

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

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4 ¹Pelayo Acevedo, Vanesa Alzaga, Jorge Cassinello, Christian Gortázar.

5 Instituto de Investigación en Recursos Cinegéticos (IREC, CSIC-UCLM-JCCM), Ronda de
6 Toledo S/N, Ciudad Real 13071, Spain.

7 **¹Corresponding author:**

8 Pelayo Acevedo

9 Instituto de Investigación en Recursos Cinegéticos (IREC, CSIC-UCLM-JCCM), Ronda de
10 Toledo S/N, Ciudad Real 13071, Spain.

11 E-mail: pelayo.acevedo@uclm.es

12 Tlf: 0034-926 295 450. Fax: 0034-926 295 451

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

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25 **Abstract**

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

41

42 **Keywords:** *Lepus castroviejo*, ENFA methodology, *Perdix perdix*, niche description,
43 Cantabrian Mountains.

44

44 **1. Introduction**

45 The knowledge of the distribution of endangered animal species and their habitat
46 requirements is essential in conservation biology (e.g., Engler et al., 2004; Whittaker et al.,
47 2005). One of the main concerns is habitat fragmentation due to land use, which has long
48 been recognized as a major threat to the preservation of biodiversity and to the viability of
49 endangered species (e.g., Hartley and Hunter, 1998; Kurki et al., 2000). However,
50 biodiversity in natural ecosystems often appears to depend on a certain degree of disturbance
51 (see White and Pickett, 1985), such as fire, flooding, storms, and herbivory (Hobbs and
52 Huenneke, 1992), as these events may play a role in increasing plant species biodiversity
53 (Waldhardt et al., 2004). Areas characterized by a mosaic structure, v.g. forests, shrub lands
54 and pastures, tend to provide very productive natural systems, suitable for certain animal
55 species, such as roe deer (*Capreolus capreolus*), Iberian lynx (*Lynx pardina*), wild rabbit
56 (*Oryctolagus cuniculus*) (e.g., Fernández et al., 2003; Acevedo et al., 2005; Michel et al.,
57 2006; Williams et al., in press.).

58 Conservation strategies have focused not only on the preservation of adequate habitat
59 areas, but also the spatial distribution of these areas throughout the landscape. To attain these
60 goals, the use of spatial models (Peterson et al., 1999; Robertson et al., 2001; Chefaoui et al.,
61 2005; Hortal et al., 2005; Soberón and Peterson, 2005; Acevedo et al., 2006; Quevedo et al.,
62 2006) has become a common practice in ecology.

63 A wide variety of predictive models has been used to simulate the spatial distribution of
64 plant and animal species (see for instance Guisan and Zimmermann, 2000; Scott et al., 2002).
65 Most of these models identify a quantitative or qualitative relationship between species
66 presence and a number of meteo-climatic, geomorphological variables and information on
67 vegetation cover, land use and anthropogenic disturbance (Austin et al., 1990; Hortal et al.,
68 2005).

69 Predictive models can easily be made from presence/absence data of a species (examples
70 at Osborne and Tigar, 1992; Brito et al., 1999; Carroll et al., 1999). However, before using
71 such information, it is necessary to have previously distinguished true absences from a mere
72 lack of information (e.g. Thuiller et al., 2004; Araújo et al., 2005). Presence data usually
73 correspond to the true presence of the species. In contrast, absences could be due to an
74 insufficient sampling effort (Hortal et al., 2005). Hence, false absences are much more
75 common than false presences. Thus, there is a need to remove these inaccurate data from
76 distributional maps (Palmer et al., 2003) and to assure the reliability of absences (Anderson,
77 2003).

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

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

88 Here we analyse habitat suitability for two emblematic animal species of the Cantabrian
89 Mountains (Asturias region, northwestern Spain), the broom hare (*Lepus castroviejo*) and the
90 Pyrenean grey partridge (*Perdix perdix hispaniensis*). Both of them are of great conservation
91 value. The broom hare is endemic to this area, whereas this partridge subspecies is endemic to
92 the northern mountains of the Iberian Peninsula, from the Galician border to the Pyrenees.
93 The IUCN (2004) considered the broom hare as species that is vulnerable to becoming

94 endangered or extinct due to habitat loss and degradation and population decline. In contrast,
95 the Pyrenean grey partridge was not considered in the Red List of Threatened Species (IUCN
96 2004). The partridges conservation value lies in the facts that it occupies the southwestern
97 edge of the species distribution in Eurasia and that it has numerous ecologically distinct
98 features (Lucio et al., 1992; Novoa et al., 2002). Populations at the edge of their distribution
99 range are of special interest (see Gortázar et al., in press) because they help in our
100 understanding of aspects such as ecological niches and threshold responses to environmental
101 change (Brown et al., 1996; Holt et al., 2005). The partridge's geographical location in the
102 Cantabrian Mountains is isolated from its nearest neighbours in the Pyrenees by more than
103 300 km, making the situation of studying population very critical. The Pyrenean grey
104 partridge was included in the Plan de Ordenación de los Recursos Naturales de Asturias
105 (PORNA) labelled as "especie singular" (a remarkable species). It has also been included in
106 Annex II of the Convention on the Conservation of European Wildlife and Natural Habitats,
107 Council of Europe, Resolution No. 6 (1998), which lists the species requiring specific habitat
108 conservation measures (http://www.eko.org.pl/lkp/prawo_html/bern_06.htm). Despite the
109 reasons for needing them, ecological studies on the broom hare and the Pyrenean grey
110 partridge in the Cantabrian Mountains are very scarce.

111 The international literature on the broom hare is circumscribed to some studies on its
112 taxonomic status (Palacios, 1976; Schneider and Leipoldt, 1983; Pérez-Suárez et al., 1994;
113 Melo-Ferreira et al., 2005; Estonba et al., 2006), whereas the few ecological studies carried
114 out on its distribution and abundance, are to be found solely in local journals (Palacios and
115 Ramos, 1979; Ballesteros, 2000, 2003), or in unpublished reports (Ballesteros et al., 1997).
116 These studies concluded that broom hares occupy habitats characterized by mountainous
117 grasslands and scrublands (mainly *Cytisus* spp., *Genista* spp., *Daboecia* spp., *Erica* spp.) and
118 small patches of woodlands (*Fagus* spp., *Quercus* spp., *Betula* spp., *Ilex* spp.). The altitude

119 range of the broom hare distribution area is between 1000 and 1900 m.a.s.l. (Ballesteros,
120 2003). This author suggests that hare population is decreasing in the peripheral areas of the
121 Cantabrian Mountains, whereas it has relatively high densities in the core of its distribution
122 area.

123 There are several studies on grey partridge biology regarding population trends (Putala
124 and Hissa, 1998; Panek, 2005), reproduction (Aebischer and Ewald, 2004), the effect of
125 predators (Potts 1986; Tapper et al., 1996; Panek, 2005) and the effect of habitat management
126 on population dynamics (Aebischer and Ewald, 2004; Bradbury et al., 2004; Bro et al., 2004;
127 De Leo et al., 2004). However, there is little known about the Iberian Peninsula subspecies
128 specifically (Lucio et al., 1992). Only a few studies on the Pyrenean populations are worth
129 being mentioned (Lescourret and Genard, 1993; Novoa et al., 2002). Habitat change is the
130 main cause of current declines in grey partridge populations. In most of Europe this decline is
131 caused by the transition from traditional to industrial agriculture (e.g., Potts, 1986; Panek,
132 2005), while the drop in the Pyrenean grey partridge population is a consequence of the
133 encroachment of dense scrublands, a necessity for this subspecies (Novoa et al., 2002), caused
134 by the decline of traditional agricultural practices. The Cantabrian partridge populations have
135 suffered from habitat loss throughout the last decades, particularly in the northern slope of the
136 Cantabrian Mountains, Asturias region (Lucio et al., 1992). The grey partridge habitat in the
137 Cantabrian Mountains is characterized by mountainous scrublands (*Genista* spp., *Daboecia*
138 spp., *Erica* spp) and deciduous forests (mainly *Fagus* spp., *Quercus* spp. and *Betula* spp.),
139 with an altitude ranging between 900 and 1200 m.a.s.l. (Lucio et al., 1992).

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

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

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

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

148

149 **2. Material and methods**

150

151 *2.1. The study region*

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

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

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

169

170 *2.2. Broom hare and Pyrenean grey partridge distribution data*

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

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

182

183 *2.3. Environmental data*

184 Environmental data came from an Asturias GIS database compiled and managed mainly by P.
185 Acevedo, and then imported and processed into the Idrisi GIS System (Clark Labs[®], 2001,
186 2004). All maps were referred to a 1 km² resolution, to fit with the spatial resolution of
187 biological data (see another example in Chefaoui et al., 2005). Many factors have been
188 described to affect population abundance and distribution of birds and mammals in the Iberian
189 Peninsula, such as ecological factors, bioclimatic parameters and human activity (e.g.,
190 Acevedo et al., 2005, 2006; Quevedo et al., 2006). In this study we selected 33 variables that
191 could act as determinants of current broom hare and Pyrenean grey partridge distribution in
192 NW Iberian Peninsula (Table I), 27 accounting for environmental traits (habitat structure,

193 vegetation characteristics and geomorphology), and 6 accounting for human impacts. Data
194 origin is as follows:

195 - Seventeen geomorphological variables were computed on a 1 km² grid resolution by
196 averaging out information extracted from a 100 x 100 m Digital Elevation Model. Mean,
197 maximum and minimum altitude (m.a.s.l.), altitude range (meters), mean, maximum, sum and
198 minimum slope (degrees), mean aspect diversity, using a 7x7 pixel kernel on a 9-categories
199 reclassified aspect map (see Clark Labs[®], 2001, 2004 for the method; and Chefaoui et al.,
200 2005 for an example of the use of this variable), and the percentages of each orientation
201 category per 1 km².

202 - Ten variables accounted for the type of vegetation. This information was obtained from
203 a high-resolution digital vegetation map of Asturias (GIS of the Environmental Thematic
204 Cartography, Government of Asturias, 1:25000). The digital map was rasterized with a 100 m
205 grid resolution and then reclassified in 10 categories to estimate the fraction of each 1 km²
206 pixel covered by mature forest (oak, beech, chestnut, etc.), pre-forest (holly, birch, ash, etc.),
207 scrub (hazel, laurel, rose, etc.), broom, heather, mountain scrub, Spanish greenweed,
208 mountain grass, urban areas, and marsh and estuary vegetation.

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

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

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

218

219 2.3. Statistical analyses

220

221 2.3.1. Niche modelling

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

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

241 Once ENFA factors were computed, habitat suitability scores for each map pixel were
242 calculated and mapped in accordance to the responses of the species to each factor. Partial

243 suitability scores were computed for each factor as the percent distance to the median scores
244 of observed presences. Habitat Suitability was then obtained as a weighted average of these
245 partial suitability scores according to the variability explained by each factor (Hirzel et al.,
246 2002).

247

248 *2.3.2. Model validation and accuracy*

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

258

259 *2.3.3. Niche analysis*

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

264 The HSM obtained for each species was reclassified (see Chefaoui et al., 2005) as either
265 very low habitat suitability (0-25), low habitat suitability (26-50), high habitat suitability (51-
266 75), or very high habitat suitability (76-100). These new maps were cross-tabulated in the GIS
267 environment to pinpoint zones of spatial coincidence where both models show at the same

268 time either very high or very low habitat suitability scores, and zones of spatial non-
269 coincidence, areas highly suitable for one species but unsuitable for the other. By means of a
270 Mann–Whitney U test, we extracted those environmental variables that characterize each of
271 these two zones, as they are significantly different to the conditions in the rest of the study
272 area. The statistical significance was corrected by means of Bonferroni tests (Perneger, 1998).

273

274

275 **3. Results**

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

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

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

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

301 Presence data of the study species showed a metapopulation structure (Fig. 1). Concerning
302 the status of these populations, 70.83% of the hare and 58.82% of the partridge populations
303 showed, neither a decreasing or increasing trend. Decreasing trends were appreciated in
304 16.67% of hare and 35.29% of partridge populations, whereas increasing population trends
305 were detected in 4.17% of hare populations and 5.88% of partridge populations.

306

307 **4. Discussion**

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

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

325

326 *4.1. Niche descriptions*

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

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

343 Kavanagh, 1997), but it also occurs commonly in intensive cereal ecosystems (e.g., Sálek et
344 al., 2004). During this century grey partridge populations have declined drastically in many
345 regions (e.g., Panek, 2005), as suggested by the reduction of hunting bags (Birkan and Jacob,
346 1988; Potts and Aebischer, 1995). The decline is mainly due to the deterioration of
347 agricultural habitats (Aebischer and Ewald, 2004). Habitat management actions are, thus, a
348 priority for grey partridge conservation strategies. For example, uncultivated structures and
349 non-crop areas are essential in aiming to keep biodiversity in agricultural landscapes
350 (Freemark and Kirk, 2001) and to maintain grey partridges' survival and reproduction rates
351 (e.g., Aebischer and Ewald, 2004; Buner et al., 2005).

352

353 *4.2. Niche overlap*

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

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

366

367 *4.3. Conservation implications*

368 Distribution of the study species in the Cantabrian Mountains, as pictured in this study and
369 from our own field experience, seems to be made of a few partially isolated populations.
370 Thus, one would assume both species would follow a metapopulation structure (sensu Levins,
371 1969) provided that occasional interbreeding does occur. However, the habitat suitability
372 models obtained in this study showed relatively well-connected suitable areas for the species.

373 Herbivory is a type of biotic disturbance that may have profound effects on the structure
374 and composition of an ecosystem, as it increases plant biodiversity and fosters the
375 proliferation of small animals' refuges and shelter in a mosaic structure (Norton-Griffiths,
376 1979; Wiens, 1985; Hobbs and Huenneke, 1992; Prins and Van der Jeugd, 1993; Miaud and
377 Sanuy, 2005). Current decline of traditional livestock activity in the area, which is used to
378 maintain patches clear from forest and a mosaic structure of pastures and scrublands, may be
379 affecting population viability of both study species, as they actively select such a landscape.
380 Thus, should further habitat or connectivity loss occur, the broom hare and the Pyrenean grey
381 partridge populations may end up disaggregated into a few isolated subpopulations, too small
382 to ensure their own long-term persistence, as has already been reported in the Cantabrian
383 capercaille (Quevedo et al., 2006).

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

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

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

396

397 **5. Conclusion**

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

410

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421

422 **6. References**

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

<i>GEOMORPHOLOGY</i>	<i>HABITAT STRUCTURE</i>
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)	<i>HUMAN IMPACT</i>
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	
	<i>MF</i>	<i>SF</i>	<i>MF</i>	<i>SF</i>
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	
	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>
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.

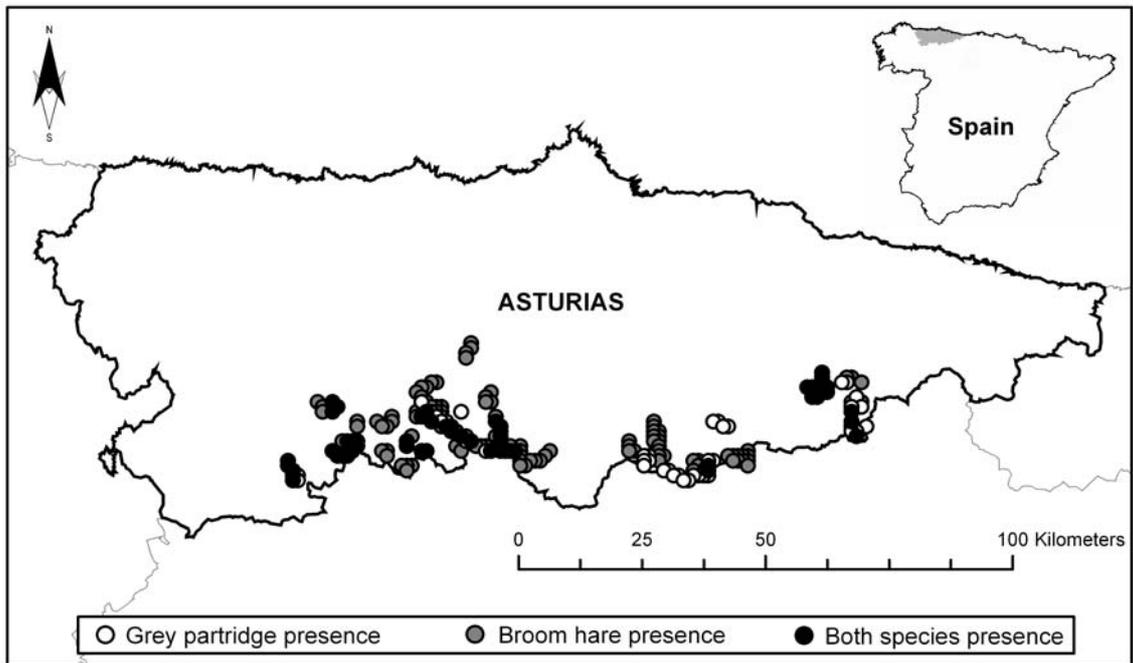


Figure 2.

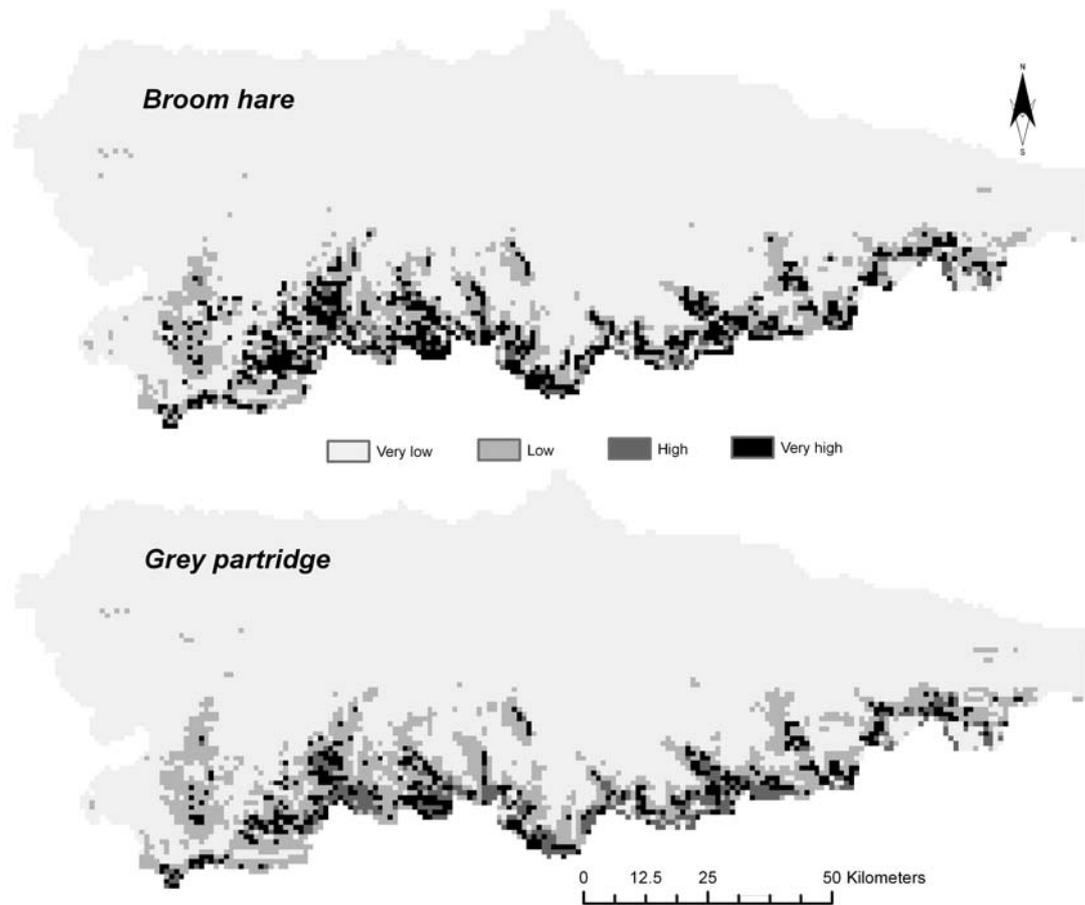


Figure 3.

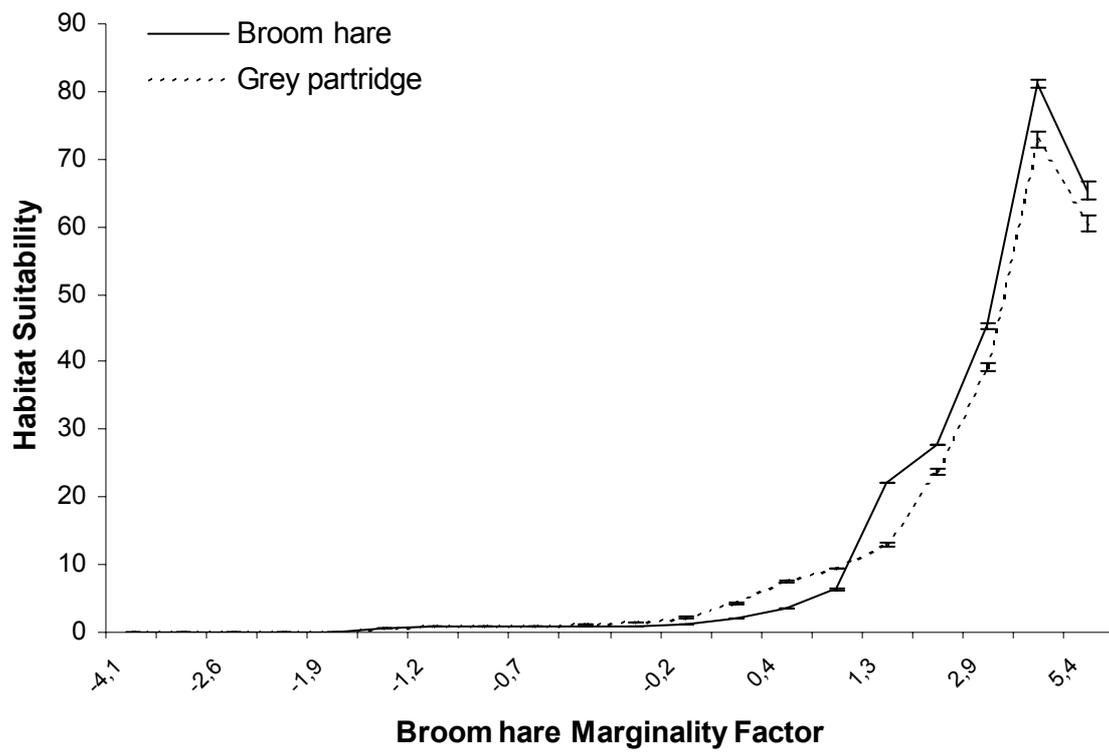


Figure 4.

