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Modelling breeding habitat preferences of Bonelli's eagle (*Hieraetus fasciatus*) in relation to topography, disturbance, climate and land use at different spatial scales

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Abstract Predictive models on breeding habitat preferences of Bonelli's eagle (*Hieraetus fasciatus*; Aves: Accipitridae) have been performed at four different spatial scales in Castellón province, East of Iberian Peninsula. The scales considered were: (1) nest site scale (1×1 km² Universal Transverse Mercator (UTM) square containing the nest); (2) near nest environment (3×3 km² UTM square); (3) home range scale (5×5 km² UTM square); and (4) landscape level scale (9×9 km² UTM square containing the above mentioned ones). Topographic, disturbance, climatic and land use factors were measured on a geographic information system (GIS) at occupied and unoccupied UTM squares. Logistic regression was performed by means of a stepwise addition procedure. We tested whether inclusion of new subset of variables improved the models by increasing the area under the receiver operator characteristic plot. At nest site scale, only topographic factors were considered as the most parsimonious predictors. Probability of species occurrence increases with slope in craggy areas at lower altitudes. At the 3×3 km² scale, climate and distur-

bance variables were included. At home range and landscape level scales, models included climate, disturbance, topographic and land use factors. Higher temperatures in January, template ones in July, higher rainfall in June, lower altitudes and higher slope in the sample unit increase probability of occurrence of Bonelli's eagle at broadest scales. The species seems to prefer disperse forests, scrubland and agricultural areas. From our results, we consider that there is a hierarchical framework on habitat selection procedure. We suggest that it is necessary to analyse what key factors are affecting Bonelli's eagle nest-site selection at every study area to take steps to ensure appropriate conservation measures. The combination of regression modelling and GIS will become a powerful tool for biodiversity and conservation studies, taking into account that application depends on sampling design and the model assumptions of the statistical methods employed. Finally, predictive models obtained could be used for the efficient monitoring of this scarce species, to predict range expansions or identify suitable locations for reintroductions, and also to design protected areas and to help on wildlife management.

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Introduction

Bonelli's eagle (*Hieraetus fasciatus*) is a large size raptor distributed from south-east Asia to the European Mediterranean region (Cramp and Simmons 1980; Del Hoyo et al. 1994; Hagemeyer and Blair 1997). The estimated population in Europe ranges from 860 to 1,100 breeding pairs (BirdLife International/EBCC 2000). The Iberian Peninsula holds approximately 80% of the European breeding pairs (Real et al. 1996). The species has experienced a large population decline in the Mediterranean region, mainly during the 1980s (Arroyo and Garza 1995; Real and Mañosa 1997; Real 2004),

and nowadays it is considered as Endangered in Spain according to IUCN categories (Real 2004) and as Least Concern worldwide (BirdLife International 2004).

In order to improve habitat management and conservation strategies, studies focusing on habitat preferences could be useful (Gil-Sánchez et al. 1996; Manly et al. 2002; Ontiveros and Pleguezuelos 2003), mainly in places where human interests and the vital needs of the birds of prey come into conflict.

Habitat selection and habitat preference have usually been used as synonyms in the literature (Jones 2001; Manly et al. 2002; Martínez et al. 2003). Manly et al. (2002) consider selection as the process in which an animal chooses a resource and preference as the likelihood that a resource will be selected if offered on an equal basis with others. By contrast, other authors consider habitat preference as the final pattern of habitat used with respect to its availability, and habitat selection as the general process involving behavioural decisions that makes an animal decide what habitat it would use (Martínez et al. 2003). Thus, habitat preferences do not necessarily correspond with the distribution of suitable resources for the species (Wiens 1989a) and in some cases individuals could be confined to suboptimal places.

Multi-scale approaches have been traditionally employed in the study of habitat preferences (Johnson 1980; Jokimäki and Huhta 1996; Store and Jokimäki 2003). Ecological patterns depend on the spatial scale at which they are analysed (Bever and Flather 1999; Levin 1992; Wiens 1989b). It has been suggested that hierarchical processes affect nest site selection (Martínez et al. 2003; Orians and Wittenberger 1991). The wide use of geographical information systems (GIS) and the development of more powerful statistical methods (Cabeza et al. 2004; Engler et al. 2004; Lehmann et al. 2002a; Sánchez-Zapata and Calvo 1999) have allowed researchers to develop new techniques in modelling species habitat preferences (Frair et al. 2004; Gibson et al. 2004; Jeganathan et al. 2004; Johnson et al. 2004; Osborne et al. 2001).

Many interesting descriptive papers concerning Bonelli's eagle breeding biology in the Iberian Peninsula have been published in past years (Arroyo et al. 1995; Real and Mañosa 1997; Gil-Sánchez et al. 2000; Balbontín et al. 2003). In contrast, the interest for the autoecology of the species has increased in recent years and some studies have tried to quantify the influence of some habitat variables, demographic parameters and prey availability on breeding success (Carrete et al. 2002; Gil-Sánchez et al. 2004; Ontiveros and Pleguezuelos 1999). As a result, the amount of information along the species' distribution range has notably increased in the Mediterranean region, particularly in the Iberian Peninsula. Notwithstanding, there are no reports about factors influencing breeding habitat preference in our study area.

The aim of this work is to investigate those topographic, disturbance, climatic and land use factors affecting the species breeding habitat preference at

four different spatial scales. We also try to evaluate the relative contribution of these different variables at each spatial scale.

Methods

Study area

The study area comprises the Castellón province (located in the east of the Iberian Peninsula; Fig. 1), covering 6,670 km²; 40°47'N, 39°42'S, 0°51'W, 0°32'E; 0–1,814 m a.s.l.. The area is geomorphologically characterised as the confluence of two mountain ranges: the Iberian System, oriented northwest–southeast, on the one hand, and the east–northeast-orientated structures of the Catalánides, parallel to the coastline, resulting on a much folded peak line. Climatologically, it belongs to the Mediterranean area, with an annual mean temperature varying between 17°C in the coast area and 8°C in the inner highlands. The annual mean precipitation varies from 400 to 900 mm, with maximum values during the autumn and minimum values in the summer (Quereda et al. 1999). In terms of bioclimatology, the study area supports an assortment in vegetation types and ecosystems (Rivas-Martínez 1987). This heterogeneity also manifests itself locally, alternating cultivation zones both irrigated and non-irrigated with forest patches dominated by pines (*Pinus* spp.) and, to a lesser extent, oaks (*Quercus* spp.) and *Juniperus* spp.

Censuses

We monitored Bonelli's eagles from 2000 to 2004. During the breeding season, all known and potential breeding territories were visited. For the latter, we monitored 85% of the potential nesting cliffs, thus may have missed an isolated reproductive pair. Observations were made with a 20–60× telescope during clear days and 300 m from nesting cliffs to avoid disturbance to the eagles (Gil-Sánchez et al. 2000; Carrete et al. 2001). A territory was considered occupied if we observed, at the minimum, nests obviously repaired with green branches, typical pair behaviour, courtship, brood rearing activity or young (Rico et al. 1999; Sánchez-Zapata et al. 2000; Carrete et al. 2001). Many pairs changed their nests during the study period to alternative ones inside the same territory (in some cases, a few metres distant on the same cliff). In these cases, we took as the reference for calculations the most used nest.

A minimum of three visits were made to every reproductive territory. A preliminary search was made between 15 January and 15 February, in which nuptial flights and copulations were observed. The first visit was made between 15 March and 1 April to confirm the presence/absence of the pairs, the existence of new nests, and possible newly-hatched chicks. The second visit took place between 15 April to 15 May to monitor the

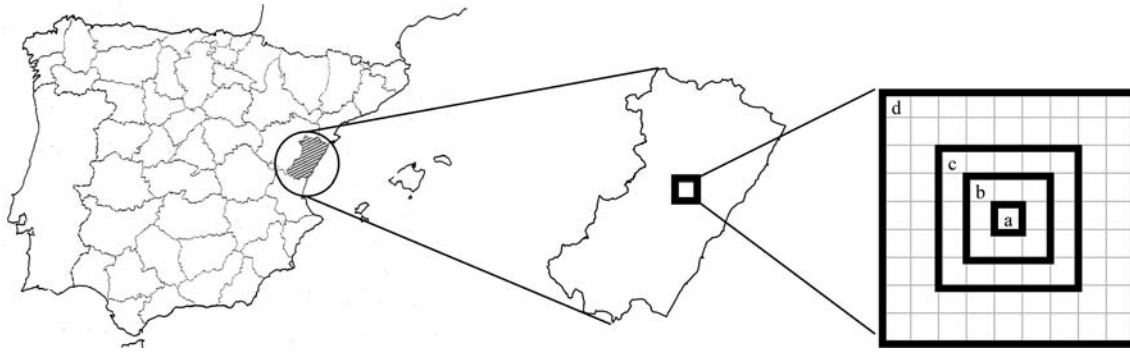


Fig. 1 Left Iberian Peninsula. Location of the study area (circle). Centre Castellón province. Right Different spatial scales considered: **a** UTM 1×1 km², **b** 3×3 km², **c** 5×5 km², **d** 9×9 km²

development of previously-detected chicks and the presence of new hatchings. Finally, a third visit was made in the period between 1 June and 30 June, to confirm breeding success, as well as the presence of late broods. We considered as fledging those young that reached 80% of plumage development or an age of 50 days (Carrete et al. 2002; Real et al. 1997).

Selection of variables and scales

To study breeding habitat preferences of Bonelli's eagle, four concentric spatial scales were considered: (1) nest site scale (1×1 km² Universal Transverse Mercator (UTM) square plot containing the nest); (2) near nest environment (3×3 km² UTM square plot); (3) home range scale (5×5 km² UTM square plot); and (4) landscape level scale (9×9 km² UTM square plot containing the above mentioned ones; Fig. 1).

A case-control design was used (Hosmer and Lemeshow 2000; Keating and Cherry 2004) corresponding to a sampling protocol C described in Manly et al. (2002). This method yields a sample of occupied and unoccupied squares independently sampled. Thus, in order to calibrate models on the factors characterising habitat preferences at each scale, 37 occupied squares and 29 unoccupied squares were chosen. Unused squares were taken spatially separated from occupied ones to avoid overlapping on higher scales (at 5×5 and 9×9 km²) with occupied ones. Bonelli's eagle is a large raptor that uses different patches for breeding and for foraging, usually separated by several kilometres. Unfortunately, detailed knowledge of the behavioural ecology, land use and territoriality of this species is not available in our study area. So as to be as similar to other habitat preference studies, the scales were assigned by researchers to fit the UTM squares in a heuristic way (Mañosa et al. 1998; Martínez et al. 2003; Ontiveros 1999; Penteriani and Faivre 1997). Furthermore, UTM squares are a common reference in ornithological studies and have been employed in broad projects like the last Spanish Breeding Bird Atlas (Martí and Del Moral 2003) allowing comparisons with other study areas.

A total of 33 variables analysed by GIS were taken into account, divided into four subsets: topographic, disturbance, climatic and land use (Table 1). These variables were selected because of they were indirect measures of breeding habitat features. Thus, they are expected to predict the realized ecological niche (Guisan and Zimmermann 2000).

Topographic variables were obtained from a Digital Elevation Model (DEM) with an accuracy of 50-m pixels of horizontal and vertical resolution. It was created by a triangular irregular network (TIN) method based on vector data of contour lines with 10 m accuracy. The slope was considered as the maximum rate of change in elevation across each triangle in the TIN. From the vectorial data of the TIN we created a raster continuous grid from which values were obtained. Disturbance and land use variables were obtained from a land-use and land-cover digital map, based on satellite imagery (0.5-m resolution), taken from 1996 to 2000 and edited from 2001 to 2003. This cartography is commercialised and available to the public in metadata shape format from Valencian Cartographic Institute (Scale 1: 10,000) (www.gva.es/icv/). Climate variables were obtained from data of the Climatic Atlas of the Valencian Community (Pérez-Cueva 1994) and the Meteorological National Institute of Spain (www.inm.es/). Data correspond from the period 1961–1990, and were improved on a digital shape by interpolation of 50-m contours by the inverse distance weighted interpolation method with 50-m horizontal resolution. This method estimates grid cell values by averaging the values of sample data points in the vicinity of each cell and is useful for predicting values in a raster from a limited sample of data points. Nest data shape was generated by the researchers and is not publicly available. In all cases, a shape containing the UTM squares for each scale was superimposed by separation. Then, we use the summarising method to calculate the variable's average or value.

Multi-collinearity test based on the variance inflation factor (VIF) analysis was calculated (Montgomery and Peck 1982) in order to avoid overparametrisation (Edwards 1985; Grand and Cushman 2003; Hobson et al. 2000; Kirk et al. 2001; Poirazidis et al. 2004).

Table 1 Description and source of explanatory variables used in habitat preference models

Name	Description and source ^a
Topographic	
Altitude	Average altitude (m) above sea level from a digital elevation model (DEM)
Orientation	Average orientation from DEM
Slope	Average slope (%) from DEM
Disturbance	
Urban	Urbanised surface
Paved	Paved roads (m)
Unpaved	Non-paved, vehicle-allowing roads
Climate	
Temperature	Average temperature (°C) on every month (January–July)
Precipitation	Average rainfall (l/m ²) on every month (January–July)
Gorzhinsky	Gorzhinsky continentality index [$K = (1.7 \times \text{thermal amplitude} / \sin \text{latitude}) - 20.4$]
Freeze	Average number of freezing days
Snowfall	Average number of snow-covered days
Land use (surface)	
Disperse forest	Forest with tree coverage < 50%
Agricultural	Irrigated and non-irrigated cultures (e.g. <i>Citrus</i> spp., <i>Rosa</i> spp., <i>Olea</i> spp.)
Unproductive	Abandoned cultures and water
Scrubland	Mediterranean scrubland areas (e.g. <i>Rosmarinus</i> spp., <i>Ulex</i> spp., <i>Pistacia</i> spp.)
Fire	Burnt areas in the last 10 years
<i>Halepensis</i>	<i>Pinus halepensis</i> forests with tree coverage > 50%
<i>Suber/faginea</i>	<i>Quercus suber</i> and <i>Q. faginea</i> forests
<i>Pinaster/sylvestris</i>	<i>Pinus pinaster</i> and <i>P. sylvestris</i> forests
<i>Nigra</i>	<i>Pinus nigra</i> forests
<i>Ilex</i>	<i>Quercus ilex</i> forests

^aSee text for details

Variables with tolerance values less than 0.1 or a VIF larger than 10 were removed from the analysis (Bowerman and O'Connell 1990). Kolmogorov-Smirnov normality test was performed for all variables (Poirazidis et al. 2004). Those that did not follow normal distribution were normalised by square root transformation (Edwards 1985; Sokal and Rohlf 1981; SPSS Inc. 1999; StatSoft Inc. 1998).

Statistical model formulation

We used logistic regression [a particular case of generalized linear models (GLMs)] for modelling Bonelli's eagle breeding habitat preferences. In general, a GLM has three components: the linear predictor, a link function and an error structure. Since the response variable (presence/absence of Bonelli's eagle) follows a binomial distribution, we used the logit as the link function. The error structure was assumed to be binomial (McCullagh and Nelder 1989).

We built 15 models at each scale, and a total of 60 models (15 models per four scales). First of all, simple models were developed using topographic (T), climatic (C), disturbance (D) and land use (U) variables by separated. Then, all possible combinations of double (i.e. T+U, C+U) and triple (i.e. T+D+U, T+C+U) subsets of variables were added to build logistic models.

We also developed a final model including all variables (T+C+D+U). This stepwise addition procedure was computed in order to test whether inclusion of a new subset of variables improved the models (in terms of increasing AUC). For each logistic regression model, standard backward stepwise procedure was used (Pearce and Ferrier 2000a), including all variables at once and removing non-significant ones stepwise by Wald's test (Johnson 1998). If the Wald statistic was significant then the parameter was included in the model (MacNally 2000). In each step, the criterion was $P=0.05$ for entry and $P=0.10$ for removal (Poirazidis et al. 2004; SPSS 1999). The Wald's test has been criticised because it is known to have major problems as have other p-based and stepwise procedures (Burnham and Anderson 2002). But, anyway, it allows the development of a great number of models and permits a heuristic approach to modelling (Seoane et al. 2004), so the procedure could be justified.

In order to select the most parsimonious model amongst a set of logistic models for each subset of variables, the Akaike's information criterion (AIC) was calculated (Akaike 1973). In our case, as the sample size divided by the number of variables is less than 40 (Burnham and Anderson 2002; Johnson and Omland 2004), a second-order AIC corrected for small sample size (AIC_c) was computed for each model. The smaller the AIC_c, the better the model (Sakamoto et al. 1986).

Receiver operating characteristic (ROC) plot was computed to assess the power of the logistic models (Gibson et al. 2004; Osborne et al. 2001; Pearce and Ferrier 2000b). This is a threshold-independent approach in the assessment of logistic regression models (Luck 2002; Manel et al. 1999; Osborne et al. 2001; Suárez-Seoane et al. 2002). The ROC curve is a plot of true positive cases (sensitivity) against corresponding false positive cases (1-specificity) across a range of threshold values (Fielding and Bell 1997; Pearce and Ferrier 2000b). The area under the ROC function (AUC) varies from 0.5 to 1, where the former corresponds with model discrimination no better than random, and the latter for a model with perfect discriminatory ability (Fielding and Bell 1997; Pearce and Ferrier 2000b). The AUC \pm standard error (SE) was displayed, and based on a non-parametric assumption (Manel et al. 2001). Models with higher AUC and less predictive variables were considered as the best models, and are highlighted in bold in Table 2. All computations were performed using SPSS version 12.0 for Windows and spatial analysis with ESRI, Inc© ArcView GIS 3.2.

Results

1×1 km² scale

The best logistic regression model identified only topographic factors as the most parsimonious predictors ($\chi^2=49,320$; $df=2$; $P<0.001$; Table 2). The best model was:

$$p(y) = -2.989 - 0.005 \times \text{altitude} + 0.377 \times \text{slope}.$$

The probability of occurrence of Bonelli's eagle decreases with altitude, but is increased by the slope of the square. The inclusion of climatic, disturbance and land use variables did not improve the predictive power of the only topographic model. The model performance could be considered as good, with an AUC value slightly higher than 90%.

3×3 km² scale

Differences of nest-site level, disturbance and climatic factors were considered as best predictors of Bonelli's eagle occurrence in the logistic regression analysis ($\chi^2=90,519$; $df=6$; $P<0.001$; Table 2). The best model was:

$$p(y) = 413.618 + 3.042 \times \text{precip.june} - 17.270 \\ \times \text{precip.july} - 20.120 \times \text{snowfall} + 0.811 \\ \times \text{urban} - 0.006 \times \text{paved} - 0.030 \times \text{unpaved}.$$

This model predicts high probabilities of Bonelli's eagle occurrence in areas with higher rainfall in June,

urban areas, and less rainfall in July, snow precipitation, and kilometres of paved and unpaved roads.

The model classified correctly 100% of squares, with the highest model performance possible, an AUC value equal to 1. The inclusion of topographic and land use factors did not improve the final model performance (Table 2).

5×5 km² scale

For this scale, the most parsimonious model ($\chi^2=90,523$; $df=15$; $P<0.001$; Table 2) was obtained by including all subset of factors. The model was:

$$p(y) = 20586.791 + 1012.940 \times \text{temp.january} - 1297.769 \\ \times \text{temp.july} - 37.466 \times \text{precip.may} + 104.770 \\ \times \text{precip.june} - 29.854 \times \text{precip.july} + 2.1 \\ \times 10^{-5} \times \text{disperseforest} + 1.2 \times 10^{-5} \times \text{agricultural} \\ - 0.305 \times \text{squnproductive} + 0.117 \times \text{sqscrubland} \\ - 2.2 \times 10^{-4} \times \text{pinaster} - 2.1 \times 10^{-4} \times \text{nigra} \\ + 0.010 \times \text{paved} - 1.568 \times \text{altitude} - 7.630 \\ \times \text{orientation} + 82.309 \times \text{slope}.$$

The model performance was excellent and correctly distinguished between all occupied and unoccupied squares. Only 46.6% models exceeded an AUC of 0.8 (S1).

9×9 km² scale

The best logistic regression model identified disturbance, climatic and land use factors as the most parsimonious predictors ($\chi^2=90,523$; $df=18$; $P<0.001$; Table 2). The model was:

$$p(y) = 51332.835 + 4301.630 \times \text{temp.january} - 4740.465 \\ \times \text{temp.july} + 1024.043 \times \text{gorzinsky} + 59.456 \\ \times \text{precip.april} - 148.443 \times \text{precip.may} + 253.303 \\ \times \text{precip.june} - 164.985 \times \text{precip.july} + 3.8 \times 10^{-5} \\ \times \text{disperseforest} + 4.029 \times 10^{-5} \times \text{agricultural} \\ - 0.270 \times \text{squnproductive} + 7.326 \times 10^{-5} \\ \times \text{scrubland} + 0.133 \times \text{sqhalepensis} + 2.055 \times 10^{-5} \\ \times \text{fire} - 1.0 \times 10^{-4} \times \text{pinaster} - 4.133 \times 10^{-5} \\ \times \text{nigra} - 1.3 \times 10^{-4} \times \text{ilex} + 1.451 \times \text{urban} \\ - 0.004 \times \text{unpaved}.$$

This model correctly classified 100% of squares. The inclusion of topographic factors did not improve the final model (Table 2).

Table 2 Logistic regression models for topographic (T), disturbance (D), land use (U), and climate (C) factors

Scale	Model	-2 log likelihood	K	AIC _c	AUC ± SE	Significance	Sensitivity
1×1	T	41.20	3	47.59	0.90 ± 0.04	< 0.001	0.95
	D	72.13	4	80.78	0.73 ± 0.07	0.001	0.95
	U	46.04	8	64.57	0.84 ± 0.05	< 0.001	0.89
	C	78.27	4	86.92	0.66 ± 0.07	0.023	0.81
	T+D	41.20	3	47.59	0.90 ± 0.04	< 0.001	0.95
	T+U	30.40	12	60.28	0.89 ± 0.05	< 0.001	0.92
	T+C	38.40	4	47.06	0.89 ± 0.05	< 0.001	0.92
	D+U	37.21	10	61.21	0.89 ± 0.05	< 0.001	0.95
	C+U	41.43	7	57.36	0.85 ± 0.05	< 0.001	0.87
	D+C	55.00	7	70.93	0.76 ± 0.06	< 0.001	0.84
	T+D+C	38.40	4	47.06	0.89 ± 0.05	< 0.001	0.92
	T+C+U	38.40	4	47.06	0.89 ± 0.05	< 0.001	0.92
	T+D+U	41.20	3	47.59	0.90 ± 0.05	< 0.001	0.95
	D+C+U	35.16	8	53.69	0.91 ± 0.04	< 0.001	0.89
3×3	T+D+C+U	38.40	4	47.06	0.89 ± 0.05	< 0.001	0.92
	T	42.19	3	48.57	0.88 ± 0.05	< 0.001	0.89
	D	18.84	4	27.50	0.94 ± 0.03	< 0.001	0.92
	U	53.84	8	72.36	0.80 ± 0.06	< 0.001	0.92
	C	68.63	6	82.05	0.66 ± 0.07	0.023	0.81
	T+D	6.45	7	22.38	0.97 ± 0.03	< 0.001	0.97
	T+U	25.55	7	41.48	0.92 ± 0.04	< 0.001	0.95
	T+C	39.58	4	48.24	0.90 ± 0.04	< 0.001	0.95
	D+U	45.57	11	72.46	0.90 ± 0.05	< 0.001	0.97
	C+U	44.94	8	63.47	0.83 ± 0.06	< 0.001	0.87
	D+C	4×10⁻³	7	15.94	1.00 ± 0.00	< 0.001	1.00
	T+D+C	10 ⁻³	7	15.93	1.00 ± 0.00	< 0.001	1.00
	T+C+U	5×10 ⁻⁶	15	39.60	1.00 ± 0.00	< 0.001	1.00
	T+D+U	2×10 ⁻⁴	7	15.93	1.00 ± 0.00	< 0.001	1.00
5×5	D+C+U	13.43	4	22.08	0.99 ± 0.02	< 0.001	0.97
	T+D+C+U	0.02	7	15.95	1.00 ± 0.00	< 0.001	1.00
	T	62.24	4	70.90	0.80 ± 0.06	< 0.001	0.87
	D	82.23	2	86.42	0.62 ± 0.07	0.101	0.89
	U	62.49	4	71.15	0.77 ± 0.06	< 0.001	0.89
	C	68.63	6	82.05	0.69 ± 0.07	0.010	0.78
	T+D	58.71	5	69.71	0.80 ± 0.06	< 0.001	0.87
	T+U	49.79	7	65.72	0.86 ± 0.05	< 0.001	0.89
	T+C	57.12	4	65.77	0.83 ± 0.06	< 0.001	0.89
	D+U	64.40	5	75.40	0.77 ± 0.06	< 0.001	0.81
	C+U	48.80	12	78.69	0.80 ± 0.06	< 0.001	0.84
	D+C	58.41	7	74.34	0.74 ± 0.06	0.001	0.78
	T+D+C	53.42	5	64.42	0.84 ± 0.05	< 0.001	0.92
	T+C+U	42.26	9	63.47	0.85 ± 0.05	< 0.001	0.87
9×9	T+D+U	49.79	7	65.72	0.86 ± 0.05	< 0.001	0.89
	D+C+U	42.08	13	75.08	0.86 ± 0.05	< 0.001	0.89
	T+D+C+U	2×10⁻⁵	16	43.10	0.98 ± 0.02	< 0.001	1.00
	T	59.60	3	65.99	0.80 ± 0.06	< 0.001	0.81
	D	82.57	2	86.76	0.647 ± 0.07	0.042	0.81
	U	65.61	4	74.27	0.716 ± 0.07	0.003	0.81
	C	68.49	6	81.91	0.729 ± 0.07	0.001	0.84
	T+D	55.19	4	63.84	0.815 ± 0.06	< 0.001	0.84
	T+U	44.49	11	71.38	0.921 ± 0.04	< 0.001	0.95
	T+C	51.08	6	64.51	0.860 ± 0.05	< 0.001	0.89
	D+U	57.77	4	66.42	0.846 ± 0.05	< 0.001	0.87
	C+U	56.79	7	72.72	0.856 ± 0.05	< 0.001	0.92
	D+C	52.79	7	68.72	0.767 ± 0.06	< 0.001	0.81
	T+D+C	39.44	9	60.66	0.833 ± 0.05	< 0.001	0.84
T+C+U	45.68	7	61.61	0.887 ± 0.05	< 0.001	0.95	
T+D+U	46.98	7	62.92	0.860 ± 0.05	< 0.001	0.89	
D+C+U	6×10⁻⁵	19	54.52	1.000 ± 0.00	< 0.001	1.00	
T+D+C+U	2×10 ⁻⁵	19	54.52	1.000 ± 0.00	< 0.001	1.00	

K number of predictor variables, AUC area under ROC curve, SE standard error. Models with higher AUC and less predictive variables were considered as the best models, and are highlighted in bold

Discussion

Habitat preference models developed using GLM techniques are useful for finding relationships between habitat features and species distribution (Buckland and

Elston 1993; Bustamante and Seoane 2004; Gibson et al. 2004; Nicholls 1989). They are mathematical extensions of linear models that deal with linear relationships (Guisan et al. 2002). Our distribution models are considered to be static and to assume equilibrium, or at least pseudo-equilibrium (Guisan and Zimmermann 2000).

As the model's dependant variable (presence/absence) is based on direct field observations, they are likely to predict the realised ecological niche (Malanson et al. 1992). Hence, biotic interaction and competitive exclusion are intrinsically considered (Guisan and Zimmermann 2000).

The multi-scale approach may be especially useful to identify different key factors involved in habitat preferences (Wiens 1989b; Jokimäki and Hutha 1996, Martínez et al. 2003; Store and Jokimäki 2003). Logistic regression models obtained in our results included different factors on different spatial scales. The same subset of variables (topography, climate, disturbance and land use) were initially calculated and considered at each scale, but the final models selected different factors to reflect breeding habitat preferences. At nest site scale, only topographic factors were selected in the final model. Bonelli's eagle is a medium-large cliff nesting raptor that needs cliffs over 15–20 m in height on which to place its nests. In our study area, the species is present at altitudes ranging from sea level to 1,300 m (López-López et al. 2003). Results indicate that the probability of species occurrence increases on craggy areas at lower altitudes, as reported in other studies (Cramp and Simmons 1980; Ontiveros and Pleguezuelos 2003). The average orientation of the UTM square was not included as a significant predictor in the best model. Nevertheless, considering only nesting cliffs, a significant relationship between productivity and nest orientation has been found in Granada, southern Spain (Ontiveros and Pleguezuelos 2003), thus selecting adequate thermal environment for the survival of the embryo or the nestlings.

At the 3×3 km² scale, climate and disturbance variables were included in the final model. Climate predictors selected are related to typically Mediterranean areas, that is, dry in summer months (shown by a negative relationship with rainfall in July) and temperate in winter (shown by a negative relationship with snowfall). Cold temperatures may cause physiological stress negatively affecting breeding success (Steenhof et al. 1997). Also, snowfall avoidance could be related to the species' early laying date (Cramp and Simmons 1980). In relation to disturbance, Bonelli's eagle is considered relatively tolerant to human presence (Arroyo and Garza 1995; Gil-Sánchez et al. 1996, 2004). The higher probability of occurrence in urban areas is possibly related to racing pigeons as a food source (Carrete et al. 2002). In contrast, the eagle avoids direct human disturbance of near nest environs as indicating by the negative coefficient of paved and unpaved roads. Gil-Sánchez et al. (1996) found similar results by adjusting discriminant functions among occupied and unoccupied cliffs. It is important to note that only climate and disturbance predictors correctly classified all sample units at this scale.

At home range and landscape level scales, results are broadly similar. Our models included several predictors in both cases. It is a general rule that the more predictors

the difficult to explain the model (Guisan and Zimmermann 2000). Complex models with several predictors become too much complex and generally difficult to understand in biological terms (Burnham and Anderson 2002). Our models selected climate, disturbance, topographic (only at 5×5 km²) and land use factors when predicting Bonelli's eagle breeding habitat preferences. Mathematically, land use coefficients were almost depreciable in comparison to climatic and topographic predictors, but model accuracy increases by including these factors. Higher temperatures in January, template ones in July, higher rainfall in June, lower altitudes and higher slope in the sample unit increase the probability of occurrence of Bonelli's eagle at the broadest scales. The species seems to prefer dispersed forests, scrubland and agricultural areas. Bonelli's eagle preys mainly on rabbits (*Oryctolagus cuniculus*) and partridge (*Alectoris rufa*) (Gil-Sánchez et al. 2000; Carrete et al. 2002) which are abundant in this type of vegetation mosaic. Hence, indirectly higher probability of occurrence is probably related to prey abundance in these areas. Carrete et al. (2002) also found abandoned Bonelli's eagle territories had less scrubland area and overlooked open lands and dispersed forests to increase prey detection and hunting success for eagles.

From our results, we could consider that there is a hierarchical framework of habitat selection procedure. In other study areas, some authors had indicated cliff availability as a determinant of species distribution (Ontiveros 1999). Competitive interactions and climate conditions have also been suggested as limiting factors (Gil-Sánchez et al. 1996, 2004; Ontiveros and Pleguezuelos 2003). Trophic resources seem not to be a determinant of nest-site selection (Ontiveros and Pleguezuelos 1999, 2003) due to high species mobility, but they are relevant for global distribution (Gil-Sánchez et al. 1994). Still, we consider it necessary to analyse what key factors are affecting Bonelli's eagle nest-site selection in every study area in order to take steps to ensure appropriate conservation measures.

The combination of regression modelling and GIS will become a powerful tool for biodiversity and conservation studies (see Lehmann et al. 2002a, b for a complete compilation). It is important to note that application depends on sampling design and the model assumptions of the statistical methods employed (Keating and Cherry 2004). Furthermore, other approaches that include non-linear relationships, like generalised additive models (GAMs) (Guisan et al. 2002; Seoane et al. 2004), neural networks (Hagan et al. 1996; Haykin 1999) and the recent developed ecological niche factor analysis (ENFA) (Engler et al. 2004) implemented in the Biomapper package (Hirzel et al. 2002), would probably perform with the data of this study. Results obtained by a comparison of these methods would be interesting for conservation applications and future research. An ongoing study will involve such a predicted model surface including an accuracy test with an independent data set from other study areas (P. López-López

and C. García-Ripollés, unpublished data). Finally, predictive models obtained could be used to monitor this scarce species, predict range expansions or identify suitable locations for reintroductions (Yanez and Floater 2000), and also to design protected areas (Li et al. 1999) and to help with wildlife management (Bradbury et al. 2000).

Zusammenfassung

Modellierung der Bruthabitatpräferenzen des Habichtsadlers (*H. fasciatus*) hinsichtlich Topographie, Störung, Klima und Landnutzung in verschiedenen räumlichen Maßstäben. Vorhersagemodelle für die Bruthabitatpräferenzen des Habichtsadlers (*H. fasciatus*) wurden in vier verschiedenen räumlichen Maßstäben in der Provinz Castellón im Osten der iberischen Halbinsel durchgeführt. Die betrachteten Maßstäbe waren: (a) Nistplatz (1×1 km² Universal Transverse Mercator-, UTM-, Quadrat, das Nest enthaltend), (b) Nestnähe (3×3 km² UTM-Quadrat), (c) Home-Range (5×5 km² UTM-Quadrat) und (d) Landschaft (9×9 km² UTM-Quadrat inklusive aller vorher genannten Quadrate). Alle Faktoren zu Topographie, Störungen, Klima und Landnutzung wurden in einem geographischen Informationssystem (GIS) zwischen Rastern mit und ohne Nestern verglichen. Mit Hilfe einer schrittweise additiven logistischen Regression wurde geprüft, ob das Hinzunehmen neuer Gruppen von Variablen die Modelle verbesserten. Im Nistplatz-Maßstab wurden nur topographische Faktoren als besonders bedeutsam identifiziert. Die Wahrscheinlichkeit des Auftretens der Art stieg mit zunehmender Hangneigung in felsigen Gebieten niedriger Meereshöhe. Im 3×3 km² Maßstab wurden Klima- und Störungsvariablen eingeschlossen. Im Home-Range- und Landschafts-Maßstab enthielten die Modelle Klima-, topographische und Landnutzungsfaktoren. Höhere Temperaturen im Januar, gemäßigte im Juli, höhere Niederschlagsmengen im Juni, geringere Höhe und größere Hangneigungen erhöhen die Wahrscheinlichkeit für das Vorkommen des Habichtsadlers. Die Art scheint lockeren Wald, Strauchland und landwirtschaftliche Gebiete zu bevorzugen. Anhand unserer Ergebnisse nehmen wir an, dass die Habitatwahl einem hierarchischen System folgt. Für Schutzmaßnahmen ist es unverzichtbar, die Schlüsselfaktoren zu identifizieren, die die Habitatwahl des Habichtsadlers ortsspezifisch bedingen. Die Kombination von Regressionsmodellen und GIS erweist sich als ein sehr geeignetes Instrument in der Biodiversitäts- und Naturschutzforschung. Allerdings sind dabei das Probeverfahren und die gewählten Modellannahmen der verwendeten statistischen Methoden zu berücksichtigen. Schließlich können solche Vorhersagemodelle dazu benutzt werden, um diese seltene Art effizient zu erfassen, Vergrößerungen des Ausbreitungsgebiets vorherzusagen oder um geeignete Orte für Wiederansiedlungen zu finden. Auch können damit Schutzgebiete konzipiert und Natur- und Umweltmanagement unterstützt werden.

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