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Modelling breeding habitat preferences of Bonelli's eagle (*Hieraaetus 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 (*Hieraaetus 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 km^2 Universal Transverse Mercator (UTM) square containing the nest); (2) near nest environment (3×3 km^2 UTM square); (3) home range scale (5×5 km^2 UTM square); and (4) landscape level scale (9×9 km^2 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 km^2 scale, climate and disturbance 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.

Keywords GIS · Habitat preferences · *Hieraaetus fasciatus* · Logistic regression · Predictive models

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Introduction

Bonelli's eagle (*Hieraaetus 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; Hagemeijer 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 (Bevers 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 km^2; 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

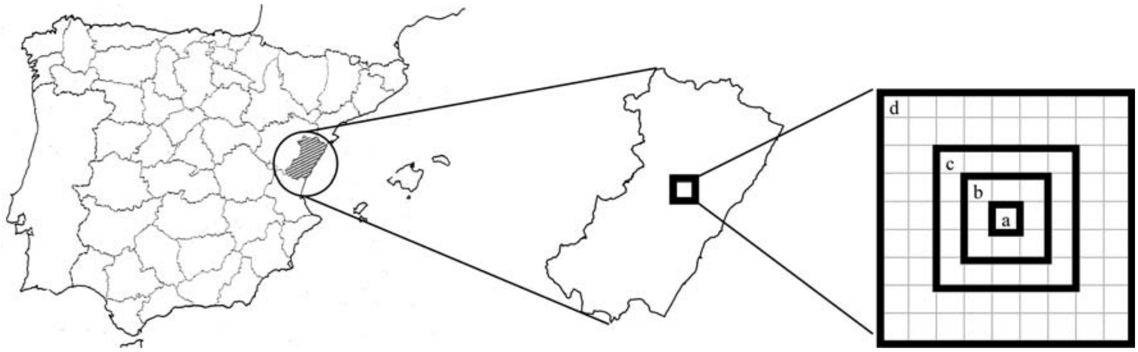

Fig. 1 *Left* Iberian Peninsula. Location of the study area (*circle*). *Centre* Castellón province. *Right* Different spatial scales considered: **a** UTM 1×1 km^2, **b** 3×3 km^2, **c** 5×5 km^2, **d** 9×9 km^2

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 km^2 Universal Transverse Mercator (UTM) square plot containing the nest); (2) near nest environment (3×3 km^2 UTM square plot); (3) home range scale (5×5 km^2 UTM square plot); and (4) landscape level scale (9×9 km^2 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 km^2) 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-colinearity 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)
Gorzinsky	Gorzinsky continentality index [$K = (1.7 \times$thermal amplitude/sin 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. *Citrus* spp., *Rosa* spp., *Olea* spp.)
Unproductive	Abandoned cultures and water
Scrubland	Mediterranean scrubland areas (e.g. *Rosmarinus* spp., *Ulex* spp., *Pistacia* spp.)
Fire	Burnt areas in the last 10 years
Halepensis	*Pinus halepensis* forests with tree coverage > 50%
Suber/faginea	*Quercus suber* and *Q. faginea* forests
Pinaster/sylvestris	*Pinus pinaster* and *P. sylvestris* forests
Nigra	*Pinus nigra* forests
Ilex	*Quercus ilex* forests

[a] See 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 ± 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 km^2 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 km^2 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 km^2 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 km^2 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
	T + D + C + U	38.40	4	47.06	0.89 ± 0.05	< 0.001	0.92
3×3	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
	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
5×5	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
	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**
9×9	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 km^2 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 km^2) 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 km^2 Universal Transverse Mercator-, UTM-, Quadrat, das Nest enthaltend), (b) Nestnähe (3×3 km^2 UTM-Quadrat), (c) Home-Range (5×5 km^2 UTM-Quadrat) und (d) Landschaft (9×9 km^2 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 km^2 Maßstab wurden Klima- und Störungsvariabeln 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 ortspezifisch 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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References

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second international symposium of information theory. Akademiai Kiado, pp 267–281

Arroyo B, Ferreiro E, Garza V (1995) El Águila Perdicera (Hieraaetus fasciatus) en España. Censo, reproducción y conservación. Colección Técnica, ICONA. Ministerio de Agricultura, Pesca y Alimentación, Madrid

Arroyo B, Garza V (1995) Factores de regresión del Águila Perdicera (*Hieraaetus fasciatus*) en España. I Congreso Internacional de Rapaces del Holártico, Resúmenes, Mérida

Balbontín J, Penteriani V, Ferrer M (2003) Variations in the age of mates as an early signal of changes in population trends? The case of Bonelli's eagle in Andalusia. Biol Conserv 109:417–423

Bevers M, Flather CH (1999) The distribution and abundance of population limits at multiple spatial scales. J Anim Ecol 68:976–987

BirdLife International (2004) Species factsheet: *Hieraaetus fasciatus*. Downloaded from http://www.birdlife.org on 2/8/2005

BirdLife International/European Bird Census Council (2000) European bird populations: estimates and trends. BirdLife International, Cambridge. BirdLife Conservation Series No. 10

Bowerman BL, O'Connell RT (1990) Linear statistical models: an applied approach, 2nd edn. Duxbury, Belmont

Bradbury RB, Kyrkos A, Morris AJ, Clark SC, Perkins AJ, Wilson JD (2000) Habitat selection and breeding success of yellowhammers on lowland farmland. J Appl Ecol 37:789–805

Buckland ST, Elston A (1993) Empirical models for the spatial distribution of wildlife. J Appl Ecol 30:478–495

Burnham KP, Anderson DR (2002) Model selection and multimodel inferences. A practical information-theoretic approach, 2nd edn. Springer, Berlin Heidelberg New York

Bustamante J, Seoane J (2004) Predicting the distribution of four species of raptors (Aves: Accipitridae) in southern Spain: statistical models work better than existing maps. J Biogeogr 31:295–306

Cabeza M, Araújo MB, Wilson RJ, Thomas CD, Cowley MJR, Moilanen A (2004) Combinig probabilities of occurrence with spatial reserve design. J Appl Ecol 41:252–262

Carrete M, Sánchez-Zapata JA, Martínez JE, Palazón JA, Calvo JF (2001) Distribución espacial del Águila Azor-Perdicera (*Hieraaetus fasciatus*) y del Águila Real (Aquila chrysaetos) en la región de Murcia. Ardeola 48:175–182

Carrete M, Martínez JE, Sánchez MA, Calvo JF, Sánchez-Zapata JA (2002) Factors influencing the decline of a Bonelli's eagle (*Hieraaetus fasciatus*) population in southeastern Spain: demography, habitat or competition? Biodivers Conserv 11:975–985

Cramp S, Simmons KEL (1980) The birds of Western Paleartic, vol 2. Oxford University Press, Oxford

Del Hoyo J, Elliot A, Sargatal J (1994) Handbook of the birds of the world, vol 2. New world vultures to Guineafowl. Lynx, Barcelona

Edwards AL (1985) Multiple regression and the analysis of variance and covariance, 2nd edn. Freeman, San Francisco

Engler R, Guisan A, Rechsteiner L (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. J Appl Ecol 41:263–274

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

Frair J, Nielsen SE, Merrill EH, Lele SR, Boyce MS, Munro RHM, Stenhouse GB, Beyer HL (2004) Removing GPS collar bias in habitat selection studies. J Appl Ecol 41:201–212
Gibson LA, Wilson BA, Cahill DM, Hill J (2004) Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. J Appl Ecol 41:213–223
Gil-Sánchez JM, Molino F, Valenzuela G (1994) Parámetros reproductivos y de alimentación del Águila real (*Aquila crhysaetos*) y del Águila perdicera (*Hieraaetus fasciatus*) en la provincia de Granada. Aegypius 12:47–52
Gil-Sánchez JM, Molino-Garrido F, Valenzuela-Serrano G (1996) Selección de hábitat de nidificación por el Águila perdicera (*Hieraaetus fasciatus*) en Granada (SE de España). Ardeola 43:189–197
Gil-Sánchez JM, Molino F, Valenzuela G, Moleón M (2000) Demografia y alimentación del Águila-azor Perdicera (*Hieraaetus fasciatus*) en la provincia de Granada. Ardeola 47:69–75
Gil-Sánchez JM, Moleón M, Otero M, Bautista J (2004) A nine-year study of successful breeding in a Bonelli's eagle population in southeast Spain: a basis for conservation. Biol Conserv 118:685–694
Grand J, Cushman SA (2003) A multi-scale analysis of species–environment relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida–Quercus ilicifolia*) community. Biol Conserv 112:307–317
Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Model 157:89–100
Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186
Hagan MT, Demuth HP, Beale M (1996) Neural network design. PWS Publishing, Boston
Hagemeijer EJM, Blair MJ (1997) The EBCC atlas of European breeding birds: their distribution and abundance. Poyser, London
Haykin S (1999) Neural networks: a comprehensive foundation. Macmillan, New York
Hirzel AH, Hausser J, Chessel D, Perrin N (2002). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83:2027–2036
Hobson KA, Kirk DA, Smith AR (2000) A multivariate analysis of breeding bird species of western and central Canadian boreal forests: stand and spatial effects. Ecoscience 7:267–280
Hosmer DW, Lemeshow S (2000) Applied logistic regression analysis, 2nd edn. Wiley, New York
Jeganathan P, Green RE, Norris K, Vogiatzakis IN, Bartsch A, Wotton SR, Bowden CGR, Griffiths GH, Pain D, Rahmani AR (2004) Modelling habitat selection and distribution of the critically endangered Jerdon's courser *Rhinoptilus bitorquatus* in scrub jungle: an application of a new tracking method. J Appl Ecol 41:224–237
Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71
Johnson DE (1998) Applied multivariate methods for data analysts. Brooks Cole, Kansas State University, Kansas
Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. J Appl Ecol 41:238–251
Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108
Jokimäki J, Huhta E (1996) Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. Ornis Fennica 73:97–113
Jones J (2001) Habitat selection studies in avian ecology: a critical review. Auk 118:557–562
Keating KA, Cherry S (2004) Use and interpretation of logistic regression in habitat-selection studies. J Wild Manag 68:774–789
Kirk DA, Boutin C, Freemark KE (2001) A multivariate analysis of bird species composition and abundance between crop types and seasons in southern Ontario, Canada. Ecoscience 8:173–184
Lehmann A, Overton JMcC, Austin MP (2002a) Regression models for spatial prediction: their role for biodiversity and conservation. Biodivers Conserv 11:2085–2092
Lehmann A, Overton JMcC, Leathwick JR (2002b) GRASP: generalized regression analysis and spatial predictions. Ecol Model 157:187–205
Levin AS (1992) The problem of pattern and scale in Ecology. Ecology 73:1943–1967
Li WJ, Wang ZJ, Ma ZJ, Tang HX (1999) Designing the core zone in a biosphere reserve based on suitable habitats: Yanchang Biosphere Reserve and the red-crowned crane (*Grus japonensis*). Biol Conserv 90:167–173
López-López P, García-Ripollés C, Aguilar JM, García F, Verdejo J (2003) Two-spatial scale multifactor analysis on Bonelli's eagle (*Hieraaetus fasciatus*) nest-site selection in the East of Iberian Peninsula. In: Proceedings II Iberian ornithological workshop. Aveiro, Portugal
Luck GW (2002) The habitat requirements of the rufous treecreper (*Climacteris rufa*). II. Validating predictive habitat models. Biol Conserv 105:395–403
MacNally R (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between and reconciliation of ''predictive'' and ''explanatory'' models. Biodivers Conserv 9:655–671
Malanson GP, Westman WE, Yan YL (1992) Realized versus fundamental niche functions in a model of chaparral response to climate change. Ecol Model 64:261–277
Manel S, Dias J, Buckton ST, Ormenrod SJ (1999) Alternative methods for predicting species distribution: an illustration with Himalayan river birds. J Appl Ecol 36:734–747
Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. J Appl Ecol 38:921–931
Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer, Dordrecht
Martí R, Del Moral JC (eds) (2003) Atlas de las Aves Reproductoras de España. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid
Martínez JA, Serrano D, Zuberogoitia I (2003) Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. Ecography 26:21–28
Mañosa S, Real J, Codina J (1998) Selection of settlement areas by juvenile Bonelli's eagle in Catalonia. J Raptor Res 32:208–214
McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall/CRC, London
Montgomery DC, Peck EA (1982) Introduction to regression analysis. Wiley, New York
Nicholls AO (1989) How to make biological survey go further with generalized linear models. Biol Conserv 73:1–17
Ontiveros D (1999) Selection of nest cliffs by Bonelli's eagle (*Hieraaetus fasciatus*) in southeastern Spain. J Raptor Res 33:110–116
Ontiveros D, Pleguezuelos JM (1999) Influence of prey densities in the distribution and breeding success of Bonelli's eagle (*Hieraaetus fasciatus*): management implications. Biol Conserv 93:19–25
Ontiveros D, Pleguezuelos JM (2003) Physical, environmental and human factors influencing productivity in Bonelli's eagle *Hieraaetus fasciatus* in Granada (SE Spain). Biodivers Conserv 12:1193–1203
Orians G, Wittenberger J (1991) Spatial and temporal scales in habitat selection. Am Nat 137:29–49
Osborne PE, Alonso JC, Bryant RG (2001) Modelling landscape-scale habitat-use using GIS and remote sensing: a case study with great bustards. J Appl Ecol 38:458–471

Pearce J, Ferrier S (2000a) An evaluation of alternative algorithms for fitting species distribution models using logistic regression. Ecol Model 128:127–147

Pearce J, Ferrier S (2000b) Evaluating the predictive performance of habitat models development using logistic regression. Ecol Model 133:225–245

Penteriani V, Faivre B (1997) Breeding density and landscape-level habitat selection of Common Buzzards (*Buteo buteo*) in a mountain area (Abruzzo Apennines, Italy). J Raptor Res 31:208–212

Poirazidis K, Goutner V, Skartsi T, Stamou G (2004) Modelling nesting habitat as a conservation tool for the Eurasian black vulture (*Aegypius monachus*) in Dadia Nature Reserve, northeastern Greece. Biol Conserv 118:235–248

Pérez-Cueva A (1994) Atlas Climático de la Comunidad Valenciana. Conselleria de Territori i Habitatge. Generalitat Valenciana, Valencia

Quereda J, Montón E, Escrig J (1999) El clima de la provincia de Castellón. In: Gimeno MA (ed) La provincia de Castellón. Servicio de Publicaciones, Diputación de Castellón, pp 51–60

Real J, Mañosa S, Codina J (1997) Post-nestling dependence period in the Bonelli's eagle *Hieraaetus fasciatus*. Ornis Fennica 75:129–137

Real J (2004) Águila-azor perdicera, *Hieraaetus fasciatus*. In: Madroño A, González C, Atienza JC (eds) Red Book of the Birds of Spain. Libro Rojo de las Aves de España. Dirección General para la Biodiversidad-SEO/Birdlife, Madrid

Real J, Mañosa S, Codina J (1996) Estatus, Demografía y conservación del Águila perdicera (Hieraaetus fasciatus) en el Mediterráneo. In: Muntaner J, Mayol J (eds) Biología y conservación de las rapaces mediterráneas. Monografía 4 SEO, Madrid, pp 55–62

Real J, Mañosa S (1997) Demography and conservation of western European Bonelli's eagle (*Hieraaetus fasciatus*) populations. Biol Conserv 79:59–66

Rico L, Sánchez-Zapata JA, Izquierdo A, García JR, Morán S, Rico D (1999) Tendencias recientes en las poblaciones del Águila Real *Aquila chrysaetos* y el Águila-Azor perdicera *Hieraaetus fasciatus* en la provincia de Valencia. Ardeola 46:235–238

Rivas-Martínez S (1987) Memoria del mapa de series de vegetación de España. Instituto Nacional para la Conservación de la Naturaleza ICONA, Madrid

Sakamoto Y, Ishiguro M, Kitagawa G (1986) Akaike information criterion statistics. KTK Scientific, Tokyo

Seoane J, Bustamante J, Díaz-Delgado R (2004) Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. Ecol Model 171:209–222

Sokal RR, Rohlf FJ (1981) Biometry. Freeman WH and Company, New York

SPSS Inc. (1999) Computer program manual. Version 10. 1. SPSS Inc. 1989–1999

StatSoft (1998) Statistica for windows (Computer program manual). StatSoft, Tulsa

Steenhof K, Kochert MN, McDonald TL (1997) Interactive effects of prey and weather on golden eagle reproduction. J Anim Ecol 66:350–362

Store R, Jokimäki J (2003) A GIS-based multi-scale approach to habitat suitability modelling. Ecol Model 169:1–15

Suárez-Seoane S, Osborne PE, Alonso JC (2002) Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. J Appl Ecol 39:755–771

Sánchez-Zapata JA, Calvo JF, Carrete M, Martínez JE (2000) Age and breeding success of a Golden Eagle *Aquila chrysaetos* population in Southeastern Spain. Bird Study 47:235–237

Sánchez-Zapata JA, Calvo JF (1999) Raptor distribution in relation to landscape composition in semi-arid Mediterranean habitats. J Appl Ecol 36:254–262

Wiens JA (1989a) The ecology of bird communities, vol 1. Foundations and patterns. Cambridge University Press, Cambridge, 539 pp

Wiens JA (1989b) Spatial scaling in ecology. Funct Ecol 3:385–397

Yanez M, Floater G (2000) Spatial distribution and habitat preferences of the endangered tarantula *Brachypelma klaasi* (Araneae: Theraphosidae) in Mexico. Biodivers Conserv 9:795–810