**The Iberian ibex is under an expansion trend but
displaced to suboptimal habitats by the presence of
extensive goat livestock in central Spain**

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2 ABSTRACT

3

4 In this paper an updated distribution of the Iberian ibex (*Capra pyrenaica*
5 Schinz, 1838) in the central Spanish region of Castile - La Mancha is shown.
6 The species is present in 19% of the study region, and in areas not cited so
7 far in the literature. A detailed analysis of habitat suitability was also carried
8 out, applying a new methodology, Ecological-Niche Factor Analysis, which
9 uses presence data to build a habitat suitability map of a given species. As
10 livestock activity is quite intense in the region, the presence of a potential
11 competitor, the domestic goat (*Capra hircus*), was included in the analyses.
12 Factors affecting ibex relative abundance were determined by means of a
13 nested stepwise multiple regression, where livestock presence/absence was
14 the nested factor. The presence of livestock has a negative effect on ibex
15 relative abundance, causing the ibex to select areas of poor, sparse
16 vegetation, cultivated lands and forests, whereas in the absence of livestock,
17 the ibex is mainly present in pasture-scrub lands and non-cultivated lands.
18 Conservation implications of these results are discussed in the context of a
19 Mediterranean region where extensive livestock grazing systems abound.

20

21 Keywords: biodiversity conservation, *Capra hircus*, *Capra pyrenaica*, livestock
22 grazing system, habitat displacement, habitat suitability analysis, resource
23 competition

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27 INTRODUCTION

28

29 To conservation biologists it is of particular interest to determine the effects of
30 invasive species on the natural history of autochthonous ones (see Lodge
31 1993). A particular example is that of exotic ungulates introduced in areas
32 where they can potentially compete with native ones (see, e.g., Cassinello et
33 al. 2004). Among the former, livestock represent a particular instance (Voeten
34 and Prins 1999), usually underestimated by conservation biologists
35 (Fleischner 1994). Although livestock graze more than one-third of the world's
36 land area, and in many instances share resources with native ungulates (see
37 de Haan et al. 1997), evidences of a negative impact on the latter are not
38 conclusive and highly debated (e.g. Saberwal 1996; Mishra and Rawat 1998;
39 Madhusudan 2004; Young et al. 2005).

40

41 The development of large, relatively permanent, agriculture-based societies
42 was the primary event initiating livestock domestication about 10,000 years
43 ago (Price 2002). With a few exceptions, ungulate domestication (e.g. cattle,
44 sheep and goats) mainly began in the Near East (Troy et al. 2001). The
45 presence of livestock in Europe goes back to Neolithic times, domestic sheep
46 and goats showing up particularly in Mediterranean countries (see, e.g.,
47 Martín Bellido et al. 2001).

48

49 The status and distribution of the Iberian ibex have been studied by several
50 authors, either in the whole peninsula (e.g. Granados et al. 2002; Pérez et al.
51 2002) or in some particular areas (e.g. Granados et al. 1998; Palomares and

Ruiz-Martínez 1993; Lasso de La Vega 1994; Pérez et al. 1994; Gortazar et al. 2000). Concerning Castile - La Mancha region, in central Spain, Granados et al. (2002) indicate that the ibex is distributed exclusively in 11% of the region, whereas Pérez et al. (2002) distinguish 51 ibex population nuclei in Spain, out of which only 4 were located in Castile - La Mancha: Serranía de Cuenca, Cabañeros National Park, Sierra de Alcaraz (connected to the well established ibex population of Sierra de Cazorla, Segura y Las Villas Natural Park, it is supposedly in expansion), and Sierra Madrona (a series of fragmented nuclei connected to other ones in Sierra Morena, Jaén province).

Here, we analyse the current distribution and habitat use of the Iberian ibex (*Capra pyrenaica* Schinz 1838) in Castile - La Mancha. We have considered it appropriate to use a political division to define our study area because in Spain conservation field is partly ruled by regional governments. This region is characterized by an intense livestock breeding activity, namely extensive sheep and goat grazing systems (see Martin Bellido et al. 2001). We have, thus, included in our analyses the presence of the domestic goat (*Capra hircus*), a close relative of the Iberian ibex and, therefore, expected to share feeding habits and ecological requirements with it; to our knowledge, no comparative studies of diet and/or spatial niche use have been made so far. Sheep, on the contrary, show a differing feeding behaviour (Martínez 2002) and probably their potential as competitor of the Iberian ibex is less pronounced.

76 The spatial prediction of species distribution is an important tool for
77 conservation biology and management planning (e.g., Hortal et al. 2005;
78 Whittaker et al. 2005). Developments of ecological and biogeographic theories
79 have been translated into different methodologies, which are able to predict
80 the distribution ranges and habitat suitability of species (see Guisan and
81 Zimmermann 2000; Ferrier et al. 2002; Scott et al. 2002), using a wide variety
82 of statistical approaches and Geographical Information Systems tools (GIS)
83 (e.g., Austin 2002; Rushton et al. 2004). The use of a Digital Elevation Model
84 (DEM) constitutes a basis for generating maps of environmental variables
85 (see Guisan and Zimmermann 2000), as it has basic outcomes, such as
86 altitude, slope or aspect, which influence the distribution of the organisms.
87 Furthermore, the use of digitalised land information database, allows a more
88 detailed analysis of factors determining species distribution.
89
90 Predictive models can easily be made from data of the presence and absence
91 of a given species (e.g., Osborne and Tigar 1992; Brito et al. 1999).
92 Nevertheless, it is necessary to distinguish true absences from a mere lack of
93 information (Thuiller et al. 2004; Araújo et al. 2005). The determination of true
94 absences of a given species in a given area is the main problem of many
95 animal presence/absence data sets (Hirzel et al. 2002; Zaniewski et al. 2002).
96 Thus, some techniques incorporate presence-only data (Hortal et al. 2005),
97 such as the relatively novel Ecological Niche Factor Analysis (ENFA) (Hirzel
98 et al. 2002). ENFA is used to determine habitat suitability starting from the
99 location of presence-only data. These maps are the result of the location of a
100 given species within the multidimensional environmental area that is defined

by considering all mapping units within the study area (Guisan and Zimmermann 2000). These habitat suitability maps indirectly reveal the species potential distribution (Hirzel et al. 2002). This approach is recommended when absence data are not available (most data banks), unreliable (most cryptic or rare species) or meaningless (invaders) (Hirzel et al. 2001), the subsequent results are to be handled with caution (e.g., Brotons et al. 2004; Engler et al. 2004). Using these data, this method characterizes the realized niche of the species from a set of environmental predictors. Thus, an application of the method could be interesting in many domains: landscape management for endangered species, better knowledge of unknown or inaccessible areas, or also better knowledge of 'new species' ecology and/or distribution (e.g. Reutter et al. 2003; Gallego et al. 2004; Chefaoui et al. 2005). This method was originally assessed in the Alpine ibex (*Capra ibex*) (Hirzel et al. 2002), but is currently widely used (see a list of publications at <http://www2.unil.ch/biomapper/bibliography.html>).

Apart from an updated distribution of the Iberian ibex in Castile - La Mancha, our aim in this study is to carry out a detailed analysis of habitat suitability of the species and determine which factors affect its abundance taking into account the influence of livestock presence/absence.

MATERIALS AND METHODS

The study area

126

127 Located in central Spain, it corresponds with Castile - La Mancha political
128 division (U.T.M. 30S 294,348-681,063 4,208,706-4,575,340), which is placed
129 at the southern plateau of the Iberian Peninsula. Politically, the region is
130 conformed of five provinces (see Figure 1), where the study species is
131 distributed unevenly. Castile - La Mancha is the Iberian region where game
132 activity is more intense. It has a surface area of 79,226 Km², which represents
133 15.7% of the whole Spanish territory. The area devoted to game activity in this
134 region is 70,000 Km² (88% of its territory), big game estates occupying 19,000
135 Km² (Junta de Comunidades de Castilla – La Mancha,
136 <http://www.jccm.es/medioambiente/mednat/cazapesca.htm>).

Figure 1 over here

137

138 The study region shows a typical Mediterranean continental climate, with dry
139 periods both in summer and winter, rains concentrated in autumn and spring,
140 and extreme temperatures during the hottest (summer) and coldest (winter)
141 seasons. Mediterranean woodland vegetation is present and it is formed of
142 oak trees (*Quercus ilex*) along with shrubs of different species (e.g., *Q.*
143 *coccifera*, *Pistacia lentiscus*, *Cistus* spp., *Rosmarinus officinalis*, etc.). Open
144 lands with scattered trees (evergreen oak savannah like habitats), the so-
145 called “dehesas”, are also common. In addition, pine woodlands (*Pinus* spp.)
146 can also be found in some elevated areas.

147

148 Apart from the Iberian ibex, other ungulate species that can be found free-
149 ranging in the study area are wild boar (*Sus scrofa*) and red deer (*Cervus*
150 *elaphus*), and to a lesser extent fallow deer (*Dama dama*), and roe deer

(*Capreolus capreolus*) (see, respectively, Rosell and Herrero 2002; Carranza 2002; Braza 2002; San José 2002).

The study species

The Iberian ibex is a wild goat endemic to the Iberian Peninsula. The IUCN (2004) considered it as at Low Risk, but near threatened (LR/nt), whereas the existing subspecies hold different qualifications. *C. p. victoriae* Cabrera, 1911 is Vulnerable (VU D2), due to the few and small areas it inhabits (see Pérez et al. 2002). *C. p. hispanica* Shimper, 1848 is at Low Risk (LC/cd), but its viability depends on current conservation programmes. This latter subspecies is widely distributed compared to the former one (ibid). Two other subspecies were also distinguished, but they are extinct nowadays: *C. p. pyrenaica* Schinz, 1838 and *C. p. lusitanica* Schlegel, 1872 (ibid). However, the distinction of these subspecies has been questioned by Manceau et al. (1999), who found no genetic differences between the two existing subspecies.

The sampling method

Presence of ibexes in the study area was assessed by means of direct field observations and by carrying out surveys (n=149) addressed to forest rangers and staff from environmental agencies of the government of Castile - La Mancha region. Information obtained by other naturalists was verified by

175 visiting areas where ibexes were reported. The sampling units were 10x10
176 km. UTM grid cells (n=905).
177
178 Survey addressees were asked to draw in a map their work area and the
179 range occupied by the Iberian ibex, red deer, wild boar and livestock. A
180 questionnaire was given to them, where they indicated the status of the
181 populations present, such as the largest group size registered, a
182 straightforward variable, easy to account for by field watchers.
183
184 In order to assess ibex abundance, we firstly relied on forest rangers and
185 environmental managers' indication of the largest group size registered. The
186 Iberian ibex is characterized by sexual segregation through most of the year,
187 but the largest group sizes are attained during the mating season (November-
188 December) according to Granados (2001), when ibexes are also more
189 conspicuous. We have confirmed that group sizes given in the questionnaire
190 refer to mixed groups observed during the mating season, when they may
191 reflect population abundance in species showing sexual segregation (see
192 Toigo et al. 1996). In addition, we validated these data by carrying out our
193 own field surveys.
194
195 During September 2003, we performed 17 field surveys consisting of line
196 transects (e.g., Burnham et al. 1980), a methodology widely used to estimate
197 relative abundance of wild goats (e.g., Alados and Escós 1996; Pérez et al.
198 1994). Average length of line transects was 3 km., and they were carried out
199 in the main areas where the Iberian ibex is present in Castile - La Mancha,

and during hours of maximum activity, i.e. at dawn and at dusk (e.g., Alados 1986). We only registered female groups, and used these data to test whether the largest group size obtained in the questionnaire was a good estimate of ibex abundance (see Results).

Habitat suitability

The ENFA computes a habitat suitability model by comparing the ecogeographical variables (EGVs) which characterize the locations where the species is detected with those present in the whole study area (Hirzel et al. 2002).

Habitat suitability for the Iberian ibex was assessed in the area where the species was more abundant according to the surveys, using 1x1 km UTM grid cells. Twenty-seven EGVs were defined, including topographical features (e.g. altitude, slope), land cover, and livestock presence (see Table 1), and normalized by a Box-Cox transformation (Sokal and Rohlf 1981). We did not considered climatic variables because of the relative homogeneity of the study area on this matter, where only slight differences can be registered, mainly due to topographic variations. Average distances to each land cover classes were calculated for each sample unit by means of “Distance Operator” tool (Idrisi32 v.32.21) (see Hirzel et al. 2002). The topographic data from a digital elevation model (DEM) carried out by the Shuttle Radar Topography Mission (European Environment Agency 2000), with a spatial resolution of 90 m., was

Table 1 over here

extracted by overlaying the DEM with the cells of 1x1 km. in a geographic information system (Idrisi32 v32.21) (see Hortal et al. 2001).

Firstly, the ENFA was run, by means of BioMapper software (Hirzel et al. 2001; 2004; see <http://www.unil.ch/biomapper/>). It computes a global marginality coefficient, expressing how, on all the EGVs, the species average differs from the global average, and a global specialization coefficient, expressing the ratio of global variance to species variance.

Formally, marginality is defined as the absolute difference between the global mean and the species mean, divided by the standard deviations of the global distribution multiplied by a constant (see Hirzel 2001 for details). A value close to one means that the species lives in a very particular habitat relative to the reference set. Similarly, specialization is defined as the ratio of the standard deviation of the global distribution to that of the study species (Hirzel 2001). A randomly-chosen set of cells is expected to have a specialization of one, while any value exceeding that score indicates some form of specialization.

The factor coefficients for the marginality factor account for the marginality of a given species in each EGV considered. It is measured as units of standard deviations of the global distribution. The higher the absolute value of a coefficient, the further the species departs from the average value of a given EGV. There are other factors which express a degree of specialization, where

the higher the value, the more restricted is the range of the study species on the corresponding variable (Hirzel 2001).

Habitat use

Information obtained from the surveys was registered in 10x10 km. UTM grid squares (n=905) by means of Idrisi32 v32.21 software (Clark Labs, Clark University). For each UTM square the frequency of occurrence of 11 ecogeographical variables (EGVs) were identified (see Table 2). These variables were obtained from CORINE Land Use/Land Cover database, spatial resolution (pixel width) of 250 m. (European Environment Agency 1996). From this information we carried out both the habitat use analysis and the study of the influence of goat livestock.

Table 2 over here

The analysis of the variables which determine habitat use (Table 2) by the Iberian ibex was assessed by a nested stepwise multiple regression analysis, using domestic goats presence/absence as the nested factor (e.g. Quinn and Keough 2002). The Iberian ibex abundance was the response variable. We designed a three step procedure to clarify the significance of the variables and their interaction with goat livestock on the Iberian ibex habitat use.

In total, 11 habitat factors were considered: 1) We discarded a number of variables with no statistical significance and avoided multicollinearity by using the Spearman Rank Correlation coefficients. 2) Each of the independent variables obtained from step 1 were then related to the dependent variable,

ibex relative abundance. Stepwise multiple regression analysis was used (Quinn and Keough 2002). 3) Variables that yielded $p < 0.05$ in step 2 were integrated into a final model which also included the nested factor of livestock presence. We carried out a nested regression analysis and obtained a final model through a backward stepwise procedure. The level of significance for step 3 was set at 5%. The statistics package used was SPSS 10.06.

RESULTS

Species distribution according to the surveys

Information covering 97.68% of the whole Castile - La Mancha region has been obtained from 149 surveys correctly filled in. Results showed that the Iberian ibex is present in 19% of the study area (175 out of 905 sampling units). Five population nuclei have been identified: Montes de Toledo mountain range, Sierra Madrona – Sierra Morena, Alto Tajo – Serranía de Cuenca, Casas Ibáñez, and south of Albacete (see Figure 1). The species is more widely distributed in Albacete province (it is present in 47% of the territory), followed by Guadalajara (21%), Cuenca (15%), Ciudad Real (12%) and Toledo province (3%).

Habitat suitability

An habitat suitability map for the study species was carried out for the province of Albacete, where the species was more abundant (see above). This meant a total number of 15,384 1x1 km. UTM grid cells. Table 1 shows average values for the EGVs that define the habitat, both in the whole study area (global mean) and in the area where ibexes were found (species mean, with standardized values). For the ENFA analysis, the variable “average distance to non-irrigated lands” was discarded due to its discontinuity. The three significant factors selected (out of 27) explained 87.6% global marginality and 75.2% global specialization. Coefficients of relationship between variables and each one of the three factors are shown in Table 3.

Table 3 over here

Global marginality was 2.03, and global tolerance was 0.49. The habitat suitability map can be seen in Figure 2. The first factor obtained, marginality factor, was essentially associated to both high altitudes and slopes, and areas distant to agro-forest lands, broadleaf woodlands, industrial areas, marshes and vineyards (see coefficients in Table 3). Ibexes are extremely sensitive to shifts from their optimal conditions on this axis. Next factors show a certain degree of specialization, being associated to areas distant to coniferous forests, sparse vegetation and human constructions, such as roads and railways, but also close to annual crops lands. Factor 3 accounts for 19.2% of specialization, so that information provided is much less accurate than that of the other two factors (see Table 3).

Figure 2 over here

Habitat use

Relative ibex abundance was assessed by the largest size group registered in each UTM grid cell considered in the study area, and obtained from the questionnaire. Previously, we determined the validity of this measure by relating it to our own average group size (see above). In our field surveys, we detected 36 ibex groups (167 animals were counted) from the 17 transects carried out in September 2003. The average group size was 4.76 ± 0.65 , and it correlated with the largest group size obtained in the questionnaire (Spearman Rank Correlation: $n=9$, $\rho=0.80$, $p=0.01$), so that the latter can be considered as an estimate of ibex abundance.

Nested stepwise multiple regression analysis showed that livestock influences habitat use of the Iberian ibex, relegating it to suboptimal vegetation areas (see Table 4). In those grid cells where domestic goat livestock ranges in sympatry with the ibex, the latter occupies preferentially cultivated lands, sparse vegetation areas and forests; whereas in absence of livestock the ibex is mainly found in pasture-scrub areas and non-cultivated lands. The marginal effect caused by distance to goat livestock herds (see Factor 3 in Table 3), is exemplified in Figure 2.

In Figure 3 the relationship between those variables which showed opposite directions, depending on the presence/absence of goat livestock, i.e. scrub land and cultures, is shown.

Figure 3 over here

DISCUSSION

347

348 Here we have updated the Iberian ibex distribution in the region of Castile - La
349 Mancha (central Spain). A habitat suitability model has also been
350 accomplished by using the ENFA technique, particularly suitable for presence-
351 only data of a given species. Our results indicate that the Iberian ibex is not
352 occupying its optimal habitat in those areas where it shares its range with
353 domestic goat herds.

354

355 On ibex distribution in the study region, it is noteworthy to point out a wider
356 presence in comparison with previous surveys (Alados 1997; Pérez et al.
357 2002). A plausible explanation is the expected increase of the species area of
358 distribution which is taking place nowadays, in part due to a natural increment
359 of population numbers due to habitat changes, game management
360 translocations (Gortazar et al. 2000) or its recovery from past sarcoptic mange
361 epizootics (Pérez et al. 1997), and a probable decrease of its hunting
362 pressure caused precisely by the incidence of this disease (see Garrido
363 2004).

364

365 Concerning risks associated to parasite infections of the ibex, the main agents
366 are host-inspecific, e.g. sarcoptic mange (Pérez et al. 1997), so that they can
367 infect any ungulate species, among other mammals. Therefore, at high host
368 densities, as it is the case in areas with high livestock densities, the availability
369 of habitat for these parasites increases, as does the risk of epizootics (see
370 Acevedo et al. 2005).

371

Specific values for marginality and tolerance indexes are bound to depend on the global set chosen as reference, so that a species might appear extremely marginal or specialised on the scale of a whole country, but much less so a subset of it (Hirzel et al. 2002). According to habitat suitability analysis carried out the Iberian Ibex is highly marginal in the studied area, and presents a medium tolerance, evidencing that, although it is placed in marginal areas in Castile - La Mancha, it seems to tolerate habitat changes, therefore compensating its marginality with the expansion to areas of relatively suboptimal habitat.

In our study, livestock seem to compete and displace the Iberian ibex from its optimal habitat, i.e. pasture-scrub lands (e.g. Chiroso et al. 2002), in those grid cells where livestock is present (see Figure 2). We have no data on social avoidance between both species, so that future research should be focused on confirming this apparent ecological displacement. Similar conclusions were obtained from a study carried out in the Great Basin, where pronghorn (*Antilocapra americana*) avoided areas grazed by sheep during winter until spring-regrowth occurred, and favoured areas temporarily rested from sheep use (Clary and Holmgren 1982; Clary and Beale 1983).

This apparent displacement of the Iberian ibex to suboptimal habitats by livestock presence is confirmed in our nested factor analysis of habitat use. The results obtained indicate that the ibex occupies different habitats depending on the presence of domestic goats. When they are present, as seen in the previous analysis of habitat suitability, the ibex is preferentially

found in suboptimal habitats, according to its resource requirements (see, e.g., Chiroso et al. 2002), i.e. sparse vegetation, cultures and woodlands; whereas when livestock is absent, the ibex mainly uses scrub lands and non-cultivated areas, where food availability according to its diet is higher (e.g., Martínez and Martínez 1987; Martínez 2000).

The question is whether both species, the ibex and the domestic goat, actually compete for resources. Resource partitioning is defined as the differential use by organisms of resources such as food and space (Schoener 1974; Begon et al. 1996), and may explain how species coexist despite extensive overlap in ecological requirements (Hutchinson 1959; MacArthur and Wilson 1967; MacArthur 1972; May 1973). On the contrary, competition is considered to be the major selective force causing this differential use of resources (Schoener 1974; 1986).

As livestock range and distribution exceed any natural expansion process, they can be considered as introduced exotic species (see, e.g., Voeten and Prins 1999), and resource partitioning with native ungulates would not be expected but, rather, a certain overlap in resource selection (see Fleischner 1994; Edwards et al. 1996; Aagesen 2000; Prins 2000). This is the case in North American steppes, where livestock replaced the bison *Bison bison* and pronghorn (Schwartz and Ellis 1981; Hartnett et al. 1997). Thus, dietary niche divergence in sympatric species can occur even at a very subtle scale (Hartnett et al. 1997). Campos-Arceiz et al. (2004) found that food overlap between Mongolian gazelles (*Procapra gutturosa*) and livestock occurred not

only at the main forage categories but also at the selection of plant parts for foraging.

Interpretation of measures of niche overlap in terms of the implications for competitive interactions is problematic (Putman 1996). High observed overlap can imply competition, but only if resources are limited. In fact, observations of high overlap might equally well be indicative of a lack of competition (see Schoener 1983; de Boer and Prins 1990; Putman 1996).

The implications these results may have on the Iberian ibex viability and expansion can be evaluated from different views. Ibex populations in the study region seem to be in expansion, particularly in the provinces of Albacete, Cuenca and Guadalajara, if we compare current abundance of the species (Figure 1) and that of former studies (e.g. Pérez et al. 2002). Therefore, currently isolated populations might enter into contact. This may imply new viability risks associated to the increase of certain diseases, such as sarcoptic mange. This disease has already been detected sporadically in Albacete province (C. Gortázar, unpublished data), so that a consequent generalization of its prevalence might occur in the near future. Finally, hunting pressure on the Iberian ibex is negligible in Castile - La Mancha: a 0.0004% (63 individuals) of total big game hunted in 1999-2003 period (Garrido 2004). Therefore, we believe that game activity is not currently disturbing the Iberian ibex expansion movements in the region.

As a conclusion, we encourage comparative studies of habitat use with other ungulate species in sympatry (including exotics), as well as a monitoring of disease prevalence and colonization process in order to assure the establishment of the species in central Spain.

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798 FIGURE LEGENDS

799

800 Figure 1. Situation of the study area (Castile - La Mancha region in central
801 Spain), the administrative provinces concerned, and its division in 10x10
802 grids, showing the presence/absence of the Iberian ibex.

803

804 Figure 2. Habitat suitability map for the Iberian ibex in Albacete province.
805 Observed Ibex distribution is outlined. The arrow indicates a potentially
806 suitable area not occupied by the ibex, and where livestock is present.

807

808 Figure 3. Relationships between Iberian ibex relative abundance and two
809 EGVs which show opposite directions depending on the presence/absence of
810 goat livestock, i.e. scrub land and cultures (see Table 4).

811

Table 1. Ecogeographical variables (EGVs) used in the ENFA. Average values in the study region are shown (global mean), together with the standardized ones, as provided by ENFA, in areas where the Iberian ibex is present (species mean). All values are in metres, except for orientation, which is in degrees.

Codes	Meaning	Global mean	Species mean
TOPOGRAPHIC			
altitud_max	Maximum altitude	507.24	0.95
aspect	Average orientation	98.49	0.87
slope	Average slope	2.82	1.44
CULTURES			
dist_agriculture	Average distance to cultivated lands	2260.56	0.82
dist_agroforest	Average distance to agroforest lands	11990.41	1.22
dist_annual_crops	Average distance to annual crops	19572.28	0.63
dist_complex_cult	Average distance to complex cultures	1933.19	0.64
dist_perm_irrigate	Average distance to irrigated cultures	1368.97	0.42
FRUIT TREE			
dist_fruit_tree	Average distance to fruit tree cultures	4249.16	0.15
dist_olives	Average distance to olive tree cultures	5388.66	0.04
dist_vineyards	Average distance to vineyards	4714.15	1.25
WOODLAND			
dist_broad_leav	Average distance to broad leaves forests	4828.36	1.05
dist_mixed_forest	Average distance to mixed forests	6194.78	0.72
dist_connifeous	Average distance to conniferous forests	3021.63	-0.34
dist_wood_scrub	Average distance to wood-scrub ecotones	1509.38	0.81
dist_sclerophyllous	Average distance to sclerophyllous areas	1421.79	0.34
SCRUBLAND			
dist_moors_heath	Average distance to moors and heaths areas	29133.07	0.56
GRASSLAND			
dist_natu_grass	Average distance to natural grass lands	2706.51	0.39
SPARSE VEG.			
dist_sparse_veg	Average distance to sparse vegetation	12196.57	-0.32
dist_bare_rocks	Average distance to bare rocks areas	24583.19	-0.05
INFRASTRUCTURE			
dist_village	Average distance to villages	3217.65	0.84
dist_industr	Average distance to industrial areas	11612.99	1.07
dist_road_rail	Average distance to roads and rails	27601.89	0.74
WATER			
dist_river	Average distance to rivers	10852.34	-0.09
dist_inland_marshes	Average distance to inland marshes	20417.79	1.38
dist_water_bodies	Average distance to water bodies	14409.52	0.09
LIVESTOCK			
dist_goat_livestock	Average distance to goat livestock	2515.05	0.07

819 Table 2. EGVs used in habitat use analysis for the Iberian ibex relative
 820 abundance dependent variable. The significance level of step 2 is provided (**
 821 $p < 0.01$, * $p < 0.05$, n.s. = non-significant). See text and Table 1 for more
 822 details.

Variables	Meaning	Significance
Goat livestock	Presence/Absence of goat livestock	**
Highest altitude	Maximum altitude (m)	n.s.
Average altitude	Average altitude (m)	n.s.
Slope	Average slope index	n.s.
Cultures	Frequency of cultures per pixel	*
Woodland	Frequency of woodlands per pixel	**
Scrubland	Frequency of scrublands per pixel	**
Grassland	Frequency of grasslands per pixel	n.s.
Sparse vegetation	Frequency of sparse vegetations per pixel	**
Infrastructures	Frequency of human infrastructures per pixel	n.s.
Water reservoir	Frequency of rivers per pixel	*

823

824

825 Table 3. Correlation between ENFA factors and the environmental descriptors
 826 (EGVs). Percentages indicate the amount of specialization accounted for by
 827 each factor. Factor 1 is Marginality factor.

828

Variable	Factor 1 (87.6%)	Factor 2 (55.4%)	Factor 3 (19.2%)
altitud_max	0.24	0.01	0.10
aspect	0.22	0.04	0.00
dist_agriculture	0.21	0.08	-0.02
dist_agro_forest	0.31	-0.09	0.32
dist_annual_crops	0.16	-0.26	0.16
dist_broad_leav	0.26	-0.02	0.00
dist_goat_livestock	0.02	-0.06	0.20
dist_coniferous	-0.09	0.51	0.61
dist_industr	0.27	0.09	0.23
dist_inland_marshes	0.35	-0.02	-0.37
dist_road_rail	0.19	0.42	0.11
dist_sparse_veg	-0.08	0.62	-0.27
dist_villages	0.21	-0.09	0.04
dist_vineyards	0.31	0.12	-0.14
dist_water_bodies	0.02	0.03	-0.34
dist_wood_scrub	0.20	-0.01	-0.01
slope	0.36	0.04	0.01

829

830

831

832 Table 4. Final model obtained for the habitat use analysis for the Iberian ibex
 833 relative abundance dependent variable (nested stepwise regression output).
 834 GL column refers to goat livestock absence (A) and presence (P). T.E. refers
 835 to the typical error. **Significance relationships are in bold.**

Parameter	GL	Estimate	T.E .	t	Probability
Intercept		3.07	0.86	3.58	<0.01
Scrub land	(A)	0.88	0.31	2.88	<0.01
	(P)	-0.94	0.30	-3.13	<0.01
Cultures	(A)	-0.53	0.27	-2.47	0.01
	(P)	0.89	0.19	4.67	<0.01
Wood land	(A)	-0.04	0.22	-0.20	0.84
	(P)	0.81	0.22	3.65	<0.01
Sparse vegetation	(A)	-0.27	3.10	-0.09	0.93
	(P)	1.45	0.45	3.19	<0.01
Water	(A)	5.62	4.02	1.40	0.16
	(P)	12.55	6.14	2.04	0.04
Goat livestock	(A)	-4.54	1.23	-3.69	<0.01
	(P)	0	0.00	.	.

836

FIGURE 1

FIGURE 2

FIGURE 3