Ecol Res
DOI 10.1007/s11284-008-0527-8

ORIGINAL ARTICLE

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Factors affecting large-scale distribution of the Bonelli's eagle *Aquila fasciata* in Spain

Received: 5 February 2008 / Accepted: 2 June 2008

Abstract We analyzed the environmental determinants of the regional distribution of Bonelli's eagle (*Aquila fasciata*) in Spain (ca. 500,000 km^2), taking into account its frequency of occurrence on UTM blocks of 50 × 50 km. We found that the distribution pattern of Bonelli's eagle was a highly predictable phenomenon based on climate, vegetation and interspecific relationships. The proportion of sunny, anticyclonic days, per year (i.e., high levels of solar radiation) was the main environmental predictor explaining the distribution and abundance pattern of the Bonelli's eagle. Sparse plant formations (mainly shrublands) had also a positive effect, while altitude, agricultural land and deciduous forests had a negative influence. The relative abundance of one of its main preys, the Red Partridge (*Alectoris rufa*), favored the probability of occurrence of Bonelli's eagle, but only in the less sunny areas located in the north of Spain. The relative abundance of its main competitor, the Golden eagle (*Aquila chrysaetos*), was slightly but positively correlated with both the distribution and the abundance of the Bonelli's eagle in the Spanish portion of the Iberian Peninsula, probably due to similarities in their habitat preferences. Finally, we did not find further regional effects of the variables describing the degree of human pressure (density of roads, urban cover, and length of power lines).

Keywords Bonelli's eagle · Distribution · Habitat modelling · Interspecific relations · Landscape and climatic variables · Spain · Raptors

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Introduction

The position of range boundaries is set by the interaction of the population processes of birth, death, and dispersal with the spatial and temporal variation in the environment (Brown et al. 1996; Gaston 2003). The limits of the entire geographic range are influenced by geographical, climatic, and landscape structure variables related to the ecological niche of the species (Brown et al. 1996). These large-scale niche relationships may be ascertained by analyzing the link between environmental variables and the spatial pattern of the species at its border limit as well as the variation of the relative abundance within range boundaries. The knowledge of biotic (e.g., prey availability, competitors), abiotic (e.g., geomorphology, climate), and habitat and landscape (e.g., vegetation structure, habitat fragmentation) variables that have an important influence on the distribution of species may provide relevant information to guide conservation efforts on large-scale geographical contexts (Lawton 1993), especially for those species with large home-ranges or patterns of juvenile dispersal. Large-scale distribution modelling usually employs the bioclimate 'envelope' approach (Berry et al. 2002; Thuiller et al. 2005) because climate is expected to exert a dominant role over biotic interactions (Hodkinson 1999). These are assumed to play a relatively minor role in governing species distributions at regional to continental scales (Pearson and Dawson 2003), especially considering the effect of interspecific competition (Wiens 1989a). Nevertheless, Davis et al. (1998) and Araújo and Luoto (2007) have clearly shown, under very different approaches, that biotic interactions could affect the distribution patterns of species—even at large scales—and thus the predictions of bioclimate 'envelope' to forecast climate-change impacts on biodiversity.

This large-scale approach is an important research program in itself but it is also relevant to examine the consistency between the perceived pattern of habitat preferences at fine-grained local scales and the factors determining distribution patterns at broader regional scales (Wiens 1989b; Grand and Cushman 2003), since species-specific ecological preferences depend upon the studied spatial scales (Bevers and Flather 1999; Lee et al. 2002; Fischer et al. 2004). This is a pertinent issue for endangered species when global recommendations within the distribution range are to be given because large-scale policies and regional conservation programmes may conflict with local prescriptions (e.g., Seoane et al. 2006). Thus, local and regional studies of species distributions should examine the similarity of both the observed patterns and the proposed mechanisms at the several arbitrarily defined scales of analysis (Rahbek and Graves 2001).

Bonelli's eagle (*Aquila fasciata*) is a sedentary and dispersive species in the western Palearctic that is mainly restricted to the Mediterranean region (Hagemaijer and Blair 1997). In the last two decades, Bonelli's eagle suffered one of the most severe population declines in Spain (> 20% over two generations), which is the main stronghold of the western Palearctic population comprising roughly 70% of the European population (Real and Mañosa 1997; Ontiveros et al. 2004). The most important causes of this severe decline are direct persecution and collision or electrocution with electric power lines (Real et al. 2001; Carrete et al. 2002). Adults are present throughout the year in the vicinity of their breeding areas while juvenile and immatures can make large dispersal movements (Real and Mañosa 2001; Cadahía et al. 2005, 2007). Several studies have been done at local scales to investigate the species habitat and climate preferences, the effect of food availability as well as the mortality and reproductive success (Sánchez-Zapata et al. 1996; Real and Mañosa 1997; Rico Alcázar et al. 2001; Carrete et al. 2002; Balbontín 2005; Cadahía et al. 2005; Gil-Sánchez et al. 2000). Muñoz et al. (2005) analyzed the overall distribution-abundance of the species in peninsular Spain using some climatic, spatial, and human variables, which allowed the identification of favorable and unfavorable areas for this species in Spain. They obtained an explanatory model based on slope of the terrain, July temperature, and precipitation. They acknowledged that projects for the conservation of this species have focused mainly on the northern limit of its range, where favorability is low and the sharpest population declines have been recorded.

The aim of this paper is to analyze the distribution of Bonelli's eagle, considering both its occurrence (presence/absence) and abundance (as estimated by the frequency of appearance in 10 × 10 km UTM squares) throughout Spain, including other variables previously not considered in the analysis of the overall distribution-abundance of the species (e.g., landscape structure, solar radiation, density of high-power electric lines, occurrence of competitor and prey species). Specific objectives are:

1. To quantify the competing roles of biotic, abiotic and landscape variables determining the regional distribution of the species
2. To examine the degree of consistency among the species' patterns of distribution and abundance at large (peninsular) versus local spatial scales.

Materials and methods

Study area

The Spanish portion of the Iberian Peninsula spans between 43.57°–36.34°N latitude and 8.7°W–2.7°E longitude. It includes a variety of climates, relief, and vegetation types despite its relatively small area (ca. 493,519 km^2). Our study area includes salient features of altitude (maximum altitude of 3,461 m), total annual precipitation (332–2,523 mm), mean annual temperature (5.7–17.9°C), and annual solar radiation (39.5–66%). Vegetation types include deciduous forest, coniferous forest, evergreen woodland and maquis, tall shrubland, dwarf shrubland, perennial grassland, and annual grassland. Within local regions, the relative extent of different vegetation types depends not only on the abiotic environment, but also on human impacts, particularly land use. Environmental characteristics of the study area can be consulted in http://www.vertebradosibericos.org/aves/atlas/mapasamb.html, under the heading *Distribution maps of environmental variables in Spain* (*Iberian Peninsula*).

Data on species distribution

Data on Bonelli's eagle distribution was obtained from the Spanish Atlas of Breeding Birds (Martí and Del Moral 2003). This atlas describes the presence–absence pattern of birds across the Spanish portion of the Iberian Peninsula in a 10 × 10 km UTM grid. Using a lower resolution 50 × 50 km UTM grid, we noted the presence of the species and counted the number of 10 × 10 km UTM squares where Bonelli's eagle was present in each 50 × 50 km cell. Although the latter defines a coarser-grained scale than the 10 × 10 km grid, it provides a higher certainty about the species occurrence in each geographic cell (note that absences are more likely to be real absences—as opposed to absences due to deficient field work—at the 50 × 50 km spatial resolution). This larger geographic scale overcomes the issues related to heterogeneity in field work, as it was not possible to invest the same amount of time in each UTM 10 × 10 km square across Spain due to logistic problems or lack of enough ornithologists in some areas. The amount of time invested in avian inventory within each selected UTM 50 × 50 km cell was, at least, 250 h (Del Moral, pers. comm.). On the other hand, the number of occupied 10 × 10 km UTM squares within blocks of 50 × 50 km provides an indirect estimation of Bonelli's eagle abundance, as the frequency of occurrence and abundance are positively related (Gaston et al. 2000). Thus, the density of breeding pairs (pairs/100 km^2) and the average frequency of occurrence of Bonelli's eagle in 10 × 10 km UTM squares, within blocks of 50 × 50 km, are positively and significantly correlated at the level of administrative provinces where the species is present in Spain (frequency of occurrence P was transformed according to $-\ln[1 - P]$ to directly relate to a measure of abundance; Tellería 1986): $r = 0.966$, $P << 0.001$, $n = 33$ provinces where the species was present in the period 2000–2005, ranging between 2,963 and 21,766 km^2 (data on Bonelli's eagle density and number of occupied 10 × 10 km squares obtained from Del Moral 2006). Therefore, the number of occupied 10 × 10 km UTM squares per 50 × 50 km block is a very good surrogate of the species population density over large areas. Moreover, the frequency of occurrence of species within larger blocks including 10 × 10 km UTM cells is also directly related to the long-term persistence probability in birds (Araújo et al. 2002).

Of all 50 × 50 km UTM cells covering the Spanish portion of the Iberian Peninsula, we only selected 199 cells. We discarded those 50 × 50 km cells covered by the sea or Portuguese or French areas not sampled by the Spanish Atlas and for which we could not obtain data in the same time span (1998–2002). Data on the species distribution can be obtained from the web Atlas Virtual de las Aves Terrestres de España (http://www.vertebradosibericos.org/aves/atlas/; Carrascal et al. 2005).

Geographical and environmental variables

We considered the following variables, measured on the UTM 50 × 50 km grid cells:

1. Mean altitude, maximum altitude and altitudinal range (difference between the minimum and maximum altitudes) of all the 250 × 250 m pixels included within each 50 × 50 km cell. Altitude was obtained from a digital elevation model (Clark Labs, 2000).
2. Total annual precipitation, mean annual temperature, and annual proportion of sunny, anticyclonic days (i.e., high levels of solar radiation). Climate variables provided by the Spanish Instituto Nacional de Meteorología.
3. Land use categories extracted from the CORINE Land Cover 1985–1990 Database (European Environmental Agency, 1991). The original CORINE land categories were merged into a set of broader categories we assumed more meaningful to Bonelli's eagle distribution, namely urban and industrial, non-irrigated arable crops, irrigated arable crops, vineyards, olive plantations, arboreal agro-pastoral systems, meadow and pastureland, shrublands, forest regrowth and dense tree plantations, broad-leaved forests, coniferous forests, and rock outcrops.
4. Roads facilitate human access and have been found to have disturbing effects on raptors (Bautista et al. 2004). A road index that incorporated information on length and width of all paved roads (provided by the Spanish Ministry for the Environment). The index was calculated weighing the length of the road by its width: a weight of three for highways with two wide lanes in each direction, two for national roads with only one lane in each direction and with wide shoulders, and one for local or regional roads with one narrower lane in each direction and with very narrow or no shoulders.
5. Length of the stream and river network and area of water bodies including reservoirs (provided by the Spanish Ministry for the Environment).
6. Latitude and longitude of the cell central points, to account for large-scale distribution gradients (i.e., spatial autocorrelation at large scales) and biogeographical effects.

These data are accessible at the *Atlas Virtual de las Aves Terrestres de España* at http://www.vertebradosibericos.org/aves/atlas/blqpdf/blq50.html.

We have also considered the frequency of occurrence, measured as the number of occupied 10 × 10 km UTM squares within blocks of 50 × 50 km, of the four most favored bird prey of Bonelli's eagle (Red-legged Partridge, *Alectoris rufa*; Jackdaw, *Corvus monedula*; Wood pigeon, *Columba palumbus*; Rock-(domestic) pigeon, *Columba livia*, and the Chough, *Pyrrhocorax pyrrhocorax*; Cramp and Simmons 1980) and a potential competitor (Golden eagle, *Aquila chrysaetos*). These data were obtained from the Spanish Atlas of Breeding Birds (Martí and Del Moral 2003) and can also be accessed at *Atlas Virtual de las Aves Terrestres de España* (Carrascal et al. 2005; http://www.vertebradosibericos.org/aves/atlas/listaspp.html).

Data analyses

The distribution pattern of the Bonelli's eagle in the Spanish portion of the Iberian Peninsula has been hierarchically analyzed using two approaches: (1) analysis of the probability of occurrence using classification trees, and (2) analysis of the number of 10 × 10 km UTM squares occupied within blocks of 50 × 50 km where the species was present using partial least squares (PLS) regression analysis (latent regression).

First, we built classification trees with species occurrence within the 50 × 50 km blocks as the response variable (absence = 0; presence = 1, see Fig. 1) and the 31 geographical, climatic, land use and species descriptors as explanatory variables. Classification tree models are a robust method for variable selection based upon a binary recursive partitioning. This non-parametric technique can select from among a large number of explanatory variables, where the response variable undergoes successive univariate splits, according to threshold values of the explanatory variables that maximize the differences between the two resulting groups of

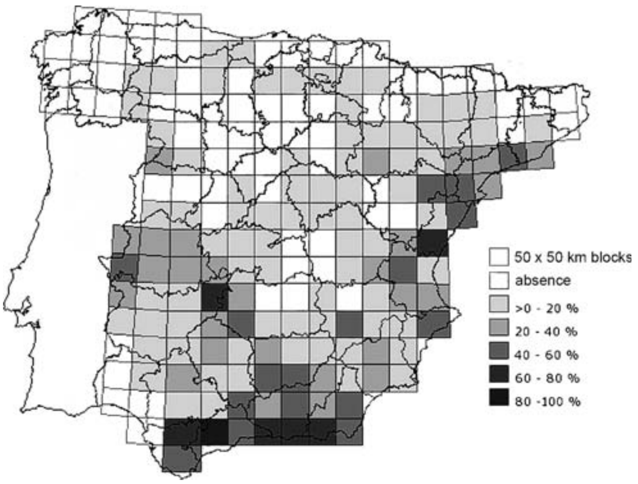

Fig. 1 Distribution map of Bonelli's eagle for the grid of 50 × 50 km UTM squares of the study area, according to the Spanish Atlas of Breeding Birds (Martí and Del Moral 2003). Frequency of occurrence, measured as the number of 10 × 10 km UTM squares within each 50 × 50 km cell where the species were recorded, is categorized in five percentage classes and depicted in a *yellow–brown* scale. The background is a digital terrain model for the Iberian Peninsula (in shades of *grey*)

samples. Classification tree analyses allow for the interpretation of datasets where there are complex non-linear relationships between response and predictor variables, and/or high-order interactions among predictor variables (Breiman et al. 1984; Venables and Ripley 1999; De'Ath and Fabricius 2000). We used the following rules to moderate tree growth: (1) groups had to include at least more than ten cases (i.e., UTM cells); (2) splits have to attain significant reductions in residual deviance (a measure of group heterogeneity) according to a χ^2 test; and (3) we applied the 1-SE rule whereby the best tree is taken from a cross-validation procedure as the smallest tree such that its estimated error rate is within one standard error of the minimum. The predictive power of the obtained classification tree was evaluated by means of a tenfold cross-validation procedure using 25 random sampling iterations. We also obtained the receiver operating characteristic (ROC) curve as a graphical plot of the sensitivity (the fraction of true positive presences) vs. [1 − specificity] (with specificity being the true negative rate) for a binary classifier system. The ROC curve depicts the discrimination power of the trees along all possible threshold values that may be used to convert continuous probabilities into a binary presence–absence variable. From the ROC diagram we calculated the area under the curve (AUC) statistic, an overall measure of the discrimination power of the classification tree, or the ability to distinguish 50 × 50 km UTM blocks with true presences from those with true absences, and its standard error following the formula of Hanley and McNeil (1982).

Second, we regressed the frequency of occurrence (in log) of Bonelli's eagle in 10 × 10 km UTM squares within blocks of 50 × 50 km where the species was present (see Fig. 1) against the set of 31 explanatory variables using PLS regression analysis. PLS is an extension of the multiple regression analysis based on a linear conversion from a large number of original descriptors to a small number of orthogonal factors (or latent components), which are designed to maximize the explanation of the response variable. The linear combinations of the explanatory variables are related to the response variable by ordinary least squares regression. These latent components may be viewed as weighted averages of predictors, where each predictor holds the residual information in the explanatory variable (Y) that is not contained in earlier components, and the quantity the latent component aims to predict is the vector of residuals resulting from regressing Y against earlier components. The interpretation of latent components was derived from the weights and loadings of original variables significant at $P < 0.01$, and the relative contribution of each variable was calculated by means of the square of predictor weights (Garthwaite 1994). The predictability of the results obtained with PLS regression applied to the whole sample ($n = 127$ 50 × 50 km blocks where Bonelli's eagle was present) was tested by means of ten validation procedures with a data-splitting strategy by which we built two-component PLS models with two-thirds of the blocks randomly selected from the original sample, and predicted the frequency of occurrence of the species in the remaining one-third of the sample.

Geographical position variables (mean latitude and longitude of each 50 × 50 or 10 × 10 km UTM square) were considered in the analyses to define geographical gradients and to control for spatial non-independence (i.e., autocorrelation), by means of a two-order polynomial of latitude and longitude (Legendre 1993). All statistical analyses were carried out using Statistica (StatSoft 2001) and S-Plus (MathSoft 1999) software packages.

Results

Probability of occurrence in 50 × 50 km blocks

The classification tree model applied to the presence–absence of Bonelli's eagle in the 50 × 50 km UTM blocks with seven splits is highly significant ($\chi^2 = 148.7$, 7 *df*, $P < 0.001$; it explained 57.1% of the observed deviance and classified correctly 87.9% of the UTM blocks (Fig. 2). AUC of this model was 0.916 (SE = 0.019), denoting a highly discriminatory power. Likewise, the cross-validation procedure indicated a good predictive power (average of correctly classified observations = 75.6%, SD = 3.2%, when using the prevalence of the species in the sample, 0.638, as the threshold to convert the continuous predicted probabilities into binary presence/absence).

The proportion of sunny, anticyclonic days, per year (i.e., high levels of solar radiation) is the main environmental predictor explaining the distribution pattern of

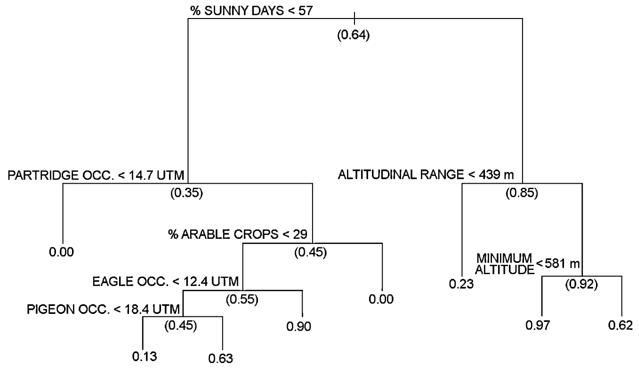

Fig. 2 Classification tree model for the occurrence of Bonelli's eagle in the study area. Values at the tips of branches are probabilities of occurrence of Bonelli's eagle in 50 × 50 km UTM squares. The splitting variables and threshold values selected refer to left branches of the tree, so that right branches met opposite conditions. PIGEON OCC.: Occurrence of rock dove

the Bonelli's eagle. Thus, the probability of occurrence of the species is very high (0.85) in blocks with more than 57% of cloudless days per year (vs. a probability of 0.35 in areas with annual solar radiation lower than 57%). In those sunnier blocks, the species prefers mountainous areas with an altitudinal range higher than 439 m and the presence of deep valleys below 581 m a.s.l. Under these conditions, the tree model predicts the maximum probability of occurrence (0.97).

In the less sunny areas (i.e., with percentage of sunny days < 57%), Bonelli's eagle shows a high preference for those UTM blocks of 50 × 50 km with a regular presence of the Red-legged partridge (more than 14.7 UTM squares of 10 × 10 km occupied within 50 × 50 km blocks). The cover of non-irrigated arable crops negatively affects the species distribution (threshold of 29%). The Golden eagle, far from having a negative influence on Bonelli's eagle distribution range, seems to be associated with it; the probability of occurrence of the Bonelli's eagle in 50 × 50 UTM blocks is greater when the Golden eagle occupies more than 12.4 UTM squares of 10 × 10 km per 50 × 50 km blocks (that is, half of the total squares within a block). Thus, both raptor species show a similar pattern of large-scale environmental preferences in Spain under low levels of sun radiation, high frequency of occurrence of the Red-legged partridge, and low cover of extensive, non-irrigated, croplands. With these environmental conditions, and when the occurrence of the Golden eagle is low, Bonelli's eagle has a higher probability of occurrence when the Rock Pigeon is widely distributed (at least, occupying more than 18.4 UTM squares of 10 × 10 km within 50 × 50 km blocks).

The less adequate areas for the species are those regions with a low proportion of sunny, anticyclonic days, per year (less than 57%) and a frequency of occurrence of its favorite prey (the Red-legged partridge) lower than 15 UTM squares of 10 × 10 km within 50 × 50 km blocks.

Table 1 Results of the partial least squares (PLS) regression analysis for the spatial variation in the frequency of occurrence of Bonelli's eagle within the area of distribution in Spain as a surrogate of the species' density (i.e., occupied UTM 10 × 10 km squares within blocks of 50 × 50 km where the species is present; see Fig. 1)

	Comp 1	Comp 2
Geographical effects and spatial autocorrelation (weights)		
Longitude	0.08	0.06
Latitude	**−0.42**	−0.09
Longitude^2	−0.07	−0.04
Latitude^2	**−0.42**	−0.09
Longitude × latitude	0.11	0.08
Geomorphological variables (weights)		
Minimum altitude	**−0.31**	−0.06
Average altitude	−0.18	0.04
Altitudinal range	0.14	0.14
Cover of limestone	0.21	**0.24**
Climatic variables (weights)		
Annual precipitation	−0.03	0.17
Mean annual temperature	0.12	−0.10
Annual proportion (%) of sunny days	**0.31**	−0.07
Landscape variables (weights)		
Cover of non-irrigated crops	**−0.29**	**−0.35**
Cover of irrigated crops	−0.04	**−0.36**
Cover of vineyards	−0.07	−0.22
Cover of olive plantations	0.12	−0.03
Cover of mosaic agriculture lands	0.09	−0.04
Cover of herbaceous habitats	0.13	0.04
Cover of shrublands	0.15	**0.36**
Cover of young forests	−0.05	0.10
Cover of deciduous forests	**−0.24**	−0.03
Cover of coniferous forests	0.15	**0.25**
Cover of bare rock	−0.03	0.06
Length of rivers	−0.13	0.01
Human impact variables (weights)		
Cover of reservoirs	0.14	**0.27**
Cover of urban areas	−0.03	−0.15
Length of highways and motor roads	−0.08	−0.19
Length of high-power electric lines	−0.09	−0.03
Competitor and prey occurrence (weights)		
Occurrence of the red-legged partridge	−0.06	−0.03
Occurrence of the rock pigeon	0.00	0.00
Occurrence of wood pigeon	−0.13	**0.29**
Occurrence of the chough	−0.08	0.12
Occurrence of the jackdaw	0.00	0.09
Occurrence of the golden eagle	0.06	**0.31**
R^2 by the whole factor (in %)	46.6	6.6
Contributions by categories of variables (R^2 in %)		
Geographical effects	17.5	0.2
Geomorphological variables	9.0	0.5
Climatic variables	5.2	0.3
Landscape variables	11.8	3.4
Human impact variables	1.8	1.5
Competitor and prey occurrence	1.3	0.7

The figures shown are the weights of each predictor variable defining the latent components that significantly ($P < 0.05$) explained the response variables (frequency of occurrence of Bonelli's eagle). Variables accounting for more than 5% of the information of each component are in bold type

Number of occupied 10 × 10 km UTM squares within 50 × 50 km blocks

Two highly significant components accounted for 53.3% of spatial variation in the frequency of occurrence of the species (Table 1). The first PLS component (46.6% of the original variance, $P << 0.001$) associates Bonelli's eagle occurrence to those areas with high levels of sun radiation, located at low altitudes in regions with a scarce cover of non-irrigated arable crops and broad-leaved forests, decreasing its frequency of occurrence from the south to the north of the Iberian Peninsula (with a maximum at mid-southern latitudes; see the negative quadratic effect of latitude). The second component is responsible for a lower amount of explained variance in Bonelli's eagle frequency of occurrence (6.6%, $P = 0.00005$), linking the species' distribution pattern positively to the frequency of occurrence of the Golden eagle and the Wood pigeon in calcareous areas with a low cover of arable crops, and a high cover of shrublands, coniferous forests, and reservoirs. Overall, frequency of occurrence is mostly explained by a south-north geographic trend, land use/land cover variables (lower in agricultural areas and higher in shrubs) and the combined effect of topography and climate (maximum at rugged mountains in warm areas). Globally, geographical position accounts for 17.7% of the original variance observed in Bonelli's eagle frequency of occurrence, landscape structure 15.2%, geomorphological variables 9.5% and climate 5.5% (obtained by summing the contributions of the two PLS components). Human impact measurements and the occurrence of prey and competitor avian species play a minor role accounting for the species density.

The PLS is well calibrated, as the intercept and slope parameters for the linear regression of observed on predicted values do not differ significantly from 0 to 1 (Observed = $a + b \cdot$ Predicted; averages [ranges] of ten validation procedures: $a = 0.22$ [−0.43 to 0.86], $b = 0.88$ [0.618–1.218], $R^2 = 38.52\%$ [26.0–63.89%]).

Discussion

Predictability of large-scale distribution of Bonelli's eagle

The distribution pattern of Bonelli's eagle is a highly predictable phenomenon considering a few number of variables: more than one-half of the variability observed in the species occurrence and frequency occupancy within 50 × 50 km UTM blocks was explained by climatic and land-cover predictors and the occurrence of other species (both prey and potential competitors). A similar result was also found by Muñoz et al. (2005) using a different subset of variables, which were biased to climatic parameters, and did not consider landscape structure or the occurrence of prey and competitor species. Nevertheless, there is a need to ascertain whether the observed large-scale patterns are related to mechanisms linked with the ecology of the species and if they are scale invariant (Wiens 1989b), because both the ecological preference and life-history patterns may depend on the spatial scale at which they are studied (Bevers and Flather 1999; and see Gil-Sánchez et al. 2005 for a particular example with the Bonelli's eagle). For example, Muñoz et al. (2005) found that the suitable areas for this species are mountainous with a Mediterranean climate characterized by hot summers and low precipitation. The effects of slope, annual precipitation, and mean temperature in July may act as surrogate variables of other more direct ecological effects related to habitat use, prey availability, or competitor occurrence.

The use of large geographical scales for analyses may lead to ignorance of the proximal factors that determine habitat selection, and similarly, habitat patterns obtained at small scales may vanish at broader ones (Wiens 1989a; Rubio and Carrascal 1994). Thus, several studies have analyzed the environmental preferences of Bonelli's eagle in Spain on a local scale, although globally no clear pattern emerges of its occupation of the territories (Ontiveros et al. 2004). This is an important concern when studying endangered or vulnerable species because the apparent geographical preferences derived from statistical models could then simply be artefacts. In the following paragraphs, the biological bases of the statistical patterns found are discussed, considering the consistencies and inconsistencies with previous studies.

Covariation with the distribution patterns of other avian species

It is well known that limits to the distribution of a species may be modified by the interactions with others (such as the availability of prey and plants used as food, or the existence of potential competitors; e.g., Anderson et al. 2002; Araújo and Luoto 2007). Thus, the density of the potential prey for Bonelli's eagle has been pointed out as a possible determinant of its distribution-abundance at local scales, although the studies published to date have not contributed conclusive results (Mañosa et al. 1998; Ontiveros and Pleguezuelos 2000; Ontiveros et al. 2005). At a regional scale, the relative abundance of the Red Partridge (measured as frequency of appearance of this species in 10 × 10 km UTM squares within 50 × 50 km blocks) is important in determining the probability of occurrence of Bonelli's eagle over large land surfaces, but only in the less sunny areas located in the North of Spain. In these northern areas (Catalonia, Burgos and the pre-Pyrenean area of Huesca and France), there is evidence that the dearth of main and alternative prey has exerted a negative effect on the reproductive success of this species (Ontiveros et al. 2004). Muñoz et al. (2005) did not consider the occurrence of the Red Partridge, but the three variables that were selected by their model (negative influence of precipitation and positive effect of slope of the terrain and July temperature) are very good surrogates of the distribution of the Red Partridge in peninsular Spain (Carrascal and Lobo 2003).

On the other hand, the relative abundance of its main competitor, the Golden eagle, does not greatly contribute to explain either the distribution or the abundance of the Bonelli's eagle at the regional scale of study (and the few instances where it does play a role, the correlation is small and positive, Table 1, Fig. 2). This absence of a negative interspecific effect has also been obtained at local scales, where the competition pressure with the Golden eagle has only a limited influence on the demography of the Bonelli's eagle (Carrete et al. 2002, 2005 López-López et al. 2004). Intraguild predation is increasingly reported as a population-limiting factor for vertebrate predators. Long-term coexistence of the intraguild prey with its predator is a common occurrence usually maintained by some form of predator avoidance, which may be achieved through distance-sensitive avoidance (i.e., selection of sites as far as possible from the intraguild predator within the same large UTM of 2,500 km^2), and/or avoidance of habitats associated with high predation risk (Sergio et al. 2007). Moreover, intraguild predation may alter habitat choices and affect density, productivity and guild structure of vertebrate mesopredators (Bonelli's eagle in this paper) as Sergio et al. (2007) have shown in a guild of owls in the Alps. This pattern of coexistence between raptor species could explain the absence of a negative relationship between the frequency of occurrence of Golden and Bonelli's eagles. At large scales, the distribution of the two species may positively correlate merely because both raptors prefer the same broad habitat characteristics (they nests in cliffs and hunt in open areas).

Geographic and climatic determinants

The purely geographic component that determines the distribution pattern of the Bonelli's eagle in Spain is small, since no geographical variable was selected in the classification tree for the probability of occurrence, and the geographical component only accounts for one-third of the explained variance in the PLS regression analysis for the species' density. The abundance of the species increases from North to South in the Iberian Peninsula (Table 1). The West to East tendency described by Ontiveros et al. (2004) was not observable. Muñoz et al. (2005) did not find any geographical influence in the distribution of Bonelli's eagle in peninsular Spain.

The topographic features make a significant contribution in accounting for the distribution and density of the species. Thus, the eagle requires mountainous areas, even if they are in the altitudinal range of 400–500 m (i.e., small hills); in other words, they avoid vast plains and valleys. Similarly, the slope has been found to explain a great part of Bonelli's eagle distribution, both at large and small scales (Sánchez-Zapata et al. 1996; Ontiveros 1999; Muñoz et al. 2005). In brief, the study species favors rugged terrains, where suitable cliffs for nesting are more common (only a small fraction of birds nest on trees, Ontiveros et al. 2004). Its greater abundance in limestone mountains is likely due to a higher availability of steep cliffs and ledges in these areas than in others where igneous rocks predominate. Nests in higher cliffs with steeper slopes have been shown to have a higher reproductive success (Ontiveros 1999).

The altitude has also an effect on both the pattern of distribution and abundance at the peninsular scale. The relationship is negative, so that the Bonelli's eagle is infrequent or scarce in areas above roughly 600 m a.s.l. (see Table 1 and Fig. 2). The basis of this association must lie in the negative correlation between altitude and annual mean temperature ($r = -0.84$, $P < 0.001$, in 199 50×50 km UTM blocks). The limiting effect of ambient temperature on the distribution, abundance and reproductive success of the eagle has been described by other authors at different scales, being more marked in the northern part of Spain with a colder climate (Ontiveros and Pleguezuelos 2003; Muñoz et al. 2005; López-López et al. 2006).

In a similar vein, the solar exposure positively affects the frequency of the appearance of the eagle, which is in agreement with the strictly Mediterranean nature of the species in the Western Palearctic. This relationship must be caused by the advantages provided to thermoregulation and flight at the nesting site. Thus, the nests are preferably located on the south-east orientations of the rocky cliffs (Ontiveros 1999; Carrete et al. 2002; Ontiveros and Pleguezuelos 2003; Gil-Sánchez et al. 2004; Balbontín 2005), possibly in order to maximize the radiant energy obtained, and reduce the expenditure of thermoregulation in the coldest period of the day during the reproductive period (see Carrascal et al. 2001; Carrascal and Díaz 2006 for a general discussion of this issue). Such southern orientations have likewise been claimed to help flight by facilitating thermal and slope soaring (Ontiveros 1999).

Landscape structure and human pressure

Land cover has an important role explaining the abundance and, to a lesser extent, the distribution of Bonelli's eagle in Spain. Sparse plant formations (mainly shrublands) have a positive effect on the frequency of the species' occurrence. This preference is consistent with the patterns found at local scales (Balbontín 2005; López-López et al. 2006), and it is explained by the greater accessibility of the main prey to Bonelli's eagle in open areas (Rabbit and Red Partridge, this latter being a highly terrestrial bird), since this feature is more important than its mere abundance (Ontiveros and Pleguezuelos 2000; Ontiveros et al. 2005). On the other hand, agricultural land and deciduous forests have a negative influence on the distribution of the species, which is consistent with the results obtained at a local scale by Carrete et al. (2002), who found that abandoned territories had larger areas of forest and extensive agriculture.

Lastly, the lack of an effect of the variables describing the degree of human pressure (other than agricultural use) on Bonelli's eagle distribution pattern at a regional scale is remarkable (see also Muñoz et al. 2005, and Li et al. 2002 for an example of tolerance to high levels of human disturbance in the endangered crested ibis, *Nipponia nippon*). This result is surprising because the electrocution in power lines is claimed to be the main cause of human-induced mortality, with a high incidence on dispersing juveniles (Mañosa and Real 2001; Real et al. 2001; Real and Mañosa 2001). Nevertheless, the younger reproductive individuals (less than 4 years of age) nest closer to roads and urban areas than adults (Penteriani et al. 2003) and several authors have described that the Bonelli's eagle occupies areas of high human density in man-made environments (Gil-Sánchez et al. 1994, 1996; López-López et al. 2004), which suggest that the species is somewhat tolerant of man. Therefore, these contrasting effects at local scales may compensate, and may not provide a clear signal at larger regional scales.

To summarize, the distribution and density of the Bonelli's eagle in Spain is explained by topography and climate, while the landscape structure and the availability of prey (mainly the Red Partridge) play a relevant, albeit secondary, role. These large-scale patterns are almost coincident with those found at local scales, which reveals that local processes often (but not always) translate into larger scale patterns of distribution. Therefore, this larger view may help, at least in the study species, to uncover the former local-scale processes.

Acknowledgments This paper was funded by projects CGL2005-02642/BOS of the Spanish Ministry of Educación y Ciencia. Claire Jasinski improved the English of the manuscript, and Juan Carlos del Moral made interesting comments on a first draft of the paper.

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