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The coexistence of the eagles *Aquila chrysaetos* and *Hieraaetus fasciatus* increases with low human population density, intermediate temperature, and high prey diversity

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Competition among species with similar ecological requirements may preclude species coexistence. However, species with similar requirements may coexist under determinate environmental conditions. Major effort is being dedicated to conserve the golden eagle (*Aquila chrysaetos*) and Bonelli's eagle (*Hieraaetus fasciatus*) in Spain, two raptors with similar ecological requirements. This work analyses how some key ecological factors correlate with the coexistence of the two eagles, which may help to optimize the conservation plannings of the two species. Findings show that low human population density favours eagle coexistence, because human presence is harmful for both eagles. Temperature is an important factor affecting the segregation of the two eagles, with Bonelli's eagle dwelling in warmer zones than the golden eagle, but overlapping in squares with intermediate temperature. High prey diversity facilitates the coexistence of the two eagles, possibly because it encourages trophic segregation. Conservation planning for both species would be enhanced by the protection of zones with low human population density, intermediate temperature, and high prey diversity, which seem to favour the coexistence of the two eagles.

Introduction

The current environmental policies worldwide generally ignore interspecific effects such as competition (Soulé *et al*. 2005), and in this way, their goals become autoecological and spatially minimalistic (Soulé *et al*. 2003). Competition among species with similar ecological requirements is one of the primary biotic factors affecting a species' distribution (Pulliam 2000). When two species with similar ecological niches are in sympatry, the competitively superior species may exclude the other (Pianka 2000). Interspecific competition, in fact, is a major source of exclusion in raptors (Newton 1979). However, some factors may facilitate coexistence among potentially competitive species, primarily habitat heterogeneity (Chesson 1985). Certainly, the incorporation of these ecological data in conservation biology must be not neglected (Crandall *et al*. 2000).

It has been suggested that golden eagle (*Aquila chrysaetos*) and Bonelli's eagle (*Hieraaetus fasciatus*) might be potentially competitive, because share their primary nesting sites (rocky cliffs), their primary prey is the rabbit (*Oryctolagus cunniculus*) and they overlap throughout most of their distribution area in western Mediterranean (Gil-Sánchez *et al*. 1994, del Hoyo *et al*. 1994, Martí & del Moral 2003). It has even been proposed that the presence of the golden eagle negatively influences the presence of Bonelli's eagle (Gil-Sánchez *et al*. 1996, Real 2004; but *see* Carrete *et al*. (2002) for one exception). However, detailed models suggest that the effect of the golden eagle on population dynamics of Bonelli's eagle is low and density-dependent (Carrete *et al*. 2005).

On the other hand, both eagle species are included in the *Red List of the Birds of Spain*, with the golden eagle catalogued as Near Threatened and Bonelli's eagle as Endangered (Madroño *et al*. 2004). These raptors are large, charismatic and scarce, and may be considered as typical flagship species in conservation (Caro & O'Doherty 2001). Conservation of flagship species is often very expensive, and management regimes of two flagship species can conflict (Simberloff 1998). Therefore, it would be useful know what factors favour the coexistence of the two species, in order to design efficient planning for the simultaneous conservation and management of both species.

In this study, we analyse at the spatial scale of peninsular Spain the relative influence of three environmental factors which have been demonstrated to be important in the distribution of both species at local scale (*see* below). These variables might affect the coexistence of the two eagles, but multivariate analyses on this topic at a large spatial scale (Iberian Peninsula) is lacking. Thus, the objective of this work is not to analyse the potential competition between the two eagles, but to examine under what circumstances their coexistence is possible.

1 Human population density: Humans negatively affect the distribution of both eagles by perturbations as well as direct persecution (Arroyo 2004, Real 2004). Human presence, therefore, may provoke the local extinction of one of the two species, or both (Hanski 1998).
2 Temperature: Bonelli's eagle is a thermophilic species (Ontiveros & Pleguezuelos 2003, Muñoz *et al*. 2005), while the golden eagle shows a much higher ecological range for temperature (Cramp 1998). Accordingly, we predict that the two eagles coexist in zones with intermediate or high temperatures, within the thermoclimatic range of peninsular Spain.
3 Prey diversity: Although their primary prey is the rabbit, both species differ in the frequency in which eat this prey, and the dietary overlap is far from complete (Jordano 1981, Gil-Sánchez *et al*. 1994). Bonelli's eagle preys relatively more on birds than the golden eagle, which, in turn, preys more on mammals (Jordano 1981, Parellada *et al*. 1984, Gil-Sánchez *et al*. 1994). Therefore, higher prey diversity should favour a trophic segregation between the two eagles, thus encouraging their coexistence.

Material and methods

Data on the distribution of both species (Fig. 1) were obtained from the Dataset of the Vertebrates of Spain (Ministerio de Medio Ambiente 2003; also *see* Martí & del Moral 2003). This dataset shows the presence/absence of each eagle in UTM squares of 10×10 km. In total, we considered 5070 squares of peninsular Spain, after excluding those without environmental data (269 squares, 4.9%). This dataset offers the most accuracy for depicting the distribution of both species in peninsular Spain, and the square size (100 km^2) is suitable to examine their coexistence, as hunting territory size is on average 199 km^2 for the golden eagle (Arroyo *et al*. 1990) and 77 km^2 for Bonelli's eagle (Sanz *et al*. 2005). Moreover, distance between nests of Bonelli's and golden eagle may be about 3 km in clumped populations of both species (Jordano

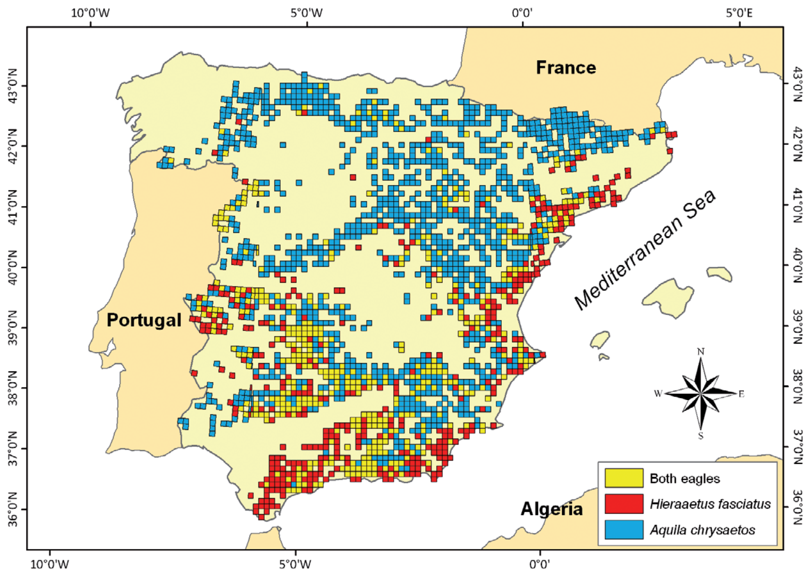

Fig. 1. Squares where presence of the golden eagle (blue), Bonelli's eagle (red), and both species (yellow) was recorded in the peninsular Spain, according to a UTM map with 10 × 10 km squares.

1981). Squares were catalogued according to the presence of the two eagles as: "No eagles", those with neither of the two species; "Golden eagle", with only golden eagle presence; "Bonelli's eagle", with only Bonelli's eagle presence; and "Both eagles", with both eagles coexisting. For the golden eagle, breeding was sure or probable in the 77.4% of the squares where the species was detected, while for Bonelli's eagle this percentage was 83%, with breeding being possible in the remaining squares where the eagles were detected (standard procedures in the atlas of breeding-bird distribution; *see* Martí & del Moral 2003).

The environmental variables used were: (1) Human population density (indiv./km^2, log-transformed). (2) Mean annual temperature (°C). Data for temperature and human population density were taken from the European Environment Agency (available at http://www.eea.europa.eu). These data were originally at the resolution of 1 × 1 km, but for analyses were up-scaled to 10 × 10 km. (3) Prey diversity, as the sum of prey species for both eagles present in each square. We considered only those prey species contributing to at least the 10% of the diet biomass of the eagles in Spain: European rabbit, red-ledged partridge (*Alectoris rufa*), wood pigeon (*Columba palumbus*), rock pigeon (*Columba livia*) and Eurasian red squirrel (*Sciurus vulgaris*) (Jordano 1981, Real 1987, Gil-Sánchez *et al*. 1994, 2000, Martínez *et al*. 1994, Ontiveros & Pleguezuelos 2000, Ontiveros *et al*. 2005). To include more prey species (with minor importance in the diet of eagles) did not significantly vary the results (data not shown). These data were taken from the Dataset of the Vertebrates of Spain (Ministerio de Medio Ambiente 2003) at a scale of 10 × 10 km. Data were managed by the GIS-program SAGA (Conrad 2005).

We first tested whether the environmental variables varied among squares according to the presence of golden eagle, Bonelli's eagle, both eagles, or neither eagle, by using ANOVA. This analysis is merely informative, giving information on the general relationship between environmental variables and the eagle presence and coexistence, but does not control for the interactions among variables. For a multivariate analysis, we performed a Generalized Linear Model (GLM) associated with a Logistic function. In this model, we used a binomial variable with two levels: "one species of eagle" and "both species of eagles" as the dependent variable, and the rest of variables (human population, temperature, prey diversity) as independent predictors. Moreover, we controlled for the spatial autocorrelation introducing as covariates the geographic variables: longitude (Long.) and latitude (Lat.) of the centre of the squares, as well as the terms

Long.^{2}, Long.^{3}, Lat.^{2}, Lat.^{3}, Long.^{2} × Lat. and Long. × Lat.^{2}, according to Legendre (1993). We did not introduce the term Latitude × Longitude because this destabilized the matrix. The introduction of these spatial variables removes most of spatial autocorrelation, and so, the effects detected are independent of the spatial structure of variables (e.g., the distribution of species). We also tested for quadratic effects of the target variables. The final model was selected by a backward step-wise process, which removed the variables that did not contribute significantly to the model. We also performed models to determine the relationship between variables and the presence of each eagle species separately. All variables had a distribution close to a normal one.

Results

The golden eagle was present in 1540 squares, in 428 (27.8%) coexisting with Bonelli's eagle. Bonelli's eagle was found in 811 squares, in 428 (52.8%) in sympatry with the golden eagle. In 3147 squares no eagle species was present (Fig. 1).

Human population was higher where only Bonelli's eagle was found than where the golden eagle was, and intermediate where both species coexisted (Table 1). Human population density did not significantly differ between squares where only Bonelli's eagle was found or those without eagle presence (unequal n HSD post hoc test: $p = 0.34$; Table 1). Human population density was the lowest where the golden eagle was present, and it was significantly lower than where Bonelli's eagle was present (post hoc: $p < 0.001$; Table 1). Mean annual temperature determined the spatial segregation of the two species. The golden eagle preferred relatively colder sites, while Bonelli's eagle preferred warmer areas. The coexistence of the two species was more probable in squares with intermediate temperature, which was considerably higher than in those squares where only the golden eagle was found (for each comparison, post hoc tests: $p < 0.001$; Table 1). Prey diversity encouraged the coexistence of the two species, this circumstance being more probable where prey diversity was higher (post hoc: $p < 0.001$; Table 1). In the squares without eagle prey diversity was significantly lower than in squares with eagles (post hoc: $p < 0.001$; Table 1).

Multivariate analyses with a GLM showed that the distribution of the golden eagle was negatively correlated with human population density and temperature, but positively correlated with prey diversity (Table 2). The distribution of Bonelli's eagle was also positively correlated with prey diversity and negatively with human population density. However, the presence of Bonelli's eagle was more probable in warmer areas, although a significant quadratic term indicated that this probability decreased for very warm sites (Table 2). Significant effects for some spatial terms show that the distributions of the two eagles vary geographically in the Iberian Peninsula.

The Generalized Linear Model showed that the coexistence of both species was more probable in squares with lower human population density, higher temperature, and higher prey diversity (Table 3). The model included a quadratic effect for temperature, which implies that the coexistence increased with temperature, but decreased at the highest temperatures (intermediate temperature seems to favour the coexistence). The spatial terms show that the coexistence between both eagles increases toward the East, in a complex form, following a cubic func-

Table 1. Mean values (SE) of three environmental variables in the groups for squares with "No eagles", "Golden eagle", "Bonelli's eagle" and "Both eagles", and the results of the ANOVA (all significant at $p < 0.001$). Raw data are shown, although statistical analyses were performed with transformed data.

Environmental variables	No eagle $n = 3147$	Golden eagle $n = 1112$	Bonelli's eagle $n = 383$	Both eagles $n = 428$	SS	MS	$F_{3,5066}$
Human population (per km^2)	126.1 (9.0)	19.4 (15.2)	65.1 (25.9)	29.0 (24.5)	565.8	188.6	213.9
Temperature (°C)	13.4 (0.05)	11.3 (0.08)	15.3 (0.13)	14.0 (0.12)	805.1	268.4	322.6
Prey-species diversity	2.87 (0.02)	3.18 (0.03)	3.18 (0.05)	3.49 (0.05)	200.1	66.7	61.7

Table 2. Results of the Generalized Linear Model on the effect of environmental variables on the distribution of the golden eagle and Bonelli's eagle. Values of the statistic Wald, *p*, and the estimate of the Logistic Regression are shown for those variables included in the final model. Model selection performed by a backward stepwise process.

	Golden eagle			Bonelli's eagle		
Variable	Wald	*p*	Estimate	Wald	*p*	Estimate
Intercept	285.77	< 0.001	–2.19	484.73	< 0.001	–4.31
Longitude	20.54	< 0.001	108.57	18.05	< 0.001	127.76
Longitude^2	5.30	0.02	11.74	4.01	< 0.05	–13.16
Longitude^3	22.59	< 0.001	–237.75	14.81	< 0.001	–247.53
Latitude	54.92	< 0.001	456.12	46.80	< 0.001	–620.27
Latitude^2	53.19	< 0.001	–901.92	46.90	< 0.001	1270.65
Latitude^3	51.09	< 0.001	444.76	46.91	< 0.001	–650.73
Longitude^2 × Latitude	5.70	0.02	–12.16	4.09	< 0.05	13.51
Longitude × Latitude^2	24.47	< 0.001	130.81	11.91	< 0.001	120.37
Human population density	170.16	< 0.001	–0.70	129.78	< 0.001	–0.74
Temperature	129.87	< 0.001	–0.74	37.34	< 0.001	4.55
(Temperature)^2	–	–	–	23.29	< 0.001	–3.28
Prey diversity	87.72	< 0.001	0.37	120.85	< 0.001	0.59

tion (Table 3). The relationship between longitude and the coexistence of the two eagles varied with latitude, as shown by a significant interaction with latitude (Table 3, *see* also Fig. 1). The deviance of the model was 0.91, and it catalogued correctly 78.8% of squares ($n = 1923$).

Discussion

It has been proposed that the presence of the golden eagle negatively affects Bonelli's eagle in Spain, competition with the golden eagle being a cause of the decline in Bonelli's eagle (review in Real 2004). This latter species has suffered a sharp population decline in Spain (Arroyo *et al*. 1995), a country that accounts for the 75% of the European population (Tucker & Heath 1994). For these reasons, a great conservationist effort is being undertaken in Spain for Bonelli's eagle (Muñoz *et al*. 2005). On the other hand, the conservation concern for the golden eagle is also substantial (Arroyo 2004). However, despite local studies suggesting that the two eagles compete (e.g. Gil-Sánchez *et al*. 1994), a set of studies suggest that the presence of the golden eagle hardly affects Bonelli's eagle (Carrete *et al*. 2001, 2002, 2005). Indeed, the findings in the present study suggest that the coexistence of the two eagles is feasible, at least at the geographical perception of 10 × 10 km UTM squares. In fact, the distribution of Bonelli's eagle overlaps with that of the golden eagle in 52.8% of the squares. Analysing three factors presumably key for the distribution and coexistence of the two eagles, we found that, in Spain, such coexistence is feasible in squares with low human population density, intermediate temperatures, and high prey diversity.

Low human population density was associated with the coexistence of the two species. As both eagles are negatively affected by the

Table 3. Results of the Generalized Linear Model on the binomial variable one species of eagle vs both species of eagle, and environmental factors (and quadratic significant terms) included in the final model by a backward stepwise process. Values of the statistic Wald, *p*, and the estimate of the Logistic Regression are shown.

Variable	Wald	*p*	Estimate
Intercept	167.25	< 0.001	–3.43
Longitude	13.99	< 0.001	33.28
Longitude^2	13.56	< 0.001	–33.59
Longitude^3	13.79	< 0.001	–33.58
Latitude	9.51	0.002	1.48
Longitude^2 × Latitude	13.14	< 0.001	33.38
Human population density	19.94	< 0.001	–0.41
Temperature	24.19	< 0.001	3.97
(Temperature)^2	15.57	< 0.001	–3.07
Prey diversity	62.45	< 0.001	0.58

human presence, the higher the human population density, the higher the probability that one or both species will go locally extinct. Several local studies have found Bonelli's eagle to be more tolerant to human presence than is the golden eagle (López-López *et al*. 2004). Here, in the univariate analysis, human population density did not significantly vary between squares with Bonelli's eagle and those without eagles. However, human population density negatively correlated with Bonelli's eagle distribution when included in a multivariate model with temperature, which positively correlated with Bonelli's eagle distribution, and with human population ($r = 0.50$; $p < 0.001$). This suggests that Bonelli's eagles are found more associated to human presence than golden eagles as a consequence of their preference for warmer zones.

Temperature was one important factor regulating the spatial segregation between the two eagles in Spain. The golden eagle is found in squares colder than those occupied by Bonelli's eagle, possibly contributing to altitudinal segregation and the avoidance of competition for resources. This altitudinal segregation mediated by temperature has been found at local scales (e.g. López-López *et al*. 2004), and related to competition between the two eagles (Gil-Sánchez *et al*. 1994). The two species belong to different biogeographic types, the golden eagle being Holarctic, and Bonelli's eagle Indoafrican (Voous 1960), therefore, being more thermophilic (Ontiveros & Pleguezuelos 2003, Muñoz *et al*. 2005; *see* also López-López *et al*. 2007). This suggests that the segregation between the two species according to temperature is due to differences in their niche for environmental temperature. In fact, both species coexisted in squares with intermediate temperature, where their niches for temperature overlapped.

Higher prey diversity favours a segregation of trophic niches, reducing interspecific competition and favouring higher predator species richness (e.g. Haddad *et al*. 2001). This also may work at the level of two species as the two eagles under study, as resource heterogeneity favours coexistence (Chesson 1985). The effect of prey diversity on the coexistence of the two species was the strongest (Table 3). Despite having similar diets, the two eagles do not completely overlap (Jordano 1981, Gil-Sánchez *et al*. 1994), and it is possible that, in sympatry, the two eagles prey on species at a different frequency. For example, Jordano (1981) found that, in Sierra Morena (southern Spain), in sympatry, the diet of Bonelli's eagle was more based on birds, and the diet of the golden eagle was more dependent on rabbit, allowing certain trophic segregation. Prey abundance also might favour eagles' coexistence (Delibes-Mateos *et al*. 2007), but prey availability seems not to be limiting for Bonelli's eagle, at least in some zones (Ontiveros *et al*. 2005).

The main threats against the golden eagle and Bonelli's eagle are persecution, habitat degradation and electrocution, and proposal for conservation measures are the diminution of the causes of mortality, nesting areas protection, sustainable human hunting of their preys, and correction of the dangerous power lines (Madroño *et al*. 2004). This study provides useful information for designing common protection areas for both species. Protection should be intensified in mountain habitats with low human population density, intermediate temperature, and high prey diversity.

In conclusion, coexistence of the golden and Bonelli's eagle in Spain is feasible under a range of conditions. Prey diversity favours eagle coexistence. Moreover, human population density seems to break coexistence, while temperature segregates the distribution of the two species, this being possible only where temperature is mean. Conservationist efforts concentrated in adequate zones for coexistence might be useful for the simultaneous conservation of the two species.

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