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Modelling the distribution of short-toed eagle (*Circaetus gallicus*) in semi-arid Mediterranean landscapes: identifying important explanatory variables and their implications for its conservation

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Abstract Mediterranean semi-arid landscapes are currently experiencing accelerated land use changes which are affecting species distributions. An important fraction of the European short-toed eagle (*Circaetus gallicus*) population, a specialised snake predator, breeds in this kind of landscapes. Information on the habitat characteristics that may affect the occurrence of this species is of paramount importance to try to evaluate how this species could be affected by ongoing territory changes. In this study, we use hierarchical partitioning analysis to identify environmental variables (natural vegetation, agricultural uses, hydrological web, topography, human pressure and climate) at two resolution scales (1 and 4 km^2) that may influence the presence of the short-toed eagle in a populated Mediterranean region in southeastern Spain. Results were highly consistent between scales. Forest was the most important variable determining the presence of the short-toed eagle in the study area, showing a positive effect, particularly those inland forests with nearby presence of sunny open scrublands where the species may find its prey. On the contrary, herbaceous crops and all variables related to human pressure, including urbanisations, dispersed houses and roads, are negatively affecting the occurrence of the species. These variables are strongly related to the main driving forces that change landscapes in our study area, including the abandonment of traditional territory uses and the expansion of urbanised areas. These results indicate that the increasing number of housing developments projected in inland areas would have a detrimental effect on the short-toed eagle, especially if they are located close to pine forests and rivers.

Keywords *Circaetus gallicus* · Habitat use · Hierarchical partitioning · Semi-arid landscapes

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Introduction

Predicting the occurrence of animals in relation to habitat has become a fundamental component in several disciplines in conservation biology including conservation planning, wildlife management and in the assessment of the impact of land use changes (see Guisan and Zimmermann 2000 for a review). This is of particular importance in concentrating efforts to preserve threatened species, especially with respect to identifying, protecting and restoring critical habitats. In all cases, knowledge of the factors that influence a species' distribution is necessary to determine whether distribution and abundance could be limited by the availability of suitable habitat or affected by territory changes.

Raptors are usually highly selective with respect to their habitat, especially regarding the availability of suitable areas for breeding (Janes 1985). Studies suggest that the analysis of raptor habitat use, particularly for territorial species, significantly contributes to the development of conservation measures for these species (e.g. Donázar et al. 1993; López-López et al. 2006, 2007; Newton et al. 1981; Suárez et al. 2000). The short-toed eagle (*Circaetus gallicus*) is a migratory bird of prey which breeds throughout the Palaearctic region from the Iberian Peninsula to India (Cramp and Simmons 1980; Mañosa 2003). The wintering areas of the species remain largely unknown, but most of the short-toed eagles breeding in Western Europe winter in tropical Africa (Cramp and Simmons 1980; del Hoyo et al. 1994). In Europe, the breeding population is 6,200–14,000 pairs and is listed as SPEC 3 (unfavourable conservation status in Europe, not concentrated in Europe; BirdLife 2009). In Spain, the current estimates reveal a population of 2,500–3,000 breeding pairs, and the species is listed as Least Concern in the Red Data Book of Birds of Spain (Madroño et al. 2004; Mañosa 2003). This species builds its nests on trees within forests with relatively low human disturbance, mainly on pines but also other tree species (Bakaloudis et al. 1998; Mañosa 2003; Thiollay 1968). However, their habitat during the breeding season is also composed of open areas where the species can find their main prey (Campión 1996; Sánchez-Zapata and Calvo 1999), snakes and other reptiles (e.g. Bakaloudis et al. 1998; Gil and Pleguezuelos 2001; Mañosa 2003). Nowadays, the species seems to be more abundant than in the past decades. However, the recent land use changes (particularly the conversion of traditional agricultural areas into urbanised areas) are thought to negatively affect the numbers of the short-toed eagle in Spain (Mañosa 2003).

An important proportion of the European short-toed eagle population breeds in Mediterranean landscapes, which are experiencing accelerated changes mainly due to the increasing urbanisation of coastal and inland areas, abandonment of traditional farming activities and expansion of modern intensified agricultural methods. Together, these changes are increasing the fragmentation of these landscapes (Serra et al. 2008). Semi-arid landscapes may be more affected by these transformations as they are more prone to desertification (García-Ruíz et al. 1996; Lasanta et al. 2000). In this context, knowledge of the habitat features that may be limiting the numbers or distribution of a given species may be of paramount importance for its conservation in an increasingly human-altered landscape (Guisan and Zimmermann 2000; Lehmann et al. 2002). In particular, slow-reproducing species which are often more sensitive to habitat alteration and disturbance may be largely affected by human-induced changes in the environment (Brambilla et al. 2006; Liberatori and Penteriani 2001; Ontiveros et al. 2004). Once the habitat requirements for a given species have been estimated, it will become easier to predict how habitat loss and transformation could affect this species.

This study has been conducted within the semi-arid region of Spain with the aim of identifying landscape-level habitat features (i.e. including both nesting and hunting habitat) which may be involved in determining the presence of the short-toed eagle during the breeding season. The study was conducted in Alicante province, one of the Spanish provinces in which land use changes are most intense. Previous studies dealing with breeding habitat selection of short-toed eagles have been conducted using regression modelling (Bakaloudis et al. 2001; Bustamante and Seoane 2004; Moreno-Rueda and Pizarro 2007; Sánchez-Zapata and Calvo 1999). These studies of short-toed eagles have shown some differences in their results, and in some cases, the variables selected as predictors of short-toed eagle occurrence could be difficult to interpret in relation to the species' biology (Bustamante and Seoane 2004), which limits their applicability to its conservation. Based on those previous studies, it is not clear which variables are most important to explain the presence of the short-toed eagle in Mediterranean landscapes. Contradictory results have been published regarding the importance of the scrublands, which have been found to have a negative (Sánchez-Zapata and Calvo 1999), a positive (Moreno-Rueda and Pizarro 2007) and at a lower scale a non-significant influence (Bustamante and Seoane 2004; Sánchez-Zapata and Calvo 1999). Also, cultivated areas have been found not to affect the distribution of this species (Bustamante and Seoane 2004; Moreno-Rueda and Pizarro 2007), whilst others found them to be important (positive effect at the 9-km^2 scale, but negative effect at the 100-km^2 scale; Sánchez-Zapata and Calvo 1999). Thus, regression modelling seems not to be adequate to distinguish which variables have a true relationship with the presence of a given species (e.g. MacNally 2000). Therefore, in the present study, we have used hierarchical partitioning analysis (Chevan and Sutherland 1991; MacNally 2000) in order to identify which variables are related to the presence of the short-toed eagle and to minimise the effect of collinearity between them.

Materials and methods

Study area

The study was carried out in Alicante province (southeastern Spain; Fig. 1). This province has an area of approx. 5,800 km^2 and is very mountainous in the North and West,

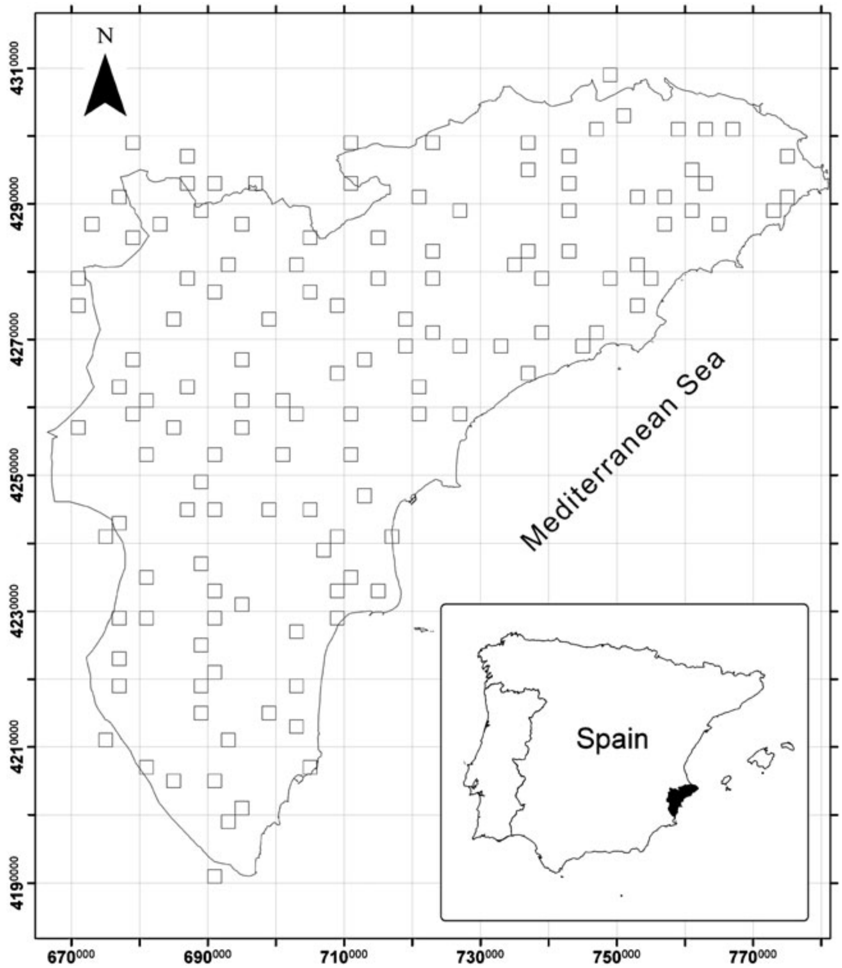

Fig. 1 Map of Alicante province and its location in SE Spain. The 10×10-km UTM grid is shown (*thin line*) along with the 2×2 squares that were randomly selected for the fieldwork of the Atlas of Breeding Birds of Alicante Province

but is mostly flat to the South and East (where coastal areas are found). Most of the province belongs to the Mediterranean semi-arid climate (Rivas-Martínez 1987). The annual mean precipitation is around 300 mm in the southern half of the study area, but between 300 and 600 mm in most other areas, and occurs mainly in autumn and spring. There is a great variety of vegetation types and ecosystems; the most abundant are scrublands followed by scrublands with trees. These patches of natural vegetation are interspersed with both intensive and non-intensive agricultural areas.

Population data of short-toed eagle

Data on the presence of short-toed eagles in the study area were collected from several sources. Firstly, all data on eagle occurrence obtained during censuses for the Atlas of Breeding Birds of the Alicante Province were used for the analyses. These censuses were conducted in a stratified random sample of 132 2×2-km UTM grid cells, covering approx. 10% of the area of Alicante province (Fig. 1). To obtain this sample, two 2×2-km cells were randomly selected within each 10×10-km UTM square. In each 1-km^2 square (within the square of 2×2 km), a linear transect of 1 km was walked on two occasions during one breeding season between 2001 and 2004. Using this information, short-toed eagles were detected in 18 1×1-km squares included in 14 2×2-km cells.

Secondly, we obtained data from the Ornithological Records of the Alicante province from 1999 to 2003 (SEO-Alicante 2001, 2002, 2006); this provided four additional presence data at the 1×1-km scale. Lastly, information of recordings of the species (until 2007) was obtained from the Conselleria de Medio Ambiente, Agua, Urbanismo y Vivienda, of the Comunidad Valenciana that contributed 29 additional records in 1×1-km squares (12 squares where short-toed eagle nests were known and 17 where repeated observations of the species were recorded). Using these last two sources, presence at the 2×2-km scale was assigned if the square included at least one presence cell at the 1×1-km scale. Overall, at the scale of 1 km^2, the species was detected in 51 squares and was considered absent in 505, whilst at the scale of 4 km^2 (2×2 km), the eagle was present in 45 squares and absent in 115. Although the characteristics of the habitats chosen for nesting, hunting or other activities may be different, all data were included in the analysis irrespective of their origin because (1) some of the squares where the species was detected during Atlas fieldwork may also be used for nesting (adequate trees to locate the nest were present); (2) the size of the sampling unit (1- or 4-km^2 squares) is big enough to include both nesting and/or hunting habitat (studies focusing on nesting habitat selection have used much smaller sampling plots for instance, 0.4 ha in Bakaloudis et al. 2001); and (3) in this study, we intended to model the probability that a piece of territory would be included within the short-toed eagle home range either for breeding or hunting. The importance of environmental variables for habitat selection can vary with spatial scale, and previous studies have shown that this is the case in short-toed eagle (Sánchez-Zapata and Calvo 1999). Therefore, we performed analyses at the two scales allowed by our data.

Predictive variables

To describe the habitat in every 1×1- and 2×2-km grid cell and given the existing knowledge on the biology of the species, we estimated a total of 26 variables representing multiple territory characteristics that could potentially affect the distribution of the eagle, i.e. extent of natural vegetation (forests, scrublands and mixtures of both), area covered by agricultural land uses, hydrological web (including both natural and artificial water bodies), topography, climate and variables related to human pressure (Table 1). Land use variables were obtained from 1:50,000 digital maps from the Spanish Ministry of Agriculture; hydrological web variables were obtained from 1:50,000 cartography of Conselleria d'Obres Publiques (COPUT, Valencian Region Government); and topographical variables were obtained from a digital elevation model derived from this last source. Infrastructure and urbanisation variables were obtained from 1:10,000 cartography of Institut Cartogràfic Valencià (Valencian Region Government). Spatial variation of temperature and rainfall was modelled from data in the climatic atlas of the Valencian Region (Pérez-Cueva 1994) using Kriging (Oliver and Webster 1990), and the resulting estimates were used to calculate the Thermicity and Ombrothermic indices as defined by Rivas-Martínez (1995, 1997). Land cover variables represent hectares of each vegetation type in every grid cell. The land use map provides general values for the scrubland and scrubland–pine mixture variables. Thus, given that topography and water availability strongly influence the development of scrubs and pines (e.g. Rivas-Martínez 1987), these variables were subdivided into types by combining these original variables with ombrotypes (semi-arid, dry, sub-humid), bioclimatic belts (thermo-Mediterranean, meso-Mediterranean, supra-Mediterranean) and aspect (North, South). In this way, 12 scrubland types and ten scrubland–pine mixture types were defined and were used to calculate the Shannon diversity index of scrubland types and pine–scrubland mixture types present in each cell. Shannon diversity index of forest types, herbaceous crops and tree crops for each cell were calculated from the cover of the forest and farming types identified in the original land use map.

The magnitude of multicollinearity among habitat variables within each variable group was evaluated by

Table 1 Groups and descriptions of the habitat variables used in the hierarchical partitioning analyses

Variable	Definition
Natural vegetation (area in ha except diversity indexes)	
Scrublands	Area covered by any kind of scrubland
ScrubPines	Area covered by a mixture of pines and scrublands
Forest	Area covered by forest
DiversityForest	Shannon diversity index of forest types present
DiversityScrubland	Shannon diversity index of scrubland types present
DiversityScrubPines	Shannon diversity index of pine–scrubland mixture types
Farming (area in ha, except diversity indexes)	
DiversityTreeFar	Shannon diversity index of tree crops present
DiversityHerbFar	Shannon diversity index of herbaceous crops
TreeFarming	Area covered by tree crops
HerbFarming	Area covered by herbaceous crops
Hydrological web	
River	Length (m) of rivers
TotArPonds	Area (m^2) covered by any kind of ponds
GullyRiverBed	Length (m) of gullies and dry riverbeds
TotalChan	Length (m) of channels and ditches
Human pressure	
Unproductive	Area covered by unproductive uses
IsolHouses	Area (m^2) covered by isolated houses
HousDevel	Area (m^2) covered by housing developments
Urban	Area (m^2) occupied by cities
PavRoad	Length (km) of paved roads
UnPavRoad	Length (km) of unpaved roads
Climatic	
DistCoast	Distance to the coast (km)
OmbrIndex	Ombrothermic index
ThermIndex	Thermicity index
Topography	
RA + 45	Rocky area with slope higher than 45%
AltMean	Average altitude (m)
Slope	Average slope

calculating the variance inflation factor (VIF; Fox 2002). When VIF is >10, we considered multicollinearity to be high (see, e.g. López-López et al. 2006). The variable with highest VIF was slope, both at the 1×1-km scale (VIF = 3.52) and the 2×2-km scale (VIF = 5.05). Therefore, we considered that multicollinearity was moderate to low.

Statistical model

Hierarchical partitioning (HP) was used to identify the most likely variables explaining the presence of short-toed eagles in our study area during the breeding season. Hierarchical partitioning computes all of the possible hierarchical models that can be developed with a set of independent predictive variables; this is to say that if *U*, *V* and *W* are variables, HP computes single-order (*U*, *V*, *W*), second-order (*UV*, *UW*, *VW*) and higher-order (*UVW*) models and tests whether the addition of a given variable produces an improvement in goodness of fit. For each independent variable, their explanatory power is segregated into the independent effect '*I*' and the effects caused jointly with other variables '*J*' (MacNally 2000). It is important to note that HP does not intend to provide a predictive model, but allows identifying variables that contribute more to a decrease of deviance by themselves, independently of the others.

All statistical analyses were conducted in R (R Development Core Team 2009). Hierarchical partitioning was conducted with the 'hier.part' package in R (Walsh and MacNally 2003) using logistic regression and log-likelihood as the goodness-of-fit measure. A HP analysis with each group of habitat variables (Table 1) was performed at both scales. The effect of spatial autocorrelation of the sampling squares was controlled by including five linear and quadratic geographical variables in all of the analyses (longitude, longitude^2, latitude, latitude^2, and longitude × latitude) calculated from the UTM coordinates of each square (Legendre 1993). As suggested by MacNally (2002), the significance of the individual contribution of each variable included in the analysis was evaluated by a randomization procedure based on 999 randomizations. In order to test the relative importance of the variables representative of each group when analysed together, a new HP analysis for each scale was made using a set of predictors that included the variable with the largest independent contribution (*I*) of each group and the five geographical variables. The VIF for these sets of predictors was also calculated and was found to be always <2 at both scales. The sign of each variable was assessed from logistic regression models. For the analyses by groups of variables, separated logistic regressions were conducted for each habitat variable plus the geographic variables, whilst in the overall analysis, a single logistic regression including all the variables was conducted.

Results

The results of the hierarchical partitioning procedure using groups of variables at the two spatial scales are shown in Table 2. Human pressure and natural vegetation were the groups of variables that explained the highest percentage of the deviance at the 1×1-km scale. At the 2×2-km scale, the highest percentage of deviance reduction was produced by topography and natural vegetation variables. The variables that had a significant effect on the occurrence of the short-toed eagle were mainly the same on both scales; the only differences were observed in scrubland area, diversity of forests (both having a significant positive effect at the 1×1-km scale but not at the 2×2-km) and in the area covered by herbaceous crops (significant at the 2×2 but not at the 1×1 scale). The variables showing the greatest independent effect on the eagle's occurrence were the area covered by forests and the mean slope at the 1×1-km and 2×2-km scales, respectively.

Analysing the results by groups of variables, at least one variable of each group had a significant effect on the presence of the short-toed eagle in Alicante province at both the considered scales. The area covered by forest was the variable with both the most independent and joint contribution in the natural vegetation variables group at the two spatial scales. The next variable of this group showing a significant effect on short-toed eagle occurrence at both scales was the diversity of scrublands. All of the significant variables that referred to natural vegetation had a positive relationship with the occurrence of short-toed eagles in the study area. From the variables related to agriculture, only the diversity of herbaceous crops (at both scales) and the area of herbaceous crops (at the 2×2-km scale) had a significant negative contribution to the presence of the short-toed eagle. All of the variables related to human pressure had a significant and negative relationship with the presence of the eagle at both scales. The extent of unproductive land use (mainly urbanised areas) and the area covered by dispersed isolated houses were the two most important variables within this group at both scales. All variables in this group presented a larger joint than independent contribution, suggesting a high degree of correlation between them. This is not surprising given that human activities tend to cluster in certain areas and that the variable unproductive land use include urban and other areas with high density of buildings and roads.

The length of rivers had a significant positive effect on the distribution of the short-toed eagle, being the only variable related to the hydrological web that had a significant contribution at both scales. Among the variables related to climatology, the distance to the coast (positive effect) and the thermicity index (negative effect) were significant at both scales. These variables also presented a

Table 2 Results of the hierarchical partitioning analyses performed with each group of habitat variables at two scales: 1 and 4 km^2

	1×1km					2×2km				
	%Dev	*I*	*J*	%*I*	*z* score	%Dev	*I*	*J*	%*I*	*z* score
Natural vegetation	19.1					20.0				
Scrublands	+	1.23	−1.12	3.77	1.91*		0.93	−0.19	4.88	1.16
ScrubPines		1.07	−1.04	3.30	1.45		0.67	−0.62	3.54	0.64
Forest	+	10.39	16.24	31.87	22.03***	+	5.33	8.26	28.04	11.47***
DiversityForest	+	1.71	0.99	5.23	3.11***		1.01	0.57	5.33	1.21
DiversityScrubland	+	2.49	1.08	7.65	4.98***	+	1.42	0.51	7.49	2.73**
DiversityScrubPines		1.06	−0.84	3.25	1.30		0.83	−0.36	4.35	0.92
Longitude		2.69	−0.51	8.24	5.31***		1.65	−0.40	8.68	3.14***
Longitude^2		2.46	−0.21	7.55	4.77***		1.56	−0.27	8.23	2.75**
Latitude		3.81	2.78	11.68	7.45***		2.21	1.77	11.66	3.83***
Latitude^2		2.75	3.84	8.43	4.00***		1.62	2.37	8.52	2.40**
Longitude × Latitude		2.94	−2.04	9.03	4.76***		1.76	−1.25	9.27	2.54**
Farming	13.1					15.6				
DiversityTreeFar		0.50	−0.17	2.24	−0.02		0.27	−0.15	1.84	−0.36
DiversityHerbFar	−	2.03	0.29	9.08	2.04**	−	1.81	0.69	12.23	1.74*
TreeFarming		1.15	0.78	5.13	0.78		0.19	0.35	1.30	−0.44
HerbFarming		1.51	−0.28	6.75	1.39	−	1.97	0.00	13.29	1.86*
Longitude		2.87	−1.52	12.86	3.31***		1.75	−0.92	11.80	1.54
Longitude^2		4.70	−3.29	21.01	5.36***		2.75	−1.89	18.57	2.68**
Latitude		2.86	1.26	12.80	3.08***		1.90	0.75	12.82	1.74*
Latitude^2		2.87	1.24	12.86	2.92***		1.88	0.76	12.73	1.72*
Longitude × Latitude		3.86	−3.29	17.26	4.78***		2.28	−1.94	15.42	2.37**
Hydrological web	11.9					16.2				
River	+	2.33	−0.75	11.54	2.28**	+	2.77	−1.15	18.05	2.67**
TotArPonds		0.15	0.00	0.76	−0.50		0.53	0.77	3.42	−0.05
GullyRiverBed		0.24	0.26	1.21	−0.41		1.42	0.77	9.25	1.22
TotalChan		0.82	0.96	4.04	0.28		0.78	0.95	5.11	0.26
Longitude		2.93	−1.57	14.46	3.37***		1.92	−1.09	12.47	2.00*
Longitude^2		4.61	−3.20	22.78	5.99***		2.53	−1.67	16.48	3.29***
Latitude		2.62	1.50	12.96	3.18***		1.53	1.11	9.98	1.41
Latitude^2		2.67	1.45	13.17	2.86**		1.52	1.12	9.91	1.25
Longitude × Latitude		3.86	−3.30	19.09	4.43***		2.35	−2.01	15.33	2.69**
Human pressure	19.4					17.7				
Unproductive	−	5.10	14.53	15.41	11.86***	−	2.72	8.26	16.15	5.85***
IsolHouses	−	5.56	13.88	16.81	11.96***	−	2.40	6.42	14.25	4.81***
HousDevel	−	2.45	4.50	7.42	4.05***	−	1.50	3.60	8.93	2.47**
Urban	−	1.67	2.42	5.06	2.79**	−	1.40	3.15	8.31	2.18*
PavRoad	−	2.12	5.07	6.42	3.97***	−	1.09	2.56	6.45	1.84*
UnPavRoad	−	4.88	11.16	14.76	11.09***	−	1.31	3.00	7.81	2.37**
Longitude		2.19	−0.19	6.61	4.81***		1.09	0.06	6.47	1.61
Longitude^2		1.75	0.33	5.30	3.46***		0.91	0.28	5.40	1.44
Latitude		2.96	3.10	8.97	6.85***		1.79	1.88	10.63	3.54***
Latitude^2		2.18	3.89	6.59	3.68***		1.37	2.30	8.14	1.96*
Longitude × Latitude		2.20	−1.37	6.64	3.62***		1.26	−0.79	7.46	1.69*
Climate	13.2					15.2				
DistCoast	+	2.79	6.01	12.38	3.04***	+	1.99	3.98	13.73	1.99*
OmbrIndex		1.63	−0.34	7.21	1.51		1.14	−0.08	7.90	0.75

Table 2 (continued)

	1×1km					2×2km				
	%Dev	*I*	*J*	%*I*	*z* score	%Dev	*I*	*J*	%*I*	*z* score
ThermIndex	–	5.86	7.59	25.98	8.11***	–	3.62	5.26	25.02	4.27***
Longitude		2.38	−1.02	10.56	2.70**		1.52	−0.69	10.46	1.38
Longitude^2		3.88	−2.47	17.18	4.46***		2.33	−1.47	16.11	2.54**
Latitude		1.65	2.47	7.32	1.52		1.09	1.56	7.50	0.70
Latitude^2		1.62	2.50	7.17	1.75*		1.04	1.61	7.17	0.66
Longitude × Latitude		2.75	−2.19	12.19	3.01**		1.75	−1.42	12.11	1.62
Topography	16.1					20.7				
RA + 45	+	2.88	−2.59	10.50	3.52***	+	3.36	−3.25	17.11	3.51***
AltMean	+	5.20	8.56	18.96	6.42***	+	3.12	5.61	15.87	3.70***
Slope	+	7.55	−0.25	27.50	10.25***	+	5.98	−1.28	30.48	7.40***
Longitude		2.18	−0.82	7.94	2.15*		1.27	−0.44	6.46	0.97
Longitude^2		3.04	−1.63	11.09	3.49***		1.63	−0.77	8.29	1.47
Latitude		2.00	2.13	7.27	1.94*		1.41	1.24	7.18	1.17
Latitude^2		1.95	2.16	7.12	1.97*		1.36	1.29	6.90	1.19
Longitude × Latitude		2.64	−2.08	9.62	3.26***		1.51	−1.17	7.71	1.25

%Dev is the percentage of deviance accounted for a logistic regression model including all variables in each group. *I* and *J* are respectively the independent and joint contribution of each habitat variable in group models. %*I* is the percentage of the group total *I* accounted for in each habitat variable. The sign of each variable is obtained from a logistic regression model for each habitat variable plus geographic variables. *Z* score is the randomization test for the independent contributions of each predictor variables calculated from 999 randomizations

*$p<0.05$, **$p<0.01$, ***$p<0.001$

large joint contribution since climate varies with geography, and distance to the coast and the thermicity index are negatively correlated. However, the fact that they presented a significant independent contribution suggests that their effect on the eagle presence is not due to this correlation. Finally, the three topographic variables (mean slope, mean altitude and rocky areas) all had a significant and positive effect on the occurrence of short-toed eagles in Alicante province at the two scales.

The overall models, which were created using the variable with the greatest independent effect of every group of variables in a single hierarchical partition analysis, resulted in a significant contribution of all the variables at both scales (Table 3). These models explained a slightly higher percentage of the deviance than that explained by any variable group in the previous analyses (Table 2). The area covered by forests was the variable with the greatest explanatory power at the two scales considered, whilst the importance of the slope was reduced significantly in the overall model. Thermicity index and human pressure (represented by isolated buildings at the 1×1-km scale and unproductive uses at the 2×2-km scale) were the next two most important variables according to their independent contribution. Altogether, these three variables explained approximately 50% of the deviance reduction at both scales. Herbaceous crops and rivers had relatively small contributions in the overall model according to their results in group models.

Discussion

In this paper, we have evaluated the habitat variables that may explain the occurrence of the short-toed eagle in Alicante province during the breeding season. Hierarchical partitioning was used to evaluate the relative "explanatory power" of the predictive variables (Chevan and Sutherland 1991; MacNally 2000) at two spatial scales. This revealed a strong consistency between the scales since 15 out of 18 significant variables were the same. At the 1×1-km scale, the groups of variables that explained most deviance were human disturbance and natural vegetation, whilst at the 2×2-km scale, the most important groups were topography and also natural vegetation and human pressure.

The variable that had both the highest independent and joint contribution at the 1×1-km scale was the area covered by forests, which was positively related to the presence of the short-toed eagle. This land use variable was also very important at the 2×2-km scale. Moreover, in the models developed with the selection of variables with the largest independent contribution of each group, forest was the most important variable at both scales (Table 3). Forests are

Table 3 Results of hierarchical partitioning analyses performed with the variable with the highest independent contribution of each group at two scales (1 and 4 km^2)

	1×1 km						2×2 km				
Variables	Sign	*I*	*J*	%*I*	*z* score	Variables	Sign	*I*	*J*	%*I*	*z* score
Forest	+	7.89	17.64	20.67	18.84***	Forest	+	3.85	9.69	16.96	7.85***
DiversityHerbFar	−	1.80	1.76	4.72	3.39***	HerbFarming	−	1.27	1.68	5.61	1.97*
River	+	2.08	0.35	5.45	3.79***	River	+	1.73	0.71	7.61	2.82**
IsolHouses	−	5.75	14.49	15.09	11.06***	Unproductive	−	3.32	8.57	14.64	6.07***
ThermIndex	+	5.50	15.13	14.42	12.19***	ThermIndex	+	3.38	9.96	14.89	6.82***
Slope	+	3.33	7.85	8.74	7.15***	Slope	+	1.97	5.09	8.69	3.45***
Longitude	−	2.28	−0.20	5.99	3.87***	Longitude	−	1.38	−0.14	6.09	2.35**
Longitude^2	−	2.15	0.01	5.64	4.11***	Longitude^2	−	1.33	−0.04	5.88	2.22**
Latitude	−	2.90	3.42	7.61	6.13***	Latitude	−	1.72	2.25	7.58	3.29***
Latitude^2	−	2.16	4.15	5.67	3.40***	Latitude^2	+	1.37	2.60	6.06	1.85*
Longitude×Latitude	+	2.29	−1.42	6.00	3.65***	Longitude×Latitude	+	1.36	−0.85	5.98	1.70*
%Dev	22.4					%Dev	23.9				

%Dev is the percentage of deviance accounted for a logistic regression model including all variables. *I* and *J* are respectively the independent and joint contribution of variable. %*I* is the percentage of the total *I* accounted for each habitat variable. The sign of each variable is obtained from a logistic regression model including all variables. *Z* score is the randomization test for the independent contributions of each predictor variable calculated from 999 randomizations

*$p<0.05$, **$p<0.01$, ***$p<0.001$

important for short-toed eagles because they nest on trees (e.g. Bakaloudis et al. 2001). This is in agreement with the results of Sánchez-Zapata and Calvo (1999) who found in the nearby province of Murcia that pine tree forests were the variable with the highest relationship to the breeding density of this species at both the 9- and 100-km^2 scales and with those of Bustamante and Seoane (2004) whose best habitat models for short-toed eagle included this variable. Contrary to these findings, Moreno-Rueda and Pizarro (2007) did not detect differences of forest area between squares with the presence or absence of this species in a study area that partially overlaps that of Bustamante and Seoane (2004) and using the same scale as these authors. Therefore, Moreno-Rueda and Pizarro (2007) excluded this variable from their model on the basis of the possible lack of independence between land use variables. The HP analyses in the present study has shown that despite the potential multicollinearity between land use variables, the effect of forest cover may be of paramount importance as a determinant of the probability of presence of this species at several spatial scales.

The diversity of scrublands was found to have a positive significant contribution to the occurrence of short-toed eagles at both scales. Additionally, the total area of scrublands was only slightly significant at the 1×1-km scale. In previous studies, the effect of scrublands was unclear; for example, Sánchez-Zapata and Calvo (1999) reported that this land use variable was not significant at the 9-km^2 scale, but it had a negative effect at the 100-km^2 scale. Also, at the 100-km^2 scale, Moreno-Rueda and Pizarro (2007) found a positive effect of scrubland on short-toed eagle occurrence in Granada province (south-eastern Spain), whilst Bustamante and Seoane (2004) did not find a relationship at this scale in a study area that included Granada province. However, despite these diverse results, our analyses show that the diversity of scrublands, which may be used as a hunting habitat, may have a true independent contribution to explain the distribution of this eagle. Particularly, areas with a high diversity of scrublands may be important for the species as they may create edges between different habitat types, which may be related to a high abundance of prey (Wisler et al. 2008).

All of the variables related to human pressure had a significant negative effect on the presence of the species in the study area at both scales. The most significant variables at both scales were the area covered by unproductive land use and the area covered by urbanisations or isolated buildings. Unproductive land use is a mix of areas uncovered by vegetation, mainly urban-related land uses. The urbanisation variable did not include urban areas, but recent housing developments in a former rural countryside. In this sense, the recent transformations of rural areas into urbanised areas, including urbanisations and dispersed houses, may negatively affect the availability of suitable habitat during the breeding season for the short-toed eagle. Also, the roads, both paved and unpaved, had a negative effect on the eagles' occurrence. Variables directly related to human pressure on landscape, other than agricultural land uses, were previously taken into account only in the studies of Bustamante and Seoane (2004) (percent of urban use) and Moreno-Rueda and Pizarro (2007) (population density), and both studies found a non-significant influence of these variables at the 100-km^2 scale. Bakaloudis et al. (2001) found a negative effect of human disturbance close to the nest (35.7-m radius plots). The present study is the first to provide evidence of negative effects of several types of human activity on the species at a landscape scale. It is important to stress that we have detected a negative effect not only of land uses covering large and continuous areas of terrain, such as unproductive land use or urban cover, but also of spatially scattered land uses and infrastructure, such as isolated buildings and unpaved roads.

In the analysis of the influence of topography, all of the considered variables were found to have a positive effect on the short-toed eagle occurrence at both scales, with the variable slope contributing the most. This may reflect a preference for mountainsides, where eagles can take advantage of rising thermal updrafts that are developed here, using them to soar and save energy during their search for food (Jiménez and Jaksic 1989). Within the climate group, the variable with the largest independent contribution was the thermicity index (at both scales), and when analysed together with the best variable from each group, the thermicity index becomes the second or third most important variable depending on the scale. In this latter model, the thermicity index had a positive relationship, suggesting that in areas with appropriate vegetation (mainly pine forests) and low human pressure, the eagle is more likely to occur in warmer places. Since the short-toed eagle is specialised in feeding on reptiles, this correlation may be related to the preferences of its prey for warm sunny areas. Among the other studies of the species, only Moreno-Rueda and Pizarro (2007) included variables related to temperature; however, they did not detect any effect of these variables. Given that they modelled the distribution at a 100-km^2 scale, it is likely that within such a large area, a wide variation in temperature occurs, for instance between south and north slopes of mountains, and the importance of this variable would be diluted.

The distance to the coast is not strictly a climatic variable, but is correlated with climate as the sea influences seasonality and daily temperature oscillations and has a strong effect on local weather conditions. According to our results, this variable had a significant effect on the distribution of eagles after controlling for temperature (thermicity index) and geography. In addition, if the distance to the coast was included in the HP analyses performed with the best variables from each group, it was identified as the fourth most important variable (11.6% of total *I*, results not shown) ahead of slope, river and herbaceous crops, which suggests that the distance to the coast had an effect irrespective of other analysed variables. Thus, it appears that appropriate habitats located in inland areas of the province have a greater probability of being included in a short-toed eagle territory than similar coastal areas. One possibility to explain this result is that another variable affecting this species negatively, and not measured in this study, increased in forests closer to the coast. One candidate for such a variable could be fragmentation of forests, which is more intense in Mediterranean coastal areas (Serra et al. 2008). However, it is known that short-toed eagles may nest in small forests, provided that suitable nearby open habitats are available for hunting (Bakaloudis et al. 1998; Thiollay 1968). Thus, it seems more likely that a decrease in quality in the matrix surrounding coastal forests, associated with increasing human population density, could explain this result.

There is no consensus on the possible impact of cultivated land on habitat use by short-toed eagle. Bustamante and Seoane (2004) and Moreno-Rueda and Pizarro (2007) found no effect of cultivated lands, whilst Sánchez-Zapata and Calvo (1999) found a positive effect of herbaceous extensive agriculture (mostly cereals) at a 9-km^2 scale, but a negative effect of herbaceous intensive agriculture at a 100-km^2 scale. In our analyses, we have detected a negative effect at both scales of all crop variables analysed, although only the variables of herbaceous crops were significant. This result may be due to our herbaceous crop variables including both extensive and intensive farming, the latter having a greater negative impact on the eagle (Sánchez-Zapata and Calvo 1999). In any case, the variables related to agriculture had the lowest effect on the eagle distribution according to their low independent contribution.

The length of rivers was the only significant variable in the hydrological web group that was positively related to the presence of short-toed eagles. This variable was also included in the predictive models for this species developed by Bustamante and Seoane (2004) in Andalusia, but in contrast, Moreno-Rueda and Pizarro (2007) did not find a relationship between the length of rivers and short-toed eagle presence in the Granada province. The former authors only modelled short-toed eagle distribution within potential habitats for the species, and in this way, they may have been able to detect more subtle habitat effects despite working with 10×10-km squares. Although rivers are often considered as a topographic variable, at the same time, rivers are accompanied by riparian habitats that might constitute the true factor influencing species distributions. In the case of short-toed eagle, rivers could provide closer trees for nesting in some Mediterranean semi-arid areas where forests are poorly developed. Bustamante and Seoane (2004) also found a positive relationship between eagle occurrence and mean spring–summer vegetation index, which is positively correlated with water availability in semi-arid regions (Quevedo and Francés 2008). This suggests that short-toed eagles would select more productive areas. It is expected that as an ecosystem increases in productivity, more energy will be available at the top of the food chain, and hence, more prey would be available for top-level predators (e.g. Arim et al. 2007). Given that the short-toed eagle may be considered as a top-level predator (Gil and Pleguezuelos, 2001), we suggest that this relationship between short-toed eagle distribution and water courses or humidity in Mediterranean areas may be mediated by increasing reptile prey availability in more productive habitats.

The major driving forces of land use change in semi-arid landscapes of southeastern Spain in the last decades have been identified by several authors (see Martínez et al. 1997; Peña et al. 2007). One of these forces is the abandonment of traditional land uses, including wood or firewood extraction and traditional dry farming. The increasing availability of water resources and market demands has resulted in two other strong driving forces: intensification of agriculture and urbanisation. Thus, the areas in which traditional farming has been abandoned have followed two opposite processes, the invasion of scrubland and pine forests on the one hand and the intensification of agriculture or spreading of housing developments (mainly urbanisations) and dispersed houses for tourism on the other. These are processes that, according to our results, have opposite effects on short-toed eagles. Despite the effect of fires, analyses of chronosequences in some parts of our study area have shown that forest cover has increased during the last four decades between 20% and 30% (Martínez et al. 1997; Peña et al. 2007). However, urbanised areas have increased much more, especially in coastal areas (e.g. 21-fold in La Marina Baixa, northeastern Alicante province; Peña et al. 2007) rather than in non-coastal areas (virtually unchanged in some mountainous areas; Martínez et al. 1997). In other regions where a similar process of forest recovery occurred, the population of this species has increased (Mañosa 2003, 2004), and although in our study area there are no censuses of the species during this time, the probable result is that the abandonment of traditional land uses has favoured the species in inland areas. In the Mediterranean provinces of southeastern Spain, urbanisation close to the coast has reached near-saturation, and therefore, an increasing number of housing developments are being projected in inland areas. This expansion of urbanisation towards inland areas would have a detrimental effect on the short-toed eagle, especially if they are located close to pine forests and rivers.

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