

1 **Prospects for population expansion of the exotic**
2 **aoudad (*Ammotragus lervia*; Bovidae) in the Iberian**
3 **Peninsula: clues from habitat suitability modelling**

4
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26 ABSTRACT

27 We studied the geographic distribution and habitat suitability of an introduced
28 ungulate, the aoudad (*Ammotragus lervia*), that is currently expanding its
29 range in southeastern Iberian Peninsula. We assessed the niche of the
30 species using Ecological Niche Factor Analysis (ENFA) on i) environmental
31 variables (climate and habitat type), and ii) potential aoudad landscape
32 avoidance and human disturbance variables. We compared both niche
33 descriptions to study the impact of human interference on niche selection of
34 the species. ENFA models were calibrated using data on the population
35 grown from the original release location, in Sierra Espuña mountains, and
36 validated using data from another free-ranging population, originated
37 independently in the Alicante province. The habitat suitability model for the
38 purely environmental niche predicts a potential distribution along a SW-NE
39 axis in the study area, following the Cordillera Sub-Bética mountain range,
40 being constrained by low winter precipitation, high altitude, high terrain slope
41 and the presence of forest. In addition to these ecological traits, roads and
42 landscape use restricted the environmental range potentially available for the
43 species. Since the aoudad is a potential competitor of native ungulates and a
44 threat to endemic flora, prospects for its potential dispersion might be of great
45 conservation value.

46

47 Keywords: biological invasions, ENFA, exotic ungulates, habitat suitability
48 modelling, Iberian Peninsula, realized niche

49

50

51 INTRODUCTION

52 Both passive and active human actions have facilitated the transportation of
53 species outside their original distribution range and habitats. Introduction of
54 exotic species has become a serious issue in conservation ecology, resulting
55 in the birth of a new discipline, the study of biological invasions (e.g.
56 Hengeveld 1989; Lodge 1993; Ruesink *et al.* 1995; Mooney & Hobbs 2000;
57 Sax *et al.* 2005). It has been generally assumed that invasive alien species
58 pose one of the greatest threats to biodiversity (Diamond 1989; Wilcove *et al.*
59 1998; but see also Sax & Brown 2000; Brown & Sax 2004; Gurevitch & Padilla
60 2004; Didham *et al.* 2005; Borges *et al.* 2006). In this context, the interest in
61 game species has played a major role in spreading many exotic mammals
62 (e.g., Crosby 1986; Macdonald *et al.* 1988; Jaksic *et al.* 2002; Richardson *et*
63 *al.* 2003). These introductions were often carried out without regard for their
64 effects on the environment, e.g. threats to native species and endemic flora
65 (e.g., Mack & D'Antonio 1998).

66

67 The aoudad, *Ammotragus lervia* Pallas 1777, is a North African caprid
68 successfully introduced as a game species in mountainous desert regions of
69 Texas, New Mexico and California in USA (Ogren 1965), and southern Spain
70 (Cassinello 2000). The aoudad has shown a formidable capacity to establish,
71 spread and extend its distribution (Gray 1985; Cassinello *et al.* 2004), two
72 characteristics typical of biological invasions (Williamson 1996). During the
73 phase of establishment of an invasive species a series of factors that
74 determine success operate in a stochastic manner primarily on mortality and
75 sex ratios. Spread occurs when an established population grows in size and

76 increases in distribution, thereby escaping stochastic extinction effects (Soulé
77 1987).

78

79 Very few individuals are required for introduced ungulate populations to
80 become established (Forsyth & Duncan 2001). The aoudad, which is native to
81 the Saharan Desert mountains where resources are scarce and sparsely
82 distributed, encountered richer habitats where it was introduced in USA and
83 Spain. Increased food availability, along with a scarcity of competitors and
84 predators, allowed high birth rates, and a swift spread of the population (see
85 Wolf *et al.* 1996). Following Colautti & MacIsaac's (2004) terminology, in this
86 region the aoudad is in the process of changing from Stage III (localized and
87 not dominant) to Stage IVa (widespread but not dominant). Here we analyse
88 several environmental and anthropogenic factors (both humanized landscape
89 configuration and human degree or disturbance) that might be influencing the
90 spread of the introduced aoudad population in southeastern Spain. This
91 knowledge may help to establish management procedures to prevent further
92 range expansion, and reduce the potential negative effects of the aoudad on
93 native fauna and flora.

94

95 The relationship between environmental variation (temperature, precipitation,
96 humidity) and the survival of a species can be used to model its potential
97 response to environmental gradients (Austin *et al.* 1990). These descriptions
98 can be used to produce predictive maps of species distribution (see reviews at
99 Guisan & Zimmermann 2000; Ferrier *et al.* 2002; Scott *et al.* 2002; Guisan &
100 Thuiller 2005), as well as to describe the characteristics of the niche of the

101 species (see, e.g., Peterson *et al.* 1999; Robertson *et al.* 2001; Soberón &
102 Peterson 2005; Araújo & Guisan, in press). In conjunction with the use of
103 modern statistics, predictive models have become powerful tools to address
104 relationships between species and their environment, being increasingly
105 common in ecological literature. They gained importance as a research tool
106 on conservation issues (see Araújo & Guisan 2006; Guisan *et al.* 2006),
107 especially to assess the effect of climatic change on the distribution of
108 organisms (e.g., Thuiller *et al.* 2006), to study species niche (Guisan &
109 Zimmermann 2000) and the spatial patterns of biodiversity (e.g., Hortal *et al.*
110 2004). A variety of methods have been used to analyse the ecological niche
111 of the species from data on their presence (see Guisan & Zimmermann 2000;
112 Soberon & Peterson 2005). Among others, there are methods based on
113 presence-only data, such as BIOCLIM (Hortal *et al.* 2005); methods that can
114 handle with presence-only data, among others, such as ENFA, GARP (e.g.,
115 Anderson 2002) or MAXENT (see, e.g., Guisan *et al.* 2006); methods based
116 on both presence and absence (or pseudoabsence) data, such as GLM (Lobo
117 *et al.* 2006) (see a review of the performance of a number of methods at Elith
118 *et al.* 2006). In addition to these methods, others try to develop resource
119 selection methods from data on the abundance of the species (e.g., Olivier &
120 Wotherpoon 2005; Boyce 2006; Meyer & Thuiller 2006).

121

122 The adaptation of niche theory to species distribution modelling is currently
123 under debate (Soberón & Peterson 2005; Araújo & Guisan in press). Since,
124 current terminology is rather ambiguous, and therefore could be misleading
125 for the development of a general framework (Araújo & Guisan in press), a

126 clear definition of the niche concepts used is needed when studying the
127 geographic response of a species. To clarify the two different expressions of
128 the geographic response of the aoudad, we use two different definitions of
129 aoudad's geographic response based on Soberón & Peterson's (2005) and
130 Araújo & Guisan's (2006) recent works: *Environmental Niche* (similar to
131 Soberón & Peterson's Fundamental Niche), which is merely the response of
132 the species to abiotic factors, and *Observed Niche* (following Araújo & Guisan
133 in press), which includes its interactions with the biotic part of the studied
134 systems, in our case landscape configuration and human disturbance. In fact,
135 following Araújo & Guisan (2006), the Environmental Niche could be better
136 described as the Observed Environmental Niche, but we have preferred the
137 term Environmental Niche throughout the text for the sake of clarity.

138

139 Ecological Niche Factor Analysis (ENFA; Hirzel 2001; Hirzel *et al.* 2001, 2002)
140 provides a good tool to describe the geographic expression of the niche of a
141 species. This ordination technique identifies the main gradients that a species
142 responds to in an area. ENFA uses presence-only, presence/absence or
143 abundance data to compute a number of orthogonal factors from several
144 predictors. Since these factors are built to maximize the discrimination
145 between the areas where the species is present, compared to the rest of the
146 region, they might be seen as the most important gradients the species is
147 responding to in the study area (Hirzel *et al.* 2002; see also Chefaoui *et al.*
148 2005). It is then assumed that the response of a species along the principal
149 axes constitutes a description of its observed niche (i.e. the spatial expression
150 of its niche with regard to habitat conditions included within the predictors).

151 ENFA methodology has been successfully used to model the environmental
152 response of other caprids in their native range (*Capra ibex*, Hirzel 2001;
153 *Capra pyrenaica*, Acevedo *et al.* 2006) as well as of reintroduced populations
154 (e.g., *Gypaetus barbatus* in Switzerland, Hirzel *et al.* 2004a). Note that several
155 other approaches are available to build spatial predictions from presence only
156 data (Hortal *et al.* 2005; see a comparison in Elith *et al.* 2006).

157

158 We used ENFA, as well as the derived niche description method proposed by
159 Chefaoui *et al.* (2005; see also Hortal *et al.* 2005), to: a) model the potential
160 distribution of the introduced aoudad in the southeastern Iberian Peninsula; b)
161 study the environmental determinants underlying the aoudad's spatial
162 response (i.e. its environmental niche); and c) evaluate the effect of landscape
163 structure and human disturbance on such response (i.e. its observed niche).

164

165 METHODS

166

167 The Study Area

168 To properly define the geographic niche of a species within a given region, the
169 area used to investigate the species' relationship with environmental variables
170 should encompass extreme conditions present in the region. Thus, to carry
171 out ENFA analyses, we chose a study area that contains both the aoudad
172 population nuclei, and the coastal and mountain environments present in SE
173 Iberian Peninsula. The study area was 340 km wide and 270 km long, and
174 61961 km² corresponded to dry land (UTM 29N geographic reference system;
175 NW corner: 450,000, 4,330,000; SE corner: 790,000; 4,060,000; Figure 1),

176 including the Sierra Nevada mountain range in the SW (rising over 3400
177 m.a.s.l.), Segura coastal basin in the east (with mean altitudes below 20
178 m.a.s.l.), as well as several other mountain ranges and high-altitude plains.
179 The study area comprised a number of sub-areas defined by the vegetation
180 succession series present, which identify plant communities and soil
181 composition (Rivas Martínez 1987). Mediterranean bushlands, oak trees
182 (*Quercus* spp.) and reforestations with *Pinus halepensis* and *P. pinaster*
183 abound in the study area (see details in Cassinello *et al.* 2004).

184

185 The Study Species

186 The aoudad, a North African caprid (subfamily Caprinae), is now a common
187 inhabitant of southeastern Spain having been introduced as a small
188 population (16 males and 20 females) in Sierra Espuña Natural Park in 1970
189 (see details in Cassinello 2000; Cassinello *et al.* 2004). Since then the
190 population has increased rapidly and by 1990 around 2,000 individuals were
191 estimated to inhabit the Sierra Espuña and surroundings mountains (ARMAN
192 1991). A sarcoptic mange episode affected the aoudad population in 1991,
193 during which time the numbers of aoudad decreased by over 90% (González-
194 Candela & León-Vizcaíno 1999). However, the aoudad population recovered
195 very quickly in the area, and is currently estimated to be over 1,000 individuals
196 (González-Candela *et al.* 2001). Apart from the population that originated in
197 the Sierra Espuña, since 1990 another free-ranging population of aoudads
198 has established in the Alicante province, originating from escapes from two
199 game estates in the area (Serrano *et al.* 2002; Cassinello *et al.* 2004).

200

201 Data Origin

202 Distributional data

203 The aoudad presence data come from Cassinello *et al.* (2004), and were
204 obtained by surveys conducted intermittently during 3 years (from 1999 to
205 2001), mainly during August, September and October, the beginning of the
206 mating season, when animal visibility is enhanced (Solbert 1980; Gray &
207 Simpson 1982, 1983; J. Cassinello, pers. obs.).

208

209 In geographically explicit analyses, the spatial resolution (grid cell size)
210 constitutes a key decision for the accuracy and reliability of the results (see
211 Chefaoui *et al.* 2005). In this study, we transformed the available data on
212 aoudad presence (Cassinello *et al.* 2004) from 100 x 100 m UTM grid cells to
213 a 1 x 1 km UTM grid cells. This could create error and scale problems, but
214 previous studies have shown a degree of correlation in species' distribution
215 patterns across narrow ranges of scales (Hartley *et al.* 2004).

216

217 Since free-ranging aoudads in the study area have two independent
218 population nuclei, we used one population to calibrate ENFA models (Sierra
219 Espuña population nucleus, n=60 records), and the other, as an independent
220 set, for the empirical evaluation of the predictive maps (Alicante population
221 nuclei, n=22 records).

222

223 Environmental data

224 Data from an Iberian GIS database compiled and managed by J. M. Lobo, A.
225 Jiménez-Valverde, R. M. Chefaoui and J. Hortal (for details contact JH, or see

226 <http://www.biogeografia.com/> for additional information) was imported and
227 processed into the raster-based Idrisi GIS System (Clark Labs 2001, 2004). A
228 set of GIS maps for the study area was produced, including a number of
229 continuous variables that were thought to determine the aoudad distribution
230 (see below). All of the variables were extracted at a 1-km² resolution,
231 corresponding to the chosen resolution of aoudad presence data. This grain
232 size chosen for the analyses is a consensus between the spatial accuracy of
233 biological data, the mobility of the aoudad, and the large spatial extent used
234 (see another example at Chefaoui *et al.* 2005).

235

236 Many climatic and ecological factors have been used to explain the variations
237 in population abundance and distribution of ungulate species in the Iberian
238 Peninsula (e.g., Acevedo *et al.* 2005, 2006). Here, we selected 42 variables
239 that could act as determinants of current aoudad distribution in SE Iberian
240 Peninsula; 38 accounting for environmental variation (climate, habitat
241 structure, vegetation characteristics and geomorphology), one index of the
242 adequacy of landscape to aoudads, and four for direct human disturbance
243 (Table 1):

244

245 i) Seventeen climate variables were obtained from the monthly values of the
246 digital version of the Spanish National Climate Atlas (provided by the
247 Instituto Nacional de Meteorología; freely available at <http://www.inm.es/>);
248 four accounting for seasonal precipitations (mm), twelve accounting for the
249 mean, maximum and minimum temperature at each season (°C), and one
250 accounting for the annual range of temperatures (°C).

251 ii) Nine geomorphology variables were extracted for each 1 km² pixel from an
252 Iberian Digital Elevation Model of 100 m pixel width extracted from a global
253 DEM (Clark Labs 2000); mean, maximum and minimum altitude (m.a.s.l.),
254 altitude range (meters), mean, maximum and minimum slope (degrees),
255 percentage of area with slopes greater than 30°, and mean aspect
256 diversity, using a 7x7 pixel kernel on a 9-categories reclassified aspect map
257 (see Clark Labs 2001, 2004 for the method; and Chefaoui *et al.* 2005 for an
258 example of the use of this variable).

259 iii) Habitat structure variables were obtained from the 250 m pixel width land
260 use information of the CORINE NATLAN European project (EEA 2000); six
261 variables accounting for land cover (Table 1) were extracted as
262 percentages of each land category per 1 km² pixel, whereas mean land use
263 diversity was obtained with the same technique as aspect diversity.

264 iv) Five variables account for the type of vegetation available, according to its
265 nutritional value; the information on vegetation composition coming from
266 the digital version of the Spanish National Forest Map (Ruiz de la Torre
267 2002) was rasterized to a 100 m pixel width resolution, and reclassified to
268 obtain the surface of each 1 km² pixel occupied by pine trees (*Pinus sp.*),
269 xeric-leaved trees (*e.g.*, *Quercus ilex*, *Juniperus sp.*), humid-leaved trees
270 (*e.g.*, *Quercus pyrenaica*, *Fraxinus sp.*), xeric-leaved bushes (*e.g.*, *Cistus*
271 *sp.*), and humid-leaved bushes (*e.g.*, *Pistacia sp.*).

272 v) A landscape avoidance index was created by combining available land use
273 map and the degree of alteration made by human activity in comparison to
274 natural habitats. This index was based on potential land avoidance by the
275 aoudad rather than landscape preference or use, and could be applicable

276 to most Mediterranean wild ungulates. We have denominated it Wild
277 Ungulates Land Avoidance Index (WULAI). Land use variables receive a
278 score proportional to the rareness of encountering aoudads in these
279 landscapes, i.e., the further to the original habitat the higher the score (up
280 to 100). Thus, in the original CORINE NATLAN map (100 x 100 m. pixel
281 resolution; EEA 2000) we assigned 100 to urban and other constructed
282 areas; 50 to irrigated croplands; 30 to fruit orchards and patchy crops; 20 to
283 vineyards; 10 to dry crops, olive groves, managed grasslands and mosaic
284 of crops and natural vegetation; and finally 0 landscape avoidance to
285 forest, bare rock, bushlands and natural grasslands. WULAI scores were
286 averaged across each square kilometre, ranging from 0 (minimum
287 avoidance, maximum use) to 100 (maximum avoidance, minimum use).

288 vi) Finally, four distance variables account for potential human disturbance
289 (see, e.g., Osborne *et al.* 2001; Schadt *et al.* 2002): the distance to urban
290 areas, roads, and first order roads (highways and national level roads),
291 calculated with the Distance Operator tool of Idrisi 32 software. In addition,
292 the distance to the Sierra Espuña population nucleus (DSE), i.e. the
293 original release location (Cassinello 2000), was used in several analyses,
294 to account for the recent dispersion of the species (see Acevedo *et al.*
295 2005).

296

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

299

300 Statistical Analyses

301 Niche modelling

302 ENFA analyses were conducted using BioMapper (Hirzel *et al.* 2004b; freely
303 available at <http://www.unil.ch/biomapper/>). This software uses the ENFA
304 methodology to produce predictive maps of habitat suitability (i.e., potential
305 distribution) from GIS information (see applications at Hirzel 2001; Hirzel *et al.*
306 2001, 2002; Hirzel & Arlettaz 2003; Gallego *et al.* 2004; Hirzel *et al.* 2004a;
307 Chefaoui *et al.* 2005; Hortal *et al.* 2005; Acevedo *et al.* 2006). We developed
308 two different ENFA analyses, one to describe the Environmental Niche
309 (herein, environmental niche model) using the variables in the first four of the
310 above-mentioned groups and using all variables present in the six groups
311 above to describe the likely Observed Niche. These analyses, and the
312 resulting habitat suitability maps, are produced in two steps:

313

314 1. ENFA was used to characterize the response of the aoudad to the main
315 variations of the used predictors in the study area. ENFA analysis
316 identifies two key components of species environmental niches:
317 *marginality* and *tolerance*, that is, how rare are the conditions selected by
318 the species within the context of the studied region, and how tolerant is the
319 species to modifications of these conditions produced by secondary
320 gradients (see Hirzel 2001 and Hirzel *et al.* 2002). Computationally,
321 *marginality* is a measure of the distance between the central trend of the
322 species environmental selection and the mean environmental conditions of
323 the region in the most important environmental gradient (i.e. the higher the
324 marginality, the more extreme the conditions with regard to the area
325 studied), and *tolerance* measures the range width with regard to all

326 gradients present in the study area (see below), that is, how the species
327 tolerates environmental variations (varying from 0 to 1; i.e. the closer to 0,
328 the more specialist the species). In this context, the *specialisation* of a
329 species is defined as the inverse of its *tolerance*. In our study, aoudad
330 presence data was used to identify a number of orthogonal factors in the
331 predictors, accounting for the maximum differentiation between mean
332 conditions for the study area, and mean conditions where the aoudad was
333 found. The first factor (Marginality Factor) accounts for the marginality of
334 the species, whereas the other factors (Specialization Factors) account for
335 the species' response to other secondary environmental gradients.

336

337 2. Once ENFA factors are computed, habitat suitability scores for each pixel
338 are calculated and mapped in accordance to the responses of the species
339 to each factor. Partial suitability scores are computed for each factor as the
340 percent distance to the median scores of observed presences, and Habitat
341 Suitability is obtained as a weighted average of these partial suitabilities,
342 according to the variability explained by each factor. These scores are
343 then mapped using the ENFA factor maps (Hirzel *et al.* 2002).

344

345 Model validation and accuracy

346 Two measures of how the resulting suitability model explains the observed
347 data were used: *Explained Information*, which accounts for the total variability
348 of the species distribution explained by the model, and *Explained*
349 *Specialisation*, which accounts for additional variability in the Marginality and

350 Specialisation Factors that is not included in the Explained Information
351 measure (Hirzel *et al.* 2004b).

352

353 Since both Explained Information and Explained Specialisation measures are
354 derived from the observed data, no assessment of how the model can be
355 extrapolated to the rest of the region is made. However, before using the
356 ENFA results or habitat suitability maps (HSMs), we needed to evaluate their
357 accuracy in describing the actual spatial response of the aoudad. A good way
358 to assess the real accuracy of any spatial prediction is to use independent
359 data to determine how model predictions perform outside the boundaries of
360 the data used in developing the ENFA. We used two different validation
361 strategies based in such assumption to determine a) the predictive power of
362 the ENFA model within the range of the population used to calibrate it (*within-*
363 *data validation*; i.e. the accuracy to describe the distribution of the Sierra
364 Espuña population), and b) its ability to predict the geographic responses of
365 other aoudad populations (*external validation*; i.e., placed outside of the
366 bounds of the range used to develop the model). While the former measures
367 how the model fit into the data, the latter gives a measure of the generality of
368 the niche description of the species. Within-data validation was made through
369 the Jackknife cross validation procedure implemented in Biomapper 3.0
370 software (Hirzel *et al.* 2000; Boyce *et al.* 2002). Briefly, the data originally
371 used for the ENFA analysis is partitioned in several spatially-aggregated
372 groups; each group is extracted once from the original dataset, the models is
373 recalibrated according to the new dataset, and the prediction results are
374 compared to the group of data plots extracted; this procedure is repeated as

375 much times as groups defined (see Boyce *et al.* 2002 for details). Model
376 accuracy is measured as the agreement between independent and calibration
377 data, using Spearman correlations. For the external validation, we used the
378 presence data from Alicante population nuclei; the predictions of the Sierra
379 Espuña model are compared with the presences in Alicante, and the degree
380 of agreement between predictions and independent data is measured using
381 Spearman correlations. This way, a truly empirical evaluation of the generality
382 of the ENFA model in describing aoudad distribution is performed using an
383 independent population.

384

385 Niche analysis

386 Following Chefaoui *et al.* (2005), we assume that the variation of habitat
387 suitability scores across environmental gradients provides a description of the
388 shape of the species' response to such gradients. To obtain a graphic
389 representation of this response, we divided the Marginality Factor scores in 20
390 homogeneous intervals, and the average habitat suitability scores at each
391 interval were represented for each habitat model (see Chefaoui *et al.* 2005;
392 Hortal *et al.* 2005).

393

394 To evaluate the relationship between the habitat suitability maps obtained in
395 the two models, they were reclassified to obtain suitable areas (HS scores
396 between 50-75) and highly suitable areas (HS scores >75) for each model,
397 and then, we analysed the surface occupied by them.

398

399 RESULTS

400

401 **Description of the Environmental Niche**

402 Thirty-one environmental variables were used for the ENFA analysis, being
403 reduced to four factors that explained 77.5% of the variance (Table 2). The
404 marginality factor (first axis) explained a lowest percentage (0.73%) than
405 specialization. The specialization factors (2, 3 and 4) explained 38.35%,
406 26.61%, and 11.81%, respectively. The maximum and mean slopes and
407 altitude range were, in that order, the variables with the highest marginality
408 coefficients, i.e., the scores of these variables in the presence cells differed
409 from their mean values in the study area (Table 2). The coefficients for these
410 variables were positive, which showed that aoudads were associated to rough
411 and craggy areas. Maximum and minimum altitude had the highest
412 coefficients of the specialization factors, so that the aoudad distribution was
413 specially restricted by these variables. The marginality factor coefficient
414 obtained for the aoudad was 1.29, which showed that there was an important
415 separation of the species from the central part of the main environmental
416 gradient shaping the aoudad distribution in the study area. In contrast, the
417 global tolerance value was 0.31, which suggests a relatively small
418 specialization (i.e. reduced tolerance to environments far from its optimum) of
419 the species in this region.

420

421 The HSM of the environmental niche model (Figure 2a) showed a high
422 probability of appearance of the aoudad in the centre of the study area,
423 following a southwest – northeast axis. Jackknife validations indicate that such
424 potential map is reliable (*within-data validation*; mean *Spearman R* = 0.92),

425 showing also a high predictive capacity when is extrapolated to the area
426 where Alicante population is present to perform an empirical validation
427 (*external validation*; mean *Spearman R* = 0.60).

428

429 **Prospects on the observed niche**

430 Thirty-seven environmental, landscape and human disturbance variables were
431 included in the ENFA to develop the observed niche model (see Table 3).
432 These variables were reduced to four factors explaining 75.6 % of the
433 variance (Table 3). Such reduction in explained variability from the
434 environmental niche model comes from the higher complexity in the
435 description of the region, provided by the new variables, which might be
436 uncorrelated with the environmental ones used in the other model. Since
437 ENFA is an ordination technique, based in the differences between the central
438 trends of species and the whole region in the hyperspace formed by the
439 descriptor variables used, the higher the number of uncorrelated variables, the
440 more complex the description of variability, and thus the smaller the variability
441 explained when these variables are incorporated to the analysis.

442

443 The marginality factor explained the lowest percentage (0.17%) of
444 specialization in this model. The specialization factors (2, 3 and 4) explained
445 34.39%, 22.60%, and 18.43%, respectively. The proximity to the original
446 release location, followed by the maximum and mean slopes, and the altitude
447 range were the variables with higher marginality coefficients, i.e., the scores of
448 these variables in the presence cells differed from their mean values in the
449 study area (Table 3). As in the environmental niche model, this result

450 indicates that aoudads show a preference for using rough and craggy areas.
451 Similarly, maximum and minimum altitude had the highest coefficients
452 amongst the specialization factors. The marginality coefficient obtained was
453 1.55, demonstrating and even higher separation of the species from the
454 central part of the environmental gradient. The global tolerance value was
455 0.27, which suggests that the aoudad is relatively specialized in this region of
456 Southern Spain. The HSM (Figure 2b) showed a high probability of
457 appearance of the aoudad in the centre of the study area following a
458 southwest – northeast axis, but this distribution was more patchily than in the
459 environmental niche model. Again, Jackknife validation indicates that the
460 predictive map of aoudad's observed niche is reliable (*within-data validation*;
461 mean *Spearman R* = 0.92), also showing a high predictive capacity when is
462 validated with the Alicante population (*external validation*; mean *Spearman R*
463 = 0.61).

464

465 **Changes in Habitat Suitability**

466 The variation of mean habitat suitability scores of both environmental and
467 observed niche models along the gradient identified by the marginality factors
468 can be seen in Figure 3. Both models showed similar environmental
469 adaptations; however, the observed niche model was more restricted and had
470 lower habitat suitability values than the environmental niche model.

471

472 The suitable areas (HS>50) in the environmental model covered 7.78% of the
473 study area (4823 km²) 34.77% of this area was suitable, and 12.32% was
474 highly suitable (HS>75) in the observed niche model (1677 and 594 km²,

475 respectively). On the other hand, the highly suitable areas in the introduced
476 model covered 1.39% of the study area (861 km²), being 76.07% suitable and
477 36.01% highly suitable in the observed niche model (655 and 310 km²,
478 respectively).

479

480 DISCUSSION

481 We performed an analysis of the factors determining habitat suitability (both in
482 the environmental and observed niches) in the introduced aoudad population
483 in southeastern Spain. The species currently occupies several mountainous
484 areas of the Cordillera Sub-Bética mountain range. Two main zones can be
485 distinguished from the presence data, the one originating from the first release
486 in Sierra Espuña Natural Park in 1970, which comprises a wide-ranging
487 population; and a second one, further north, originating from escapes from a
488 couple of hunting estates in Alicante (see Cassinello *et al.* 2004). Since data
489 on habitat suitability in its native range in North Africa is not available, we
490 have used nuclei from one of these zones (Alicante) as an independent test to
491 determine the reliability of the geographic expression of both niche
492 descriptions calculated from the other (Sierra Espuña nucleus).

493

494 **Habitat suitability of the aoudad in Spain**

495 According to our characterization of its environmental niche (see Figure 2a),
496 the aoudad selected areas characterized by a low winter precipitation regime,
497 high altitudes and terrain slopes as well as with the presence of forest lands.
498 These results agree with the habitat selection expected for a mountain
499 ungulate such as the aoudad, where rocky and precipitous areas abound,

500 from the sea level up to the extent of snow-free altitudes (see Shackleton
501 1997). This niche characterization for the aoudad is highly reliable, as our
502 maps showed a high predictive power when validated using the second
503 population in Alicante. Therefore, we suggest a high potentiality for this exotic
504 ungulate to conquer new areas around its current distribution range in
505 southern Spain.

506

507 The description of aoudad's current habitat suitability varies when landscape
508 avoidance and anthropogenic variables are included in the analysis to
509 develop the observed niche model. When landscape avoidance and human
510 disturbance effects are included in the ENFA model, it appeared that the
511 aoudad was associated with less mountainous areas, with higher
512 temperatures, forest and dryland crop areas (see Table 3). Human land use
513 data will also be more patchily distributed than environmental parameters,
514 therefore contributing to a more patchy distribution. This resulted in a
515 narrower, more patchy suitability map (Figure 2b), due to the landscape and
516 human disturbance constraints added to ENFA calculations. The high
517 coefficients obtained for the distance to the original release locality indicate
518 that current aoudad distribution is clearly shaped by the location of the initial
519 release. In addition, the observed niche was narrower than the environmental
520 niche, and was also placed nearer to one of the extremes of the marginality
521 factor axis (see Figure 3).

522

523 There was an important relationship between habitat suitability for the aoudad
524 and the intensity of human disturbance; humanized landscapes with

525 moderate-to-high WULAI scores appear not to be suitable for the species. If
526 WULAI scores are plotted against HSM scores, there is a progressive
527 diminution of the maximum habitat suitability for the aoudad as its landscape
528 avoidance increases, reaching 0 above intermediate levels of disturbance
529 (Figure 4). However, the current analysis does not allow us to separate the
530 effects of different types of land use on the aoudad range expansion. These
531 single effects could be even stronger than that measured by our landscape
532 use index, so the exact effects of landscape modification by humans on
533 aoudad dispersion remain untested. As an example, distance to roads
534 presents more explanatory power than WULAI (see Table 3), an effect of
535 using a complex mixture of land use categories (EEA 2000) within a single
536 index (see Methods). Thus, further analyses are needed to unravel the
537 individual effects of these human impacts on aoudad habitat selection.

538

539 **Conservation concerns**

540

541 Most ungulate species in Spain are currently expanding in range (e.g., the
542 Iberian ibex; Pérez *et al.* 2002; Acevedo *et al.* 2006). Some species are
543 occupying new habitats that may have not supported large herbivores for a
544 long time; consequently, local plant species may have evolved without
545 recovering high grazing pressure, so that they may not be tolerant to a more
546 intensive herbivore presence. Furthermore, the increasing presence of
547 allochthonous ungulates, such as the European mouflon (*Ovis aries musimon*)
548 and the aoudad, make things worse as they may particularly threaten local
549 plant species (Rodríguez-Piñero & Rodríguez-Luengo 1992). It has been seen

550 that exotic species can substantially influence the composition and structure
551 of plant and animal communities, alter nutrient and water cycles, and change
552 disturbance regimes (e.g. Parker *et al.* 1999; Mack *et al.* 2000; Holmgren, M.
553 2002).

554

555 This work shows that the potentially high expansion capacity of the exotic
556 aoudad in the south of Spain is resulting from the similarity of the host habitat
557 to that of the region of origin, North Africa. In Spain, the aoudad has not yet
558 reached suitable areas located at much higher altitudes (i.e., Sierra Nevada
559 mountain range), which is the native land of the Iberian ibex. We hypothesize
560 that if the aoudad reaches these areas, potential competition may arise with
561 the ibex, given the biological similarities of these caprid species. In addition,
562 the Sierra Nevada (a Spanish National Park) is known to be an important
563 hotspot for Iberian plants, both in terms of richness and endemism (see
564 Castro Parga *et al.* 1996; Lobo *et al.* 2001). Therefore, if the aoudad reached
565 the region, many endangered endemic plants could be at a higher risk. Given
566 this potential threat, it is important to develop strategies to prevent the aoudad
567 dispersing through the suitable areas located in the western limits of its
568 current distribution (see Figure 2). Our analysis has identified several
569 constraints to the dispersal of the aoudad associated with the intensity of
570 human disturbance and land use. This suggests that further investigations on
571 the individual effects (e.g., management of cultivated landscapes, grazing
572 intensities and competition with livestock) could help to design land use
573 strategies that are able to create a landscape matrix which offers a high
574 frictional effect on aoudad dispersal.

575

576

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595

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830

831

832 FIGURE CAPTIONS

833 Figure 1.- Location of the study area in southeastern Spain. Province
834 boundaries are shown. The records of the aoudad presence are depicted. The
835 southernmost group (circles) corresponds to the dispersion of the Sierra
836 Espuña nucleus, whereas the eastern ones (squares) are the nuclei in the
837 Alicante province. The geographic coordinate system shown is the UTM.

838

839 Figure 2.- Habitat Suitability Maps for a) the environmental niche model, and
840 b) the observed niche model. The scale on the right shows habitat suitability
841 values (0 = low suitability; 100 = high suitability). The geographic coordinate
842 system shown is the UTM.

843

844 Figure 3.- Variation of the mean habitat suitability scores along the gradient
845 defined by the marginality factor. As the marginality factors for both models
846 were highly correlated, we plotted them against the one from the
847 environmental niche model. The marginality factor was divided into 20
848 intervals, and mean values per interval are shown.

849

850 Figure 4.- Relationship between the habitat suitability for the aoudad, and the
851 Wild Ungulates Land Avoidance Index (WULAI) from the observed niche
852 analysis (see Figure 2b).

- Variables used in the analyses (including abbreviations). See text for details and data sources.

	<i>Geomorphology</i>	<i>Vegetation</i>
Precipitation in winter (mm)	Alt Mean altitude (m)	VHTr Humid-leave tree area (%)
Precipitation in autumn (mm)	AltMx Maximum altitude (m)	VXTr Xeric-leave tree area (%)
Precipitation in spring (mm)	AltMn Minimum altitude (m)	VHBsh Humid-leave bush area (%)
Precipitation in summer (mm)	AltRn Altitude range (m)	VXBsh Xeric-leave bush area (%)
Mean temperature in winter (°C)	Slp Mean slope (°)	VPTr Pine tree area (%)
Mean temperature in autumn (°C)	SlpMx Maximum slope (°)	
Mean temperature in spring (°C)	SlpMn Minimum slope (°)	
Mean temperature in summer (°C)	Slp30 Area with slope higher than 30° (%)	
Maximum temperature in winter (°C)	AspDv Aspect diversity (H' index)	
Maximum temperature in autumn (°C)		
Maximum temperature in spring (°C)	<i>Habitat structure</i>	<i>Landscape use</i>
Maximum temperature in summer (°C)	HFr Forest area (%)	WULAI Landscape Avoidance Index
Minimum temperature in winter (°C)	HCFr Coniferous forest area (%)	
Minimum temperature in autumn (°C)	HBFr Broadleaved forest area (%)	<i>Human disturbance</i>
Minimum temperature in spring (°C)	HBsh Bushland area (%)	DUr Distance to urban areas (km)
Minimum temperature in summer (°C)	HGrS Grassland area (%)	DRd Distance to the nearest road (l
Annual range of temperatures (°C)	HDC Dryland crops (%)	DHw Distance to the nearest highw
	LUDV Land use diversity (H' index)	DSE Distance to Sierra Espuña nuc

Table 2. Coefficients of the variables used in the environmental niche ENFA.

Variable codes as in Table 1.

Variable	Marginality	Factor 2	Factor 3	Factor 4
1 HFr	0.324	0.000	0.000	0.000
2 HBsh	0.023	0.000	0.000	0.000
3 VXBsh	0.131	0.000	0.000	0.000
4 VPTr	0.205	0.000	0.000	0.000
5 HDc	-0.125	0.000	0.000	0.000
6 AltMx	0.231	0.702	0.707	0.731
7 AltMn	0.017	-0.636	-0.64	-0.662
8 AspDv	0.077	0.000	0.000	0.000
9 LUDv	-0.023	0.000	0.000	0.000
10 Alt	0.184	0.000	0.000	0.000
11 SlpMx	0.438	0.000	0.000	0.000
12 Slp	0.386	0.000	0.000	0.000
13 SlpMn	0.155	0.000	0.000	0.000
14 PW	-0.142	0.000	0.000	0.000
15 PF	-0.012	0.000	0.000	0.000
16 PSp	-0.086	0.000	0.000	0.000
17 PSm	-0.034	0.000	0.000	0.000
18 AltRn	0.361	-0.149	-0.15	-0.155
19 TRn	-0.052	0.128	0.116	0.025
20 TMxW	-0.016	0.000	0.000	0.000
21 TMxF	-0.083	0.000	0.000	0.000
22 TMxSp	-0.043	0.000	0.000	0.000
23 TMxSm	-0.101	0.000	0.000	0.000
24 TW	-0.122	0.206	0.187	0.04
25 TF	-0.171	0.000	0.000	0.000
26 TSp	-0.144	0.000	0.000	0.000
27 TSm	-0.213	-0.15	-0.136	-0.029
28 TMnW	-0.081	0.000	0.000	0.000
29 TMnF	-0.095	0.000	0.000	0.000
30 TMnSp	-0.095	0.000	0.000	0.000
31 TMnSm	-0.124	0.000	0.000	0.000

Table 3. Coefficients of the variables used in the observed niche. Variable codes as in Table 1. DSE refers to the distance to the original release location in Sierra Espuña.

Variable	Marginality	Factor 2	Factor 3	Factor 4
1 HFr	0.270	0.000	0.000	0.000
2 HBsh	0.019	0.000	0.000	0.000
3 VXBsh	0.109	0.000	0.000	0.000
4 VPTr	0.171	0.000	0.000	0.000
5 HDc	-0.104	0.000	0.000	0.000
6 AltMx	0.192	0.668	0.625	-0.694
7 AltMn	0.142	-0.605	-0.566	0.628
8 AspDv	0.064	0.000	0.000	0.000
9 LUDv	-0.019	0.000	0.000	0.000
10 Alt	0.153	0.000	0.000	0.000
11 SlpMx	0.364	0.000	0.000	0.000
12 Slp	0.321	0.000	0.000	0.000
13 SlpMn	0.129	0.000	0.000	0.000
14 PW	-0.118	0.000	0.000	0.000
15 PF	-0.010	0.000	0.000	0.000
16 PSp	-0.072	0.000	0.000	0.000
17 PSm	-0.029	0.000	0.000	0.000
18 AltRn	0.300	-0.141	-0.132	0.147
19 TRn	-0.043	0.184	-0.234	-0.144
20 TMxW	-0.013	0.000	0.000	0.000
21 TMxF	-0.069	0.000	0.000	0.000
22 TMxSp	-0.036	0.000	0.000	0.000
23 TMxSm	-0.084	0.000	0.000	0.000
24 TW	-0.101	0.296	-0.377	-0.232
25 TF	-0.143	0.000	0.000	0.000
26 TSp	-0.120	0.000	0.000	0.000
27 TSm	-0.177	-0.214	0.273	0.168
28 TMnW	-0.067	0.000	0.000	0.000
29 TMnF	-0.079	0.000	0.000	0.000
30 TMnSp	-0.079	0.000	0.000	0.000
31 TMnSm	-0.103	0.000	0.000	0.000
32 DSE	-0.473	0.000	0.000	0.000
33 DHw	0.107	0.000	0.000	0.000
34 DRd	0.184	0.000	0.000	0.000
35 DUr	0.188	0.000	0.000	0.000
36 WULAI	-0.058	0.000	0.000	0.000