Full title: Habitat suitability modelling reveals a strong niche overlap between two poorly known species, the broom hare and the Pyrenean grey partridge, in the north of Spain.

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Running title: Niche overlap between the broom hare and the Pyrenean grey partridge.

Abstract

In the present work, we derive a habitat suitability model of the broom hare and the Pyrenean grey partridge in the Cantabrian Mountains by using the Ecological Niche Factor Analysis. Both species are endemic to the northern of Iberian mountains, and because of the vulnerability of the hare to endangerment or extinction and because of the great interest in the partridge, this habitat requires specific conservation measures. Literature on these animals' biology and ecology is practically nonexistent. Habitat suitability analyses show that the hare and partridge occupy very similar ecological niches, characterized by a high percentage of broom and heather scrublands, high altitude and slope, and limited human accessibility. We have identified differences in habitat selection between the Pyrenean grey partridge and other sub-species subspecies of partridge present in central-northern Europe. Our results indicate a probable metapopulation structure for both the hare and partridge, however, according to our predictive maps, there is a high connectivity between suitable habitats. Current decline of traditional rural activities, such as mountain livestock, are affecting the mosaic landscape. This, in turn, enhances biodiversity in the area and, particularly, the viability of these valuable animal populations.

Keywords: *Lepus castroviejoi*, ENFA methodology, *Perdix perdix*, niche description, Cantabrian Mountains.

1. Introduction

The knowledge of the distribution of endangered animal species and their habitat requirements is essential in conservation biology (e.g., Engler et al., 2004; Whittaker et al., 2005). One of the main concerns is habitat fragmentation due to land use, which has long been recognized as a major threat to the preservation of biodiversity and to the viability of endangered species (e.g., Hartley and Hunter, 1998; Kurki et al., 2000). However, biodiversity in natural ecosystems often appears to depend on a certain degree of disturbance (see White and Pickett, 1985), such as fire, flooding, storms, and herbivory (Hobbs and Huenneke, 1992), as these events may play a role in increasing plant species biodiversity (Waldhardt et al., 2004). Areas characterized by a mosaic structure, v.g. forests, shrub lands and pastures, tend to provide very productive natural systems, suitable for certain animal species, such as roe deer (*Capreolus capreolus*), Iberian lynx (*Lynx pardina*), wild rabbit (*Oryctolagus cuniculus*) (e.g., Fernández et al., 2003; Acevedo et al., 2005; Michel et al., 2006; Williams et al., in press.).

Conservation strategies have focused not only on the preservation of adequate habitat areas, but also the spatial distribution of these areas throughout the landscape. To attain these goals, the use of spatial models (Peterson et al., 1999; Robertson et al., 2001; Chefaoui et al., 2005; Hortal et al., 2005; Soberón and Peterson, 2005; Acevedo et al., 2006; Quevedo et al., 2006) has become a common practice in ecology.

A wide variety of predictive models has been used to simulate the spatial distribution of plant and animal species (see for instance Guisan and Zimmermann, 2000; Scott et al., 2002). Most of these models identify a quantitative or qualitative relationship between species presence and a number of meteo-climatic, geomorphological variables and information on vegetation cover, land use and anthropogenic disturbance (Austin et al., 1990; Hortal et al., 2005).

Predictive models can easily be made from presence/absence data of a species (examples at Osborne and Tigar, 1992; Brito et al., 1999; Carroll et al., 1999). However, before using such information, it is necessary to have previously distinguished true absences from a mere lack of information (e.g. Thuiller et al., 2004; Araújo et al., 2005). Presence data usually correspond to the true presence of the species. In contrast, absences could be due to an insufficient sampling effort (Hortal et al., 2005). Hence, false absences are much more common than false presences. Thus, there is a need to remove these inaccurate data from distributional maps (Palmer et al., 2003) and to assure the reliability of absences (Anderson, 2003).

There are various other ways available to estimate potential distributions when data on absences are not reliable, such as BioMapper software (Hirzel et al., 2004a, URL: http://www.unil.ch/biomapper). This technique provides a useful alternative that relies solely on information about presences (Hirzel et al., 2001, 2002; Hortal et al., 2005), even though the obtained results were overestimated (Zaniewski et al., 2002; Engler et al., 2004).

To date, relatively few predictive models have been applied to rare and endangered animal species (e.g. Godown and Peterson, 2000; Fernández et al., 2003; Naves et al., 2003; Graf et al., 2005; Acevedo et al., 2006; Quevedo et al., 2006), despite their potential to enhance conservation management. For example, predictive models could help in identifying sites with high colonization potential.

Here we analyse habitat suitability for two emblematic animal species of the Cantabrian Mountains (Asturias region, northwestern Spain), the broom hare (*Lepus castroviejoi*) and the Pyrenean grey partridge (*Perdix perdix hispaniensis*). Both of them are of great conservation value. The broom hare is endemic to this area, whereas this partridge subspecies is endemic to the northern mountains of the Iberian Peninsula, from the Galician border to the Pyrenees. The IUCN (2004) considered the broom hare as species that is vulnerable to becoming endangered or extinct due to habitat loss and degradation and population decline. In contrast, the Pyrenean grey partridge was not considered in the Red List of Threatened Species (IUCN 2004).The partridges conservation value lies in the facts that it occupies the southwestern edge of the species distribution in Eurasia and that it has numerous ecologically distinct features (Lucio et al., 1992; Novoa et al., 2002). Populations at the edge of their distribution range are of special interest (see Gortázar et al., in press) because they help in our understanding of aspects such as ecological niches and threshold responses to environmental change (Brown et al., 1996; Holt et al., 2005). The partridge's geographical location in the Cantabrian Mountains is isolated from its nearest neighbours in the Pyrenees by more than 300 km, making the situation of studying population very critical. The Pyrenean grey partridge was included in the Plan de Ordenación de los Recursos Naturales de Asturias (PORNA) labelled as "especie singular" (a remarkable species). It has also been included in Annex II of the Convention on the Conservation of European Wildlife and Natural Habitats, Council of Europe, Resolution No. 6 (1998), which lists the species requiring specific habitat conservation measures (http://www.eko.org.pl/lkp/prawo_html/bern_06.htm). Despite the reasons for needing them, ecological studies on the broom hare and the Pyrenean grey partridge in the Cantabrian Mountains are very scarce.

The international literature on the broom hare is circumscribed to some studies on its taxonomic status (Palacios, 1976; Schneider and Leipoldt, 1983; Pérez-Suárez et al., 1994; Melo-Ferreira et al., 2005; Estonba et al., 2006), whereas the few ecological studies carried out on its distribution and abundance, are to be found solely in local journals (Palacios and Ramos, 1979; Ballesteros, 2000, 2003), or in unpublished reports (Ballesteros et al., 1997). These studies concluded that broom hares occupy habitats characterized by mountainous grasslands and scrublands (mainly *Cytisus* spp., *Genista* spp., *Daboecia* spp., *Erica* spp.) and small patches of woodlands (*Fagus* spp., *Quercus* spp., *Betula* spp., *Ilex* spp.). The altitude range of the broom hare distribution area is between 1000 and 1900 m.a.s.l. (Ballesteros, 2003). This author suggests that hare population is decreasing in the peripheral areas of the Cantabrian Mountains, whereas it has relatively high densities in the core of its distribution area.

There are several studies on grey partridge biology regarding population trends (Putaala and Hissa, 1998; Panek, 2005), reproduction (Aebischer and Ewald, 2004), the effect of predators (Potts 1986; Tapper et al., 1996; Panek, 2005) and the effect of habitat management on population dynamics (Aebischer and Ewald, 2004; Bradbury et al., 2004; Bro et al., 2004; De Leo et al., 2004). However, there is little known about the Iberian Peninsula subspecies specifically (Lucio et al., 1992). Only a few studies on the Pyrenean populations are worth being mentioned (Lescourret and Genard, 1993; Novoa et al., 2002). Habitat change is the main cause of current declines in grey partridge populations. In most of Europe this decline is caused by the transition from traditional to industrial agriculture (e.g., Potts, 1986; Panek, 2005), while the drop in the Pyrenean grey partridge population is a consequence of the encroachment of dense scrublands, a necessity for this subspecies (Novoa et al., 2002), caused by the decline of traditional agricultural practices. The Cantabrian partridge populations have suffered from habitat loss throughout the last decades, particularly in the northern slope of the Cantabrian Mountains, Asturias region (Lucio et al., 1992). The grey partridge habitat in the Cantabrian Mountains is characterized by mountainous scrublands (*Genista* spp., *Daboecia* spp., *Erica* spp) and deciduous forests (mainly *Fagus* spp., *Quercus* spp. and *Betula* spp.), with an altitude ranging between 900 and 1200 m.a.s.l. (Lucio et al., 1992).

The aim of this study was to develop predictive habitat suitability models for the broom hare and the Pyrenean grey partridge. Our specific objectives were:

1) To study the environmental niche occupied by each species in the study area.
2) To model the potential distribution of both species.

3) To review environmental requirements of both species in order to identify differences and similarities.

4) To identify habitat management strategies with the ability to improve the population status of these species.

2. Material and methods

2.1. The study region

To define the biogeographical niche occupied by a species in a given region, the study area should encompass the extreme conditions present in that region. Thus, to carry out Ecological Niche Factor Analyses (ENFA; Hirzel et al., 2002), we have chosen a geographical area that includes both sites where broom hare and grey partridge population have been observed, as well as the coastal and mountain environments present in Asturias (Fig. 1), NW Iberian Peninsula.

Asturias is included in the Eurosiberian climatic dominion of Atlantic type climate. Winters are cold, with a minimum of 6 months of potential frosts in the study area. The temperatures range from 3 - 8 ºC to -4 - 0 ºC in the coldest months. Precipitations are abundant (1400-2100 l/m2/year) and it frequently snows in winter season (e.g., Lines Escardó, 1970).

The predominant vegetation in Asturias are deciduous and mixed forests. The characteristic trees and scrubs are oak (*Quercus robur*, *Q. ilex*, *Q. petraea*, *Q. orocantabrica*, etc), beech (*Fagus sylvatica*), birch (*Betula celtiberica*), yew (*Taxus baccata*), holly (*Ilex aquifolium*), hazel (*Corylus avellana*), and several scrubs (*Genista* spp., *Cytisus* spp., *Erica* spp., *Calluna* spp., *Vaccinum* spp., *Juniperus* spp.). These deciduous forests have been under human management for a long time (Tucker and Evans, 1997).

2.2. Broom hare and Pyrenean grey partridge distribution data

Data on presence of both species were assessed by carrying out surveys addressed to Rural Agents of the Environment Agency of Asturias. Survey addressees were asked to draw their work area and the range occupied by the two study species on printed maps. They were also given a questionnaire, which aimed to indicate the status, i.e., growing trends, of the populations present. Information covered 90.03% of the whole study area.

Maps that were correctly filled were scanned at a 200-dots-per-inch (d.p.i.) resolution, and transformed into 1x1 km UTM grid cells by means of the 'Extract' tool of Idrisi GIS software (Clark Labs®, 2001, 2004). Presence data were only considered in the analyses if they were confirmed in at least three questionnaires. This restrictive criterion was used to avoid including false presences in our statistical models (see Palmer et al., 2003). The broom hare (n=164) and the Pyrenean grey partridge (n=95) presence data are shown in Fig. 1.

2.3. Environmental data

Environmental data came from an Asturias GIS database compiled and managed mainly by P. Acevedo, and then imported and processed into the Idrisi GIS System (Clark Labs®, 2001, 2004). All maps were referred to a 1 km^2 resolution, to fit with the spatial resolution of biological data (see another example in Chefaoui et al., 2005). Many factors have been described to affect population abundance and distribution of birds and mammals in the Iberian Peninsula, such as ecological factors, bioclimatic parameters and human activity (e.g., Acevedo et al., 2005, 2006; Quevedo et al., 2006). In this study we selected 33 variables that could act as determinants of current broom hare and Pyrenean grey partridge distribution in NW Iberian Peninsula (Table I), 27 accounting for environmental traits (habitat structure, vegetation characteristics and geomorphology), and 6 accounting for human impacts. Data origin is as follows:

- Seventeen geomorphological variables were computed on a 1 km^2 grid resolution by averaging out information extracted from a 100 x 100 m Digital Elevation Model. Mean, maximum and minimum altitude (m.a.s.l.), altitude range (meters), mean, maximum, sum and minimum slope (degrees), mean aspect diversity, using a 7x7 pixel kernel on a 9-categories reclassified aspect map (see Clark Labs®, 2001, 2004 for the method; and Chefaoui et al., 2005 for an example of the use of this variable), and the percentages of each orientation category per 1 km^2.

- Ten variables accounted for the type of vegetation. This information was obtained from a high-resolution digital vegetation map of Asturias (GIS of the Environmental Thematic Cartography, Government of Asturias, 1:25000). The digital map was rasterized with a 100 m grid resolution and then reclassified in 10 categories to estimate the fraction of each 1 km^2 pixel covered by mature forest (oak, beech, chestnut, etc.), pre-forest (holly, birch, ash, etc.), scrub (hazel, laurel, rose, etc.), broom, heather, mountain scrub, Spanish greenweed, mountain grass, urban areas, and marsh and estuary vegetation.

- Six variables, that accounted for the human impact on broom hare and grey partridge territories: distances to small and big population nuclei, and different types of roads (first order roads (highways), national roads, regional roads and nonasphalted roads), were calculated.

We did not consider any climatological variables, despite the fact that the realized niche of a species may be shaped by climatic conditions. However, the study area is characterized by a relative climatic homogeneity, with only slight differences related to topographic variations (similarly to Acevedo et al., 2006; Quevedo et al., 2006).

All variables were Box-Cox normalized prior to their use in the ENFA analyses.

2.3. Statistical analyses

2.3.1. Niche modelling

In our case, only presence data were available. Thus, we selected ENFA to produce predictive maps of habitat suitability (i.e., potential distribution) from GIS information (see a list of publications at http://www.unil.ch/biomapper/bibliography.html). ENFA were made using BioMapper 3.0 (Hirzel et al., 2004a; freely available at http://www.unil.ch/biomapper). These maps are produced in two steps.

First, ENFA characterizes the response of the species to the main environmental variations in the study area. ENFA transforms the original ecogeographical variables into new, uncorrelated, axes. The first axis (Marginality Factor) accounts for the marginality of the species (i.e., differences between the conditions suitable for the species and the regional average traits; see below), whereas the other axes (Specialization Factors) accounts for the species response to other secondary environmental gradients in the study area (e.g., Hirzel et al., 2004b; Hortal et al., 2005). ENFA analysis identifies two key components of species environmental niches. The first being a Marginality Coefficient, which is a measure of the distance between species niche and the mean environmental conditions of study area, and the second being Tolerance Coefficient, which measures how the species tolerates environmental variations in the analysed territory. A high Marginality Coefficient value indicates that the species' requirements differ considerably from the average habitat conditions in the study area and a Tolerance Coefficient value closer to 0 in a range from 0 to 1 indicates a higher degree of specialization.

Once ENFA factors were computed, habitat suitability scores for each map pixel were calculated and mapped in accordance to the responses of the species to each factor. Partial suitability scores were computed for each factor as the percent distance to the median scores of observed presences. Habitat Suitability was then obtained as a weighted average of these partial suitability scores according to the variability explained by each factor (Hirzel et al., 2002).

2.3.2. Model validation and accuracy

Explained Information and Explained Specialization (sensu Hirzel et al., 2004a) are two measures of how the resulting suitability model explains the observed data. These two measures account for the total variability of the species distribution explained by the model and for additional variability on the marginality and specialization factors not included in the Explained Information measure (ibid.). However, before using the ENFA results or habitat suitability maps (HSMs), we needed to evaluate their accuracy to describe the actual spatial response of the species. We assessed the robustness and predictive power of the HSMs by means of a Jackknife cross validation procedure implemented in BioMapper 3.0. software (Hirzel et al., 2004a).

2.3.3. Niche analysis

The shape of the environmental niche of the species has been described as the variation in the habitat suitability scores throughout the environmental gradient defined by the Marginality Factor (see Chefaoui et al., 2005; Hortal et al., 2005; Cassinello et al., in press). We analyzed the ecological niche of both study species according to this methodology.

The HSM obtained for each species was reclassified (see Chefaoui et al., 2005) as either very low habitat suitability (0-25), low habitat suitability (26-50), high habitat suitability (51-75), or very high habitat suitability (76-100). These new maps were cross-tabulated in the GIS environment to pinpoint zones of spatial coincidence where both models show at the same time either very high or very low habitat suitability scores, and zones of spatial non-coincidence, areas highly suitable for one species but unsuitable for the other. By means of a Mann–Whitney U test, we extracted those environmental variables that characterize each of these two zones, as they are significantly different to the conditions in the rest of the study area. The statistical significance was corrected by means of Bonferroni tests (Perneger, 1998).

3. Results

The 33 environmental variables considered were reduced to 2 factors for both species (Table II) that explained 100.00% of the variance in both cases. The percentages explained by each specialization factor can be seen in Table II.

Mean and maximum altitude, distance to nonasphalted and regional roads, and mountainous vegetation were the determinant variables on potential distribution models of both species (Table II). The scores of these variables in the presence cells differed from their mean values in the region. The accessibility to the territory, quantified as distance to human structures such as national roads, had a slightly higher influence on the broom hare model than on the partridge one. However, terrain slope had a higher influence on the grey partridge model than on the hare one. Jackknife validations indicated that both potential maps are highly reliable (mean Spearman coefficient > 0.95 for both species).

Our results showed that both species occupy marginal areas in the study region according to the main environmental gradient (broom hare Marginality Coefficient=2.19; grey partridge Marginality Coefficient=2.41, Fig. 2). These species were not tolerant to secondary environmental gradients, (both Tolerance Coefficients=0.00) thus, showing a high specialization level. The shape of the environmental niches showed that both species niches are widely overlapped in the study area (Fig. 3).

Reclassified and cross-tabulated habitat suitability maps show the areas of spatial coincidence (Fig. 4). No zones of spatial non-coincidence occurred. The results of Mann-Whitney U test to characterize zones of spatial coincidence for both species can be seen in Table III. Altitude and slope were the variables with higher relevance in the characterization of coincidence areas of both species (very high or very low habitat suitability for both species). In addition, the distance to roads and the percentage of forest and broom scrublands were also variables with significant influence in the discrimination between overlap areas and the rest of the territory.

Presence data of the study species showed a metapopulation structure (Fig. 1). Concerning the status of these populations, 70.83% of the hare and 58.82% of the partridge populations showed, neither a decreasing or increasing trend. Decreasing trends were appreciated in 16.67% of hare and 35.29% of partridge populations, whereas increasing population trends were detected in 4.17% of hare populations and 5.88% of partridge populations.

4. Discussion

The Cantabrian Mountains cover areas of great conservation value, most of them under the highest protection measures. For example, the Cantabrian mountains are home to three Natural Parks, Fuentes del Narcea y del Ibias, Somiedo, and Redes, and Picos de Europa National Park. Several endangered flagship species can be found in their domains, such as, the European brown bear (*Ursus arctos arctos*), the Cantabrian capercaille (*Tetrao urogallus cantabricus*), and lesser known species, also of great conservation relevance, but which are usually ignored in the literature. Here we presented an analysis of habitat suitability of two lesser known species of the region, the broom hare and the Pyrenean grey partridge. Both are endemic to the north of the Iberian mountain ranges and literature on their biology and ecology is practically nonexistant.

Generalized linear and generalized additive models have become very popular for predicting animal distributions (Guisan et al., 2002; Quevedo et al., 2006). Yet, although absence or pseudo-absence data are available, more robust models can be built on only presence data by using the ENFA (Hirzel et al., 2001). However, the robustness of ENFA makes it particularly suitable and efficient when data obtained do not indicate true absences, but rather lack of information (ibid.). Thus, as our data came from surveys concerned with species presence, we have used ENFA analyses to implement the suitability maps.

4.1. Niche descriptions

According to the habitat suitability analyses carried out and to the environmental niche descriptions, we have determined that the broom hare selects areas characterized by a high percentage of broom and heather scrublands, high altitude and slope, and limited human accessibility (quantified as distance to roads variables). These results are in agreement with previously reported data on broom hare habitat (Ballesteros, 2003). The Pyrenean grey partridge also selects mountainous areas in the Cantabrian Mountains, and is mainly present in areas characterized by very high altitudes, and also by low human accessibility, broom and heather scrublands and high slopes (Lucio et al., 1992). The distribution of both species are highly marginal in the study area, although, in general, the partridges is present in slightly more marginal habitats than the broom hare.

Similarly, the Pyrenean grey partridge populations inhabiting the eastern Pyrenees select areas over 1300 m.a.s.l. of altitude, hard terrain slopes, and scrub-grassland and scrub-woodland mosaics, as well as cultures in high altitudes (e.g., Genard and Lescourret, 1990). In contrast, however, the habitat selection of the other subspecies of the grey partridge is related with agrosystems in central-northern Europe, where it prefers open, low intensity, mixed farmland comprising small fields bounded by hedges and grassy habitats (e.g., Aebischer and

Kavanagh, 1997), but it also occurs commonly in intensive cereal ecosystems (e.g., Sálek et al., 2004). During this century grey partridge populations have declined drastically in many regions (e.g., Panek, 2005), as suggested by the reduction of hunting bags (Birkan and Jacob, 1988; Potts and Aebischer, 1995). The decline is mainly due to the deterioration of agricultural habitats (Aebischer and Ewald, 2004). Habitat management actions are, thus, a priority for grey partridge conservation strategies. For example, uncultivated structures and non-crop areas are essential in aiming to keep biodiversity in agricultural landscapes (Freemark and Kirk, 2001) and to maintain grey partridges' survival and reproduction rates (e.g., Aebischer and Ewald, 2004; Buner et al., 2005).

4.2. Niche overlap

In this study, we provided evidence that the ecological niches in Asturias for the broom hare and the Pyrenean grey partridge are highly overlap. We also showed that habitat suitability is very restricted for both species. Specific values for marginality and tolerance coefficients obviously depend on the global set (mean values of the environmental predictors for the entire study area) chosen as reference, so that a species might appear extremely marginal or specialized on the scale of a whole country. However, this is not so in a subset of the country, since the extent of the region studied affects model performance (Hirzel et al., 2002; Lobo et al., 2006).

The models obtained for both species identified similar zones as highly suitable. The study species coexist and are part of the same ecological niche in the Cantabrian Mountains, although we do not know to what extent they are related to dependent on each other. Thus, habitat changes and fragmentation might affect them equally.

4.3. Conservation implications

Distribution of the study species in the Cantabrian Mountains, as pictured in this study and from our own field experience, seems to be made of a few partially isolated populations. Thus, one would assume both species would follow a metapopulation structure (sensu Levins, 1969) provided that occasional interbreeding does occur. However, the habitat suitability models obtained in this study showed relatively well-connected suitable areas for the species.

Herbivory is a type of biotic disturbance that may have profound effects on the structure and composition of an ecosystem, as it increases plant biodiversity and fosters the proliferation of small animals' refuges and shelter in a mosaic structure (Norton-Griffiths, 1979; Wiens, 1985; Hobbs and Huenneke, 1992; Prins and Van der Jeugd, 1993; Miaud and Sanuy, 2005). Current decline of traditional livestock activity in the area, which is used to maintain patches clear from forest and a mosaic structure of pastures and scrublands, may be affecting population viability of both study species, as they actively select such a landscape. Thus, should further habitat or connectivity loss occur, the broom hare and the Pyrenean grey partridge populations may end up disaggregated into a few isolated subpopulations, too small to ensure their own long-term persistence, as has already been reported in the Cantabrian capercaille (Quevedo et al., 2006).

One of the consequences of low habitat connectivity is risking the viability of the peripheral local populations (Palacios and Ramos, 1979; Ballesteros, 2003). However, from our results, no clear population trends were observed over the study period on a regional scale. The general population trends registered in our surveys showed a certain stability for both study species.

A priority for conservation should be to implement the existence of ecological corridors (e.g., Meffe and Carroll, 1997), which would aid the exchange of individuals, allowing for population interbreeding. The central part of the southern slope of the Cantabrian Mountains is mostly deforested, so that it is *a priori* ecologically suitable area for both study species.

This deforestation could alleviate an eventual connectivity problem for the broom hare and grey partridge, keeping what happened with the endangered Cantabrian capercaille subpopulations (see Quevedo et al., 2006) from occur with these species .

5. Conclusion

In the present study we showed that the broom hare and the Pyrenean grey partridge exhibit a strong niche overlap, so that the viability of their populations will be enhanced by carrying out habitat conservation strategies aimed at preserving these types of habitats. More research is needed to gain knowledge on dynamics and progress of these isolated populations. Therefore, studies should be carried out to evaluate habitat management strategies, such as scrub clearance, in order to create potential dispersal corridors that facilitate the exchange of individuals between the local populations and, thus, allowing for interbreeding. Extensive livestock practices, in particular, cattle farming, have traditionally been the biggest asset to maintain a suitable habitat for the hare and the partridge, because they have aided in preserving the grass-scrubland mosaics (Ballesteros, 2003). We suggest that, among other management strategies, extensive traditional cattle uses should be considered to improve habitat suitability for both emblematic species.

6. Acknowledgements

The authors wish to thank Georges Stora and two anonymous referees for their revision of a previous version of the manuscript. Erin Corbin for revising the English. M. Álvarez, E. Álvarez, P. Collada, J. Collada and J. Marcos for their assistance during the field work. J. Naves, Alejandro and Tito helped us with the GIS variables. We are also deeply indebted to all Rural Agents of the Environment Agency of Asturias. This is a contribution to the joint project CSIC/Principado de Asturias and P. Acevedo and V. Alzaga are supported by this project. J. Cassinello is currently enjoying a Ramón y Cajal research contract at the CSIC awarded by the Ministerio de Educación y Ciencia; he is also supported by the project PBI-05-010 granted by Junta de Comunidades de Castilla-La Mancha.

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Table I. Variables used in the analyses. See text for details and data origin.

GEOMORPHOLOGY	***HABITAT STRUCTURE***
Percentage of north orientation (%)	Percentage of mature forest area (%)
Percentage of north-east orientation (%)	Percentage of pre-forest area (%)
Percentage of east orientation (%)	Percentage of shrub area (%)
Percentage of south-east orientation (%)	Percentage of broom area (%)
Percentage of south orientation (%)	Percentage of heather area (%)
Percentage of south-west orientation (%)	Percentage of mountain shrub area (%)
Percentage of west orientation (%)	Percentage of Spanish greenweed area (%)
Percentage of north-west orientation (%)	Percentage of mountain grass area (%)
Aspect diversity	Percentage of urban area (%)
Mean altitude (m)	Percentage of marsh and estuary area (%)
Maximum altitude (m)	***HUMAN IMPACT***
Minimum altitude (m)	Distance to small population nuclei (m)
Altitude range (m)	Distance to big population nuclei (m)
Mean slope (degrees)	Distance to the nearest highway (m)
Maximum slope (degrees)	Distance to the nearest national-road (m)
Minimum slope (degrees)	Distance to the nearest regional-road (m)
Sum slope (degrees)	Distance to the nearest non-asphalted-road (m)

Table II. Correlation between ENFA factors and the environmental descriptors. Percentages indicate the amount of specialization accounted for by each factor (MF is the marginality factor and SF is the specialization factor).

VARIABLES	Broom hare		Pyrenean grey partridge	
	MF	***SF***	***MF***	***SF***
Mean altitude	0.40	0.00	0.40	0.00
Maximum altitude	0.39	0.00	0.39	0.00
Minimum altitude	0.41	0.00	0.40	0.00
Altitude range	0.16	0.00	0.19	0.00
Aspect diversity	0.04	0.00	0.05	0.00
Percentage of east orientation	0.03	-0.04	0.00	-0.02
Percentage of north orientation	0.01	-0.05	0.04	-0.02
Percentage of north-east orientation	0.09	-0.04	0.10	-0.02
Percentage of north-west orientation	-0.07	0.24	-0.03	-0.45
Percentage of south orientation	-0.03	-0.04	-0.03	-0.02
Percentage of south-east orientation	-0.03	-0.04	-0.04	-0.02
Percentage of south-west orientation	0.02	-0.04	-0.01	-0.02
Percentage of west orientation	-0.02	-0.04	-0.03	-0.02
Distance to the nearest highway	-0.07	-0.28	-0.03	0.43
Distance to the nearest national-road	0.26	0.00	0.20	0.00
Distance to the nearest regional-road	0.06	0.00	0.11	0.00
Distance to big population nuclei	0.11	0.00	0.10	0.00
Distance to small population nuclei	0.15	0.00	0.18	0.00
Distance to the nearest nonasphalted road	0.22	0.00	0.31	0.00
Mean slope	0.16	0.00	0.19	0.00
Maximum slope	0.19	0.00	0.23	0.00
Minimum slope	0.07	0.00	0.05	0.00
Sum slope	0.16	0.00	0.19	0.00
Percentage of mature forest area	0.08	0.00	0.08	0.00
Percentage of mountain grass area	0.00	0.00	0.04	0.00
Percentage of marsh and estuary area	-0.01	0.89	-0.01	-0.76
Percentage of mountain shrub area	0.09	0.00	0.25	0.00
Percentage of urban area	-0.04	-0.26	-0.04	0.22
Percentage of pre-forest area	-0.01	0.00	-0.04	0.00
Percentage of shrub area	-0.02	0.00	-0.02	0.00
Percentage of broom area	0.45	0.00	0.29	0.00
Percentage of heather area	0.01	0.00	0.03	0.00
Percentage of Spanish greenweed area	0.05	0.00	0.03	0.00

Table III. Environmental variables that characterize each zone of spatial coincidence. Mann-Whitney U test coefficient (Z) and the p-value (P; ns=no significant, += significant following the Bonferroni correction) are shown. Very high (Zone A) and very poor (Zone B) habitat suitability for both species are shown.

VARIABLE	**Zone A**		**Zone B**	
	Z	***P***	***Z***	***P***
Maximum altitude	27.94	+	-70.01	+
Mean altitude	27.59	+	-68.63	+
Minimum altitude	26.96	+	-66.87	+
Maximum slope	18.95	+	-50.26	+
Mean slope	18.70	+	-50.67	+
Sum slope	18.71	+	-50.67	+
Distance to the nearest non-asphalted-road	18.59	+	-40.36	+
Altitude range	17.54	+	-49.13	+
Distance to the nearest regional-road	16.22	+	-43.25	+
Percentage of broom area	13.50	+	-34.40	+
Distance to the nearest national-road	13.10	+	-25.52	+
Minimum slope	12.79	+	-33.18	+
Distance to the nearest highway	11.49	+	-27.46	+
Percentage of mature forest area	8.20	+	-24.22	+
Percentage of south-east orientation	-5.81	+	12.74	+
Percentage of north-east orientation	5.65	+	-7.47	+
Percentage of pre-forest area	-5.63	+	11.98	+
Percentage of Spanish greenweed area	5.13	+	-13.37	+
Percentage of mountain grass area	4.49	+	-11.45	+
Percentage of south orientation	-4.35	+	7.65	+
Percentage of urban area	-4.32	+	12.10	+
Percentage of north orientation	3.99	+	-1.46	ns
Percentage of south-west orientation	-2.89	ns	1.23	ns
Aspect diversity	-2.36	ns	6.79	+
Percentage of west orientation	-2.33	ns	2.92	ns
Percentage of mountain grass area	2.33	ns	-7.83	+
Percentage of heather area	1.84	ns	-5.93	+
Percentage of north-west orientation	-1.62	ns	4.05	+
Percentage of mountain shrub area	-0.32	ns	-4.38	+
Percentage of marsh and estuary area	-0.20	ns	0.57	ns
Percentage of east orientation	-0.16	ns	5.39	+

Captions

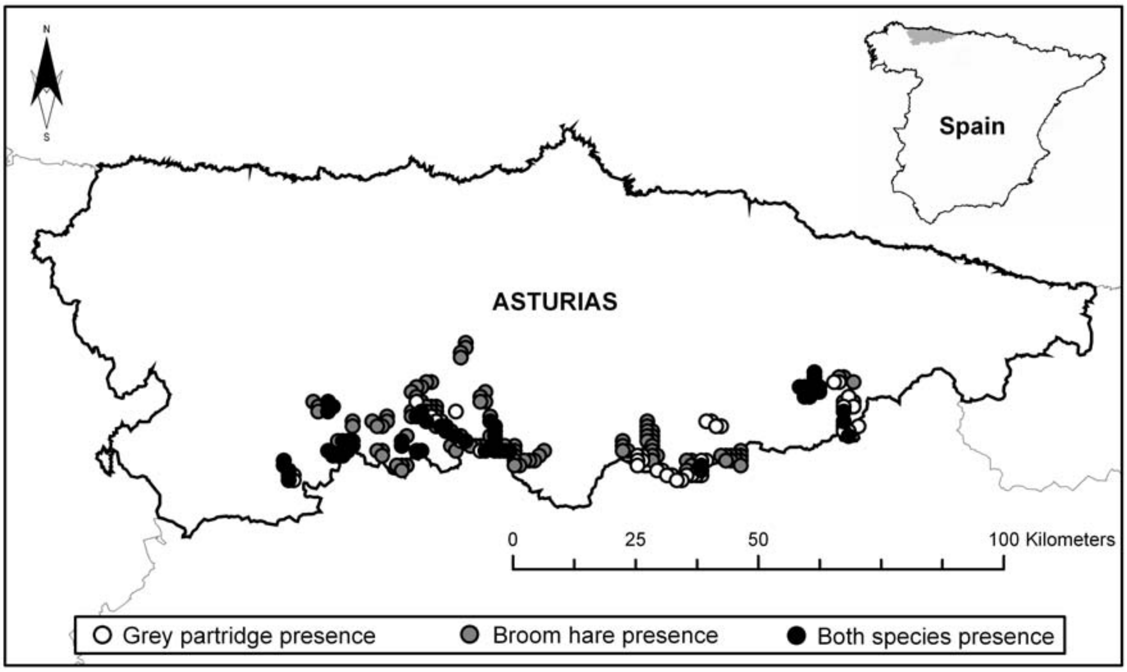
Figure 1. Geographic location of the study area (UTM 30S 225000-333000, 4760000-4816000), and presence data of the Pyrenean grey partridge (white circles), the broom hare (grey dark circles) and both species (black circles).

Figure 2. Habitat Suitability Maps for the broom hare and the Pyrenean grey partridge models. The scale shows the habitat suitability values (0 - 25 = very low suitability, 26 – 50 = low suitability, 51 – 75 = high suitability, and 76 - 100 = very high suitability).

Figure 3. Variation of mean habitat suitability scores along the marginality factor. The factor was divided into 20 intervals, and mean values are shown. As marginality factors for both models were strongly correlated, only the figure of the broom hare model was plotted.

Figure 4. Maps of the areas (in black) with: A) very high and B) very poor suitability for both species (see Material and Methods section).

Figure 1.



N
S
Spain
ASTURIAS
0
25
50
100 Kilometers
Grey partridge presence
Broom hare presence
Both species presence

Figure 2.

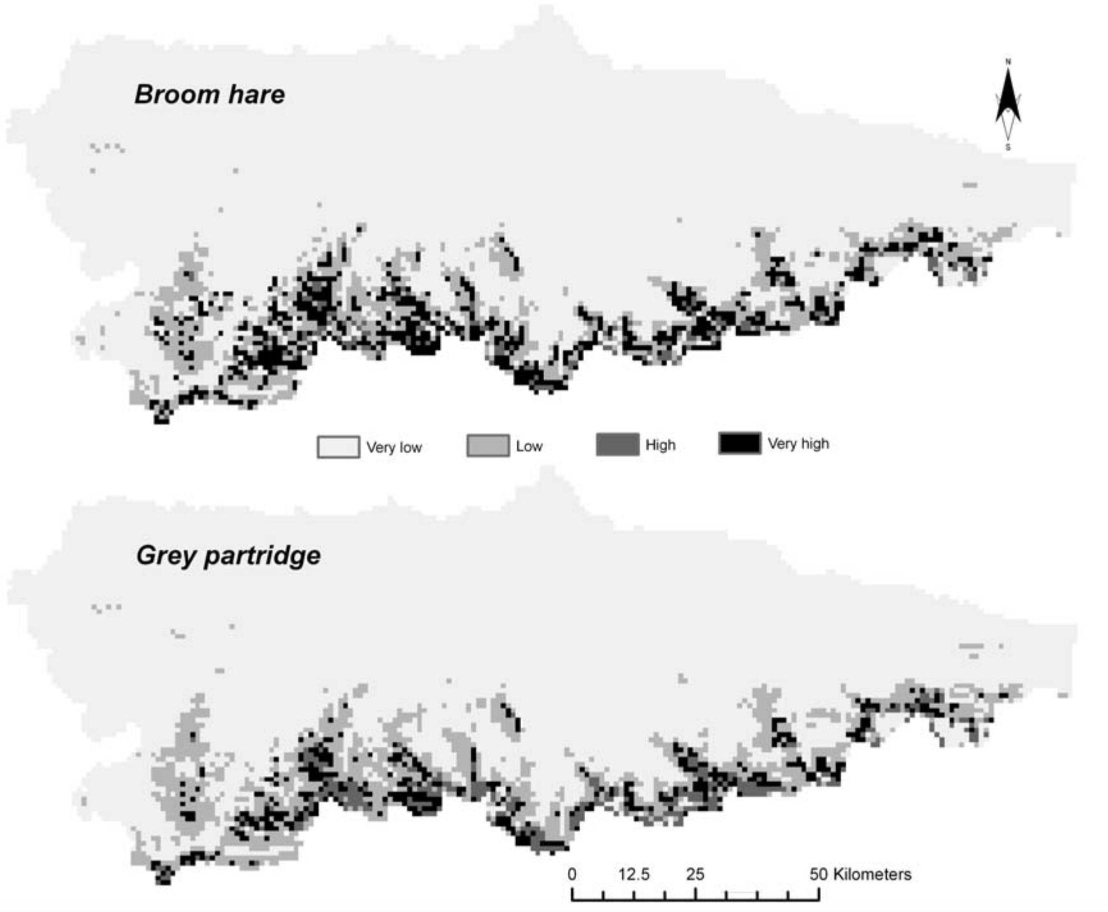
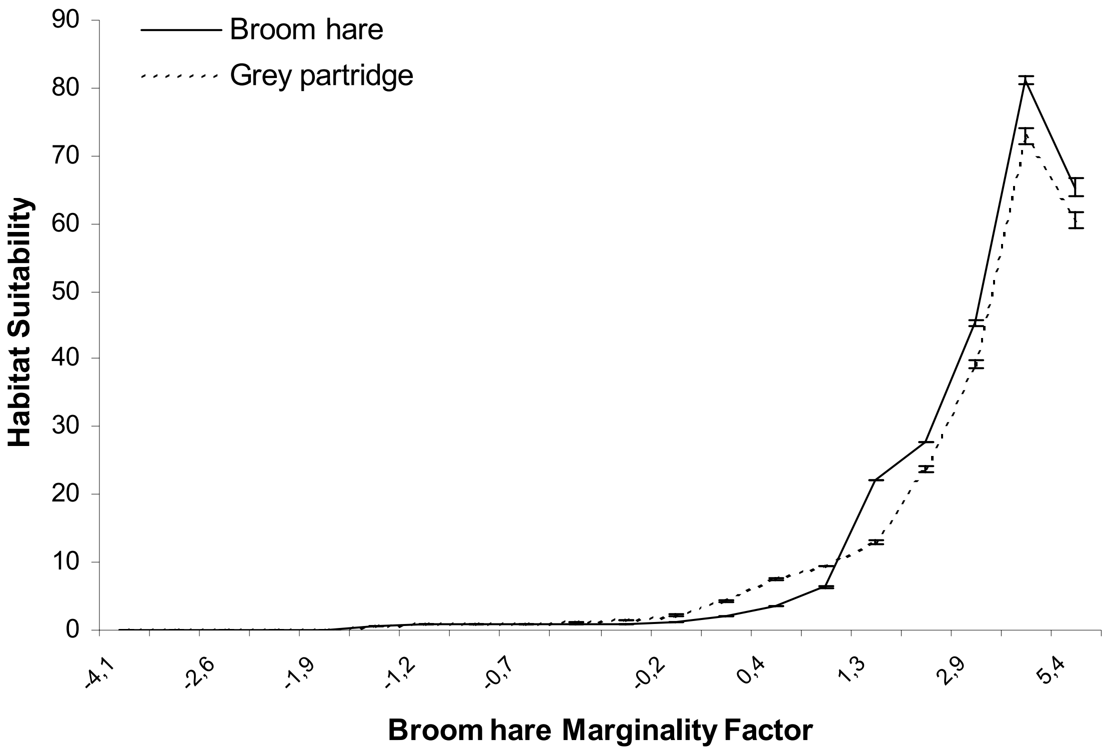

Broom hare
N
S
Very low
Low
High
Very high
Grey partridge
0
12.5
25
50 Kilometers

Figure 3.



Broom hare
Grey partridge
Habitat Suitability
90
80
70
60
50
40
30
20
10
0
-4,1
-2,6
-1,9
-1,2
-0,7
-0,2
0,4
1,3
2,9
5,4
Broom hare Marginality Factor

Figure 4.