Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Refuge as major habitat driver for wolf presence in human-modified landscapes

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Keywords
breeding areas; human-wildlife coexistence; *Canis lupus*; species range; Iberian Peninsula; large carnivores; nested-scale models; refuge availability.

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Editor: Julie Young
Associate Editor: Vincenzo Penteriani

Received 08 March 2016; accepted 20 June 2018

doi:10.1111/acv.12435

Abstract

Despite severe population declines and an overall range contraction, some populations of large carnivores have managed to survive in human-modified landscapes. From a conservation perspective, it is important to identify the factors allowing for this coexistence, including the relevant habitat characteristics associated with the presence of large carnivores. We evaluated the role of several environmental factors describing habitat quality for wolves *Canis lupus* in the humanised Iberian Peninsula, which currently holds an important wolf population at European level. We used maximum entropy and generalized linear model approaches in a nested-scale design to identify the environmental factors that are related to wolf presence at three spatial scales and resolutions: (1) distribution range: wolf presence on a 10×10 km grid resolution, (2) wolf habitat use: wolf occurrence on a 2×2 km grid and (3) dens/rendezvous sites: breeding locations on a 1×1 km grid. Refuge availability, as defined by topography, seemed to be the key factor determining wolf presence at the multiple scales analysed. As a result, wolf populations may coexist with humans in modified landscapes when the topography is complex. We found that a significant amount of favourable habitat is not currently occupied, suggesting that the availability of suitable habitat is not the limiting factor for wolves in the Iberian Peninsula. Habitat suitability outside the current range indicates that other factors, such as direct persecution and other sources of anthropogenic mortality, may be hampering its expansion. We suggest that priorities for conservation should follow two general lines: (1) protect good quality habitat within the current range; and (2) allow dispersal to unoccupied areas of good quality habitat by reducing human-induced mortality rates. Finally, we still need to improve our understanding of how wolves coexist with humans in modified landscapes at fine spatiotemporal scales, including its relationship with infrastructures, land uses and direct human presence.

Introduction

During the last century large carnivores have experienced substantial population declines and range contractions mainly due to human encroachment and direct persecution (Ceballos & Ehrlich, 2002; Ripple *et al.*, 2014; Lucas, González-Suárez & Revilla, 2016). In Europe and North America in the last three decades new conservation-oriented legislation has been passed, while natural and rural areas have experienced substantial socioeconomic changes, leading to an increase in forest cover in many temperate areas. These changes have somewhat facilitated the stabilization and even the growth of some populations of large carnivores (Chapron *et al.*, 2014; Gompper, Belant & Kays, 2015).

The case of the wolf *Canis lupus* population in the Iberian Peninsula is an example of a change in trend in recent times, showing an overall stabilization (Blanco, Reig & de la Cuesta, 1992; Torres & Fonseca, 2016). The Iberian wolf population occupies the western most part of the range in Europe. It has been isolated for generations with a very low effective population size (Hindrikson *et al.*, 2017). A hundred years ago, the species occurred through the entire Iberian Peninsula (Cabrera, 1914). During the 20th century, human persecution and the decline of populations of wild ungulates (Fernández & Azua, 2010) drove wolf populations to the brink of extinction (Valverde, 1971). The subsequent increases in wild prey and forest cover, mainly due to widespread rural exodus, coupled with partial or total protection, allowed the species to re-colonize some local areas (Blanco *et al.*, 1992; Chapron *et al.*, 2014). Nevertheless, in the last three decades, the range occupied and the number of packs have remained stable with 120 000 km^2 and around 360 packs in total (100 000 km^2 and 300 packs and 20 000 km^2 and 60 packs in Spain and Portugal respectively; Blanco *et al.*, 1992; MAGRAMA, 2016; Torres & Fonseca, 2016). Only one population remains in the Iberian Peninsula shared by Portugal and Spain, after the virtual extinction of the so-called Sierra Morena population, with no packs detected in the last census. Neither packs nor reproduction have been detected yet in the Pyrenees, although some individuals of Italian origin are arriving there (Chapron *et al.*, 2014; MAGRAMA, 2016).

The species is considered endangered in Portugal, and near threatened in Spain (Cabral *et al.*, 2005; Blanco, Sáenz Buruaga & Llaneza, 2007), been strictly protected in Portugal and protected in Spain under the Bern Convention (Annexes III and II respectively). It is also covered by the European Union's Habitats Directive (92/43/EEC): strictly protected in Portugal and in Spain south of Duero River (Annex IV), whereas in Spain, north of the Duero River, it can be subject to lethal management if justified (Annex V). The Directive also comprises a mandate for the protection of wolf habitat, by its inclusion in Annex II (Portugal, and Spain south of Duero River) from which some recommendations have recently been derived, including the identification by spatially explicit modelling of potential areas for expansion by natural recolonization (Boitani *et al.*, 2015).

Habitat models are important tools to identify the factors affecting the distribution of species and populations, but also to predict potential distributions in response to environmental changes (Martin *et al.*, 2012; Bellamy, Scott & Altringham, 2013). In order to properly model natural processes it is necessary to consider the relevant scales (Grimm *et al.*, 2005) and modelling the distribution of a species is no exception (Hortal *et al.*, 2010). In the case of wolves there are several studies suggesting that the effects of environmental variables on their distribution change follows a hierarchy of spatial scales (see Johnson, 1980). At species distribution scale (1st order selection) they can occur in areas with relatively high road densities (e.g. 0.54 km/km^2, Thiel, 1985) and without forest cover if prey availability allows (Jędrzejewski *et al.*, 2008). At the scale of individual habitat use (third-order selection), wolves move avoiding roads and areas heavily used by humans, selecting areas with high forest cover and with abundant prey (Thiel, 1985; Massolo & Meriggi, 1998; Glenz *et al.*, 2001; Houle *et al.*, 2010; Llaneza, López-Bao & Sazatornil, 2012; Zimmermann *et al.*, 2014). Wolves can also coexist with humans in areas with low vegetation cover, if the landscape is not too fragmented by settlements and roads (Eggermann *et al.*, 2011). Finally, breeding locations, that is dens and rendezvous sites (the sites used for raising pups, third-order selection) are commonly located far from human settlements and roads, on steep slopes and/or in densely forested areas (Capitani *et al.*, 2006; Ausband *et al.*, 2010; Houle *et al.*, 2010; Bassi *et al.*, 2015; Sazatornil *et al.*, 2016). Wolves exhibit a variety of adaptations that enable them to coexist with humans in modified landscapes. Therefore, investigating how environmental variables contribute to habitat quality at a variety of scales can improve our understanding of the key factors driving occurrence patterns.

We analysed key environmental variables at different spatial scales, which can potentially determine the occurrence of wolves in the Iberian Peninsula. The main objectives in this study were to: (1) understand how landscape features, human disturbance and prey availability affect wolf distribution, space use and the location of reproduction sites; and (2) identify the critical areas for wolf occurrence, including high and low habitat quality in currently occupied areas as well as high-quality unoccupied areas. We hypothesized that the predictive power of the analysed variables will change with the scale: at species distribution scale, wolf presence would be explained by large scale topographic variables; at the scale of individual habitat use, wolves would be selecting forested areas with presence of enough prey while avoiding more humanized areas; and wolves would use the farthest areas from humans to select reproduction sites. We also evaluate why wolves are spatially restricted to the NW of the Iberian Peninsula, either due to a lack of habitat availability, lack of corridors between occupied and empty sites or other factors. Since the population is shared by Portugal and Spain, this work should provide insights on habitat quality in current wolf range and future areas for recolonization where conflicting scenarios related with wolf presence may occur.

Materials and methods

Study area

The Iberian Peninsula, with an area of approximately 585 200 km^2 comprising the continental territories of Portugal and Spain, has a complex topography ranging from sea level to 3478 m (Fig. 1). The current range of the wolf is located in the north-western quadrant of the Iberian Peninsula, around the Duero basin which is surrounded by mountain ranges (Cantabrian Mountains, and Iberian and Central Systems). The central plateau is comprised by croplands, broadleaved, evergreen and coniferous forests, scrubland and urban areas. This landscape has been modified by human intervention with an intensification of activities such as transport infrastructures, agriculture, livestock raising, urbanization,

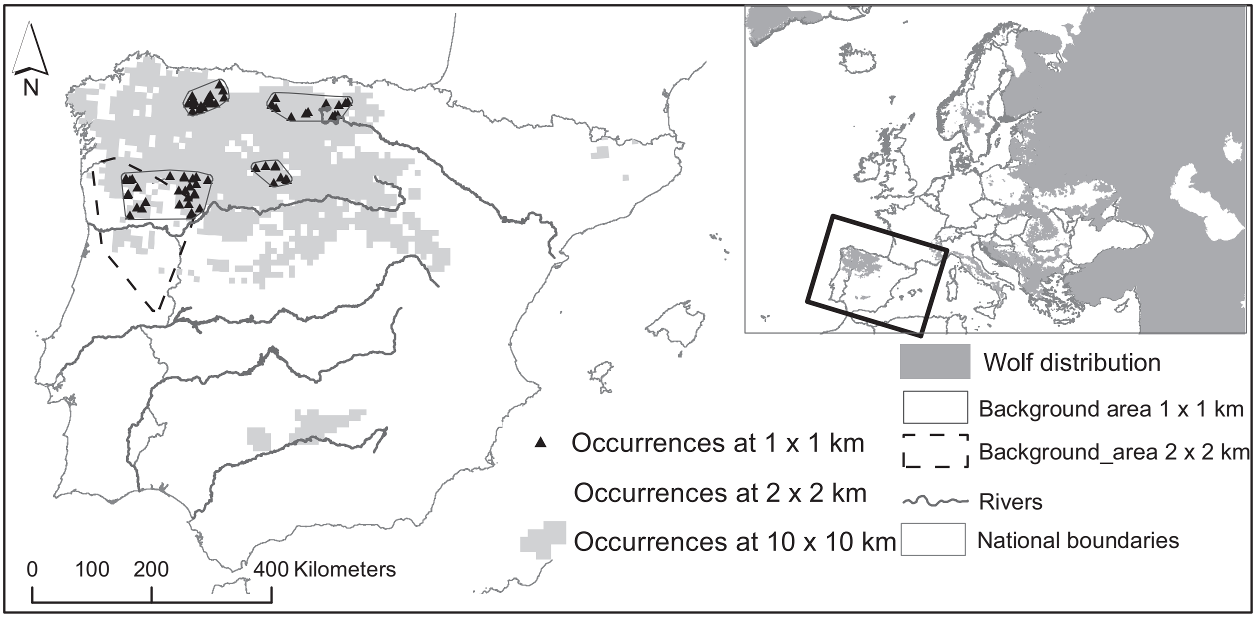

Figure 1 Wolf range in Europe with location of the study area in the Iberian Peninsula at the three spatial scales with the delineation of their respective background areas.

mining, forestry and forest fires, resulting in the depletion of vegetation cover and soil erosion (Udelhoven & Stellmes, 2007). On the other hand, in mountain areas natural vegetation cover has increased in recent times due to land abandonment by humans in the last decades (Garcia-Ruiz & Lasanta-Martinez, 1990).

Wolf data at different spatial scales

Wolf presence/absence data were compiled at three biologically meaningful spatial scales and two orders selection (*sensu* Johnson, 1980): (1) species distribution (1st order), (2) individual habitat use (3rd order) and (3) breeding sites (3rd order). Species distribution is represented by the current area of occupancy of the species at 10 × 10 km resolution (n = 1258, Fig. 1). We used data from the Portuguese wolf census, a systematic survey conducted to determine the area of presence and wolf numbers (Pimenta *et al.*, 2005) and the atlas of Spanish mammals, a compilation of wolf presence data which also includes information from a systematic census survey (Blanco *et al.*, 1992, 2007) and therefore, we do not expect spatial biases at this scale (Beck *et al.*, 2014).

At the scale of individual habitat use we use a 2 × 2 km resolution (n = 321, Fig. 1). This scale represents the space use of individuals and therefore its resolution is below the home range of the species (200 km^2 in southern Europe, Boitani, 1983; Vilà, Urios & Castroviejo, 1990). Data include a compilation of wolves' individual locations from independent studies in Portugal, including radio-tracking locations, direct observations, dead animals (except road kills), scats confirmed by genetic analyses and camera-trapping records (Álvares, 2011; Nakamura *et al.*, 2013; Eggermann *et al.*, 2011; Roque *et al.*, 2013 and unpublished data from 2002 to 2012). The original coordinates were converted to 2 × 2 km cells with presence when there was at least one observation, thus reducing the potential for spatial biases (Rondinini *et al.*, 2006; Beck *et al.*, 2014; Kittle *et al.*, 2018). Although it was not possible to estimate the sampling effort, the proportion of cells for each type of survey method was 62% radio-tracking, 25% wolf scats, 6% dead animals, 4% camera-trapping records and 3% direct observations. Around 25% of the cells have data from more than one type of method.

We defined reproduction sites at 1 × 1 km resolution using data of dens and rendezvous sites (n = 76, Fig. 1). After the pups leave the den, they use one or more rendezvous sites (also, home sites), where they wait for adults that bring them food, until the pack can travel altogether by mid-autumn (Packard, 2003). These sites are used by most individuals in a pack (95% of the individuals within a radius of 250 m, and 100% within a radius of 1 km; Stenglein *et al.*, 2011). We used den and rendezvous-site data from Northern Portugal (Vila Real and Bragança counties in Portugal during 2002–2012, authors' unpublished data) and from Northern Spain (Asturias, Cantabria and Castilla y León, between 1987 and 2013, authors' unpub. data). Rendezvous sites were determined by: (1) tracks of pups in a location, usually along with tracks of adults, (2) direct observation of pups and (3) howling of pups, usually altogether with howling adults. In all cases the locations were determined by the aforementioned observations or signs, until mid-October, when pups start leaving rendezvous sites in the Iberian Peninsula.

Environmental data

We defined environmental variables potentially explaining wolf ecological requirements at the different spatial scales.

We grouped variables into five types of information related with topography, water availability, vegetation, prey availability and human disturbance (Table 1). Variables were projected in ETRS-1989 UTM 30N and converted into a grid at the three spatial resolutions.

For topographic variables we used a Digital Elevation Model (DEM) at 100 × 100 m resolution (Robinson, Regetz & Guralnick, 2014; available at http://www.earthenv.org/DEM.html). We then calculated *Altitude* (in *m*) and *Slope* (%) as the average value within each grid data cell. We estimated water availability, *Rivers_dis* (in *m*) as the mean value within each grid cell for the three resolutions of the Euclidean distances to the nearest river calculated for a raster at 100 × 100 m. We derived the variables describing vegetation from a raster version of Corine Land Cover (CLC) 2006 with a resolution of 100 × 100 m (available at http://www.ign.es). As wolves use open areas for hunting and forest and other areas with dense vegetation as refuge (Jędrzejewski *et al.*, 2008), we reclassified the original CLC categories into open and closed land use types (Table S1). From these new categories we calculated for each grid cell the variables *Closed,* as the proportion of closed areas; *Closed_inner_dis*, as the mean Euclidean distances from the border of patches of closed vegetation to the centre of the respective patch; *Open*, as the proportion of open areas in each grid cell; *Open_dis* as the mean Euclidean distance to open areas per grid cell; *Border_closed_open*, as the ratio of border between closed and open areas per grid cell.

We included two variables to express prey availability: *Wild prey diversity* and *Livestock*. In the absence of wild prey abundance data, we used wild prey diversity by assuming that high richness of wild ungulates is associated with high availability of wild prey for wolf. *Wild prey diversity* is the number of species of native wild ungulates (wild boar, *Sus scrofa*; red deer, *Cervus elaphus*; roe deer, *Capreolus capreolus*; chamois, *Rupicapra pyrenaica*; Iberian ibex, *Capra pyrenaica*) per grid cell derived from the atlas of terrestrial mammals of Spain (Palomo, Gisbert & Blanco, 2007) and from a map of ungulates in Portugal (Vingada *et al.*, 2010); and *Livestock* is the total number of individuals (cattle, sheep and goat) per square kilometre derived from the National census of Agriculture 2011 and 2009 for Portugal and Spain, respectively, and aggregated by county (available at http://sniamb.apambiente.pt and http://www.ine.es/).

We derived the variables describing human disturbance from several data sources. From CLC, we calculated *Urban*, as the proportion of urban areas per grid cell (Table S1); *Urban_dis*, as the mean Euclidean distance to the nearest urban area per grid cell; *Agriculture*, as the proportion of agricultural area per grid cell (Table S1); *Agriculture_dis*, as the mean Euclidean distance to the nearest agricultural area per grid cell. In the case of roads, we rasterized at

Table 1 Description of the environmental variables used to model wolf occurrence in the Iberian Peninsula at three spatial scales

Variable	Definition (unit)	Dataset	Source
Topography			
Altitude	Average elevation above sea level (km)	MDT100	Robinson *et al.*, 2014
Slope	Average slope (%)	MDT100	Robinson *et al.*, 2014
Water availability			
Rivers_dis	Average Euclidian distance to rivers (km)	Rivers	SNIAMB; IGN
Vegetation			
Closed	Proportion of closed areas; see Table S1	CLC 2006	IGN
Closed_inner_dis	Average Euclidian distance from the border of patches of closed vegetation towards their centre (m); see Table S1	CLC 2006	IGN
Open	Proportion of open areas; see Table S1	CLC 2006	IGN
Border_closed_open	Proportion of border between closed and open areas; see Table S1	CLC 2006	IGN
Prey availability			
Wild prey diversity	Number of wild ungulates species	Ungulate atlas	Palomo *et al.*, 2007; Vingada *et al.*, 2010
Livestock	Livestock density (number of animals/km^2)	National census of Agriculture 2011 and 2009 for Portugal and Spain, respectively, and aggregated by county	INE; SNIAMB
Human disturbance			
Urban	Proportion of urban areas; see Table S1	CLC 2006	IGN
Urban_dis	Average Euclidian distance to urban areas (km); see Table S1	CLC 2006	IGN
Agriculture	Proportion of agriculture areas; see Table S1	CLC 2006	IGN
Roads_dis	Average Euclidian distance to roads (km);	Road network	IGN; IGeoE

The source of the variables corresponds to: IGeoE (Instituto Geográfico do Exército, https://www.igeoe.pt); IGN (Instituto Geográfico Nacional, https://www.cnig.es); INE (Instituto Nacional de Estadística http://www.ine.es/); Robinson *et al.*, 2014 (http://www.earthenv.org/DEM.html); and SNIAMB (Sistema Nacional de Informação de Ambiente http://sniamb.apambiente.pt).

100×100 m the vector datasets describing the network of paved roads, and to obtain the variable *Roads_dis* we calculated the mean Euclidean distance to the nearest road per grid cell. Calculations and transformations of variables were done using ArcMap 9.3 (ESRI, 2008) and Idrisi Taiga software package (Clark Labs, 2009).

Analyses

We run distribution models at the three scales. As model techniques can produce divergent results (Thuiller, 2004; Pearson *et al.*, 2006), we used two approaches to ensure that our results were consistent: (1) MaxEnt, a distribution modelling approach which uses presence-only data applying maximum entropy modelling (Phillips, Anderson & Schapire, 2006; Phillips & Dudík, 2008; Phillips *et al.*, 2009; Elith *et al.*, 2011) and (2) Generalized Linear Models (GLM), commonly used in distribution modelling (Guisan & Zimmermann, 2000; Guisan, Edwards & Hastie, 2002). In order to avoid multicolinearity among environmental variables we calculated Spearman′s correlation between each pair of variables. Strongly correlated variables (>0.7) were removed from the analyses (Zuur, Leno & Elphick, 2010), retaining the one more correlated with the dependent variable (Tables S2, S3, S4, S5, S6, S7). We randomly selected 80% of presences to run the model and the remaining was used for model validation.

MaxEnt analyses

On the basis of our hypothesis, goals and data quality we used a specific combination of options in the parameters of MaxEnt for each scale (Merow, Smith & Silander, 2013). First, to calculate the probability of wolf presence we used a transformation of the relative occurrence rate called logistic transformation (Phillips *et al.*, 2006). Background areas were selected based on the questions which we are asking at each scale. At distribution scale our goal was to know the environmental factors that determine the species range in the Iberian Peninsula in order to evaluate the potential for future range expansions. Therefore, we used as background area the historical range of the species which includes the entire Iberian Peninsula (4824 background points). At the scales of habitat use and breeding site selection we aimed to understand which factors may be limiting space use within the area of wolf presence. Therefore as background area we used the area defined by the minimum convex polygon of presences plus a buffer distance calculated as the radius of an average-size circular home range (8 km, Boitani, 1983; Vilà *et al.*, 1990; 6477 background points for habitat use and 9967 points for breeding site analyses respectively).

We used the default settings of MaxEnt to define the convergence threshold. In order to limit model complexity, avoid model overfitting and also facilitate the interpretation of the results, we restricted the analysis to linear and exponential effects. We explored a range of regularization coefficient values for each scale and retained the value which maximized the AUC of the cross-validation data set.

Generalized linear model analyses

We also performed the analyses applying GLMs with a binomial distribution and logit link function using the ‘glm’ function in the ‘stats’ package in R-Program (R Core Team, 2016). In the same background areas as the previous analyses we extracted the same number of random pseudoabsences as available presences (Iturbide *et al.*, 2015). We used 80% of the data to estimate the models and 20% for validation. For each scale we calculated all possible combinations of models among uncorrelated variables. For each model we calculated the ΔAICc (the difference between the minimum AICc of all models and the AICc of each model) and the Akaike Weight. Parameter estimates were calculated based on model averaging for models within ΔAICc < 2, which allows for formal inference from multiple models (Burnham & Anderson, 2004; Lukacs, Burnham & Anderson, 2010). We evaluated the validity of each model with the validation data set, and calculated the correct classification rate (the proportion of all cases that were predicted correctly), the sensitivity (the proportion of true positives that were predicted correctly) and the specificity (the proportion of negatives that were predicted correctly, Fielding & Bell, 1997).

Nested prediction

For each technique we used the coefficient estimates of the best model or the average-estimated coefficients of best models (ΔAICc < 2) at each scale to predict the potential distribution/habitat use/reproduction of wolves. We nested (restricted) the prediction of wolf habitat use within the area predicted by the distribution range model and that of breeding sites to the area obtained with the habitat use model. As our absence data were pseudoabsences, we established a cutoff for low high-quality areas for wolves based on the 90th percentile training presence at each scale (Liu *et al.*, 2005; Bean, Stafford & Brashares, 2012; Merow *et al.*, 2013), for both techniques (MaxEnt and GLM), therefore leaving out 10% of the observed presences of the training dataset.

Results

Overall, the results obtained with both methods were reasonably consistent in the predicted suitable areas at different spatial scales and in the variables involved, showing a low discrepancy between both model techniques (Table 2, Fig. 2). Variables varied in their contribution across scales (Table 2). At the scale of the distribution range, both techniques identified *Altitude* as the most relevant variable, with a quadratic effect in the case of MaxEnt and a direct positive effect in the case of GLM. *Rivers_dis*, *Urban* and *Wild prey diversity* were also relevant variables in the GLM, been negatively associated with the presence of wolves. At the scale of habitat use, for both techniques, *Altitude* provided the major contribution with a positive association with wolf presence. In the case of the GLM *Wild prey diversity* was also important and was positively associated with wolf presence. Finally, distance to roads provided the major

Table 2 Selected variables explaining wolf occurrence in the Iberian Peninsula at each of the three spatial scales, considering permutation importance and the relationship with wolf presence ('+' for positive linear, '−' for negative linear and '∩' for quadratic) for the MaxEnt model, and relative importance and averaged parameter estimates (and standard errors SE) for the selected GLMs explaining wolf presence at different scales. Estimates and SE with '−' indicate that the variable was not included in the subset of models used to calculate model averaging

Model/variable	MaxEnt Permutation importance (relationship)	GLM Relative importance	Estimate (SE)
Distribution range scale (10 × 10 km²)			
Topography			
Altitude	60.6 (∩)	1.00	2.33 (0.179)*
Slope	7.1 (+)	0.56	−0.01 (0.009)
Water availability			
Rivers_dis	24.2 (−)	1.00	−1.46 (0.152)*
Vegetation			
Closed	1.9 (+)	0.56	0.21 (0.264)
Border closed open	0.8 (+)	0.39	0.73 (1.416)
Human disturbance			
Urban	2.3 (−)	1.00	−8.75 (1.995)*
Prey availability			
Wild prey diversity	2 (+)	1.00	−0.27 (0.060)*
Livestock	1.2 (−)	0.83	0.00 (0.001)*
Habitat use scale (2 × 2 km²)			
Topography			
Altitude	74.2 (+)	1.00	4.34 (0.554)*
Slope	0.4 (+)	0.23	0.00 (0.009)
Water availability			
Rivers_dis	2.2 (+)	0.59	0.20 (0.241)
Natural vegetation			
Closed	0.3 (+)	0.50	−0.55 (1.294)
Open	8.3 (+)	0.71	1.78 (1.414)
Human disturbance			
Urban	0 (−)	0.05	−0.09 (0.709)
Agriculture	11.3 (−)	0.65	−1.35 (1.499)
Prey availability			
Wild prey diversity	0.7 (+)	1.00	0.47 (0.199)*
Livestock	2.6 (−)	–	–
Breeding site scale (1 × 1 km²)			
Topography			
Altitude	6.5 (+)	0.08	−0.03 (0.246)
Slope	0.4 (∩)	0.88	−0.03 (0.024)
Water availability			
Rivers_dis	0 (+)	–	–
Natural vegetation			
Closed_inner_dis	4.8 (+)	0.91	1.19 (0.707)†
Open	25.3 (−)	0.50	−1.028 (1.424)
Human disturbance			
Urban_dis	0 (∩)	0.08	0.00 (0.020)
Roads_dis	63 (∩)	1.00	1.19 (0.273)*
Agriculture	0 (−)	0.34	−0.46 (0.880)

*$P < 0.05$; †$P < 0.10$.

contribution for both methods in models of breeding sites. However, the relationship with the presence of breeding sites was slightly different; in MaxEnt the relationship was quadratic (positive up to a certain distance and then negative) whereas in GLM *Roads_dis* was positively related with breeding sites.

For MaxEnt models the AUC showed values of 0.73, 0.80 and 0.74 for 10 × 10 km, 2 × 2 km and 1 × 1 km respectively (Table S8). The threshold probability values obtained using the 90th percentile training presence at each scale were: 0.31, 0.24 and 0.22 for MaxEnt and 0.37, 0.35 and 0.28 for GLM at 10 × 10 km, 2 × 2 km and 1 × 1 km scales respectively (Tables S9, S10 and S11). With these cut-off values, GLM validation showed a correct classification rate for absences of 0.50, 0.58 and 0.60 for 10 × 10 km, 2 × 2 km and 1 × 1 km scales respectively (note that, as expected given the cut-offs, it was 0.90 for presences).

The potential wolf distribution range predicted by Maxent and GLM models covered 55 and 59% of the Iberian Peninsula respectively. The potential habitat for wolf within the predicted potential distribution using the nested approach covered 33% and 38% and the potential areas for breeding sites only covered 20 and 25% of the Iberian Peninsula for MaxEnt and GLM models respectively (Fig. 2). Within the current wolf range, the models predicted a potential high-quality area of 90% for both methods at distribution range scale, 56 and 64% at the scale of habitat use and 31 and 40% at breeding site scale for MaxEnt and GLM respectively.

Using the nested approach we could identify three types of areas: (1) high-quality areas within the current wolf range, (2) low-quality areas within the current wolf range and (3) high-quality areas outside the wolf range (Fig. 2). The current wolf range occupied only 35% and 33% of the high-quality areas predicted by the distribution range models for the Iberian peninsula; 37 and 36% of the predicted area at the scale of individual habitat use; and 34 and 34% of the areas predicted as suitable for reproduction, for MaxEnt and GLM models respectively (Fig. 2A). Low-quality areas within the current wolf range included small areas in the North of Portugal, the lower Duero basin and at the North East of the current distribution (Fig. 2B). Outside the current wolf range, high-quality areas represented 36 and 39% of the Iberian Peninsula at distribution range scale, 30 and 24% at the scale of individual habitat use and 13 and 17% at reproduction scale, for MaxEnt and GLM models respectively (Fig. 2C). These currently unoccupied but potentially favourable areas were located in key mountain ranges such as the Pyrenees, Baetic Systems, western Central System including Portugal and the Iberian System (Fig. 2C).

Discussion

The wolf is an important apex predator at the ecosystem level (Estes *et al.*, 2011; Ripple *et al.*, 2014). It is the only

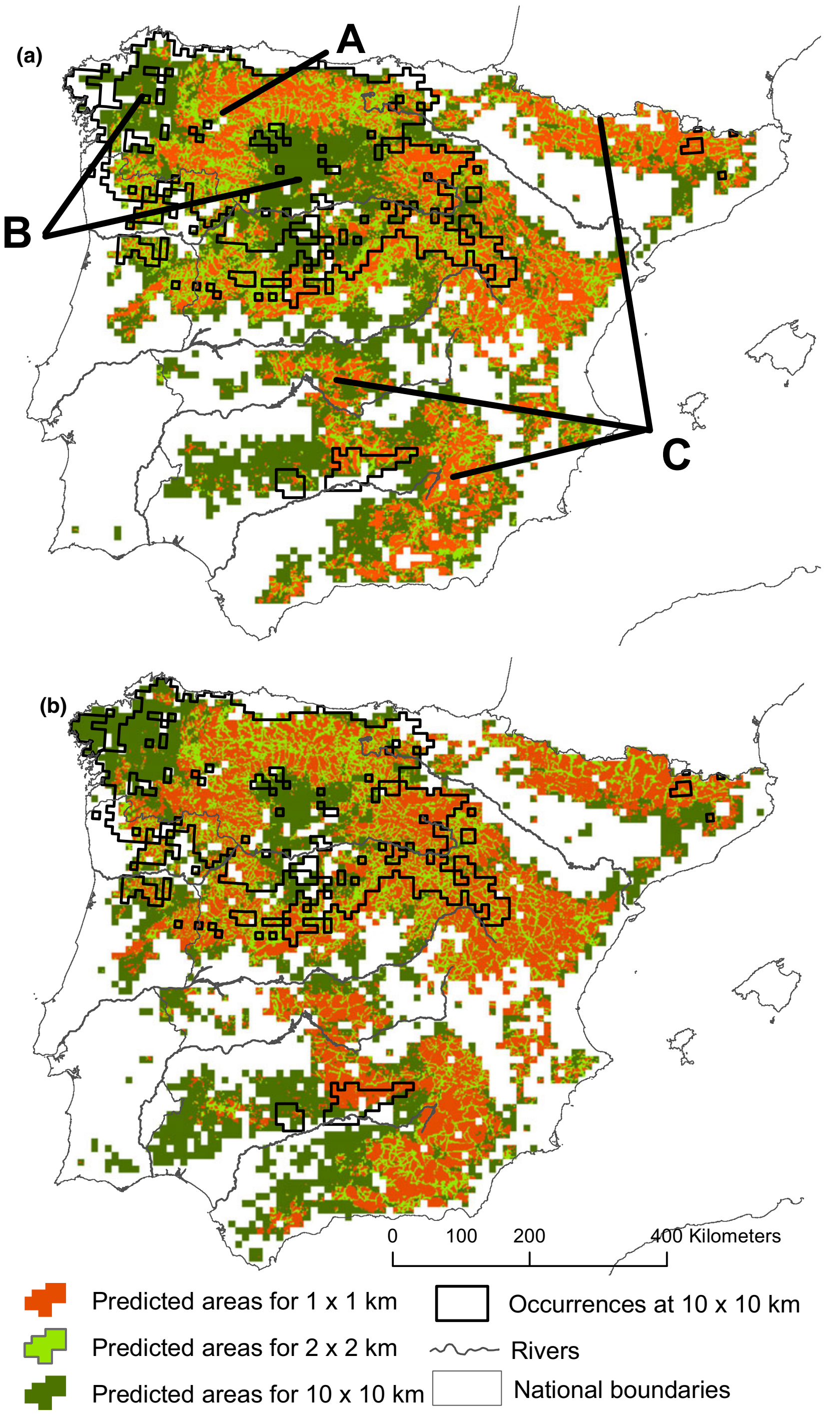

Figure 2 Current wolf range in Iberian Peninsula (black outlined squares) and predicted areas for wolf occurrence (10 × 10 km), habitat selection (2 × 2 km) and breeding sites (1 × 1 km), using MaxEnt (a) and GLM (b) model results. Predictions are nested and therefore, areas suitable for reproduction are also suitable for habitat use, and areas suitable for habitat use are also suitable for wolf range. Capital letters represent examples of high-quality areas inside current wolf range (A), low-quality areas inside the current range (B) and high-quality areas outside the current range (C) Kml files for (a) and (b) (Supporting Information Figure S1). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

large carnivore in many areas of the Iberian Peninsula, preying on wild ungulates, and using extensively farm refusal, but also feeding on domestic animals where husbandry practices are unsuitable (Cuesta *et al.*, 1991). Therefore, a good understanding of the environmental determinants of wolf space use at multiple scales is required to design science-based conservation and management strategies. In this study, we found that a complex topography, defined by the combination of altitude with proximity to rivers, and avoidance of highly humanized areas seemed to be the key factors determining wolf presence in the Iberian Peninsula. In addition, our findings show evidences that a hierarchical habitat selection process have been taking place. We found that in this human-modified landscape, wolves follow a pattern of responses in order to avoid high exposure to humans at a large scale, select areas with enough food availability at intermediate scales, and try to prevent human encounters when choosing breeding sites. The overall interpretation of these results indicates that habitat quality in our study area is mainly determined by the presence of areas acting as refuges from humans. We also found that there is a large amount of potentially good habitat for wolves in the Iberian Peninsula, including large tracts of unoccupied areas.

Key environmental factors for wolf range, habitat use and breeding locations

Topographical and anthropogenic factors seemed to shape wolf range in human-modified landscapes. Long-term persecution may have forced wolves to avoid direct human pressures. Indeed, a rugged terrain can provide safeguard by limiting human accessibility (Llaneza *et al.*, 2012; Ahmadi, López-Bao & Kaboli, 2014). However, a long coexistence with humans may have helped the species to develop adaptations to deal with varying levels of human exposure at smaller scales. Interestingly, the richness of wild prey species and refuge (altitude) seemed to greatly influence wolf habitat selection whereas domestic prey abundance was not an important factor. In fact, wild ungulates are essential for wolf populations in some regions (presence of at least one or two species present; Barja, 2009; Cuesta *et al.*, 1991; Fernández-Gil, 2004). In other areas, such as parts of Galicia, Portugal, or the Duero basin, the depletion of wild ungulate populations has led wolves to rely on livestock when vulnerable to predation, or human refuse (mainly from farms), including carrion of domestic animals (Cuesta *et al.*, 1991; Torres *et al.*, 2015). In these areas the exposure to direct human persecution is substantially increased (Newsome *et al.*, 2016). Remaining undetected by humans seemed to be the key driver in the selection of breeding sites in areas with enough refuge and food (Grilo *et al.*, 2002; Lesmerises, Dussault & St-Laurent, 2012; Dellinger *et al.*, 2013). At a small scale, distance to roads and to other human activities provided a good proxy for human disturbance and risk of mortality as shown by other studies (Linnell *et al.*, 2000; Bassi *et al.*, 2015; Sazatornil *et al.*, 2016).

Potentially suitable but unoccupied areas in the Iberian Peninsula

Our findings showed that the current wolf range in the Iberian Peninsula is not limited by a lack of suitable habitat. At a coarse scale, at least 55% of the Iberian Peninsula seemed to be favourable for wolves in terms of refuge, but only 21% is currently occupied. Given that the distribution of the species has barely changed since the mid-1980s and the significant amount of favourable habitat outside the current wolf range, other factors not quantified here may be limiting wolf expansion and hampering its further recovery. The main causes of mortality in the Iberian Peninsula are human-related (e.g. culling, hunting, poaching, poisoning and road kills), even within protected areas, and in strictly protected populations (Blanco *et al.*, 1992; Colino-Rabanal, Lizana & Peris, 2011; López-Bao *et al.*, 2015). High human-induced mortality rates (Blanco & Cortes, 2007; Barroso & Pimenta, 2008) may be limiting the number of animals available to disperse and colonize suitable areas. Even with relatively low rates of legal culling and hunting, effective dispersal can be hampered when a population has low genetic variability due to severe historical bottlenecks (Pilot, Greco & von-Holdt, 2014). It is, therefore, crucial to evaluate the role of human-induced mortality in determining the spatial distribution of the wolf in the Iberian Peninsula.

Implications for management and conservation

There is a large disparity in how wolves are managed in different places of the Iberian Peninsula based on the legal and conservation status that the species has in Portugal and Spain, and among different Spanish regional administrations, each with full competence on wolf management. Nevertheless, there is a common mandate to preserve this unique population, including the full protection of the animals south of Duero River, under Habitats Directive 92/43/EEC. A key challenge to define a science-based strategy to effectively protect this population and their habitat is the mismatch between the spatial distribution of habitat and its management (Trouwborst, 2014).

The area currently occupied by the species is highly heterogeneous in quality, with large tracts of good quality habitat associated with mountain ranges. *A priori*, these areas should be acting as sources of individuals since wolf packs are present and reproduce regularly. The long-term persistence of the whole population and the recolonization of vacant areas rely on the dispersing individuals born in good quality areas. In addition, the functional role of wolves at ecosystem level requires their protection in these areas. Although wolves in the Iberian Peninsula rely mostly on wild prey (Cuesta *et al.*, 1991; Barja, 2009), some areas are conflicting hotspots due to inadequate husbandry practices (Blanco *et al.*, 1992). As a result, regular culling is being applied in Spain, including within some National Parks (Fernández-Gil *et al.*, 2016). Therefore, the potential role of these good quality areas as key sites for the conservation of the whole population may be compromised even if located in areas with the highest level of protection.

In areas of lower quality, where wolves are also present and reproduce, we can expect a higher exposure to humans. In these heavily modified landscapes in terms of loss of native vegetation, wolves rely on farm refuse and livestock and, to a lesser extent, on wild ungulates (Cuesta *et al.*, 1991). These areas have a low availability of landscape refuge, making wolves very vulnerable to human-caused mortality. In fact, it has been observed that the expansion of the road network in areas with low habitat quality is positively related with high rates of wolf road kill and other sources of human-related mortality, including poaching (Colino-Rabanal *et al.*, 2011). In low-quality areas, the remnant fragments of vegetation offering some protection should be protected since wolves rely on them for refuge. Low-quality areas could be acting as sinks if mortality rates are high. In such a case, their maintenance would depend on the arrival of dispersing individuals from more productive areas and where survival rates are higher. However, these *a priori* expectations may not hold if human-induced mortality is biased following habitat quality. It is therefore necessary to evaluate the association in the spatial distribution of damages and wolf mortality in relation with habitat quality within the areas of current presence.

We identified extensive areas with good quality habitat where wolves are not currently present. The mobility of dispersing wolves is very high and therefore the potential for re-colonization of the Pyrenees, the Central System and the Iberian System should be high. In the case of the Pyrenees, the apparent bottleneck in the corridor linking this area with the Cantabrian range may limit the connectivity (Fig. 2) and therefore, the protection of natural vegetation and the creation of new patches that can act as stepping stones may favour a natural re-colonization from the west. It is interesting to note that wolves are arriving to the Pyrenees from the eastern Italian-Alpine population, crossing large areas of apparently very low-quality habitat (Louvrier *et al.*, 2018), instead of coming from the western region of the Peninsula. Both western Central System and southern Iberian System show also continuity in habitat quality with the main current range. The colonization of these large areas with very low human density may be limited by the intense lethal management performed in the main range, including at the south of the Duero river, where wolves are in theory protected by the Habitats Directive (Trouwborst, 2014). Thus, human-induced mortality should be carefully examined in order to identify the critical levels that allow for re-colonization.

Our results strongly suggest that the coordination of organisms and agencies acting at multiple levels, from local to cross-boundary (e.g. nature conservation institutions, forest, wildlife and road agencies) is crucial for a successful management and conservation of wolf populations in the heterogeneous habitat quality provided by human-modified landscapes. In particular for the Iberian Peninsula, a coordinated effort between Portugal and Spain is required to balance the protection and management of the shared wolf population. Finally, this study is an example of the use of available data from different sources and across scales to conduct a comprehensive analysis to define priorities for wolf conservation.

Acknowledgements

This study was conducted in the framework of a research project Wildlife corridors: Spatial modelling of human pressure and its usefulness for Iberian wolf conservation (PTDC/AAC-AMB/111457/2009) funded by Fundação para a Ciência e Tecnologia (FCT) from Ministry of Education and Science of Portugal and the Spanish Agencia Estatal de Investigación from the Ministry of Economy, Industry and Competitiveness (CGL2017-83045-R AEI/FEDER UE, co-financed with FEDER). C. Grilo and S. Roque were supported by FCT through Post-doctoral grant (SFRH/BPD/64205/2009) a pre-doctoral grant (SFRH/BD/12291/2003) respectively. P. M. Lucas was funded by the National Science Centre in Poland (2016/22/Z/NZ8/00121) through the BiodivERsA call (project BearConnect, national funders ANR/DLR-PT/UEFISCDI/NCN/RCN). We also thank the Association for the Conservation of the Iberian Wolf Habitat (ACHLI) for funding wolf monitoring. We specially thank Raquel Godinho and Diana Castro (CTM/CIBIO) for genetic analysis of wolf scats, and to Ana Guerra, Ana Pedro, Duarte Cadete, João Bernardo, Sara Pinto and Vitor Ramiro (Grupo Lobo) for conducting scats surveys. We thank the associate editor Vicenzo Penteriani, Nuria Selva and three anonymous reviewers for their constructive comments which helped us to improve the manuscript.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Table with original categories of the CLC and the categories applied to reclassified in the vegetation classes used to model the wolf occurrence in Iberian Peninsula.
Table S2. Table of correlation values between environmental variables at 10 × 10 km scale used to model wolf distribution range in Iberian Peninsula.

Table S3. Table of correlation values between environmental variables at 2 × 2 km scale used to model wolf habitat use in Iberian Peninsula.
Table S4. Table of correlation values between environmental variables at 1 × 1 km scale used to model wolf breeding sites in Iberian Peninsula.
Table S5. Results of univariate GLMs used to select correlated variables at 10 × 10 km scale.
Table S6. Results of univariate GLMs used to select correlated variables at 2 × 2 km scale.
Table S7. Results of univariate GLMs used to select correlated variables at 1 × 1 km scale.
Table S8. Results of AUC (Test data) of MaxEnt models at 10 × 10 km, 2 × 2 km and 1 × 1 km scales for different values of the Beta Multiplier parameter.
Table S9. Results for threshold values for MaxEnt models at 10 × 10 km scale to determine the environmental factors related to wolf range distribution in the Iberian Peninsula. We used the threshold value for 10th percentile training presence.
Table S10. Results for threshold values for MaxEnt models at 2 × 2 km scale to determine the environmental factors that are related to wolf habitat use in Iberian Peninsula. We used threshold value for 10th percentile training presence.
Table S11. Results for threshold values for MaxEnt models at 1 × 1 km scale to determine the environmental factors related to the location of wolf breeding sites in the Iberian Peninsula. We used the threshold value for 10th percentile training presence.
Figure S1. kml files for Fig. 2a and b.