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Linking density, productivity and trends of an endangered species: The Bonelli's eagle in Spain

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ABSTRACT

Whether regional population density is a good indicator of environmental quality according to demographic variables such as breeding success or short-term population trends is controversial. In this paper we analyze the interrelationships among regional population density, breeding success and recent population trends of an endangered species, Bonelli's eagle in the Iberian Peninsula. We also analyze the different influence of geographical, climatic, landscape structure and human impact variables on regional variation in those demographic variables. Breeding success was higher and population decrease was lower in those areas where the population density of Bonelli's eagle was greater. Breeding success, density and recent population trends of Bonelli's eagle were tightly related, increasing from northern to southern Iberian Peninsula (with highest figures at intermediate latitudes), and as sun radiation increased, and altitude decreased. Breeding success and population density were significantly lower in the periphery of the distribution range than in core areas in the Iberian Peninsula. Population trends between 2000 and 2005 were also more negative (decreasing) in the periphery. Overall, these results suggest that population density in this endangered species of large home-range is a good indicator of environmental quality and reproductive output, and that peripheral populations occupy low-suitability areas with lower breeding success, where negative short-term population trends are more likely.

1. Introduction

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; Gaston, 2003). The position of the range boundary is set by the interaction of the population processes of birth, death, and dispersal with the spatial and temporal variation in the environment. The understanding of species' geographic ranges and their borders is particularly important in the case of endangered species, in which the knowledge of the factors involved in the definition of range boundaries are useful for understanding both the changes in the distribution area and the determinants of species numbers. The demographic processes in populations, including survival, reproductive success and dispersal, will underlie the dynamic patterns of occurrence and abundance for a study species in a given area. Indeed, demographic dynamics may differ among large-scale zones within the distribution range of a species, whereas at local scales demographic parameters vary according to fine-grained variables compounding habitat quality. Such contrasting scale-dependent results have been repeatedly found when analysing large-scale population trends or reproduction success: these typically differ among areas within the regional distribution of a species (Both et al., 2004; trends: Julliard et al., 2004; Seoane and Carrascal, 2008; reproduction: Sanz, 1998). A well known explanation to account for the variation of the species' performance across its range is the abundant-centre model, which assumes a constant degradation of the environmental conditions for a species, from an optimal centre towards the marginal edges of distribution (reviewed in Sagarin et al., 2006). According to this model we should expect a reduction in the density and productivity from core areas (that would function as source populations of emigrant propagules) to edge areas (that would act as population sinks).

Variation of species abundances across large geographic scales is central to ecological biogeography. Much effort has been made in modelling species distribution and determining which variables explained the variation of species' abundances (Guisan et al., 2006;

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Rodriguez et al., 2007), predicting abundance from presence–absence data (e.g., He and Gaston, 2000; Holt et al., 2002; Conlisk et al., 2009), or testing different methods for modelling species distributions (e.g., Segurado and Araújo, 2004). Nevertheless there is considerably less information documenting whether variation in animal abundance on large spatial scales is linked to demographic parameters such as breeding output or population trends. Van Horne (1983) warned that density could be a misleading indicator of environmental quality if it was negatively correlated with other demographic variables such as breeding success or survival. The basis of this relationship is that a small number of dominant, reproductively successful individuals could displace a large number of young and other subordinate individuals to marginal areas where they become more abundant, according to a settlement pattern known as the Ideal Pre-emptive Distribution that has been recorded for several raptor species (Pulliam and Danielson, 1991; Krüger and Lindström, 2001; Sergio and Newton, 2003). This potential relationship casts doubts about the value of population density as a surrogate of environmental quality. Such a mismatch is of special concern, as population density is in many cases the only ecological parameter that can be feasibly studied over large areas to define protection priorities and to carry out environmental assessment (Brawn and Robinson, 1996; Vickery et al., 1992; but see the review by Bock and Zach, 2004). Consequently, conservation biologists are recommended to be cautious when relying on abundance estimations as surrogates of habitat quality, which is more accurately described with labour-intensive demographic research (Johnson, 2007). Thus, there is clearly a need for studies that evaluate the value of bird abundance as a guide to establishing conservation priorities, especially over large regions where managers and conservation planners cannot normally afford more intensive research.

Bonelli's eagle (*Aquila fasciata*) is a polytypic raptor species whose nominate subspecies *fasciata* spreads out southern Europe and North Africa, east to India and south China. It has a large home-range, both for adults and juveniles (e.g., López-López et al., 2004; Balbontín, 2005; Cadahia et al., 2005; Sanz et al., 2005). In the Western Palearctic it is a sedentary species mainly restricted to the Mediterranean region (Hagemaijer and Blair, 1997). The Iberian Peninsula is the main stronghold of the Western Palearctic population, comprising roughly 70% of the European population (Ontiveros et al., 2004; Real and Mañosa, 1997). The population of Bonelli's eagle has markedly declined over most of the Western Palearctic. Its European breeding population is very small (less than 1000 pairs), and decreased substantially between 1970 and 1990, although some populations were stable during 1990–2000 (Burfield and Van Bommel, 2004). In Spain there was not a clear increase from 2000 to 2005 (Del Moral, 2006; apparent changes have been attributed to differences in knowledge about the potential territories prospected during the two years of census, or to differences between years in sampling effort), although some areas experienced positive population trends (Gil-Sánchez et al., 2004). The large amount of knowledge obtained for this species regarding its ecology and behaviour in the last 20 years (see review by Ontiveros, 2007) make it suitable for the analysis of the ecological biogeography of the species, and for testing within a large-scale scheme whether species abundance in a globally scarce species is linked to other demographic parameters related to persistence or probability of extinction.

The main aims of this work are twofold. Firstly, we test if regional population density in a species with a large home-range is a good indicator of environmental quality according to demographic descriptors (breeding success and short-term population trends). Secondly, we explore the environmental determinants (geographical, climatic, landscape structure and human impact effects) of large-scale variation in these demographic descriptors of Bonelli's eagle in Spain.

2. Material and methods

2.1. Study area and species

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. 580,673 km^2).

Information on reproductive performance, local density (in pairs per square kilometer) and population trends of Bonelli's eagle were gathered in 2005 during the last national census for the species and compiled per administrative province in Del Moral (2006). The Bonelli's eagle had been monitored by regional agencies in Spain most intensively since the last decade, but a simultaneous census with a common methodology was lacking. In 2005, SEO/BirdLife promoted a national-wide census based on a net of regional coordinators (one per each administrative province) having previous experience with this and other raptors' censuses. The local field work was done mostly by personnel belonging to local environmental agencies and by semi-professional ornithologists (amounting to more than 150 people).

At least five visits to areas suspected to contain breeding territories were done between the first of January and the fifth of March to detect occupancy (if no pair was registered in a given territory, two additional visits were done between the first of April and the end of May to make sure it was unoccupied). Breeding parameters were estimated in a sample of the monitored territories in each region (roughly 50–75% of them), which were visited at least two more times to confirm the number of pairs that begun to breed (between 5th and 30th March) and the reproductive success (between 30th March and 30th May). Records were made with telescopes from lookouts far from nests during the first and the last hours of the day, thus minimizing disturbances to the birds and maximizing the probabilities of detection.

Bonelli's eagle was present in 33 out of 50 Spanish provinces in 2000 (Del Moral, 2006; Fig. 1). Productivity was measured in 2005 as the number of young fledged per established territorial pair, because this is the most suitable demographic parameter for describing the population growth rate (however, the results were qualitatively similar when using reproductive success, measured as the number of young fledged per hatching pair: $r = 0.870$, $n = 32$ provinces with breeding attempts in 2005, $p < 0.001$). Recent population trends were estimated as the percentage change between the two last population censuses in 2000 and 2005: (birds in 2005 − birds in 2000)/birds in 2000. Provincial densities were estimated as the total number of breeding pairs of Bonelli's eagle divided by the occupied 10 × 10 km UTM squares of each province. This abundance measure is indicative of the maximal ecological density in those favourable areas for the species, and it is also correlated with total provincial density (obtained dividing number of pairs by the total area of the province; $r = 0.48$, $n = 33$, $p = 0.005$). See Appendix for detailed information of Bonelli's eagle in the studied provinces.

2.2. Geographical and environmental variables

Data on variables were obtained for the 32 provinces where Bonelli's eagle was present in 2005, considering the environmental data for all the 10 × 10 km UTM squares they include. We considered the following variables: latitude and longitude of the province baricenters, to account for large-scale distribution gradients (i.e., spatial autocorrelation at large scales) and biogeographical effects;

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Fig. 1. Map of Spain showing the provinces where the species was present in the period 2000–2005 (marked in grey and black). In grey peripheral provinces; in black the remaining occupied core provinces; in white, provinces where the species either went extinct or there have been no recent records (see the text for more details)*: Huelva, where Bonelli's eagle became extinct in the study period 2000–2005.

mean altitude, maximum altitude and altitudinal range (difference between the minimum and maximum altitudes; obtained from a Digital Elevation Model; Clark Labs, 2000); total annual precipitation, mean annual temperature, and annual proportion of sunny, anticyclonic days (i.e., high levels of solar radiation; provided by the Spanish Instituto Nacional de Meteorología); land use categories extracted from the CORINE Land Cover 1985–1990 Database (European Environmental Agency, 1991); length of all paved roads (provided by the Spanish Ministry for the Environment); length of the stream and river network and area of water bodies including reservoirs (provided by the Spanish Ministry for the Environment). The original CORINE land categories were merged into a set of broader categories that were more meaningful for the large-scale distribution of Bonelli's eagle (Carrascal and Seoane, 2009), namely urban and industrial, non-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.

2.3. Data analyses

Productivity of Bonelli's eagle in each province was regressed against a set of 26 explanatory variables using partial least squares (PLS) regression analysis. This technique is an extension of the multiple regression analysis where the effects of linear combinations of several predictors on a response variable (or multiple response variables) are analyzed. PLS is specially useful when the number of predictor variables is similar or higher than the number of observations (i.e., overfitting), there are more than one response variable, and predictors are highly correlated (i.e., there is strong collinearity; Hubert and Branden, 2003; Abdi, 2007; Carrascal et al., 2009). Associations are established with latent factors extracted from predictor variables that maximize the explained variance in the dependent variables. These latent factors are defined as linear combinations constructed between predictor and response variables, so the original multidimensionality is reduced to a lower number of orthogonal factors to detect the structure in the relationships between predictor variables and between these latent factors and the response variables. The extracted factors account for successively lower proportions of original variance. The interpretation of latent components was derived from the weights and loadings of original variables (Garthwaite, 1994). The relative contribution of each variable to the derived factors was calculated by means of the square of predictor weights.

Geographical position variables (mean latitude and longitude of each province) 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).

We analyzed the spatial differences in productivity, population density and trend by comparing these demographic parameters on core versus peripheral provinces with non-parametric Kruskal–Wallis tests. We consider the provinces comprising of the continuous distribution from the Mediterranean to be the core area ($n = 23$, note that part of this core range is coastal and thus an unavoidable edge), while those covering the discontinuous edge of the distribution, farther from the coast, were considered peripheral ($n = 10$, including also Huelva where Bonelli's eagle became extinct in the study period 2000–2005).

All the statistical analyses were carried out using Statistica (StatSoft Inc., 2001).

3. Results

The PLS regression of Bonelli's eagle population density, productivity and recent population trends per province resulted in two significant latent components, explaining 46.0% of the total observed variance in the response variables: 39.1% for productivity, 63.8% for population density and 35.3% for population trends (PLS1: 34.4%, $p < 0.001$; PLS2: 11.6%, $p < 0.001$). The first component (PLS1 in Table 1) positively relates population density, productivity and recent population trends: the productivity was higher and the population decrease between years 2000 and 2005 was lower in those provinces where the population density of Bonelli's eagle was greater. The second component (PLS2) identifies a subtle pattern of relationship between only population trend and density. Fig. 2 summarizes the patterns of relationships among the response variables.

The variables with higher weights in the first PLS component were average latitude of the provincial baricenters (both the linear and quadratic terms with negative signs), the proportion of sunny, anticyclonic days, per year (positively) and altitude (both the minimum and average altitude with negative weights; Table 1). Thus, the tightly related productivity, density and recent population trends of Bonelli's eagle increased from north to south of Spain (with highest figures at intermediate latitudes), and as sun radiation increased, and altitude decreased. Fig. 3 shows the intense relationship between these two sets of variables. The second PLS component (PLS2) positively and significantly associates population trend and density. This component positively relates the residual variation in population trend and density, after removing the effect of component PLS1 in Fig. 3, with cover of non-irrigated herbaceous crops, and negatively with other kind of agriculture lands (vineyards, olive plantations and arboreal agro-pastoral systems) and the length of high-power electric lines.

Table 1
Results of the partial least squares (PLS) regression analysis for the spatial variation in the productivity, density and recent population trends of Bonelli's eagle in 32 Spanish provinces (see Fig. 1). The figures shown are the weights of each predictor variable defining the latent components that significantly explained the linear combination of response variables (population density, productivity and recent population trends) of Bonelli's eagle. Variables with loadings significant at $p < 0.05$ and accounting for more than 5% of the information of the component are in bold type.

	PLS1	PLS2
Response variables		
Productivity	**0.61**	0.05
Population trends	**0.36**	**0.80**
Population density	**0.70**	**0.60**
Predictor variables		
Longitude	−0.08	0.07
Latitude	**−0.43**	−0.17
Longitude^2	0.10	0.00
Latitude^2	**−0.43**	−0.17
Longitude × Latitude	−0.05	0.10
Minimum altitude	**−0.33**	−0.18
Average altitude	**−0.26**	−0.13
Altitudinal range	0.15	0.06
Annual precipitation	−0.01	−0.01
Mean annual temperature	0.20	−0.01
% Sunny days	**0.43**	0.27
Cover of non-irrigated crops	−0.08	**0.40**
Cover of vineyards	−0.06	**−0.29**
Cover of olive groves	0.16	**−0.32**
Cover of arboreal agro-pastoral systems	0.16	**−0.43**
Cover of herbaceous habitats	0.15	−0.08
Cover of shrub lands	0.00	−0.11
Cover of young forests	−0.20	−0.20
Cover of deciduous forests	−0.17	0.02
Cover of coniferous forests	−0.04	0.07
Cover of bare rock	0.16	−0.25
Length of rivers	−0.04	0.14
Cover of reservoirs	0.05	−0.10
Cover of urban areas	0.04	−0.05
Length of highways and motor roads	0.01	0.00
Length of high-power electric lines	−0.07	**−0.33**

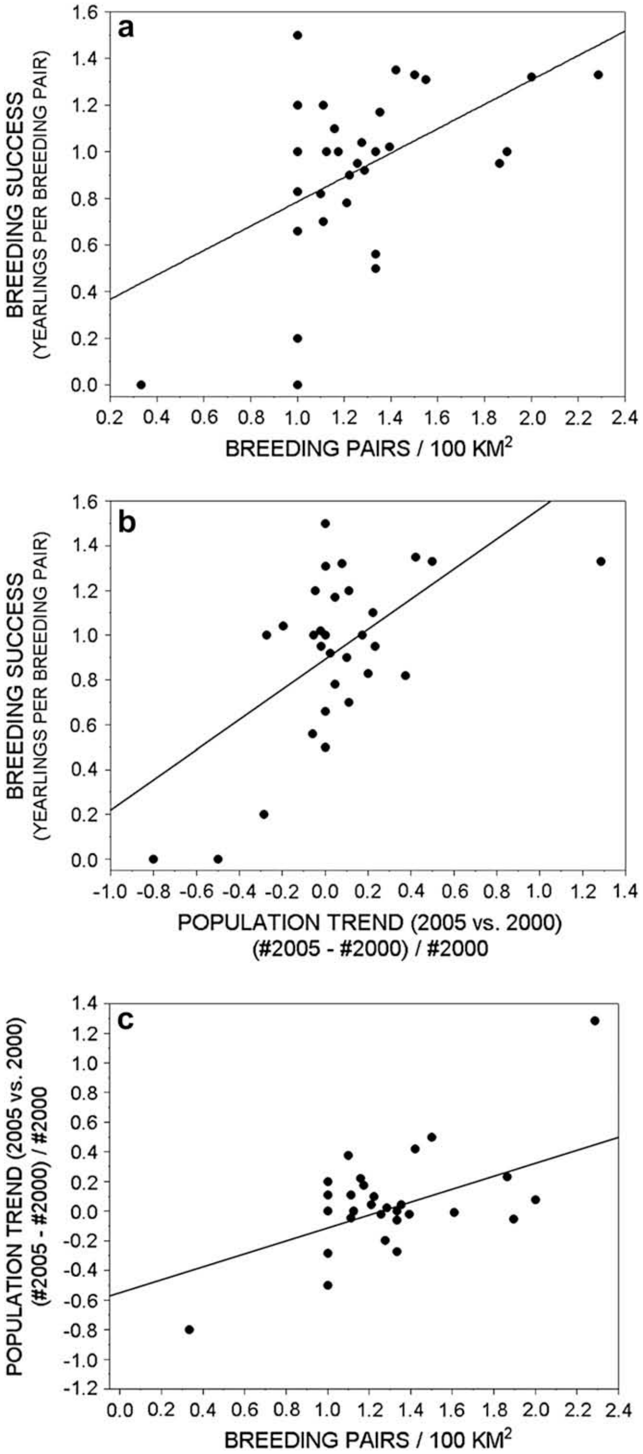

Fig. 2. Plots of productivity versus (a) breeding pairs per 100 km^2 in occupied 10 × 10 UTMs and (b) population trends, and of breeding pairs per 100 km^2 in occupied 10 × 10 UTM versus population trends (c) in the 32 Spanish provinces where the species was present and attempted to breed in 2005.

Productivity and population density were significantly lower, and population trends between 2000 and 2005 were more negative, in the periphery of the distribution range in Spain (Kruskal–Wallis tests: $p = 0.023$, $p = 0.048$ and $p = 0.013$, respectively, Fig. 4).

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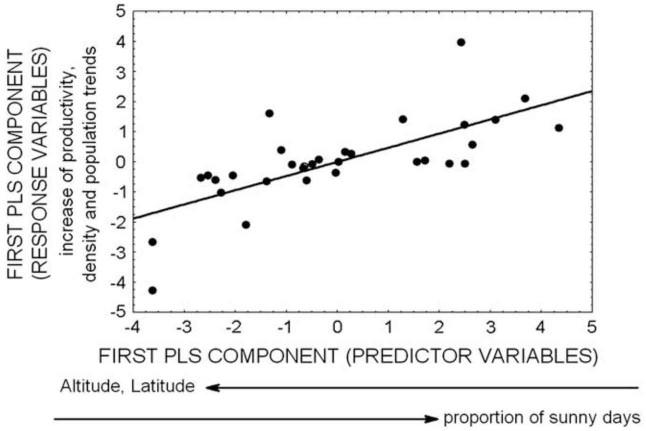

Fig. 3. Relationship between the response variables (productivity, density and recent population trends of the Bonelli's eagle) and the predictor environmental variables in the 32 Spanish provinces where the species was present and attempted to breed in 2005.

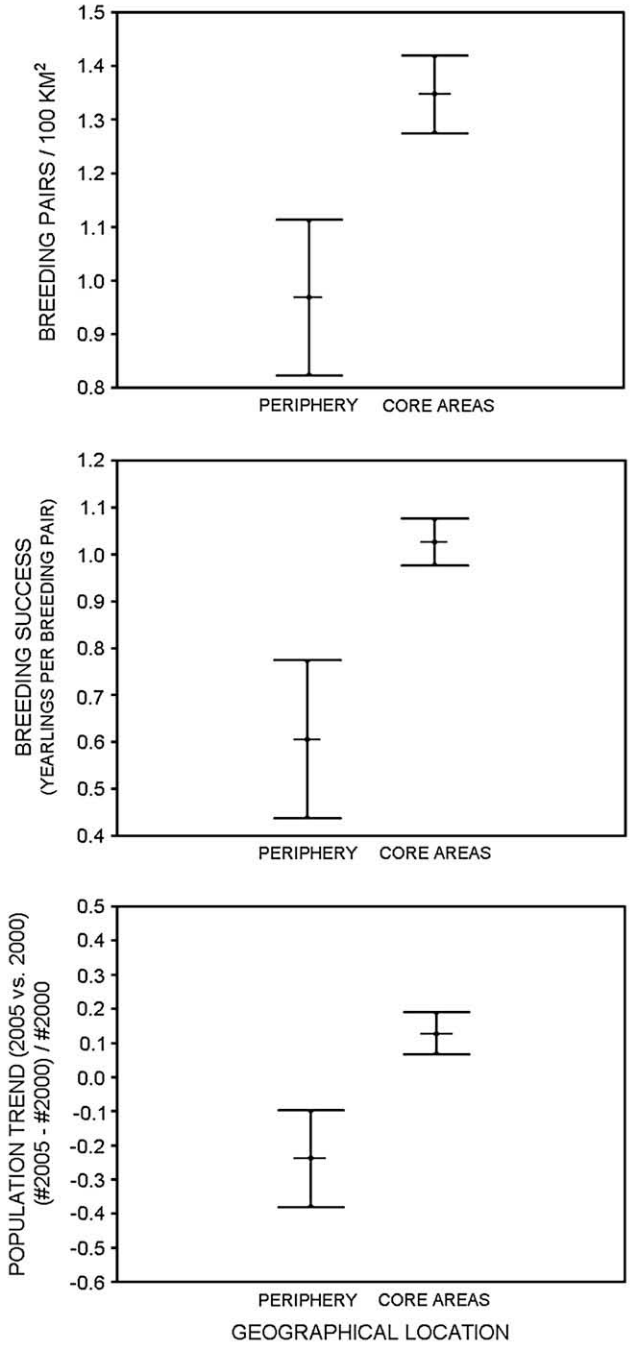

Fig. 4. Means and standard errors of breeding pairs per 100 km^2 in occupied 10 × 10 km UTM squares (top), productivity (middle) and population trends (bottom) for peripheral ($n = 10$, including Huelva where Bonelli's eagle became extinct in the study period 2000–2005) and core areas ($n = 23$) of the Bonelli's eagle distribution in Spain.

4. Discussion

Density-dependent processes in saturated populations generally lead to a negative relationship between breeding performance and population density (Newton, 1998; Paradis et al., 2002). However, these patterns may be reversed in low-density populations where the species is considerably below carrying capacity throughout its geographical range, or is suffering the Allee effect because individuals have difficulties in finding mates (Courchamp et al., 1999). This Allee effect is expected to be detected mainly in marginal, peripheral and isolate small sub-populations with low density and breeding output, and thus negative population trends. We found a positive relationship between productivity, density and recent population trend, which suggests that the Spanish population of Bonelli's eagle show a very large spatial heterogeneity in these three demographic parameters, and that it may be suffering from a high mortality or low productivity that maintain it below carrying capacity. High mortality of the breeding segment of the population has been observed (Real et al., 2001) and, as a consequence, juvenile floater individuals find and occupy vacant territories, or mate with owners of territories after the disappearance of one of the members of a breeding pair (see Balbontín et al., 2003; Penteriani et al., 2006, and Soutullo et al., 2008 for long-lived Mediterranean raptors). This reduction in age at first breeding and productivity has been proposed as a consequence of unnatural events caused by human persecution in the Bonelli's eagle (Balbontín et al., 2003).

Our results support the value of population density of Bonelli's eagle as an index of environmental quality for the species, because it was positively correlated with both breeding success and population trends. This pattern, obtained at a very broad spatial scale, is relevant for large-sized bird species for which only low population densities in their preferred habitats can be expected (Carrascal and Tellería, 1991), because population density is usually the only ecological parameter that can be feasibly studied over large areas to define protection priorities and to carry out environmental assessment (Brawn and Robinson, 1996; Vickery et al., 1992). This result is not consistent with Van Horne's (1983) concern about animal abundance as a misleading indicator of environmental quality, but agrees with the review by Bock and Zach (2004) showing that birds in Northern Hemisphere are usually more abundant in habitats where per capita reproduction is highest, regardless of the type of bird or habitat, degree of territoriality and migratory status. Nevertheless, human impact may hamper the ability of birds to recognize and occupy the best suited places for reproduction, decreasing the intensity of relationship between population density and breeding success (Bock and Zach, 2004). This seems not to be the case for Bonelli's eagle in Spain, because the younger reproductive individuals (less than 4 years of age) usually nest in less favourable areas (closer to roads and urban areas than adults; Penteriani et al., 2003), and

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several authors have described that the Bonelli's eagle occupies areas of high human density in man-made environments (Gil-Sánchez et al., 1994; López-López et al., 2004). Moreover, there is a lack of an effect of the variables describing the degree of human pressure (see cover of urban areas, and length of highways and motor roads in Table 1) on Bonelli's eagle breeding success at a regional scale. Nevertheless, Soutullo et al. (2008) have pointed out that protecting the areas of temporary settlement used by juveniles, minimizing the risk of electrocution in power lines and preventing human persecution, should be a priority in management actions for the Spanish population of the Bonelli's eagle. Moreover, only a relative small decrease in pre-adult mortality (20%) during the first two years of life was enough for the stabilization of the Spanish metapopulation. Therefore, systematic censuses to monitor population density of Bonelli's eagle may be used to define conservation priorities in this endangered species in the Iberian Peninsula (see: López-López et al., 2007a).

Reproductive performance was higher in the core provinces than in the peripheral ones, where high favourability areas for the species are scarce and dispersed, and most of the territory either is unfavourable or has an intermediate adequacy (Muñoz et al., 2005). Population trends were likewise positive in core provinces but negative in peripheral ones. According to Muñoz et al. (2005), the spatial variation in regional favourability for Bonelli's eagle could be explained by a balance between source-sink or metapopulation dynamics, where adult mortality is the key factor in determining the result. More recently, Soutullo et al. (2008) have shown that when the interchange of individuals among sub-populations is taken into account, pre-adult mortality plays the key role in determining the overall population trend. Floaters (mainly juvenile birds dispersing from natal areas) may enter the breeding population only when adult mortality is high and the availability of suitable unoccupied territories increases (Balbontín et al., 2003; Penteriani et al., 2006). Then, these floaters would not readily replace deceased territorial individuals in low-quality territories, and unfavourable areas would act as sinks showing population declines. Moreover, breeding success of dispersers making their first breeding attempts is low (Cadahia et al., 2007). Our analyses are in agreement with this line of reasoning and suggest that Bonelli's eagle populations in peripheral provinces may be best viewed as sink areas depending in the long run on the emigrant individuals from the core areas. Viewed from a more general perspective, our findings match the common result in territorial raptors that the best quality individuals occupy the best territories and have higher fecundities, likely because foraging or other skills improve with age and the more experienced birds outcompete the others.

According to land use variables, open country agricultural areas had a positive effect, while more densely vegetated agro-pastoral environments (vineyards, olive groves and holm oak parklands) had a negative influence on population trends and density of the Bonelli's eagle. This pattern is consistent with the results obtained at a local scale by Carrete et al. (2002), and may be explained by the greater accessibility of the main prey to Bonelli's eagle (Rabbit and Red Partridge) in open areas, since this feature is more important than its mere abundance (Ontiveros and Pleguezuelos, 2000; Ontiveros et al., 2005). Solar radiation positively, and altitude negatively, also affected the breeding success 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 at the nesting site. Thus, the nests are preferably located on the south-east orientations of the rocky cliffs (Ontiveros, 1999; Ontiveros and Pleguezuelos, 2003; Gil-Sánchez et al., 2004; López-López et al., 2007b), 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 (which starts during the Northern Hemisphere winter).

The abundant-centre hypothesis predicts that species' abundances are typically greatest at the centre of their geographical ranges and uniformly decline towards the edges following a continuous degradation of the environmental conditions for a species (see review by Sagarin et al., 2006 and references therein). However, the model has been recently criticized on the grounds of having a low (and equivocal) empirical support and leading to ambiguous predictions (Sagarin and Gaines, 2002; Sagarin et al., 2006). The testing of the abundant-centre hypothesis requires that care should be taken to sample the edges appropriately (Sagarin and Gaines, 2002) and that a range of densities exists to compare the assumed centres of distribution with those edges. In this work the range edges of Bonelli's eagle are not under-sampled because the species reaches its distribution boundary in the study area, where, in addition, it has the highest observed densities and population size of the whole Western Palearctic. Therefore, the species and the geographic scenario of this paper allow testing the prediction of the abundant-centre 'general rule'. The results support the hypothesis considering that the population density of the species decreased towards the boundary of the range in the Iberian Peninsula (see Figs. 1 and 3).

If peripheral populations occupy low-suitability areas with a reduced probability of being colonized and behave as demographic sinks, what consequences should be considered for the conservation of the Bonelli's eagle? In our opinion the conservation efforts should not be restricted to those areas in the periphery of the distribution range following regional interests that are based on the relative rarity of the species within geopolitical units (see also Muñoz et al., 2005), which, however, do not necessarily reflect its global rarity or conservation relevance (Rodrigues and Gaston, 2002). Conservation efforts are probably best invested in areas of high potential environmental suitability (e.g., Lawton, 1993; Sergio and Newton, 2003; but see Lesica and Allendorf, 1995; Nathan et al., 1996) where human impacts need still to be corrected (see Ontiveros et al., 2004 for a review of these impacts). The emigration of individuals from healthy populations in core areas would eventually be beneficial to those in the periphery (Muñoz et al., 2005). However, a complete conservation strategy should also take into account factors at larger scales such as the presence of areas that attract juveniles during natal dispersal (Cadahia et al., 2005; López-López et al., 2007a). This is specially important in the Spanish metapopulation of the Bonelli's eagle as the decrease in pre-adult mortality during the first two years of life was more important for the stabilization of the metapopulation than similar decreases in the values of adult mortality (Soutullo et al., 2008). Contrary to these views, international EU-funded conservation projects (LIFE programme) are being normally directed towards peripheral populations in low-suitability areas, and conservation plans typically do not pay enough attention to the dispersal process (Muñoz et al., 2005).

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Appendix I

Summary of the results of the 2005 breeding Bonelli's eagle census (compiled and modified from tables in Del Moral 2006). **Province**: administrative units for which data were gathered. **Center/Periphery**: C for provinces within the core area of distribution in peninsular Spain, P for those in the periphery (a dash is used for provinces with no records of breeding eagles). **N2005** and **N2000**: number of breeding pairs for the 2005 and the 2000 censuses (*: assigned considering a more precise census in 2002). **Prod**: productivity, measured as the number of young fledged per established territorial pair (number of monitored territories in brackets). **UTM**: Number of occupied 10 × 10 km UTM squares. **Km^2**: size of the province (in km^2). **dUTM**: density of breeding pairs per occupied 10 × 10 km UTM square, measured as N2005/UTM (note that density for Burgos is 0.33 pairs/100 km^2 because it has three occupied territories in three squares but just a single breeding pair – the other two territories being occupied by singles).

Province	Center/ Periphery	N2005	N2000	Prod	UTM	km^2	dUTM
Álava	P	1	2	0.00 (1)	1	2963	1.00
Albacete	C	22	16	0.82 (22)	20	14858	1.10
Alicante	C	20	21	1.20 (20)	18	5816	1.11
Almería	C	69	56	0.95 (62)	37	8774	1.86
Badajoz	P	49	50	0.95 (41)	39	21766	1.26
Barcelona	C	11	10	0.90 (11)	9	7733	1.22
Burgos	P	1	5	0.00 (1)	3	14022	0.33
Cáceres	P	45	44	0.92 (79)	35	19868	1.29
Cádiz	C	42	39	1.32 (38)	21	7436	2.00
Castellón	C	27	23	1.00 (27)	23	6679	1.17
Ciudad Real	C	23	22	0.78 (23)	19	19813	1.21
Córdoba	C	36	38	1.00 (31)	19	13769	1.89
Cuenca	C	16	17	0.56 (16)	12	17141	1.33
Gerona	C	4	4	0.50 (4)	3	5910	1.33
Granada	C	54	38	1.35 (40)	38	12531	1.42
Guadalajara	C	14	14	1.00 (14)	14	12167	1.00
Huelva	P	0	2	–	0	10128	0.00
Huesca	P	3	2	1.33 (3)	2	15626	1.50
Jaén	C	37	46	1.04 (23)	29	13489	1.28
La Rioja	C	6	5	0.83 (6)	6	5045	1.00
Lérida	P	4	4	1.00 (4)	4	12150	1.00
Madrid	C	2	2	1.50 (2)	2	8028	1.00
Málaga	C	79	79*	1.31 (52)	51	7308	1.55
Murcia	C	23	22	1.17 (23)	17	11313	1.35
Navarra	P	3	3	0.66 (3)	3	10391	1.00
Salamanca	P	8	11	1.00 (8)	6	12349	1.33
Sevilla	C	16	7	1.33 (9)	7	14036	2.29
Tarragona	C	46	47	1.02 (44)	33	6303	1.39
Teruel	C	10	9	0.70 (10)	9	14804	1.11
Toledo	C	10	9	1.20 (10)	10	15370	1.00
Valencia	C	44	36	1.10 (26)	38	10763	1.16
Zamora	P	5	7	0.20 (5)	5	10561	1.00
Zaragoza	C	18	18	1.00 (27)	16	17274	1.13

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