

1 **Invasive exotic aoudad (*Ammotragus lervia*) as a major**
2 **threat to native Iberian ibex (*Capra pyrenaica*): A**
3 **habitat suitability model approach**

4

5 **Pelayo Acevedo¹, Jorge Cassinello^{1*}, Joaquín Hortal^{2,3,4**}, Christian**
6 **Gortázar¹**

7

8 ¹Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM.
9 Ronda de Toledo s/n, 13071 Ciudad Real, Spain

10 ²Biodiversity and Global Change Lab., Museo Nacional de Ciencias Naturales, CSIC.
11 C/José Gutiérrez Abascal 2, 28006 Madrid, Spain

12 ³Departamento de Ciências Agrárias, CITA-A. Universidade dos Açores. Campus de
13 Angra, Terra-Chã, Angra do Heroísmo, 9701-851 Terceira (Açores), Portugal

14 ⁴Center for Macroecology, Institute of Biology, University of Copenhagen.
15 Universitetsparken 15, DK-2100 Copenhagen O, Denmark

16

17 Running head: Niche relationships between Iberian ibex and aoudad

18

19 *Author for correspondence:

20 Dr. Jorge Cassinello

21 Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM.

22 Ronda de Toledo s/n, 13003 Ciudad Real (Spain)

23 E-mail: jorge.cassinello@uclm.es

24 ** Present address: NERC Centre for Population Biology, Division of Biology,

25 Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY,

26 UK

27

28 **ABSTRACT**

29 The introduction of alien species to new environments is one of the main threats
30 to the conservation of biodiversity. One particularly problematic example is that
31 of wild ungulates which are increasingly being established in regions outside
32 their natural distribution range due to human hunting interests. Unfortunately,
33 we know little of the effects these large herbivores may have on the host
34 ecosystems. This study deals with a first comparative analysis of the habitat
35 requirements of two ungulate species that may be facing competition for
36 resources in the south of Europe: the native Iberian ibex (*Capra pyrenaica*) and
37 the exotic aoudad (*Ammotragus lervia*). The aoudad is a North African caprid
38 introduced in 1970 as a game species in southeastern Spain. It has adapted
39 well and populations have been freely expanding since then. ENFA is used to
40 describe the realized niche of both species where their distribution ranges
41 merge. Both species occupy marginal areas of rugged terrain in the region.
42 Marginality is higher for the Iberian ibex, which also presents a higher tolerance
43 of secondary environmental gradients than the aoudad. Highly suitable areas
44 for each species are secondarily-suitable for the other. Reclassified and cross-
45 tabulated habitat suitability maps showing the areas of potential spatial
46 coexistence and differences in ecological traits between both species are
47 provided. The results obtained do not allow inferring resource competition
48 between these species. However, current aoudad expansion could result in it
49 invading the favoured habitats of the ibex. Inadequate hunting policy and
50 monitoring, and increasing climatic resemblance of the study region to the
51 native aoudad areas, due to a strong desertification process, are facilitating a
52 high rate of expansion. We strongly recommend to eradicate or, at least,

53 monitor these exotic populations, and promote active conservation practices, if
54 one wants to preserve the unique natural resources present in this European
55 region.

56

57 **Keywords:** Biological invasions; ENFA; Habitat suitability modelling; Iberian
58 Peninsula; Resource competition; Ungulates

59

60 INTRODUCTION

61 Alien invasive species are considered by the IUCN Species Survival
62 Commission to be the second largest threat to indigenous species, following
63 habitat destruction (Bergmans & Blom 2001). The introduction of alien species
64 in regions beyond their natural distribution ranges may alter the host
65 ecosystems, thus affecting the viability of native fauna and flora (e.g., Diamond
66 1989; Wilcove *et al.* 1998). However, recent evidence postulates that
67 dominance of alien species over native ones is actually a consequence of
68 degraded ecosystems which facilitate the spread of such aliens (see reviews in
69 Gurevitch & Padilla 2004; Didham *et al.* 2005). Concerning ungulates, sport
70 hunting is among the main driving forces behind the expansion of various
71 species throughout the world (see, e.g., Macdonald *et al.* 1988; Gortázar *et al.*
72 2000; Jaksic *et al.* 2002).

73

74 Rapid increases in the populations of large herbivores in the Iberian Peninsula
75 are provoking their local overabundance (Cassinello 2000; Gortázar *et al.*
76 2006). These high densities are resulting in a serious threat for plant
77 communities due to overgrazing pressures (McNaughton 1979; Mace 1991; van
78 de Koppel *et al.* 1999). Thus, several non-native ungulates, including feral goats
79 (*Capra hircus*), the European mouflon (*Ovis aries musimon*) and the aoudad
80 (*Ammotragus lervia*), pose a serious risk and might be responsible for the
81 rarefaction and extinction of endemic plants (Nogales *et al.* 2006).

82

83 Uncontrolled exploitation and poaching along with habitat loss and
84 fragmentation used to be the main threat to native European ungulate

85 populations. However, current hunting regulations have led to their recovery
86 and even expansion in most countries (e.g., Sidorovich *et al.* 2003; Geisser &
87 Reyer 2004; Acevedo *et al.* 2007). Such expansion is noteworthy in areas
88 where game activity is not allowed, *i.e.*, protected lands and those close to
89 urban zones (e.g. Whittaker *et al.* 2001; Cahill *et al.* 2003). In the Iberian
90 Peninsula, the expansion of the wild boar, *Sus scrofa*, has been recorded over
91 several decades (Sáez-Royuela & Tellería 1986; Gortázar *et al.* 2000; Acevedo
92 *et al.* 2006). Other recent examples are roe deer, *Capreolus capreolus*
93 (Acevedo *et al.* 2005) and Iberian ibex, *Capra pyrenaica* (Pérez *et al.* 2002;
94 Acevedo *et al.* 2007). Current distribution of the latter is a consequence of both
95 natural and unnatural expansion processes, where most of translocations were
96 carried out posterior to 1970, particularly during 1980s and 1990s (Pérez *et al.*
97 2002). Also, such expansion may rely on recent habitat changes, *i.e.*
98 abandonment of agricultural lands, game management translocations (Gortázar
99 *et al.* 2000), its recovery from past sarcoptic mange epizootics (Pérez *et al.*
100 1997), and a decrease in hunting pressure on the species, probably caused by
101 the incidence of this disease (see Garrido 2004).

102

103 Of special concern is the aoudad, an African generalist ungulate, which has
104 been successfully introduced outside its African range as a game species in
105 USA and Spain. There, it has adapted formidably to Mediterranean-like regions,
106 where food resources are abundant, in contrast with the desert lands occupied
107 in its native African range. In these areas, the abundance of resources, along
108 with the scarcity of competitors and predators, results in high birth rates and a
109 quick spread of the population (see Wolf *et al.* 1996). Due to this, the aoudad

110 has rapidly adapted to southern Iberian habitats, presenting elevated population
111 growth rates (Cassinello 2000; Cassinello *et al.* 2004). The effects that this alien
112 species may cause on native flora and fauna are yet uncertain, although its
113 potential as a competitor of native ungulates has already been postulated,
114 mainly based on diet overlap between the aoudad and desert bighorn, *Ovis*
115 *canadensis nelsoni* (Simpson *et al.* 1978) and mule deer, *Odocoileus hemionus*
116 (Krysl *et al.* 1980).

117

118 The relationships between environmental gradients and the adequacy for the
119 survival of the populations of a species can be used to model the potential
120 response of the species to these gradients (Austin *et al.* 1990). Such description
121 can be used to produce predictive maps of species distribution (Guisan &
122 Zimmermann 2000; Araújo & Guisan 2006), and to describe the characteristics
123 of the niche of the species (*e.g.*, Chefaoui *et al.* 2005; Soberón & Peterson
124 2005; Araújo & Guisan 2006; Acevedo *et al.* in press). Two kinds of predictive
125 maps can be obtained for a species, describing i) current distribution or ii)
126 habitat suitability (*i.e.*, potential distribution). The latter could serve as a tool for
127 the study and threat assessment of biological invasions, as habitat suitability
128 can be used as an indicator of the risk for a particular territory to be invaded by
129 the alien species (*e.g.*, Cassinello *et al.* 2006).

130

131 The Ecological Niche Factor Analysis (ENFA, Hirzel *et al.* 2002) models habitat
132 suitability by comparing the environmental response of the species to the
133 environmental characteristics of the entire study area. This methodology can be
134 used to develop habitat suitability maps from raw presence data. Therefore,

135 ENFA is recommended when absence data are not available (most databases),
136 unreliable (most cryptic and rare species) or meaningless (invaders) (Hirzel *et*
137 *al.* 2001). Recently, it has been proposed that a species niche can be described
138 using ENFA results (Chefaoui *et al.* 2005; Acevedo *et al.* in press). Given that
139 the factors identified by ENFA represent the main environmental gradients that
140 are shaping the spatial response of the species in the study region, it can be
141 assumed that the response of a species to these gradients constitutes its
142 realized niche. Therefore, the distribution of habitat suitability scores through
143 these factors could be used to describe and study the characteristics of the
144 realized niche of species, as well as niche differentiation among several related
145 species (Chefaoui *et al.* 2005; Hortal *et al.* 2005; Acevedo *et al.* in press). Here,
146 the realized niche is intended as the portion of the fundamental niche where the
147 species is currently present, rather than where is competitively dominant (the
148 original definition of Hutchinson 1957; see discussion in Soberón & Peterson
149 2005; Araújo & Guisan 2006).

150

151 In this study, we compare habitat requirements and habitat suitability for native
152 Iberian ibex and exotic aoudad inhabiting the southeastern Iberian Peninsula,
153 according to their current distribution (Pérez *et al.* 2002; Cassinello *et al.* 2004;
154 Acevedo *et al.* 2007). Our goal is to compare the environmental requirements of
155 both species to identify differences and similarities (see Acevedo *et al.* in
156 press), and advance whether competition for resources and threats to the
157 Iberian ibex could be expected. To do this, we use ENFA and the niche
158 description proposed by Chefaoui *et al.* (2005) to characterize the response of
159 both ungulate species to the main environmental variations in the study area, as

160 well as to predict their potential distribution. This is the first attempt to compare
161 ecological traits between aoudads and Iberian ibexes, as to date no field study
162 whatsoever has been carried out in the regions where both species coexist. The
163 results are used to assess the potential impacts of current aoudad expansion in
164 the conservation of ibex populations.

165

166 A recent study by Cassinello *et al.* (2006) used a similar methodology to assess
167 the ecological niche of the aoudad in southeastern Spain, discriminating
168 between environmental and anthropogenic variables. The present study goes a
169 step forward, exploring potential niche overlap between the aoudad and its
170 close relative of the native Iberian fauna, namely, the Iberian ibex.

171

172 **METHODS**

173 **The study area**

174 We have chosen a geographic extent that hosts the environmental extremes
175 present in the SE Iberian Peninsula (*i.e.*, from coast to mountain), the current
176 area of expansion of the aoudad (Cassinello *et al.* 2004). This encompasses an
177 area 340 km wide and 270 km long (61,961 km² of land area; UTM 29N
178 geographic reference system; NW corner: 450,000-4,330,000; SE corner:
179 790,000-4,060,000; Fig. 1), including the Sierra Nevada mountain range in the
180 SW (rising over 3,400 m.a.s.l.), the Segura coastal basin in the east (with mean
181 altitudes below 20 m.a.s.l.), as well as several other mountain ranges and high-
182 altitude plains, such as the Sierra Espuña (the site where the introduced
183 aoudad population first became established), the Sierra María, the Sierra de
184 Los Filabres, and the Cazorla, Segura y Las Villas Natural Park.

185

186 **Data origin**

187 *Aoudad and Iberian ibex distributional data*

188 Aoudad distribution data (Cassinello *et al.* 2004; Fig. 1) come from field
189 observations and interviews with local shepherds, hunters, biologists and park
190 managers from regional environmental agencies, and verified by visits to the
191 areas where aoudads were reported. Iberian ibex distribution data were also
192 obtained by means of field observations and interviews with forest rangers and
193 staff from environmental agencies (Pérez *et al.* 2002; Acevedo *et al.* 2007).

194

195 *Environmental data*

196 Many climatic and ecological factors have been described to affect the
197 population abundance and distribution of ungulate species in the Iberian
198 Peninsula (*e.g.*, Acevedo *et al.* 2005, 2006). We selected 12 variables that
199 could act as determinants of current aoudad and Iberian ibex distribution in SE
200 Iberian Peninsula, also encompassing the range of climatic and ecological traits
201 present in the study region (Table 1). Ten of these variables account for
202 environmental variations (climate, habitat structure, vegetation characteristics
203 and geomorphology), and the other two do for human impact.

204

205 Data comes from an Iberian GIS database compiled and managed by J. M.
206 Lobo, A. Jiménez-Valverde, R. M. Chefaoui and J. Hortal. Climate variables
207 were obtained from the monthly values of the digital version of the Spanish
208 National Climate Atlas (provided by the Instituto Nacional de Meteorología;
209 available at <http://www.inm.es/>). Geomorphology variables were calculated from

210 an Iberian Digital Elevation Model of 100 m pixel width. Habitat structure
211 variables were obtained from the 250 m pixel width land use information of the
212 CORINE NATLAN European project (EEA 2000). Finally, two variables
213 accounting for human pressure on aoudad and ibex populations were obtained:
214 distance to urban areas (*i.e.* to the urban and industrial categories following
215 CORINE land cover map), and distance to the nearest road (including
216 motorways and national and local roads, extracted from the Spanish National
217 Digital Atlas, courtesy of the Instituto Geográfico Nacional; <http://www.ign.es/>).

218

219 We would like to point out that, although CORINE land cover maps are known
220 to present low spatial accuracy and some spatial errors (see, *e.g.*, Felicísimo &
221 Sánchez-Gago 2002), the CORINE 2000 version has largely improved these
222 aspects (see the updated reports available at
223 <http://dataservice.eea.europa.eu/dataservice/>). Also CORINE data have been
224 qualified as well suited for distribution modelling, even for habitat specific
225 species such as marshland birds (Virkkala *et al.* 2005). Therefore, it is doubtful
226 that these drawbacks in CORINE data result in misrepresentations of the
227 relationship between the study species and habitat characteristics.

228

229 All variables were handled and processed in a GIS environment (Clark Labs
230 2004). Information was extracted at 1 km² grain (1 x 1 km pixels). Such
231 resolution has been chosen as a compromise between the spatial resolution of
232 biological data (see discussion at Chefaoui *et al.* 2005; see also Acevedo *et al.*
233 2007, in press) and the scale at which the interaction between the two species
234 might be important. Using a coarser grain we could have been able to find

235 stronger relationships with the environmental predictors (see, e.g., Huettmann &
236 Diamond 2006), but our results would be less relevant for the assessment of
237 potential interactions between populations of both species. All variables were
238 Box-Cox normalized prior to their use in the ENFA analyses.

239

240 **Statistical analyses**

241 *Niche modelling*

242 BioMapper 3.0 (Hirzel *et al.* 2004; <http://www.unil.ch/biomapper>) was used to
243 model the niche of the study species. This software uses ENFA to produce
244 predictive maps of habitat suitability (*i.e.*, potential distribution) from GIS
245 variables (see applications at <http://www2.unil.ch/biomapper/bibliography.html>).
246 How these maps are produced has already been explained in detail in former
247 works (Hirzel *et al.* 2002; Cassinello *et al.* 2006).

248

249 *Model validation and accuracy*

250 Explained Information (ExI) and Explained Specialisation (ExS) are used to
251 measure how the resulting suitability model explains the observed data. The
252 former accounts for the total variability of the species distribution explained by
253 the model, whereas the latter accounts for additional variability on the
254 marginality and specialisation factors not included in the Explained Information
255 measure (Hirzel *et al.* 2004). In addition, the robustness and predictive power of
256 the HSMs were assessed by means of the spatially explicit Jackknife cross-
257 validation procedure implemented in Biomapper software (Boyce *et al.* 2002;
258 Hirzel *et al.* 2002).

259

260 *Niche description*

261 ENFA analysis identifies two descriptors of species environmental niches:
262 marginality and tolerance coefficients (see above). We also describe the shape
263 of the environmental niche of the species as the variation in the habitat
264 suitability scores throughout the environmental gradient defined by the
265 Marginality Factor (see Chefaoui *et al.* 2005; Hortal *et al.* 2005; Acevedo *et al.*
266 in press). To do this, Marginality Factor scores were divided into a number of
267 homogeneous intervals, and mean habitat suitability scores at each interval
268 were represented for each species. In addition, the HSM map obtained for each
269 species was reclassified (see Chefaoui *et al.* 2005; Acevedo *et al.* in press) in
270 three categories according to HSM scores: low habitat suitability (0-33); medium
271 habitat suitability (34-66) and high habitat suitability (66-100). These new maps
272 were cross-tabulated in the GIS environment to pinpoint zones suitable for the
273 two study species (high habitat suitability for the Iberian ibex and high habitat
274 suitability for the aoudad), where coexistence and competition could occur. The
275 environmental variables that characterize each zone were examined using
276 Bonferroni corrected ANOVA analyses (Perneger 1998).

277

278 **RESULTS**

279 The 12 environmental variables considered were reduced to three factors in
280 both ENFA analyses (see Table 2), explaining 82.34% and 83.20% of the
281 variance in the aoudad and Iberian ibex distributions, respectively. The first
282 axes explained very low percentages of the specialization for both species (<
283 4%).

284

285 Maximum and mean slopes, altitude range and presence of forests were the
286 variables with higher scores in the marginality factor for the aoudad model,
287 while low summer temperatures, maximum altitude, mean slope and winter
288 rainfall were so in the ibex model. Temperature range and winter rainfall
289 presented the higher coefficients at the specialization factors for the two
290 species, which thus show similar secondary restrictions (Table 2).

291

292 Both ungulate species occupy marginal areas in the study region (aoudad
293 marginality coefficient = 1.15; ibex marginality coefficient = 2.08, see Fig. 2).
294 However, although the Iberian ibex is more marginal than the aoudad in its
295 environmental selection according to the main environmental gradient in the
296 region, this species is quite tolerant to the secondary environmental gradients
297 (tolerance coefficient = 0.84). Therefore, ibex distribution appears to be more in
298 equilibrium with regional conditions than aoudad distribution, which is less
299 tolerant of secondary gradients (tolerance coefficient = 0.68). Moreover, highly
300 suitable areas for each species were secondarily suitable for the other one (Fig.
301 2).

302

303 The HSMs thus obtained are highly reliable, since our model validation
304 produced the following outcome: ExI = 66%, ExS = 83%, and average
305 Spearman coefficient at Jackknife validations of 0.97 for the ibex, and ExI =
306 65%, ExS = 82%, and Spearman coefficient = 0.95 for the aoudad.

307

308 Reclassified HSMs for both species are shown in Fig. 3, where areas of low,
309 medium and high habitat suitability are depicted. Cross-tabulated HSMs show

310 the areas of spatial coexistence between both species (*i.e.*, highly suitable for
311 both species) as well as those areas highly suitable for each exclusively (Fig.
312 4). High suitability areas were significantly different in ecological traits for the
313 two species (Table 3, Fig. 5), and were also different from the sites highly
314 suitable for both species.

315

316 **DISCUSSION**

317 One of the possible adverse consequences of the presence of the exotic
318 aoudad in the south of Europe is its effect on other taxonomically related native
319 ungulates, or on ecologically convergent species. Here we present the first
320 study on habitat similarities between aoudad and Iberian ibex, according to data
321 on the distribution of both species in the southeast of the Iberian Peninsula.

322

323 **On the methodological approach**

324 The ENFA-based methodological approach used here (based on Chefaoui *et al.*
325 2005) could be of great utility for the study of the realized niches of most
326 species, as well as for monitoring the potential spread of invasive species
327 (Cassinello *et al.* 2006). Since the seminal works of Austin, Nicholls and
328 Margules (Margules *et al.* 1987; Nicholls 1989; Austin *et al.* 1990), Generalized
329 Linear and Generalized Additive Models (GLM and GAM, respectively), linked
330 to GIS applications, have become very popular in species distribution
331 predictions (*e.g.*, Guisan *et al.* 2002; Nogués-Bravo & Martínez-Rica 2004).
332 When absence or pseudo-absence data are available, more robust habitat
333 models can be built from these techniques (*e.g.*, Engler *et al.* 2004; but see
334 Hirzel *et al.* 2001). However, in the specific case of invading species, some

335 times these species are not yet occupying all their potential habitats in the
336 landscape, and ENFA could produce better results than GLM, as 'absence data'
337 of this species would not be reliable (Hirzel *et al.* 2001).

338

339 Given that both the Iberian ibex and the aoudad are under remarkable
340 expansion processes in the study region (Cassinello 2000; Pérez *et al.* 2002;
341 Cassinello *et al.* 2004; Acevedo *et al.* 2007), we used ENFA analyses to
342 implement maps of the potential distribution of both species. In addition, ENFA
343 could also be more useful than a GLM when ecological interpretation is the aim
344 of the study, even in situations where a GLM provides higher correlations to the
345 observed data (Hirzel *et al.* 2001). The niche-description methodology derived
346 by Chefaoui *et al.* (2005), based in such premises, is used here to describe the
347 realized niches of both caprids in southeastern Iberian Peninsula. However,
348 ENFA results usually overestimate habitat suitability (Zaniewski *et al.* 2002;
349 Engler *et al.* 2004); therefore, such limitation should be considered when
350 interpreting our results.

351

352 **Niche description for the study species**

353 The Iberian ibex and the aoudad occupy restricted habitats in the study area.
354 However, the ibex presents a higher tolerance of secondary environmental
355 gradients than the aoudad. This might suggest that the aoudad has as yet not
356 reached all potentially suitable areas in the region, some of them being located
357 at higher altitudes. According to the known biology and ecology of the aoudad
358 (*e.g.*, Ogren 1965; Shackleton 1997; Cassinello 1998), and from our results
359 (see Fig. 1 and Cassinello *et al.* 2006), the species shows a strong potential to

360 reach and settle in other mountainous regions native to the Iberian ibex, such
361 as the Sierra Nevada mountain range (part of the Spanish National Parks
362 network since 1999).

363

364 According to our analyses, the aoudad selects areas characterized by high
365 slopes and altitude ranges, and an important presence of forests (see also
366 Cassinello *et al.* 2006). Such requirements agree with the habitat selection
367 made by the aoudad both in its native North African range (Shackleton 1997)
368 and in the regions where it has been introduced (Johnston 1980; Cassinello
369 2000). On the contrary, although the Iberian ibex also selects mountainous
370 areas, these are more marginal than those used by the aoudad, characterized
371 by low summer temperatures and high altitudes, and, to a lesser extent, by high
372 slopes (see also Acevedo *et al.* 2007) and high winter rainfall. In these areas,
373 food availability according to its diet is expected to be higher (Martínez &
374 Martínez 1987; Martínez 2000).

375

376 The results of this study defined a series of ecological traits that can be easily
377 related to the mountain ranges where the two study species are predominantly
378 found in the southeast of Spain (see Fig. 1). Thus, the aoudad ranges a wide
379 variety of mountainous regions of very different altitudes and scattered
380 throughout the study area (see Fig. 3a), whereas the ibex is found in spatially
381 restricted areas, in the mountain ranges with higher elevations in the study area
382 (Fig. 3b).

383

384 Cross-tabulated HSMs allowed the comparison between areas highly suitable
385 for one of the study species (but not for the other) and areas highly suitable for
386 both species (the areas of potential coexistence). Differences found between
387 the ecological variables included in the analyses can be explained by the
388 characteristics of the mountain ranges concerned. Basically, we appreciate
389 higher marginality values and lower plasticity in the Iberian ibex than in the
390 aoudad, which comparatively tends to act as a generalist in terms of habitat
391 preference (e.g., Gray & Simpson 1980; Escós & Alados 1992). Also, areas of
392 coexistence are more similar in terms of climate to highly suitable areas
393 exclusively of the ibex, so that before a hypothetical competitive situation, the
394 native caprid may be at an advantage. It is noticeable that the aoudad
395 significantly selects areas with lower winter rainfall and higher mean summer
396 temperatures, thus resembling its North African origin (Shackleton 1997).
397 Finally, the areas highly suitable for the aoudad are closer to urban areas and
398 roads than are those of the Iberian ibex, probably because of the higher niche
399 plasticity of aoudads and the location of their release site, the Sierra Espuña
400 and surrounding mountains (see Cassinello 2000).

401

402 **Implications for conservation**

403 A competition conflict could arise in areas of potential coexistence between the
404 Iberian ibex and the aoudad, due to the *a priori* biological similarities of both
405 caprids (Schaller 1977). Current distribution of the study species already
406 overlaps (Fig. 1), and our HSMs indicate that this overlap might increase in
407 time. If the aoudad reaches core native areas of the Iberian ibex (e.g., Sierra

408 Nevada, Sierra de Cazorla), the viability of ibex populations might be
409 compromised. But, would the aoudad actually be a threat to the Iberian ibex?

410

411 Given our results, currently the areas of coexistence of both species are
412 potentially scarce (merely 14.8% of all the highly suitable areas for the ibex) and
413 tend to be approaching to optimal conditions for the ibex. However, we are
414 probably not witnessing yet all the competitive potential between both species,
415 since the aoudad seems to have not yet reached its optimum. Nevertheless, as
416 Putman (1996) highlights, it is problematic to extract the implications for
417 competitive interactions from measures of niche overlap. High levels of overlap
418 can imply competition, but only if resources are limited. In fact, observations of
419 high overlap might equally well be indicative of a lack of competition (de Boer &
420 Prins 1990; Putman 1996). On the other hand, species segregation can also be
421 a result of competition. In our case, however, the aoudad has only recently
422 reached the domain of the Iberian ibex, so that we would not expect that
423 competition leading to segregation has already happened between both
424 species. As far as we know, it would be then premature to indicate whether the
425 aoudad will or will not be a threat to the native ibex and to which degree.

426

427 Despite this reasoning, recent evidence showed the displacement of the Iberian
428 ibex to suboptimal habitats by extensive goat livestock presence in central
429 Spain (Acevedo *et al.* 2007). This should alert us on possible similar effects in
430 southeastern Spain caused by the aoudad, a species strongly gregarious (Gray
431 & Simpson 1982; J. Cassinello, pers. obs.).

432

433 There is also another threat to be considered. Both study species are colonizing
434 new habitats in the south of Spain and their expansive movements are
435 noticeable (Pérez *et al.* 2002; Cassinello *et al.* 2004; Acevedo *et al.* 2007),
436 although both have experienced similar population decreases due to sarcoptic
437 mange episodes few years ago (Pérez *et al.* 1997; González-Candela & León-
438 Vizcaíno 1999). Concerning to future sarcoptic episodes, as the current ibex
439 distribution in the study region is characterized by isolated nuclei (see Fig. 1;
440 Pérez *et al.* 2002), contacts between them would be less probable than
441 contacts with hypothetically infected aoudad populations, which may occupy
442 larger extensions in the study area. Thus, if the aoudad acts as a vector of this
443 disease, it would then represent a risk for the ibex.

444

445 The increasing presence of exotic ungulates in Spain, due to sport hunting
446 introductions (*i.e.* the European mouflon and the aoudad), may particularly
447 threaten local plant species (Rodríguez-Piñero & Rodríguez-Luengo 1992). In
448 the case of the aoudad, its expansion might put the threatened, highly endemic
449 flora of Sierra Nevada at serious risk. The critical importance of such a
450 mountain range for the conservation of Iberian plant biodiversity (see, *e.g.*,
451 Castro Parga *et al.* 1996; Blanca *et al.* 1998; Lobo *et al.* 2001) means that
452 monitoring the aoudad grazing habits (both intensity and grazed species) in its
453 expanding range should be a priority.

454

455 Finally, there is a series of factors that may determine the current degree of
456 Iberian ibex and aoudad expansion and the effects caused by the latter on
457 native fauna and flora. Recent climatic changes and the strong desertification

458 which is taking place in the southeast of Spain (e.g., Puigdefábregas &
459 Mendizábal 2004), resulting in lower rainfall regimes and higher mean annual
460 temperatures, may cause significant habitat changes which will favour the
461 expansion of a desert caprid, such as the aoudad. On the other hand, the
462 strong interest displayed in the aoudad by private game estates in the south of
463 Spain, and the subsequent risk of animals escaping from badly maintained
464 fences (Cassinello *et al.* 2004; P. Acevedo, direct observations), may speed up
465 this colonization process and therefore exacerbate their effects on the host
466 ecosystem.

467

468 To sum up, when looking at cumulative effects, the presence of the exotic
469 aoudad in the southeast of the Iberian Peninsula should be considered as a
470 major problem for the ecosystem. Although current evidences do not yet show
471 straight threats, we should start taking measures to prevent them to occur, as
472 we are dealing with an invasive alien species which should be strictly controlled
473 (see, e.g., Bergmans & Blom 2001; Wittenberg & Cock 2001;
474 http://www.iucn.org/en/news/archive/2001_2005/press/alien2001.html;
475 Genovesi & Shine 2003). One straightforward action to be taken should be the
476 eradication of the species. This may confront with opposite interests by hunters
477 and owners of game estates, and mainly with the difficulty of carrying out such
478 an enormous task on a population of probably more than 2,000 individuals
479 spread out across an extremely large area (Cassinello 2000; Cassinello *et al.*
480 2004). But time is critical, and if no action is taken in the near future, the ongoing
481 expansion of the species will reduce the possible management alternatives.

482

483 **ACKNOWLEDGEMENTS**

484 Our gratitude to F. Huettmann and two anonymous reviewers for their useful
485 comments and suggestions on a previous version of our manuscript. We thank
486 J.M. Lobo, A. Jiménez-Valverde, D. Nogués-Bravo and M.B. Araújo for the
487 outcome of hours of conceptual and practical discussion on niche modelling.
488 We are also indebted to J.M. Lobo, A. Jiménez-Valverde and R.M. Chefaoui for
489 their work on the original GIS database. The Spanish Instituto Nacional de
490 Meteorología kindly provided climate data for such database. PA has benefited
491 from a contract from the Universidad de Castilla-La Mancha. JC holds a Ramón
492 y Cajal research contract at the CSIC awarded by the Ministerio de Educación y
493 Ciencia (MEC), and is also supported by the project PBI-05-010 granted by
494 Junta de Comunidades de Castilla-La Mancha. Finally, JH was supported by a
495 Portuguese FCT (Fundação para a Ciência e Tecnologia) grant
496 (BPD/20809/2004), and also by the Spanish MEC project CGL2004-0439/BOS.

497

498 **REFERENCES**

499 Acevedo, P., Alzaga, V., Cassinello, J. & Gortázar, C. In press. Habitat
500 suitability modelling reveals a strong niche overlap between two poorly
501 known species, the broom hare and the Pyrenean grey partridge, in the north
502 of Spain. *Acta Oecologica*.

503 Acevedo, P., Cassinello, J.& Gortázar, C. (2007). The Iberian ibex is under an
504 expansion trend but displaced to suboptimal habitats by the presence of
505 extensive goat livestock in central Spain. *Biodiversity and Conservation*, DOI
506 10.1007/s10531-006-9032-y.

507 Acevedo, P., Delibes-Mateos, M., Escudero, M.A., Vicente, J., Marco, J. &
508 Gortázar, C. (2005). Environmental constraints in the colonization sequence
509 of roe deer (*Capreolus capreolus* Linnaeus, 1758) across the Iberian
510 Mountains, Spain. *Journal of Biogeography*, **32**, 1671-1680.

511 Acevedo, P., Escudero, M.A., Muñoz, R. & Gortázar, C. (2006). Factors
512 affecting wild boar abundance across an environmental gradient in Spain.
513 *Acta Theriologica*, **51**, 327-336.

514 Araújo, M.B. & Guisan, A. (2006). Five (or so) challenges for species
515 distribution modelling. *Journal of Biogeography*, **33**, 1677-1688.

516 Austin, M.P., Nicholls, A.O. & Margules, C.R. (1990). Measurement of the
517 realized qualitative niche: environmental niches of five *Eucalyptus* species.
518 *Ecological Monographs*, **60**, 161-177.

519 Bergmans, W. & Blom, E. (ed.) (2001). *Invasive Plants and Animals. Is There a*
520 *Way Out?* The Netherlands Committee for IUCN, Amsterdam.

521 Blanca, G., Cueto, M., Martínez-Lirola, M.J. & Molero-Mesa, J. (1998).
522 Threatened vascular flora of Sierra Nevada (southern Spain). *Biological*
523 *Conservation*, **85**, 269-285.

524 Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002).
525 Evaluating resource selection functions. *Ecological Modelling*, **157**, 281-300.

526 Cahill, S., Llimona, F. & Gràcia, J. (2003). Spacing and nocturnal activity of wild
527 boar *Sus scrofa* in a Mediterranean metropolitan park. *Wildlife Biology*, **9**, 3-
528 13.

529 Cassinello, J. (1998). *Ammotragus lervia*: a review on systematics, biology,
530 ecology and distribution. *Annales Zoologici Fennici*, **35**, 149-162.

531 Cassinello, J. (2000). *Ammotragus* free-ranging population in the south-east of
532 Spain: a necessary first account. *Biodiversity and Conservation*, **9**, 887-900.

533 Cassinello, J., Acevedo, P. & Hortal, J. (2006). Prospects for population
534 expansion of the exotic aoudad (*Ammotragus lervia*; Bovidae) in the Iberian
535 Peninsula: clues from habitat suitability modelling. *Diversity and Distributions*,
536 **12**, 666–678.

537 Cassinello, J., Serrano, E., Calabuig, G. & Pérez, J.M. (2004). Range
538 expansion of an exotic ungulate (*Ammotragus lervia*) in southern Spain:
539 ecological and conservation concerns. *Biodiversity and Conservation*, **13**,
540 851-866.

541 Castro Parga, I., Moreno Saiz, J.C., Humphries, C.J. & Williams, P.H. (1996).
542 Strengthening the Natural and National Park system of Iberia to conserve
543 vascular plants. *Botanical Journal of the Linnean Society*, **121**, 189-206.

544 Chefaoui, R.M., Hortal, J. & Lobo, J.M. (2005). Potential distribution modelling,
545 niche characterization and conservation status assessment using GIS tools:
546 a case study of Iberian *Copris* species. *Biological Conservation*, **122**, 327-
547 338.

548 Clark Labs (2004). *Idrisi Kilimanjaro version 14.02. GIS software package*. Clark
549 Labs, Clark University, Worcester.

550 de Boer, W.F. & Prins, H.H.T. (1990). Large herbivores that strive mightily but
551 eat and drink as friends. *Oecologia*, **82**, 264-274.

552 Diamond, J.M. (1989). Overview of recent extinctions. *Conservation for the*
553 *Twenty-first Century* (ed. by D. Western and M.C. Pearl), pp. 37-41. Oxford
554 University Press, Oxford.

555 Didham, R.K., Tylianakis, J.M., Hutchinson, M.A., Ewers, R.M. & Gemmell, N.J.
556 (2005). Are invasive species the drivers of ecological change? *Trends in*
557 *Ecology and Evolution*, **20**, 470-474.

558 EEA (2000). *NATLAN. Nature/land cover information package*. European
559 Environment Agency, Luxembourg.

560 Engler, R., Guisan, A. & Rechsteiner, L. (2004). An improved approach for
561 predicting the distribution of rare and endangered species from occurrence
562 and pseudo-absence data. *Journal of Applied Ecology*, **41**, 263-274.

563 Escós, J. & Alados, C.L. (1992). Habitat preference of Spanish ibex and other
564 ungulates in Sierras de Cazorla y Segura (Spain). *Mammalia*, **56**, 393-406.

565 Felicísimo, A.M. & Sánchez-Gago, L.M. (2002). Thematic and spatial accuracy:
566 a comparison of the Corine Land Cover with the Forestry Map of Spain.
567 *AGILE 2002 Proceedings*, pp. 109-122. Association Geographic Information
568 Laboratories Europe, Palma de Mallorca.

569 Garrido, J.L. (2004). Aprovechamientos por especies y autonomías. *II Máster*
570 *en Conservación y Gestión de los Recursos Cinegéticos*. Unpublished report,
571 Ciudad Real.

572 Geisser, H. & Reyer, H.U. (2004). Efficacy of hunting, feeding, and fencing to
573 reduce crop damage by wild boars. *Journal of Wildlife Management*, **68**, 939-
574 946.

575 Genovesi, P. & Shine, C. (2003). *European Strategy of Invasive Alien Species*.
576 Convention on the Conservation of European Wildlife and Natural Habitats.
577 Standing Committee. 23rd Meeting. Council of Europe Publishing,
578 Strasbourg.

579 González-Candela, M. & León-Vizcaíno, L. (1999). Sarcoptic mange in Barbary
580 sheep (*Ammotragus lervia*) population of Sierra Espuña Regional Park
581 (Murcia). *Galemys*, **11**, 43-58.

582 Gortázar, C., Acevedo, P., Ruiz-Fons, F. & Vicente, J. (2006). Disease risks
583 and overabundance of game species. *European Journal of Wildlife*
584 *Research*, **52**, 81-87.

585 Gortázar, C., Herrero, J., Villafuerte, R. & Marco, J. (2000). Historical
586 examination of the status of large mammals in Aragon, Spain. *Mammalia*, **64**,
587 411-422.

588 Gray, G.G. & Simpson, C.D. (1980). *Ammotragus lervia*. *Mammal Species*, **144**,
589 1-7.

590 Gray, G.G. & Simpson, C.D. (1982). Group dynamics of free-ranging Barbary
591 sheep in Texas. *Journal of Wildlife Management*, **46**, 1096-1101.

592 Guisan, A., Edwards, T.C. & Hastie, T. (2002). Generalized linear and
593 generalized additive models in studies of species distribution: setting the
594 scene. *Ecological Modelling*, **157**, 89-100.

595 Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in
596 ecology. *Ecological Modelling*, **135**, 147-186.

597 Gurevitch, J. & Padilla, D.K. (2004). Are invasive species a major cause of
598 extinctions? *Trends in Ecology and Evolution*, **19**, 470-474.

599 Hirzel, A., Helfer, V. & Métral, F. (2001). Assessing habitat-suitability models
600 with a virtual species. *Ecological Modelling*, **145**, 111-121.

601 Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002). Ecological-niche
602 factor analysis: How to compute habitat- suitability maps without absence
603 data? *Ecology*, **83**, 2027-2036.

604 Hirzel, A.H., Hausser, J. & Perrin, N. (2004). *Biomapper 3.0*. Laboratory for
605 Conservation Biology, University of Lausanne, Lausanne.

606 Hortal, J., Borges, P.A.V., Dinis, F., Jiménez-Valverde, A., Chefaoui, R.M.,
607 Lobo, J.M., Jarroca, S., Brito de Azevedo, E., Rodrigues, C., Madrugá, J.,
608 Pinheiro, J., Gabriel, R., Cota Rodrigues, F. & Pereira, A.R. (2005). Using
609 ATLANTIS - Tierra 2.0 and GIS environmental information to predict the
610 spatial distribution and habitat suitability of endemic species, *A List of the*
611 *Terrestrial Fauna (Mollusca and Arthropoda) and Flora (Bryophyta,*
612 *Pteridophyta and Spermatophyta) from the Azores* (ed. by P.A.V. Borges, R.
613 Cunha, R. Gabriel, A.F. Martins, L. Silva, and V. Vieira), pp. 69-113. Direcção
614 Regional de Ambiente and Universidade dos Açores, Angra do Heroísmo
615 and Ponta Delgada. <http://sram.azores.gov.pt/lffa/>.

616 Huettmann, F. & Diamond, A.W. (2006). Large-scale effects on the spatial
617 distribution of seabirds in the Northwest Atlantic. *Landscape Ecology*, **21**,
618 1089-1108.

619 Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on*
620 *Quantitative Biology*, **22**, 415-427.

621 Jaksic, F.M., Iriarte, J.A., Jiménez, J.E. & Martínez, D.R. (2002). Invaders
622 without frontiers: cross-border invasions of exotic mammals. *Biological*
623 *Invasions*, **4**, 157-173.

624 Johnston, D.S. (1980). Habitat utilization and daily activities of Barbary sheep.
625 *Symposium on Ecology and Management of Barbary Sheep* (ed. by C.D.
626 Simpson), pp. 51-58. Texas Technical University Press, Lubbock.

627 Krysl, L.J., Simpson, C.D. & Gray, G.G. (1980). Dietary overlap of sympatric
628 Barbary sheep and mule deer in Palo Duro Canyon, Texas. *Symposium on*

629 *Ecology and Management of Barbary Sheep* (ed. by C.D. Simpson), pp. 97-
630 103. Texas Technical University Press, Lubbock.

631 Lobo, J.M., Castro, I. & Moreno, J.C. (2001). Spatial and environmental
632 determinants of vascular plant species richness distribution in the Iberian
633 Peninsula and Balearic Islands. *Biological Journal of the Linnean Society*, **73**,
634 233-253.

635 Macdonald, I.A.W., Graber, D.M., DeBenedetti, S., Groves, R.H. & Fuentes,
636 E.R. (1988). Introduced species in nature reserves in Mediterranean type
637 climatic regions of the world. *Biological Conservation*, **44**, 37–66.

638 Mace, R. (1991). Overgrazing overstated. *Nature*, **349**, 280-281.

639 Margules, C.R., Nicholls, A.O. & Austin, M.P. (1987). Diversity of *Eucalyptus*
640 species predicted by a multi-variable environmental gradient. *Oecologia*, **71**,
641 229-232.

642 Martínez, T. (2000). Diet selection by Spanish ibex in early summer in Sierra
643 Nevada. *Acta Theriologica*, **45**, 335-346.

644 Martínez, T. & Martínez, E. (1987). Diet of Spanish wild goat, *Capra pyrenaica*,
645 in spring and summer at the Sierra de Gredos, Spain. *Mammalia*, **51**, 547-
646 557.

647 McNaughton, S.J. (1979). Grazing as an optimization process: grass-ungulate
648 relationships in the Serengeti. *The American Naturalist*, **113**, 691-703.

649 Nicholls, A.O. (1989). How to make biological surveys go further with
650 Generalised Linear Models. *Biological Conservation*, **50**, 51-75.

651 Nogales, M., Rodríguez-Luengo, J.L. & Marrero, P. (2006). Ecological effects
652 and distribution of invasive non-native mammals on the Canary Islands.
653 *Mammal Review*, **36**, 49-65.

654 Nogués-Bravo, D. & Martínez-Rica, J.P. (2004). Factors controlling the spatial
655 species richness pattern of four groups of terrestrial vertebrates in an area
656 between two different biogeographic regions in northern Spain. *Journal of*
657 *Biogeography*, **31**, 629–640.

658 Ogren, H. (1965). *Barbary sheep*. New Mexico Department of Game and Fish
659 Bulletin 13, Santa Fe.

660 Pérez, J.M., Ruiz, I., Granados, J.E., Soriguer, R.C. & Fandos, P. (1997). The
661 dynamics of sarcoptic mange in the ibex population of Sierra Nevada in
662 Spain: Influence of climatic factors. *Journal of Wildlife Research*, **2**, 86-89.

663 Pérez, J.M., Granados, J.E., Soriguer, R.C., Fandos, P., Marquez, F.J. &
664 Crampe, J.P. (2002). Distribution, status and conservation problems of the
665 Spanish Ibex, *Capra pyrenaica* (Mammalia : Artiodactyla). *Mammal Review*,
666 **32**, 26-39.

667 Perneger, T.V. (1998). What is wrong with Bonferroni adjustments. *British*
668 *Medical Journal*, **136**, 1236-1238.

669 Puigdefábregas, J. & Mendizábal, T. (2004). Prospects for desertification
670 impacts in Southern Europe. *Environmental Challenges in the Mediterranean*
671 *2000-2050* (ed. by A. Marquina), pp. 155–172. Kluwer Academic Publishers,
672 Netherlands.

673 Putman, R.J. (1996). *Competition and Resource Partitioning in Temperate*
674 *Ungulate Assemblies*. Chapman and Hall, London.

675 Rodríguez-Piñero, J.C. & Rodríguez-Luengo, J.L. (1992). Autumn food-habits of
676 the Barbary sheep (*Ammotragus lervia* Pallas 1777) on La Palma Island
677 (Canary Islands). *Mammalia*, **56**, 385-392.

- 678 Sáez-Royuela, C. & Tellería, J.L. (1986). The increased population of Wild Boar
679 (*Sus scrofa*) in Europe. *Mammal Review*, **16**, 97-101.
- 680 Schaller, G.B. (1977). *Mountain Monarchs: wild sheep and goats of the*
681 *Himalaya*. Univ. of Chicago Press, Chicago.
- 682 Shackleton, D.M. (1997). *Wild Sheep and Goats and their Relatives: Status*
683 *Survey and Conservation Action Plan for Caprinae*. IUCN, Gland,
684 Switzerland.
- 685 Sidorovich, V.E., Tikhomirova, L.L. & Jedrzejewska, B. (2003). Wolf *Canis lupus*
686 numbers, diet and damage to livestock in relation to hunting and ungulate
687 abundance in northeastern Belarus during 1990-2000. *Wildlife Biology*, **9**,
688 103-111.
- 689 Simpson, C.D., Krysl, L.J., Hampy, D.B. & Gray, G.G. (1978). The Barbary
690 sheep: a threat to desert bighorn survival. Trans. *Desert Bighorn Council*, **22**,
691 26-31.
- 692 Soberón, J. & Peterson, A.T. (2005). Interpretation of models of fundamental
693 ecological niches and species' distribution areas. *Biodiversity Informatics*, **2**,
694 1-10.
- 695 van de Koppel, J., Rietkerk, M. & Weissing, F.J. (1999). Catastrophic vegetation
696 shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology*
697 *and Evolution*, **12**, 352-356.
- 698 Virkkala, R., Luoto, M., Heikkinen, R.K., & Leikola, N. (2005). Distribution
699 patterns of boreal marshland birds: modelling the relationships to land cover
700 and climate. *Journal of Biogeography*, **32**, 1957-1970.

701 Whittaker, D., Manfredo, M.J., Fix, P.J., Sinnot, R., Miller, S. & Vaske, J. (2001).
702 Understanding beliefs and attitudes about an urban wildlife hunt near
703 Anchorage, Alaska. *Wildlife Society Bulletin*, **29**, 1114-1124.

704 Wilcove D.S., Rothstein, D. & Dubow, J. (1998). Quantifying threats to imperiled
705 species in the United States. *Bioscience*, **48**, 607–615.

706 Wittenberg R. & M. Cock (2001). *Invasive Alien Species: A Toolkit of Best*
707 *Prevention and Management Practices*. GISP/CAB International, Wallingford,
708 UK.

709 Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. (1996). Avian and mammalian
710 translocations: update and reanalysis of 1987 survey data. *Conservation*
711 *Biology*, **10**, 1142–1154.

712 Zaniwski, A.E., Lehmann, A. & Overton J.M. (2002). Predicting species spatial
713 distributions using presence-only data: a case study of native New Zealand
714 ferns. *Ecological Modelling*, **157**, 261-280.

715

716 **FIGURE CAPTIONS**

717

718 Figure 1.- Presence data of the Iberian ibex (black dots) and the aoudad (grey
719 dots), and location of the study area. Provinces borders are shown along with
720 the main mountain ranges where the species can be found.

721

722 Figure 2.- Variation of mean habitat suitability scores along the marginality
723 factor. The factor was divided into 20 intervals, and mean HSM values are
724 shown. As marginality factors for both models were highly correlated, only one
725 was used for plot the figure, the ibex model.

726

727 Figure 3.- Habitat suitability maps for the study species: a) the aoudad, and b)
728 the Iberian ibex. Habitat suitability scores have been reclassified in three
729 categories (0-33 = low suitability, 34-66 = medium suitability, and 67-100 = high
730 suitability).

731

732 Figure 4.- Map showing the highly suitable areas (habitat suitability > 66) for
733 each one of the study species, as well as the areas of potential coexistence.

734

735 Figure 5.- Plots showing mean ($\pm SE_{95\%C.I.}$) values of some ecological variables
736 present in highly suitable areas for the aoudad, aoudad and Iberian ibex
737 (potential coexistence areas) and Iberian ibex. Statistically significant
738 differences are indicated in Table 3. (a) Percentage of forest and shrubland
739 areas; (b) maximum altitud and slope; (c) winter rainfall and mean summer

740 temprature; (d) distances to urban areas and roads. We have added solid and

741 dotted lines between the suitable areas in order to clarify the different trends.

742

743 Table 1.- Variables used in the analyses (and their measurement units).
 744 Average values are shown for the whole study region (global), and for the areas
 745 where the aoudad and the Iberian ibex are present.

VARIABLES (UNIT)	Means		
	Global	Aoudad	Iberian ibex
CLIMATE			
Winter rainfall (mm)	132.92	108.65	209.14
Summer rainfall (mm)	46.29	40.73	61.69
Mean summer temperature (°C)	22.95	21.9	19.28
Annual range of temperatures (°C)	15.33	15.21	15.58
GEOMORPHOLOGY			
Maximum altitude (m)	806.46	1066.77	1670.46
Altitude range (m)	101.14	187.37	204.59
Mean slope (degrees)	5.56	10.40	11.21
Maximum slope (degrees)	12.23	23.01	22.24
HABITAT STRUCTURE			
Forest area (%)	11.86	33.17	39.80
Shrubland area (%)	27.72	33.88	17.08
HUMAN PRESSURE			
Distance to urban areas (m)	3974.88	5714.69	7335.62
Distance to the nearest road (m)	2050.21	2915.65	3431.15

Table 2.- Coefficients of the variables used in ENFA, and percentages explained by marginality (MF) and specialization factors (SF).

Variables	Aoudad model			Iberian Ibex model		
	MF	SF 1 (43.49%)	SF 2 (17.53%)	MF	SF 1 (48.01%)	SF 2 (14.54%)
Forest area	0.36	0.00	0.01	0.26	0.07	-0.14
Shrubland area	0.03	0.15	0.03	0.02	0.11	-0.27
Maximum altitude	0.26	-0.28	0.26	0.47	-0.10	-0.37
Distance to the nearest road	0.25	0.07	0.02	0.22	0.01	-0.08
Distance to urban areas	0.25	0.09	-0.10	0.27	0.04	-0.15
Maximum slope	0.49	0.11	-0.15	0.25	0.20	-0.04
Mean slope	0.43	-0.07	-0.36	0.28	-0.09	-0.05
Winter rainfall	-0.16	0.58	-0.33	0.28	0.30	-0.40
Summer rainfall	-0.04	-0.51	0.41	0.21	0.09	0.40
Altitude range	0.40	-0.03	0.23	0.27	-0.01	0.13
Annual range of temperatures	-0.06	-0.44	-0.66	0.04	-0.89	-0.15
Mean summer temperature	-0.24	-0.27	-0.07	-0.49	0.15	-0.61

Table 3.- Environmental differentiation between the areas of potential coexistence of the aoudad and the Iberian ibex, and the areas suitable to each one of these species (HS > 66 in both models). Results of the analyses of variance are shown; ANOVA test coefficient (F), Bonferroni-corrected p-value (ns = no significant, ***p ≤ 0.0001); the areas with significantly higher values for a given dependent variable in each comparison are indicated (A = aoudad, C = potential coexistence, and I = Iberian ibex).

Variables	Aoudad vs. potential coexistence			Aoudad vs. Iberian ibex			Iberian ibex vs. potential coexistence		
	F	p-value	area with a higher mean value	F	p-value	area with a higher mean value	F	p-value	area with a higher mean value
Forest area	56.52	***	C	72.13	***	I	8.34	ns	-
Shrubland area	19.28	***	A	0.82	ns	-	14.75	***	I
Maximum altitude	612.68	***	C	3212.16	***	I	27.82	***	I
Distance to the nearest road	48.89	***	A	43.11	***	I	95.35	***	I
Distance to urban areas	30.23	***	C	94.01	***	I	0.12	ns	-
Maximum slope	0.30	ns	-	70.04	***	I	13.84	***	I
Mean slope	0.52	ns	-	225.10	***	I	57.60	***	I
Winter rainfall	814.17	***	C	1046.59	***	I	65.42	***	C
Summer rainfall	1168.11	***	C	941.18	***	I	84.14	***	C
Altitude range	2.89	ns	-	209.29	***	I	64.14	***	I
Annual range of temperatures	193.29	***	C	150.00	***	I	96.73	***	C
Mean summer temperature	498.62	***	A	2222.7	***	A	15.61	***	C

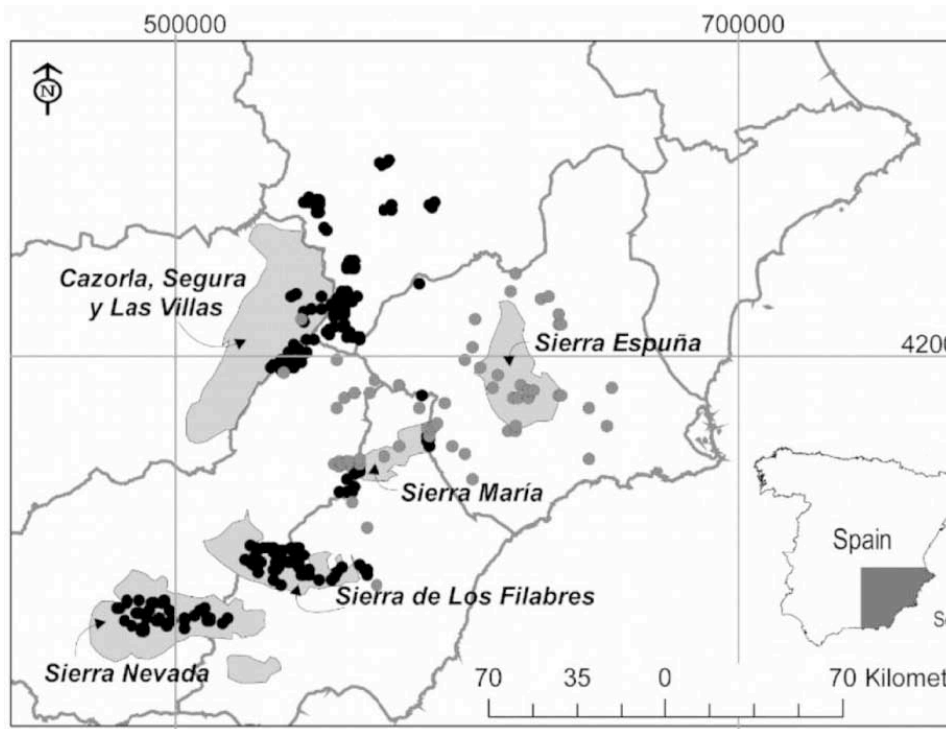


FIGURE 1

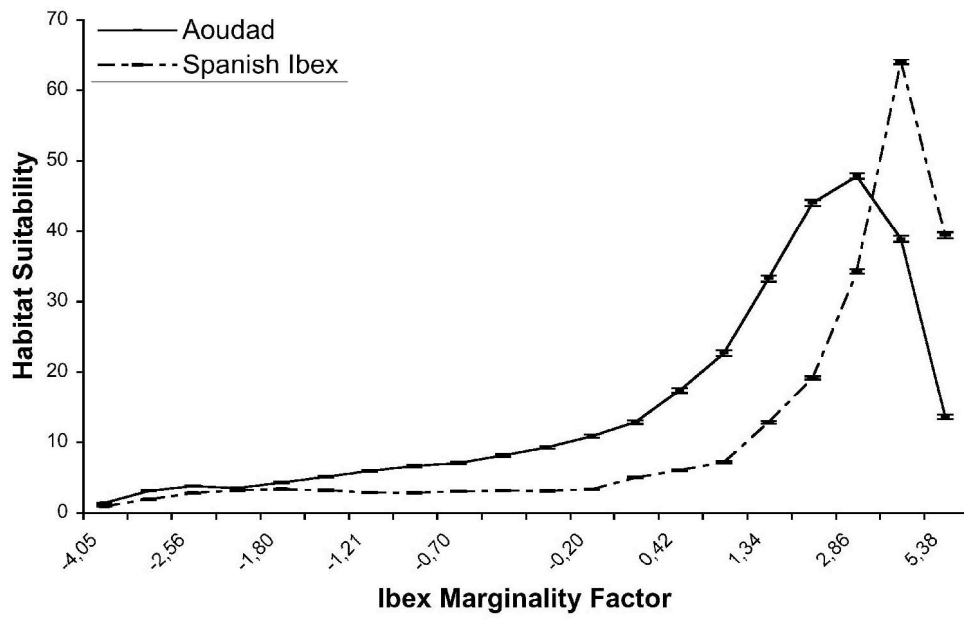


FIGURE 2

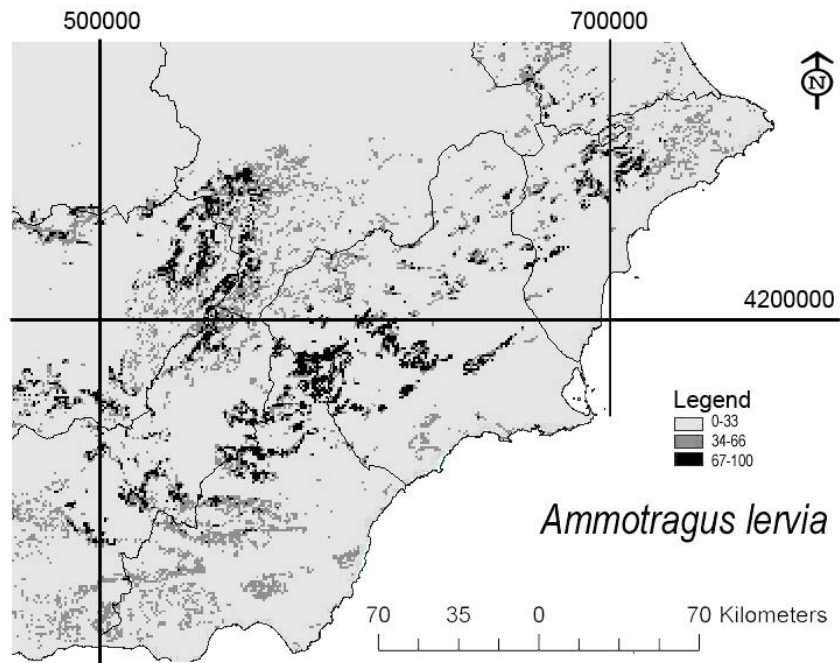


FIGURE 3a

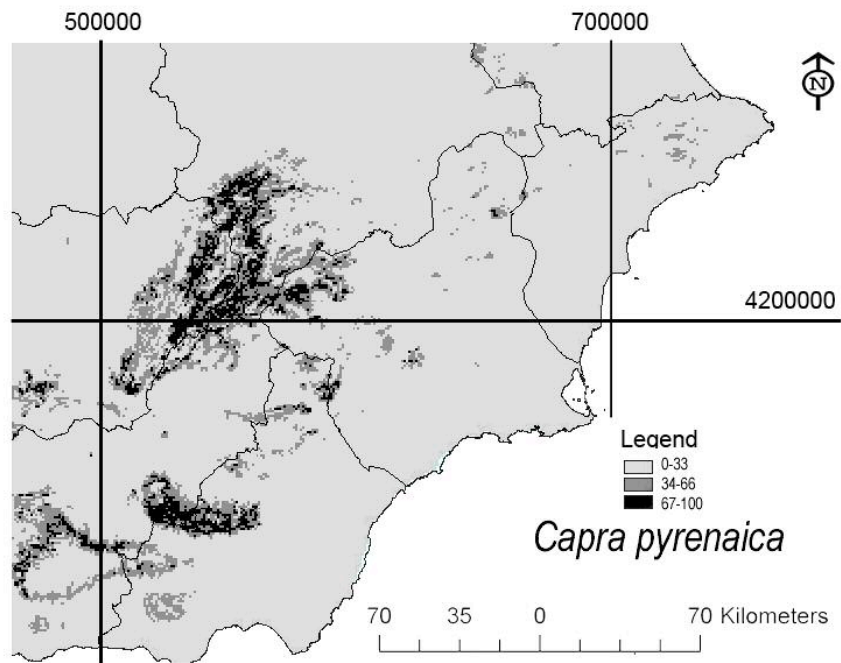


FIGURE 3b

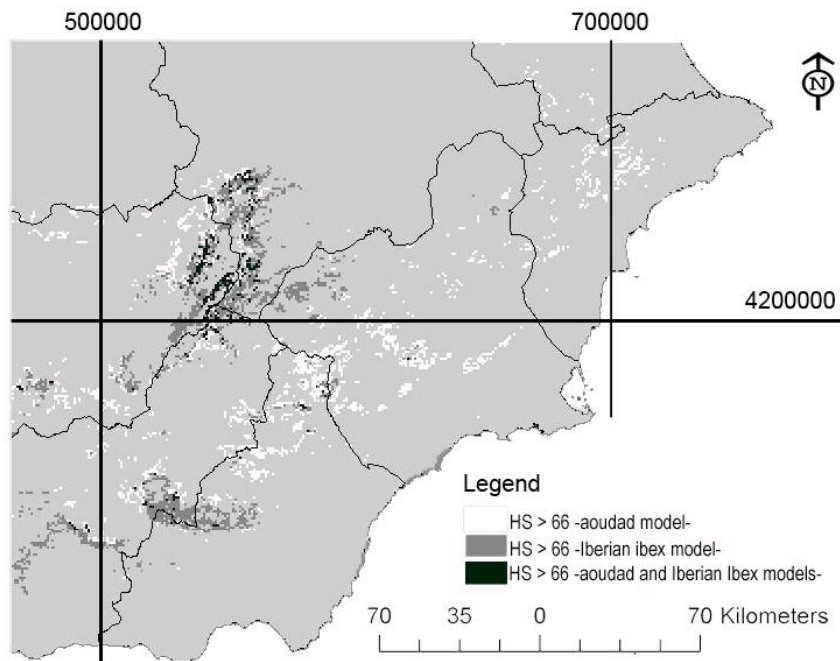


FIGURE 4

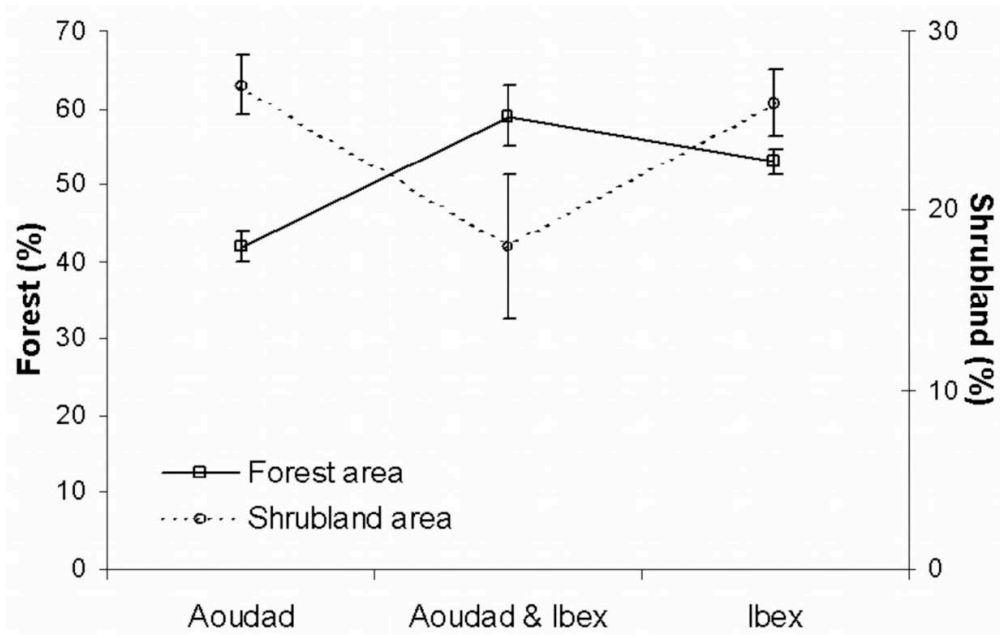


FIGURE 5a

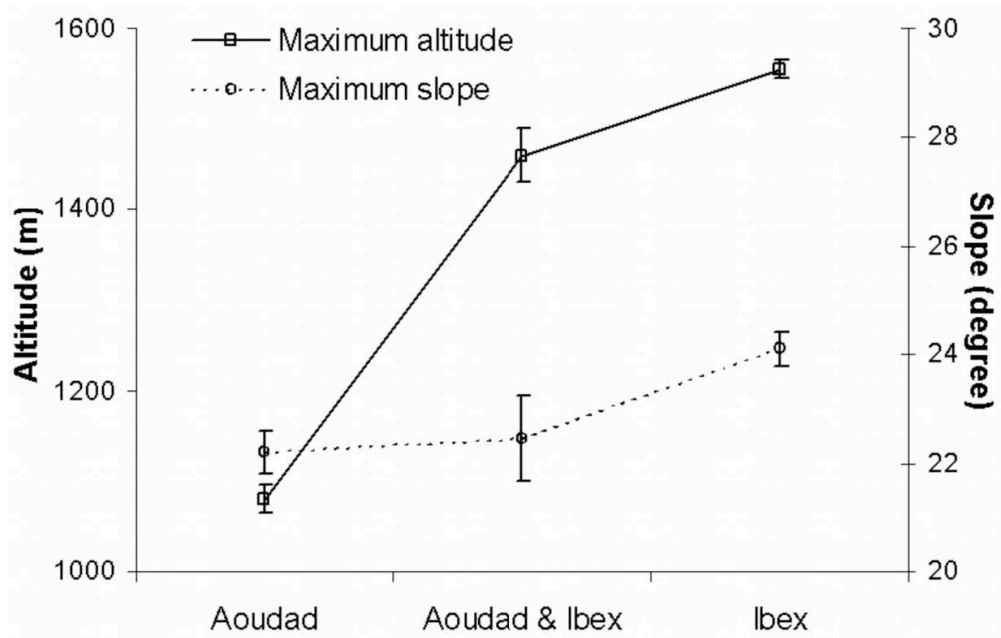


FIGURE 5b

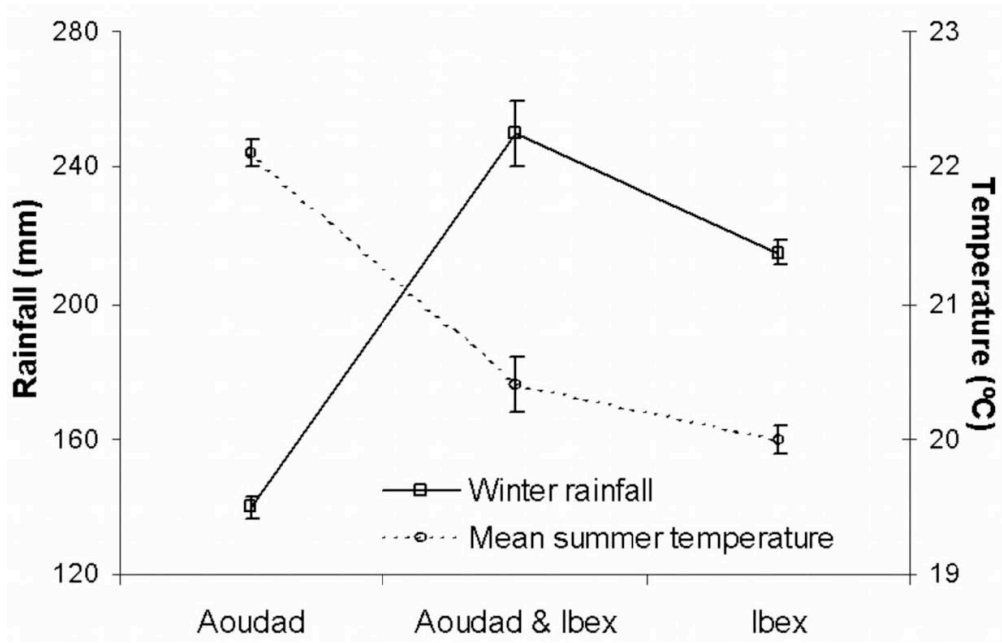


FIGURE 5c

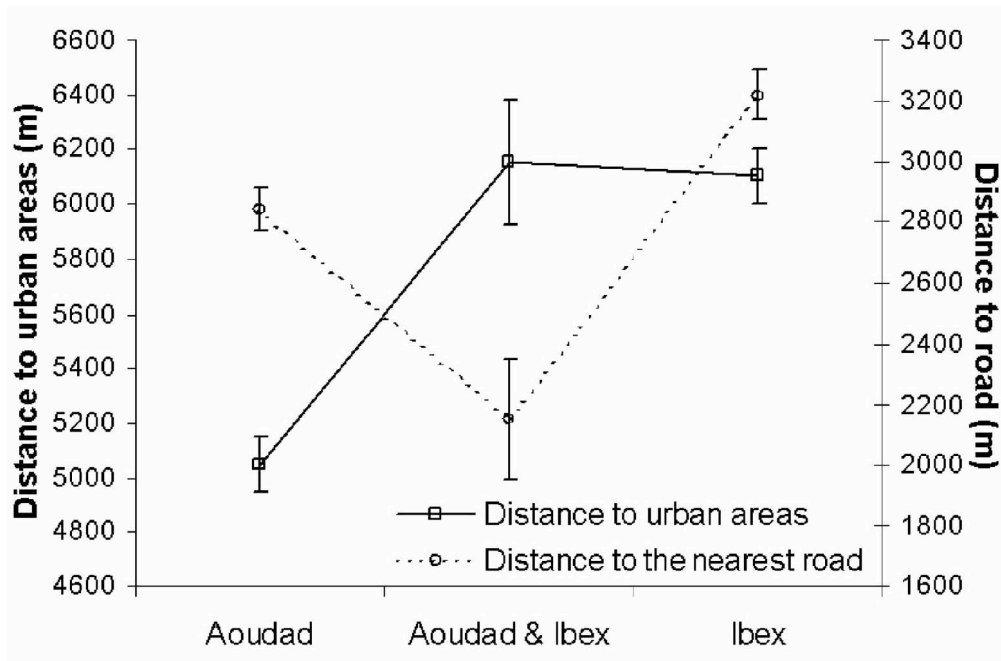


FIGURE 5d