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*Chapter 5*

**MODELING DISJUNCT CARNIVORE  
DISTRIBUTIONS: THE CASE OF THE WOLF  
(*CANIS LUPUS*) IN THE IBERIAN PENINSULA**

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**ABSTRACT**

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The gray wolf (*Canis lupus*) is a generalist species whose distribution was originally the widest among wild carnivores but suffered a marked regression due to human persecution during the 19th and 20th centuries. Legal protection after 1970 allowed wolves to recover significant parts of their range, including, in some cases, heavily humanized and modified landscapes. Nowadays, many wolf populations keep expanding, although the viability of many others is still at risk due to small population sizes and loss of genetic diversity. The Iberian Peninsula holds Western Europe's largest wolf population, which is currently divided into two distinct nuclei: a large and practically continuous one spreading through most of the northern half of this region, and a smaller and subdivided one in a southern mountainous area. A distribution model based on the whole Iberian wolf distribution overlooked the southern nucleus, suggesting biogeographic differences between them. This can happen due to local adaptation events, and points to the need for caution when modelling species or populations with disjunct distributions. When we modelled both wolf nuclei separately, the southern nucleus showed indeed different environmental and biogeographical properties, with a trend towards a metapopulation structure. We discuss the implications of these models for the conservation and management of wolves in the Iberian Peninsula and of other species facing similar biogeographic situations elsewhere.

## INTRODUCTION

The wolf (*Canis lupus* L., 1758) is a generalist and highly adaptable carnivore that was once widely spread across the northern hemisphere, which made it the wild mammal with the broadest natural distribution. Yet, human persecution during the nineteenth and twentieth centuries eliminated it from much of its original range. By the mid of the twentieth century, wolf distribution was basically reduced to the northern half of North America, northern and central Asia, eastern Europe, southern Scandinavia and the Mediterranean peninsulas, and wolf populations were mostly relegated to remote undisturbed areas. However, worldwide legal protection in the early 1970s allowed the species to recolonize a significant part of its former distribution range, including highly altered and humanized landscapes (Mech 1995, Route & Aylsworth 1999, Boitani 2000). Nowadays, many wolf populations are expanding significantly, although the viability of many others

is still at risk due to low population sizes and loss of genetic variability (Ellegren 1999, Vila et al. 2003).

In the Iberian Peninsula (SW Europe), wolf regression became patent during the twentieth century. Wolf populations reached their minimum in the 1970s, but later Blanco et al. (1990, 1992) and Arberas et al. (1999) found that many Iberian wolf populations were recovering rather than heading for extinction. Two main distribution nuclei currently occur in the Peninsula, one occupying a large and, at this scale, virtually continuous area in the northwest, including N Portugal and NW Spain; and the other occurring in a relatively small area and divided in two separate populations in Sierra Morena, S Spain (Figure 1). Although the Iberian wolf population is the largest in Western Europe (IUCN, 2010), the wolf is currently considered endangered in Portugal (Cabral et al., 2005) and nearly threatened in Spain (Palomo & Gisbert, 2002; Palomo et al. 2007). The Iberian wolf population suffered a recent bottleneck and currently presents low levels of heterozygosity and a distinctive genetic structure (vonHoldt et al. 2011) with some unique mitochondrial haplotypes (Pilot et al. 2010). Although it is not consensual, some authors consider that Iberian wolves constitute a separate subspecies (*C. l. signatus* Cabrera, 1907; Palomo & Gisbert, 2002).

As a large carnivore, the wolf plays an important role at the top of food chains, so helping maintain the equilibrium of ecosystems. The disappearance of wolves, as well as other large carnivores, from areas where they originally occurred has remarkable consequences on prey community structure and on subtle but important ecological patterns involving interspecific behavioral relationships (Berger 1999). On the other hand, wolf recovery has boosted up old conflicts with humans, generated mainly by predation on domestic livestock and on wild ungulates where they are an economically important hunting resource (Blanco et al. 1992, Fico et al. 1993, Mech 1995, Treves et al. 2004). Management plans are therefore needed to allow for the conservation of wolves, protecting their vulnerable populations, whilst minimizing the damages caused by expanding, well-established populations.

Corsi et al. (1999) defended a landscape approach as the most adequate for the management of this wide-ranging species. National species surveys, whether or not included in species distribution atlases, are a most useful basis for such studies, as they provide comprehensive data suitable for analyzing the distribution of species on a wide scale. Large-scale distribution models can be applied even when country-wide information is limited (Corsi et al. 1999), and extrapolated to predict potential distribution of species on finer resolution scales (Barbosa et al. 2003, 2010, Araújo et al. 2005). They can also forecast

the evolution of species' distribution ranges, their responses to environmental change, and the probability of persistence of different populations (Araújo & Williams 2000, Real et al. 2009). A biogeographical perspective may also be important in the assessment of the conservation status of disjunct population nuclei (Acevedo & Real 2011).

Here we model wolf distribution in the Iberian Peninsula, investigating whether one model can account for both distribution nuclei or if separate models are necessary. We also compare the factors that describe the areas occupied by each nucleus, and discuss the implications of these models for the conservation and management of the wolf and other large carnivores alike, in the study area as well as in other parts of its extensive range.

## METHODS

The study area was the Iberian Peninsula, at the south-western edge of Europe (Figure 1). This is a nearly 600,000-km<sup>2</sup> heterogeneous region comprising the mainland territories of Portugal and Spain, and linked to the European continent by a narrow and mountainous isthmus. It thus constitutes a discrete biogeographical unit appropriate for studies on species distributions (e.g. Real et al. 2009, Barbosa et al. 2010) – especially so in this case, as the Iberian wolf population is genetically distinct from the remaining European populations (vonHoldt et al. 2011).

Distribution data consisted of Iberian wolf presences and absences on UTM 10×10-km grid cells (Figure 1). Data from Portugal were taken from I.C.N. (1997) and are the result of a national wolf survey held in 1997 and previous years. Data for Spain were taken from a mammal distribution atlas (Palomo & Gisbert 2002) which gathered distribution records of various sources from a roughly similar time period. We modeled distribution data from the Iberian Peninsula altogether and from the two disjunct wolf nuclei separately to see whether a single model could account for the whole peninsular distribution of this species or, on the contrary, if two different models were needed. For the modeling of each nucleus, presences of wolves from the other nucleus were treated as absences.

Predictor variables, representative of physiography, climate and human activity (Table 1), were digitized and interpolated by Barbosa et al. (2003, 2009). We corrected the values of solar radiation according to Barbosa et al.

(2011). The variables were chosen on the basis of availability at this scale and relation to factors that may influence wolf distribution more directly. Our aim was not to create explanatory models with the variables directly conditioning wolf distribution, but rather to predict its potential distribution on the basis of available variables, which are assumed to be correlated with more proximate causal factors (see Austin 2002, Robertson et al. 2003). Models that rely on indirect links between environmental variables and species presence can predict distribution at least as well as mechanistic models built on variables more directly related to species physiology (Austin 2002, Robertson et al. 2003).

**Table 1. Variables used to model the distribution of *Canis lupus*, in alphabetical order of their code. Sources: (1) U. S. Geological Survey (1996); (2) Font (1983, 2000); (3) I.G.N. (1999); data on the number of inhabitants of urban centers taken from Enciclopédia Universal (<http://www.universal.pt>) for Portugal and from the Instituto Nacional de Estadística (<http://www.ine.es>) for Spain, both in 1999**

Code	Variable
<i>aet</i>	Mean annual actual evapotranspiration (mm) (=minimum[ <i>PET</i> , <i>Prec</i> ])
<i>alti</i>	Mean altitude (m) <sup>(1)</sup>
<i>altr</i>	Altitudinal range (m)
<i>d100</i>	Distance to the nearest town with more than 100,000 inhabitants (km) <sup>(3)</sup>
<i>d500</i>	Distance to the nearest town with more than 500,000 inhabitants (km) <sup>(3)</sup>
<i>dfro</i>	Mean annual number of frost days (minimum temperature $\leq 0^{\circ}\text{C}$ ) <sup>(2)</sup>
<i>dhi</i>	Distance to the nearest highway (km) <sup>(3)</sup>
<i>dpre</i>	Mean annual number of days with precipitation $\geq 0.1$ mm <sup>(2)</sup>
<i>hjan</i>	Mean relative air humidity in January at 07:00 hours (%) <sup>(2)</sup>
<i>hjul</i>	Mean relative air humidity in July at 07:00 hours (%) <sup>(2)</sup>
<i>inso</i>	Mean annual insolation (hours/year) <sup>(2)</sup>
<i>lati</i>	Latitude (degrees N) <sup>(3)</sup>
<i>long</i>	Longitude (degrees E) <sup>(3)</sup>
<i>mp24</i>	Maximum precipitation in 24 hours (mm) <sup>(2)</sup>
<i>pet</i>	Mean annual potential evapotranspiration (mm) <sup>(2)</sup>
<i>prec</i>	Mean annual precipitation (mm) <sup>(2)</sup>
<i>rpm</i>	Relative maximum precipitation (=MP24/Prec)
<i>slop</i>	Mean slope (degrees) (calculated from <i>Alti</i> )
<i>srad</i>	Mean annual solar radiation (kwh/m <sup>2</sup> /day) <sup>(2)</sup>

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<i>temp</i>	Mean annual temperature (C) <sup>(2)</sup>
<i>tjan</i>	Mean temperature in January (C) <sup>(2)</sup>
<i>tjul</i>	Mean temperature in July (C) <sup>(2)</sup>
<i>vhum</i>	Annual relative air humidity range (%) ( $= HJan-HJul $ )
<i>vtem</i>	Annual temperature range (C) ( $=TJul-TJan$ )

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The UTM 10×10 km grid and the limits of the study area were downloaded from the EDIT Geoplatform (Sastre et al. 2009). We used Quantum GIS 1.7 (Quantum GIS Development Team, 2010) and its GRASS plugin (Geographic Resources Analysis Support System; GRASS Development Team 2010) to clip the grids with the limits of the study area. The values of the variables were averaged over the UTM cells with the *raster* package in R 2.11 (R Development Core Team 2010).

To avoid a spurious effect of surface area on the probability of the species being present, only complete UTM cells, and not those that were cut by study area borders or the unions between UTM zones, were used for model building. This left a total number of 5464 analyzed UTM cells, 1239 of which (22.7%) had wolf presence records. The northern nucleus had 1185 presence cells (corresponding to a 21.7% prevalence in the whole study area), while the southern nucleus had the remaining 54 cells (1.0% prevalence). The models were then applied to the whole study area of 6180 cells for which average values of the variables could be obtained.

We modeled wolf presences and absences using the favorability function described by Real et al. (2006), which is a generalized linear model that corrects the effect of the uneven proportion of presences and absences in the analyzed sample. In this way, output model values strictly reflect environmental favorability for the species or population, independently of its prevalence in the study area, thus enabling direct between-model comparison even among species or populations with very different prevalence (Real et al. 2006; Jiménez-Valverde & Lobo 2006). This function has been successfully used to build comparable models for different species (Real et al. 2009, Barbosa & Real 2012), for parts of the distribution of the same species in different countries (Barbosa et al. 2009) and for different subspecies within the same species (Acevedo & Real 2011), for example.

Statistical theory predicts an increase in false findings when a large number of variables is analysed, due to the increase in type I errors under repeated testing. García (2003) recommended controlling type I errors in

ecological research by evaluating the false discovery rate (FDR). We controlled this error using the procedure for all forms of dependency among test statistics (Benjamini and Yekutieli, 2001), and only accepted variables under a FDR value lower than 0.05.

Variables were then included in the models using a stepwise procedure (Araújo et al., 2005; Bulluck et al., 2006; Arntzen & Espregueira-Themudo, 2008) using SPSS Statistics 17.0 and the forward conditional option. Stepwise selection is a useful and effective tool to infer distribution patterns inductively from observed data, when no theory or previous hypotheses exist about the importance of each variable (Guisan & Zimmermann, 2000; Real et al., 2009).

**Table 2. Variables (and their coefficient estimates in parentheses) selected to predict the distribution of the Iberian wolf and the distributions of the northern and southern nuclei separately. Variables are grouped according to the factors they are associated with. Variable codes as in Table 1. \*Models excluding spatial variables**

Factor	Iberia	North	South	Iberia*	North*
Intercept	(-63.332)	(-126.998)	(-267.755)	(-11.545)	(-8.368)
Topography	alti (0.002)	alti (0.002)			alti (-0.001) altr (0.001)
	slop (0.057)				
Energy	pet (0.007)	pet (-0.016)	aet (0.025)	aet (-0.001)	aet (-0.002)
	inso (-0.002)		pet (0.044)		pet (-0.012)
	temp (-0.426)	temp (-0.327)		inso (-0.001)	
				temp (-0.614)	temp (-0.636)
	tjul (0.325)	tjul (0.291)			tjan (0.127)
		srاد (0.744)	srاد (37.055)		tjul (-0.265)
Continentality	dfro (0.041)	dfro (0.037)	dfro (0.072)		
			vtem (1.81)	vtem (-0.128)	
Water	dpre (-0.029)	dpre (-0.037)	dpre (-0.124)		dpre (0.01)
	hjan (0.173)	hjan (0.158)		hjan (0.422)	hjan (0.349)
				hjul (-0.144)	
	vhum (-0.086)			vhum (-0.173)	
Location	lati (0.979)	lati (2.733)			
	long (-0.959)	long (-1.188)			
Disturbance			pm24 (0.025)		pm24 (-0.008)
				rmp (-10.082)	rmp (-9.74)
Human	d500 (0.004)	d500 (-0.007)		d500 (0.013)	d500 (0.01)
			dhi (-0.052)		



The capacity of each model to discriminate between the wolf presences and absences was assessed with the Area Under the receiver operating characteristic (ROC) Curve (AUC). This is a widely used model evaluation measure that provides a single-number discrimination measure across all possible classification thresholds for each model, thus avoiding the subjective selection of one threshold (Fielding & Bell 1997). We remark that, as any discrimination measure, the AUC depends on thresholds (just not on one particular threshold) to convert continuous model predictions into binary classifications, and it is conditioned by species prevalence (e. g., Lobo et al. 2008). We thus performed also the Hosmer & Lemeshow goodness-of-fit test to assess the calibration of the models, i. e., the reliability of model predictions (Liu et al. 2009).

## RESULTS

The predictions obtained from the total Iberian wolf data reflected mainly the distribution of the (substantially larger) northern nucleus, overlooking the southern one (Figure 1a). A single model was thus unsuitable to account for the whole Iberian wolf distribution. This was not due to the inclusion of spatial variables (latitude and longitude) in the models, as excluding these variables (Table 2) produced a highly similar model that still overlooked the southern nucleus (Figure 2a). The distributions of the two spatially segregated wolf nuclei thus needed to be modeled separately.

**Table 3. Evaluation measures of the of total, northern and southern Iberian wolf distribution models. \* Models excluding spatial variables;  $p$ : significance**

Model	Area Under the Curve (AUC)	Hosmer & Lemeshow calibration statistic (H-L)
Iberia	0.948	221.101, $p < 0.001$
North	0.978	18.127, $p = 0.020$
South	0.993	52.036, $p < 0.001$
Iberia*	0.931	207.503, $p < 0.001$
North*	0.959	28.820, $p < 0.001$

All models included variables related to topography, continentality, environmental energy and water availability. The total and the northern Iberian wolf models included also human activity and spatial situation, with a trend for more favourable areas towards the north and the west (Table 2).

When modeling was repeated without the spatial variables for the Iberian and the Northern Iberian populations, the obtained potential distribution maps were highly similar (Figure 2) and predictions were highly correlated with those of the models with spatial variables (Pearson's  $r = 0.919$  for both the Iberian population and the northern nucleus,  $p < 0.001$ ).

All models attained high discrimination capacity as given by AUC, whereas model calibration varied more widely (Table 3). The distribution of the northern wolf nucleus could also be well predicted by the overall Iberian model (AUC = 0.971 for the complete Iberian model, AUC = 0.956 for the Iberian model without spatial variables). However, the same did not occur for the southern wolf nucleus, with the Iberian model completely failing to predict its presence (AUC = 0.335 for the complete Iberian model, AUC = 0.285 for the Iberian model without spatial variables, indicating predictions were even worse than random).

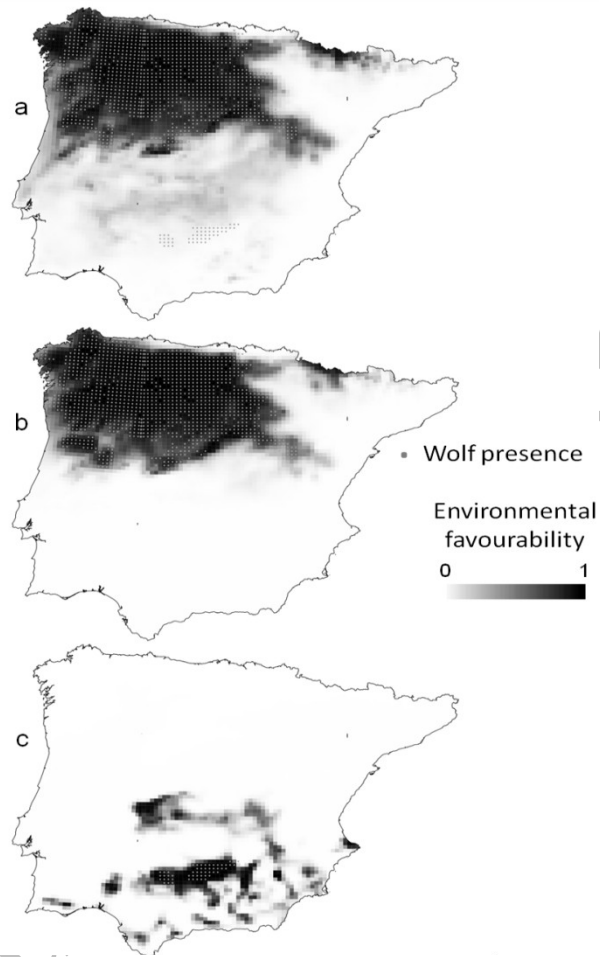


Figure 1. Wolf (*Canis lupus*) occurrence on 10x10-km UTM grid cells [data from I. C. N. (1997) for Portugal and Palomo & Gisbert (2002) for Spain] and the favourability models obtained for the whole Iberian distribution (a) and for the northern (b) and southern nuclei (c) separately.

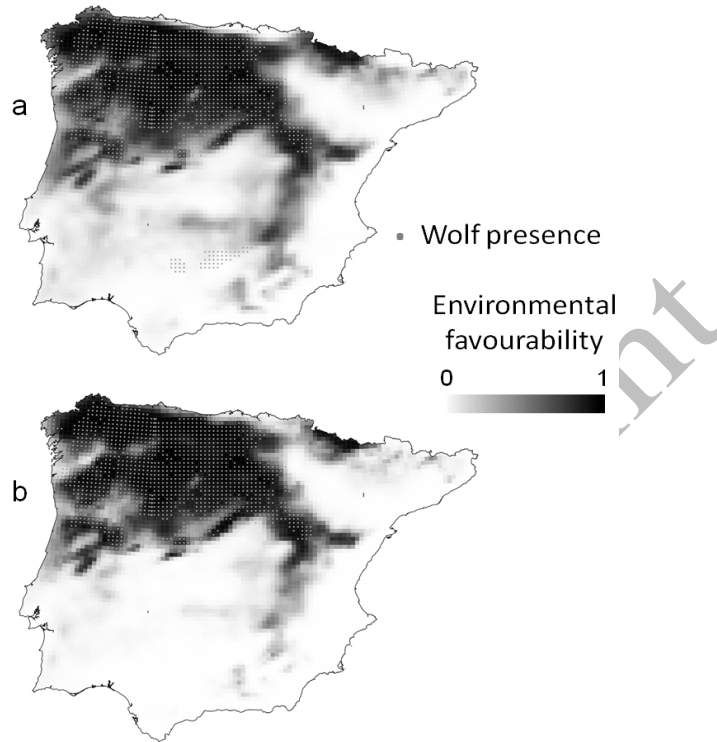


Figure 2. Wolf (*Canis lupus*) occurrence on 10x10-km UTM grid cells [data from I. C. N. (1997) for Portugal and Palomo & Gisbert (2002) for Spain] and the favourability models obtained for the whole Iberian distribution (a) and for the northern nucleus (b) without spatial variables.

## DISCUSSION

Our results show that the two main Iberian wolf nuclei respond to different environmental factors. The environmental favorability maps obtained for the two nuclei were clearly different, and the Iberian model was manifestly incapable of predicting the distribution of the southern nucleus (Figure 1).

The fact that the Iberian model mainly predicted the distribution of the northern nucleus is probably due to the much greater weight of this nucleus within the data set, given the large difference in the numbers of presences of both nuclei (Figure 1). It is important to remark that the incapacity of the Iberian model to predict the southern nucleus was not due to the inclusion of spatial variables in the analysis. These variables might indeed have restricted

favorable predictions to the northern region, which contained most of the analysed occurrences; however, repeating the modeling procedure without using any spatial variables just produced very similar models (Figure 2), showing that it was not the spatial variables that were restricting the Iberian model to the northern half of the Peninsula.

Blanco & Cortés (2002) defended that wolf distribution is conditioned mainly by human activity and not by environmental factors, which would be demonstrated by this species' wide overall distribution. However, even a tolerant species is affected by environmental conditions, especially when human pressure restricts it to more adverse regions, where previously non-limiting factors may become decisive. In addition, human activity is itself affected by environmental factors, and the two are often inseparable (although not indistinguishable) when analyzing their impact on species distribution.

The areas occupied by the northern and southern wolf nuclei are similar in some characteristics, namely low water availability, moderate to high environmental energy and high continentality (Table 2), which may be related to ecological factors. Continentality, for example, is related with winter severity, which can favour wolves by debilitating their natural prey (Mech et al. 1988b).

Although wolf distribution has been associated negatively with road density by several authors (e. g. Thiel, 1985; Mech *et al.*, 1988a; Mladenoff *et al.*, 1995), none of the three models presented here identify the distance to highways as positive for wolf presence. These results agree with Mech (1995), who noted that, in North America, wolf recovery after official protection also led to the colonization of much more open, accessible and densely populated areas with greater road density. Also Jędrzejewski *et al.* (2004) found no influence of roads on the distribution and abundance of wolves in Northern Poland, although there was a negative influence of highways and human settlements. The main menace posed by roads seems to come not from accidents, but rather from accessibility to humans and types of land use (see also Thiel 1985).

Despite some environmental similarities between the northern and southern wolf areas, our results suggest that the two nuclei show different spatial responses to the environmental constraints. There is a possibility that wolves from the northern nucleus have adapted to live in more humanized landscapes and to use artificial food sources, which may have helped their expansion. Several studies have indicated that although wolves tend to avoid the proximity to densely populated areas, they start to tolerate them when their

population grows or when good habitat becomes scarcer (Mech *et al.*, 1988a; Mech, 1995; Mladenoff *et al.*, 1999). Wolves have, in general, an extraordinary capacity to adapt and re-colonize areas if they are given the chance. Route & Aylsworth (1999) identified direct persecution and habitat destruction, caused by road building and the expansion of agricultural and urban areas, as the main threats to wolves at a global level, but they also pointed out that, given prey abundance and non excessive persecution, wolf populations recover rapidly.

The southern nucleus, in spite of its localized distribution, does not seem limited by space but rather by environmental factors related to energy availability, humidity and environmental disturbance. The model obtained for this nucleus points to a metapopulation structure in the spatial configuration of favorable areas, with the species occupying only two separated fractions of the main, core, and continuous favorable patch (see Figure 2B).

Connectivity seems to be of lower relevance for the northern wolf populations. The influence of spatial situation on the northern wolf nucleus reflects autocorrelation in distribution, which limits wolf presence to the vicinity of other presence areas. This autocorrelation in wolf distribution cannot be explained solely by autocorrelation in the analysed environmental predictors, since, in such case, purely spatial variables such as latitude and longitude would not add a significant predictive ability to the model. Consequently, this pure spatial effect may be interpreted as a consequence of aspects of this population's own dynamics, namely dispersal capacity (Legendre 1993, Barbosa *et al.* 2003). This may indicate a trend of the northern nucleus to keep expanding its range, as it is not limited only by environmental factors but also by the proximity of actual areas of presence.

Other top predators inhabiting the Iberian Peninsula, such as the Iberian lynx (*Lynx pardinus*) and the Iberian imperial eagle (*Aquila adalberti*), are in danger of extinction after restricting their diets to a staple prey, the wild rabbit (*Oryctolagus cuniculus*), whose populations have suffered strong declines (e. g. Real *et al.* 2009). In contrast, the ability of wolves to adapt their feeding habits has allowed them to recover notably after protective measures were taken. However, the models obtained here suggest that this process may not be generalizable to both Iberian wolf nuclei, as the southern nucleus is facing lack of connectivity between environmentally favorable areas. Given that species with disjunct distributions can show subspecific variation in their habitat requirements, due to local adaptation (Stockwell & Peterson, 2002; McPherson *et al.*, 2004), the plans for conservation and management of wolf populations in the Iberian Peninsula should take into account that the northern

and southern nuclei have different biogeographical (and probably also ecological) traits, and thus should be treated independently.

A similar situation was recently observed for the two extant subspecies of Iberian wild goat *Capra pyrenaica* (Acevedo & Real 2011). Habitat fragmentation may be in the origin of disjunct distributions, when the movement between suitable fragments is disrupted. Species with disjunct distributions often show different responses to environmental gradients due to local adaptations (Stockwell and Peterson, 2002; McPherson et al., 2004), and they can become divergent enough for different genetic lineages to evolve. Such biogeographic drift might give rise to sub-speciation. Studies on spatial genetic structure of grey wolves have included the Iberian population, but with sampling limited to the northern nucleus (Pilot et al. 2010, vonHoldt et al. 2011). It would be interesting to genetically compare the wolves from the northern and the southern Iberian nuclei.

Disjunct distributions have relevant implications for species conservation and management, since they have different biogeographical, and probably ecological, characteristics, and should thus be considered independently when management strategies are designed (Acevedo & Real 2011). Disjunct distributions are also a crucial aspect to consider when transferring models in space or time, since under these circumstances the predictive capacity of the models may be strongly reduced under new scenarios (Barbosa et al. 2009, Acevedo & Real 2011).

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