Eagles in Sardinia, giving hope for the success (at least in relation to the competition factor) of the ongoing reintroduction project for the Bonelli's Eagle.

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