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Human-induced range expansion of wild ungulates causes niche overlap between previously allopatric species: red deer and Iberian ibex in mountainous regions of southern Spain

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Game species exploitation usually causes an increase in their distribution, further from their own dispersal potential, but we know too little about the ecological effects that these human-induced expansions may produce. The realized niche of the red deer was analyzed by means of habitat suitability modelling in the present study. Two populations inhabiting different geographic areas have been distinguished according to their origin, one is native to the study area and the other was translocated as a result of human hunting interests. Translocated red deer showed strong distributional overlap with the native Iberian ibex. However, a comparative analysis of the potential distribution of native red deer and Iberian ibex populations did not yield a significant niche overlap. Thus, we conclude that the observed niche overlap between the Iberian ibex and the red deer in the study area would not have taken place without human intervention. We discuss these results in the light of biological invasions and native species translocation programmes, and conclude that human-induced range expansion of native species should be regarded as a specific case of invasive species.

Introduction

The present expansion of both native and non-native large herbivores in Europe has been well documented (e.g. Gortázar *et al.* 2000, Pérez *et al.* 2002, Acevedo *et al.* 2005, Ward 2005, Acevedo *et al.* 2007a). There may be indirect causes for these expansions, such as land use changes (e.g., agricultural abandonment, Acevedo *et al.* 2006), or the creation of protected areas and conservation reserves (e.g. Alados 1997). But there are certain policies that are promoting range expansion in wild ungulates: an increased control of game exploitation and poaching (*see* Acevedo *et al.* 2006), and translocations and introductions of wild ungulate populations (*see* Falk-Petersen *et al.* 2006) driven by hunting interests (Gortázar *et al.* 2000, Whittaker *et al.* 2001, Cassinello *et* *al*. 2006). Unfortunately, we are not aware of the effects that these ungulate expansions may exert on the host ecosystems (*see* Acevedo *et al*. 2007a).

The concept of native species is not based on ecological assumptions, but rather on whether the presence of a species in a given area is natural, and not caused by human intervention; whereas a non-native species is one occupying an area outside its natural past or present range and dispersal potential (Falk-Petersen *et al*. 2006). According to niche theory, a given species is optimally present in any habitat offering the fundamental requirements for it to survive, grow and reproduce, i.e., the fundamental niche (Hutchinson 1957). However, in the context of species competition, the niche actually occupied is usually smaller, and it is called the realized niche (*ibid*.).

The use of niche theory for species distribution modelling has been widely studied and is currently under debate (Pulliam 2000, Araújo & Guisan 2006). However, current terminology is ambiguous, and could be misleading for the development of a general framework (Araújo & Guisan 2006), so that a clear definition of niche concepts is needed when studying the geographic response of a species. To clarify the expression of the geographic response of the study species, we followed Araújo and Guisan's (2006) recent work, where interactions between biotic traits and climate, landscape configuration and human disturbance are taken into account (*see* also Cassinello *et al*. 2006, Acevedo *et al*. 2007a).

A non-native species may successfully inhabit an area provided its realized niche is accomplished. If this establishment is coupled with an expansion of its range, then it is regarded as an invasive species (Falk-Petersen *et al*. 2006). The degree of disturbance caused by invasive species on the host ecosystem depends on their ability to establish, reproduce and spread (Bright & Smithson 2001), i.e., on becoming "naturalized" (Falk-Petersen *et al*. 2006), which, in turn, is affected by the presence of predators, competitors, parasites and/or diseases (Hengeveld 1989).

Spatially explicit models are being increasingly applied to predict species' potential distributions and to derive habitat suitability maps (e.g. Guisan & Zimmermann 2000). Most models are empirically deduced, relating observed patterns of occupancy to environmental parameters (Corsi *et al*. 2000). Despite their wide application, such models also have a series of drawbacks (Wiens 2002). One rarely considered point is that spatial models may fail to depict the species' distribution area because past anthropogenic disturbances or other historical factors may have confounded the underlying patterns of habitat use (Baumann *et al*. 2005).

The Iberian red deer (*Cervus elaphus hispanicus* Hilzheimer 1909) is one of twelve red deer subspecies currently recognized, which were originally distributed throughout Eurasia and the Maghreb (Geist 1998). During the last glacial period (the Würm glaciation), which ended 10 000 years bp, large Eurasian herbivores were relegated to southern and more temperate areas. Since then, a natural process of recolonization occurred, which was historically accelerated by human intervention due to an increasing interest in game species and their husbandry (e.g. Anderson 1985). Thus, deer were progressively reintroduced in the whole continent, including the Iberian Peninsula (e.g. Braza *et al*. 1989, Soriguer *et al*. 1994; Fig. 1). Currently, red deer are widely distributed in the Iberian Peninsula, except for the northwestern corner and the east coast (Carranza 2002; Fig. 1). This impressive human-mediated expansion has promoted their presence in areas traditionally within the natural range distribution of other large herbivores, such as the Iberian ibex, *Capra pyrenaica* (*see* Fig. 2), a typical mountain ungulate.

The aim of the present study was to determine, by means of a habitat suitability modelling approach, whether the current niche overlap between the red deer and the Iberian ibex could be the result of a natural colonization process of the former from their original native areas, without human intervention.

Material and methods

The study area

To accurately define the realized niche (Araújo & Guisan 2006) of a species within a given region, the area used to investigate the species'

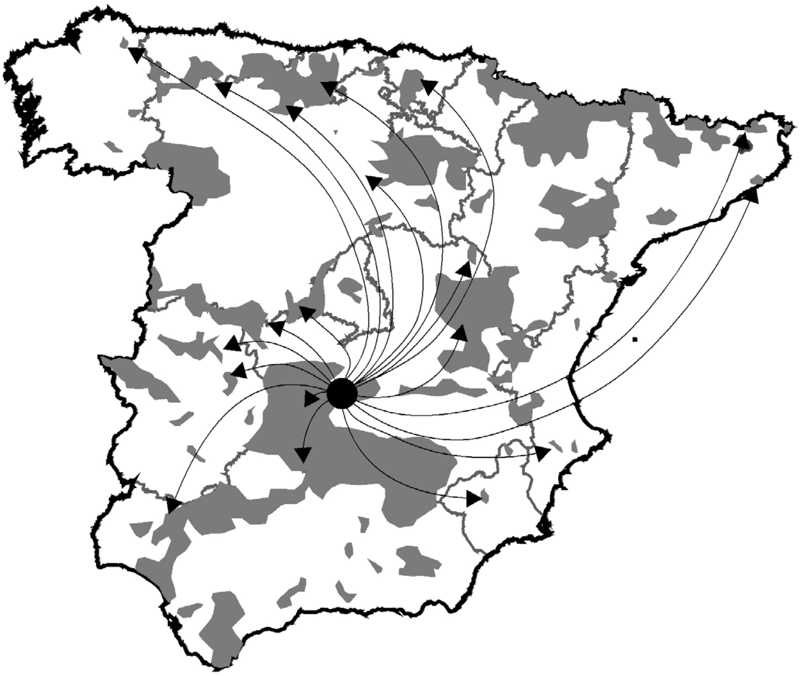

Fig. 1. Map of Spain showing Montes de Toledo location (black dot), a native red deer area, and the direction (arrows) where the species was translocated to (Centro Quintos de Mora, 1970–1990, unpubl. report). Current red deer distribution is depicted in grey (adapted from Carranza 2002).

relationship with environmental variables should include extreme conditions present in the region (e.g. Austin 2002). For this reason, we chose a study area that includes a strong environmental gradient and settled red deer and ibex populations.

The study area is located in the SE of the Iberian Peninsula. It is 340 km wide and 270 km long, where 61 961 km^2 corresponded to dry land (UTM 29N geographic reference system; NW corner: 450 000, 4 330 000; SE corner: 790 000; 4 060 000; Fig. 2), including the Sierra Nevada mountain range in the SW (rising over 3400 m a.s.l.), the Segura river basin in the east (with mean altitudes below 20 m a.s.l.), as well as several other mountain ranges and high-altitude plains (*see* more details in Cassinello *et al*. 2006, Acevedo *et al*. 2007a).

Distribution data

Red deer distributional data were obtained from literature sources (e.g. Braza *et al*. 1989), but mainly from the *Atlas de los Mamíferos Terrestres de España* (Carranza 2002), a volume widely used in biogeographical studies (e.g. Barbosa *et al*. 2003, Real *et al*. 2008). The presence of red deer in areas with scarce information was established by means of field observations carried out in September 2003, following a methodology similar to Acevedo *et al*. (2007a). The autochthonous or native population nucleus refers to deer presence in historical times, without human intervention; whereas the allochthonous nucleus stems from human translocations according to Braza *et al*. (1989) (*see* Fig. 2). We transformed the available data of deer presence from several scales to 1 × 1 km UTM grid cells, which is the most convenient scale given the available local cartographic and climatic information (*see* Acevedo *et al*. 2007a, 2007b). Using this information, we built a habitat suitability model for the native red deer population (present in 258 grid cells, Braza *et al*. 1989).

Iberian ibex distributional data were the same as those used in a previous study (Acevedo *et al*. 2007b), and were mainly extracted from Pérez *et al*. (2002), and Acevedo and Cassinello (2009) where the Iberian ibex distribution was recently updated. All data were transformed to the same scale used for red deer presence, i.e. 1 × 1 km UTM grid cells. We considered 199 grid cells with ibex presence for analyses (*see* Fig. 2).

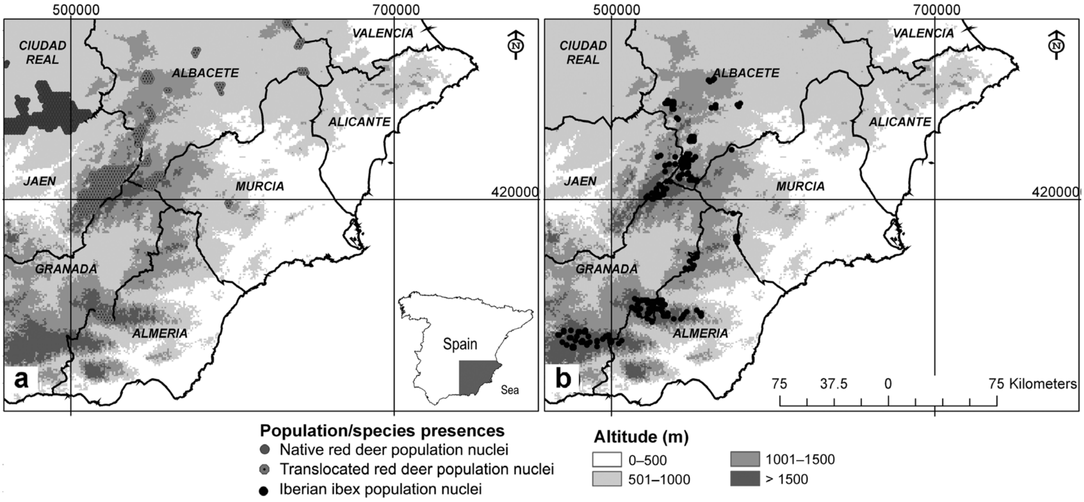

Fig. 2. Distribution of ungulate populations in the study area: (**a**) native and translocated red deer presence (Braza *et al.* 1989); (**b**) Iberian ibex presence (Pérez *et al.* 2002, Acevedo *et al.* 2007b).

Environmental data

Many factors have been described as important for the abundance and distribution of ungulate species in the Iberian Peninsula (e.g. Acevedo *et al*. 2005, 2006, 2007a, 2007b, Real *et al*. 2008). We selected 17 variables that could act as constraints for red deer and Iberian ibex distributions in the SE Iberian Peninsula (Table 1); these variables cover the range of climatic and ecological traits present in the study region.

All climate variables are courtesy of the

Table 1. Variables used in the analyses (including abbreviations), and results of each univariate model (GLM binomial with logarithmic link function). The Wald statistics and significance (*** $p < 0.001$, ns = non-significant) are shown.

Variables (unit)	Codes	Red deer	Iberian ibex
Climate			
Winter rainfall (mm)	PW	76.88***	265.91***
Summer rainfall (mm)	PSm	0.11 ns	170.81***
Mean summer temperature (°C)	TSm	127.06***	256.73***
Annual range of temperatures (°C)	TRn	163.23***	16.69***
Geomorphology			
Maximum altitude (m)	AltMx	3.09 ns	245.84***
Altitude range (m)	AltRn	14.99***	238.87***
Mean slope (degrees)	Slp	9.02***	256.21***
Maximum slope (degrees)	SlpMx	3.13 ns	223.60***
Habitat structure			
Forest area (%)	HFr	2.52 ns	279.40***
Distance to coniferous forest area (m)	DCFr	22.16***	109.64***
Distance to broadleaved forest area (m)	DBFr	3.34 ns	55.98***
Bushland area (%)	HBsh	56.66***	1.94 ns
Xeric-leave bush area (%)	HXBsh	3.56 ns	11.10***
Distance to humid-leave bush area (m)	DHBsh	18.49***	12.12***
Human presure			
Distance to urban areas (m)	DUr	127.22***	187.84***
Distance to the nearest road (m)	DRd	152.21***	163.83***
Landscape Avoidance Index	WULAI	82.80***	114.26***

Spanish *Instituto Nacional de Meteorología* (http://www.inm.es/). Geomorphology variables were obtained from an Iberian Digital Elevation Model of 100-m pixel width. Habitat structure variables were obtained from the 250-m pixel width land use information of the CORINE NATLAN European project (EEA 2000). Finally, we obtained three variables representing human activity in the study. First, distance to urban areas (i.e. to urban and industrial categories following the CORINE land use map), and distance to the nearest road (including motorways, national and local roads, extracted from the Spanish National Digital Atlas, courtesy of the *Instituto Geográfico Nacional*, http://www.ign.es/). For more details about the data sources, *see* Cassinello *et al*. (2006) and Acevedo *et al*. (2007a).

In addition, we used the Wild Ungulate Land Avoidance Index (WULAI), an index based on the degree of landscape alteration by human activities, and the resultant potential avoidance of that area by wild ungulates (*see* details in Cassinello *et al*. 2006).

We evaluated the relationships between the response variable and the predictors considering their polynomial functions (linear, quadratic and/or cubic) in order to include possible curvilinear relationships (Austin *et al*. 1990). An initial exploratory analysis of the different predictors showed that all response curves were mainly of a $y = x + x^2$ type, providing a basis for ignoring polynomial terms higher than quadratic (Engler *et al*. 2004). All variables were handled and processed using the Idrisi 32 software (Clark Labs 2004). All predictors were standardized to 0 mean and 1 standard deviation to eliminate the effect of different measurement scales.

Statistical analyses

The two statistical methods used to model the study species were: (i) Ecological Niche Factor Analyses (ENFA), and (ii) Generalized Linear Models (GLM). In this study, ENFA was only used to obtain pseudo-absences from which distribution models were built using GLMs (Engler *et al*. 2004, Jiménez-Valverde *et al*. 2007, 2008). The use of ENFA-weighted pseudo-absences is a way to improve quality, increasing the accuracy of GLM-based potential distribution maps (Engler *et al*. 2004).

ENFA (Hirzel *et al*. 2002) is a method based on the comparison between the environmental niche of a species and environmental characteristics of the entire study area (stored as GIS layers). Hence, ENFA only needs a set of presence data and a set of background GIS predictors (Hirzel *et al*. 2001). Since most information is usually explained by a few first factors (*see ibid*.), only these are used to compute the final habitat suitability map (HS map). All cells are allocated a HS value that is proportional to the distance between their position and the position of the species' optimum range in the new factorial space.

The generation of pseudo-absences was done using ENFA predictions, i.e. the HS map. Absences were chosen at random, but only in areas where predictions by ENFA were lower than 0.1. This criterion is similar to the one followed by Engler *et al*. (2004), although more restrictive, in order to minimize the risk of generating absences in areas which are favourable to the species. To avoid bias due to the inclusion of an excessively high number of absences (Kink & Zeng 2001), they were 10 times higher than the number of presences (*see* Lobo *et al*. 2006). All ENFA analyses were performed using the Biomapper software (Hirzel *et al*. 2004).

GLMs are an extension of classical multiple regressions (McCullagh & Nelder 1989; for the application of GLMs in habitat suitability studies *see* Guisan *et al*. 2002), allowing non-normal response variables to be modelled. GLMs (binomial, with a logarithmic link function) were used to model presences/pseudo-absences of the study species. To select the most parsimonious model, we used a forward stepwise model-selection procedure (*see* Engler *et al*. 2004). The statistic used to select the final model was the Akaike Information Criteria (AIC; Akaike 1973). All calculations were made using the STATISTICA software (StatSoft 2001).

The Receiver Operating Characteristic (ROC, Zweig & Campbell 1993), from a plot of sensitivity (ratio of correctly predicted positives to total number of positive cases) and specificity (ratio of correctly predicted negative cases to total number of negative cases), was used to measure model performance (e.g. Lobo *et al*. 2006). To compare observed and predicted maps, the continuous probability variable generated by logistic regression should be converted to a binary one (presence-absence), selecting a threshold cut-off point which minimizes the difference between sensitivity and specificity (Liu *et al*. 2005). The area under the ROC function (AUC), independent of the presence/pseudo-absence threshold (Fielding 2002), is the best measure of model prediction accuracy.

To evaluate the relationship between the HS maps of both models, they were reclassified to obtain highly suitable areas for each species, and then their overlap was analysed. In addition, we analysed the spatial relationships between habitat suitability maps and the presence of the translocated red deer.

Results

First, we produced the ENFA models, which were quite robust, as the explained variance was over 78%. Based on habitat units with a suitability < 0.10 according to the ENFA analysis, a series of random pseudo-absences were selected (2580 for the red deer model and 1990 for the Iberian ibex model).

Univariate logistic regressions identified the variables to include in the final models (Table 1). Annual temperature range and the proportion of forest cover were the variables that best explained red deer and Iberian ibex presence, respectively. Overall, the Iberian ibex model identified more variables related to topography as candidates for the final models than the red deer model.

With the stepwise model selection procedure based on AIC (*see* Table 2), the final models were selected (Table 3). The simplest models for the red deer and Iberian ibex datasets explained 84% and 79% of the deviance in the presence *vs*. pseudo-absence habitat units, respectively. Scores of AUC for both red deer and Iberian ibex models (0.97 for both models), sensitivity (98.45% and 95.98%, respectively) and specificity (98.18% and 96.03%, respectively) showed that the models are statistically robust. Both red deer and Iberian ibex models, considering these parameters, can be regarded as outstanding (*sensu* Hosmer & Lemeshow 2000). Cut-off values were fixed at 0.24 and 0.26 for red deer and Iberian ibex, respectively.

Six variables were included in the red deer final model, representing all the predictor groups considered in the analyses. In the Iberian ibex model, seven variables were selected, including the predictor groups, but in this case variables related to geomorphology and habitat structure were more influential than in the red deer model. Habitat suitability indices, i.e., the probability

Table 2. Summary of the stepwise model selection procedure based on Akaike Information Criterion (AIC) for the two study species. D^2 = percentage of the explained deviance. Variable codes as in Table 1.

	D^2	AIC
Red deer		
TRn	66.83	383.24
TRn + DHBsh	79.63	358.19
TRn + DHBsh + DUr	82.34	313.37
TRn + DHBsh + DUr + WULAI	82.89	305.85
TRn + DHBsh + DUr + WULAI + PW	83.38	299.39
TRn + DHBsh + DUr + WULAI + PW + AltMx	84.13	288.41
Iberian ibex		
AltMx	60.01	533.24
AltMx + DCFr	60.62	525.21
AltMx + DCFr + TRn	68.18	424.44
AltMx + DCFr + TRn + HXBsh	69.67	404.49
AltMx + DCFr + TRn + HXBsh + DHBsh	75.16	331.25
AltMx + DCFr + TRn + HXBsh + DHBsh + DUr	77.00	306.78
AltMx + DCFr + TRn + HXBsh + DHBsh + DUr + SlpMx	78.61	285.26

(P) of habitat units being occupied (*see* Fig. 3) were calculated as:

$$P = \frac{e^y}{1 + e^y}$$

were y is the linear combination of the selected factors in the final models.

Highly suitable areas (HS > 0.50) for the native red deer population covered 4.34% of the study area, of which only 13.47% was also highly suitable for the Iberian ibex. Similarly, highly suitable areas for the Iberian ibex covered 13.19% of the study area, of which 4.43% was highly suitable for red deer (*see* Fig. 3). These results suggest that there is only a slight overlap in the ecological niche of the native populations of both species.

Nevertheless, habitat suitability values obtained for native deer in sites occupied by translocated red deer populations were very small and significantly different ($F_{1,510} = 5828.16$, $p < 0.0001$; *see* Fig. 4). Habitat suitability scores obtained for the Iberian ibex model in sites where red deer had been translocated were very similar to scores obtained for the ibex, although statistically significant differences were detected ($F_{1,445} = 11.66, p = 0.001$; *see* Fig. 4).

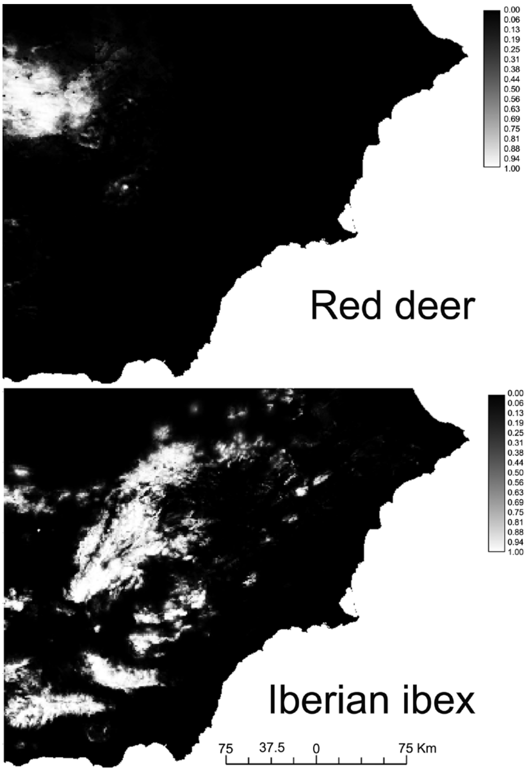

Fig. 3. Habitat suitability maps for Iberian red deer and ibex in southeastern Spain. The scale on the right shows habitat suitability values (0 = low suitability; 1 = high suitability).

Discussion

In this study, we provide evidence that niche overlap between the Iberian ibex and the red deer in the mountainous regions of southeastern Spain would probably not have taken place without human intervention, i.e., individual translocations. This evidence is derived from the fact that deer presence in these areas, where ibex are

Table 3. Coefficients and significance values of the exploratory variables entered in the final models for the study ungulate populations. Variable codes as in Table 1. *** $p < 0.001$.

Variable codes	Red deer		Iberian ibex	
	Estimate	Wald	Estimate	Wald
(Intercept)	–15.30	81.01***	–7.64	132.58***
WULAI	–1.08	10.35***	–	
DUr	0.63	13.06***	0.96	35.56***
AltMx	1.95	13.27***	2.24	105.53 ***
PW	–2.28	18.04***	–	
DHBsh	–3.44	60.27***	1.40	37.30***
TRn	11.34	102.68***	2.35	45.51***
DCFr	–	–	–7.27	44.18***
HXBsh	–	–	–1.10	21.67***
SlpMx	–	–	1.03	19.92***

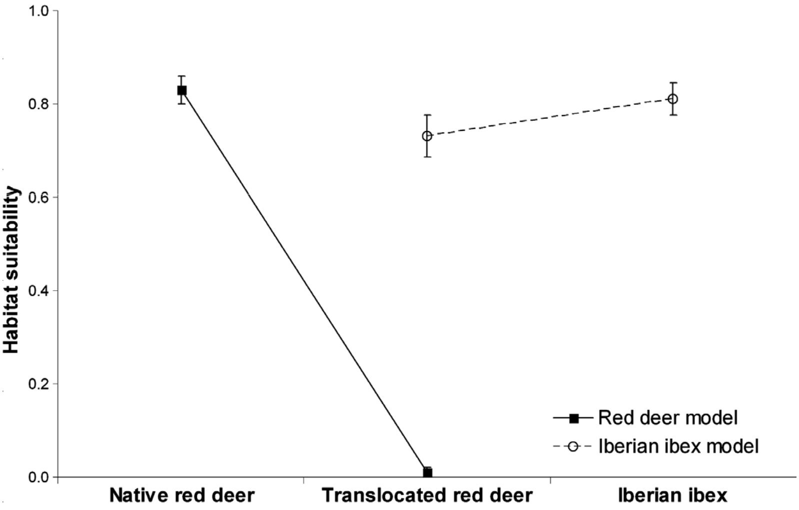

Fig. 4. Habitat suitability mean (± SE) values for both native and translocated red deer populations obtained from the red deer model (black squares). Habitat suitability values for the translocated red deer and the Iberian ibex presences obtained from the Iberian ibex model (white circles). Lines that join the suitable areas of a given model have been added in order to clarify the different trends.

native, cannot be explained by the natural expansion of native deer populations, according to its habitat suitability model.

Methodological considerations

GLM models using ENFA-weighted pseudo-absences (*see* Engler *et al*. 2004), could be of great utility for the study of the realized niche of many species (e.g. Jiménez-Valverde *et al*. 2008). GLM and Generalized Additive Models, linked to GIS applications, are very popular approaches to study species distributions (e.g. Guisan *et al*. 2002, Jiménez-Valverde *et al*. 2007, 2008). When absence or pseudo-absence data are available, more robust habitat models can be built using these techniques (e.g. Engler *et al*. 2004; but *see* Hirzel *et al*. 2001) in relation with other procedures named 'profile', e.g. ENFA.

Another justification for the methodology used here is that we obtained a low prevalence of species presence, and GLM models using ENFA-weighted pseudo-absences are more sensitive to spatial resolution (data quality) than to number of occurrences (data quantity) (Engler *et al*. 2004).

Niche analyses for the study species

Red deer translocations to the Iberian Peninsula, basically in response to game interests (Braza *et al*. 1989, Gortázar *et al*. 2000; *see* Fig. 1), have been carried out without preliminary ecological studies. Areas where red deer have been translocated to may be suitable for sport hunting but 'unsuitable' for red deer according to habitat requirements of the native red deer populations. They are typically rough, high altitude areas with low productivity, often home to the native Iberian ibex.

The presence of a species in areas with low scores of suitability is indicating a high ecological plasticity of the species, as was reported for roe deer (*Capreolus capreolus*) in Spain (Acevedo *et al*. 2005). One of the main results from our study is that red deer express a high ecological plasticity (e.g. Hofmann 1985, Gebert & Verheyden-Tixier 2001), adapting to suboptimal ecological conditions in areas where they have been translocated to (Mátrai *et al*. 2004). A given species occupying unsuitable areas may be interpreted in different ways: (i) the species is expanding its geographical range in the study area and these 'unsuitable' areas could be used as dispersal corridors, as was reported for roe deer (Acevedo *et al*. 2005), (ii) it might be the result of interspecific competition in which one species has been forced to occupy suboptimal habitats, as was reported in the Iberian ibex (Acevedo *et al*. 2007b), or (iii) it might be a result of historical factors, such as human-induced ones, which modulate the species distribution (Real *et al*. 2008). The presence of red deer in 'unsuitable' areas in Spain, according to the ecological requirements of native populations, is a clear example of human-induced expansions of this species.

The successful establishment of these populations, in habitats outside their ecological range and beyond their dispersal potential, connects them with non-native invasive species (*see* Falk-Petersen *et al*. 2006), which may cause severe ecological disturbances in the host environment, so that, if not removed, at least they should be carefully monitored (e.g. Moriarty 2004). Such disturbances can affect the autochthonous vegetation, other native animal species, and, indirectly, the viability of the translocated deer population. It is noticeable that these deer translocations may be harmful not only because of their potentially alien nature, but also because of the increasing herbivory pressure on the ecosystem.

Our results suggest that translocated red deer have a similar distribution than the native Iberian ibex, since their presence maps strongly resemble each other (Fig. 2). Native red deer, however, present a different potential distribution in the study area (*see* Fig. 3), with just a slight overlap with the Iberian ibex distribution. Thus, we postulate that the native red deer would never have reached the areas currently occupied by translocated populations and as a consequence of this, we should not expect a niche overlap between native red deer and the Iberian ibex.

However, the presence of translocated red deer in habitats typically occupied by the Iberian ibex may represent a threat to the latter. A large diet overlap between both species has been reported (Martínez *et al*. 1992), so that interspecific competition might occur, particularly when resources are limited. Unfortunately, it is not possible to infer interspecific competition with the analyses carried out in this study, and more experimental studies are required. If competition does take place, there is a potential risk of displacement of the Iberian ibex population to suboptimal habitats, as reported for other localities where domestic livestock are present (Acevedo *et al*. 2007b). One probable advantage for red deer when competing for resources is its larger body size in relation to that of the Iberian ibex (e.g. Gordon 1989).

When high population densities are reached, together with limited food availability, high parasite abundances can be expected due to a loss of fitness and increased aggregations (Gortázar *et al*. 2006, Acevedo *et al*. 2007c). This could be another negative effect of wildlife introductions. A probable example of this phenomenon was observed in the case of sarcoptic mange (*Sarcoptes scabiei*) outbreaks detected in the Iberian ibex populations of Cazorla (León-Vizcaíno *et al*. 1999).

Since these human-induced translocations have promoted the presence of red deer in new habitats, where the species has successfully established, we might be facing a particular case of biological invasion. This involves two essential stages: transport of an organism to a new location (Mack *et al*. 2000), and establishment and population increase at the invaded locality (Veltman *et al*. 1996). A third stage, applicable to most invasions, is regional spread from initially successful populations (Shigesada & Kawasaki 1997). The effects of environmental constraints on translocated red deer populations in SE Spain may have been mitigated by game management strategies, such as the use of fences, protection against predators at estates, and extra feeding and watering (*see* Vicente *et al*. 2006). On the other hand, an invader will be at an advantage if its maintenance requirements are lower than those of a resident even under harsh environmental conditions, or if it has a better response to increased resources than the resident species (Shea & Chesson 2002). Also, the dominance of alien species over native ones may actually be a consequence of degraded ecosystems, which facilitate the spread of the former (Gurevitch & Padilla 2004, Didham *et al*. 2005).

Final statement: clear-cut definition of native and alien species

The definition of a native species is not always clear, as highlighted by species introduction programmes, where this definition is either absent or unclear (Rees 2001). This lack of clarification may produce severe ecological damage when species translocations take place in host ecosystems to which they are alien. We should follow strict rules when defining native species, taking into consideration both historical and paleontological facts as well as current environmental conditions of the locality where the introduction is to be carried out (*see ibid*.).

In this paper, we presented some evidence that native species may be restricted to certain environments or habitats, and particular care should be taken when promoting their translocation elsewhere. This is the case for red deer translocated to mountainous regions of southern Spain. We, thus, postulate than native species promoted beyond their native areas may 'behave' as alien species, adapt to the new habitats and could become a risk to the native fauna and flora, in a similar manner as true exotic or alien species (*see* Cassinello *et al*. 2006, Acevedo *et al*. 2007a).

Following the IUCN Technical Guidelines on *ex situ* populations (IUCN 2002, Maunder & Byers 2005), whenever feasible, conservation measures should always be directed towards *in situ* populations (i.e., in their natural habitats) or, alternatively, towards populations managed through *ex situ* techniques (i.e., the conservation of components of biological diversity outside their natural habitats [Glowka *et al*. 1994]). Such techniques include reproduction propagation, germplasm banking, applied research, reinforcement of existing populations and re-introduction into the wild or controlled environments (IUCN 2002). However, a clear-cut separation between natural populations, based on proper knowledge of a species' natural history, and historically wrongly translocated or introduced populations, may help to stimulate interest and induce consensus against some present day introductions, which are increasingly recognized as a major threat to biodiversity. Furthermore, even when a complete eradication of alien species is unfeasible, at least their unambiguous identification may lead to the establishment of more rigorous biodiversity priorities at the local, national, and international levels. Finally, how can we properly deal with current biological invasions if we do not distinguish yesterday's mistaken introductions?

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