

Brown bear habitat suitability in the Pyrenees: transferability across sites and linking scales to make the most of scarce data

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Summary

1. Identification of suitable habitats for small, endangered populations is important to preserve key areas for potential augmentation. However, replicated spatial data from a sufficient number of individuals are often unavailable for such populations, leading to unreliable habitat models. This is the case for the endangered Pyrenean brown bear *Ursus arctos* population, with only about 20 individuals surviving in two isolated groups.

2. We conducted habitat suitability analyses at two spatial scales (coarse and local). Given the limited available data, we used information from the nearby Cantabrian brown bear population in Spain to develop a two-dimensional model (human and natural variables) at a coarse scale, based on logistic regression, which we applied in the Pyrenees. At a local scale, we used bear presence in the Pyrenees to describe the population's ecological niche and develop a habitat suitability model using presence-only methods. We combined these models to obtain a more integrative understanding of bear requirements.

3. The coarse-scale model showed a good transferability to the Pyrenees, identifying preference for areas with high forest connectivity, mast trees, rugged terrain and shrubs and avoidance of areas with anthropogenic structures. The local-scale model was consistent with the coarse-scale model. Bears showed a trade-off between food resources (scarcer at high elevations) and human presence (higher at low elevations).

4. Our models illustrated that there is unoccupied good habitat for bears in the Pyrenees that could host new individuals. Combining two scales allowed us to identify areas that should be prioritized for management actions and also those that should be easier to manage for bears.

5. *Synthesis and applications.* Our study illustrates how a nested-scale approach, combining coarse data from a different population and fine-scale local data, can aid in the management of small populations with limited data. This was applied to remnant brown bear populations to identify priorities for conservation management.

Key-words: attractive sink habitat, Cantabrian Mountains, carnivore conservation, habitat model, nested scales, Pyrenees Mountains, Source habitat, spatial scale, transferability, *Ursus arctos*

Introduction

Predictive models that identify and characterize habitat suitability are important tools in conservation planning and

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management (Schadt *et al.* 2002). The scale of the analyses depends on the question (Noss *et al.* 1996; Schadt *et al.* 2002): large-scale models reveal coarse population patterns and processes more akin to whole-species distributions (Guisan & Zimmermann 2000), whereas high-resolution models offer complementary results on individual requirements and their responses to local environmental variability (Martin *et al.* 2010). It is particularly important to identify the general processes that govern habitat use in different populations. From an evolutionary perspective, general coarse-scale processes should be congruent across populations, even if actual limiting factors differ among areas, although local outcomes may differ owing to adaptations to local conditions. Large-scale global models should be transferable over broad ranges of habitats to be consistent tools for species conservation and management (Guisan & Zimmermann 2000; Klar *et al.* 2008). Transferability is especially important for rare and elusive animals, and for small populations with low-quality data, because of a lack of replicated spatial data for enough individuals. In such cases, results might be seriously biased by the idiosyncrasy of a few individuals, often involving overfitting some specific properties of the relict area and thus reducing the biological relevance of the results owing to serendipity.

One way to overcome data availability problems is to build broad-scale models using coarse-scale data from a different population, assuming that the model can be applied successfully to the focal population. Model transferability is only possible using process-based models, which tend to contain a reduced set of variables closely linked to the limiting factors (Vanreusel, Maes & Van Dyck 2007) and assuming the same limiting environmental factors in both areas. Identifying those variables is relatively easy if strong environmental gradients exist (large study areas), allowing for land uses or vegetation types of varying quality. The performance of such a model can be evaluated using the data available from the area of interest. Thus, one should be able to coarsely describe a reduced set of relevant variables and coarsely identify areas of unoccupied potential habitat. Finally, the available local data can be analysed at a finer scale to obtain more detailed information on the local management-relevant factors. This nested approach allows a global contextual description without losing the species perspective (including an easier transfer of knowledge across sites) and maximizes the available data to identify locally relevant limiting factors.

The management and conservation of large carnivores is a difficult task, because of their large spatial requirements (Noss *et al.* 1996) and the socio-political context (Breitenmoser 1998; Treves & Karanth 2003). Many species have small populations with a precarious conservation status, because of the loss and fragmentation of their primary habitats by human activities and infrastructures, resulting in closer proximity to humans and therefore conflicts (Linnell, Swenson & Andersen 2001). This is especially true in central Europe, where landscapes are crowded, modified and fragmented and where protecting sufficient suitable habitats often involves international administrative borders (Linnell, Salvatori & Boitani 2008). The Habitat Directive of the Natura 2000 network sets a legal framework

for transboundary management of habitats for 'favourable conservation status' in the European Union (EU) for some species, including the five species of large carnivores. The implementation of this network requires the identification of areas of high habitat quality.

The brown bear *Ursus arctos* almost went extinct in Europe in the past century and now is found in small, isolated populations in central and western Europe (Breitenmoser 1998; Linnell, Swenson & Andersen 2001), with one of the most endangered populations in the Pyrenees (France–Spain, Fig. 1a). After decades of persecution, this population became protected in 1979 but contained only 5–6 individuals in 1996. Following two augmentation releases from Slovenia, three adult females in 1996–1997 and four adult females and one adult male in 2006 (Linnell, Salvatori & Boitani 2008), the population has increased. Its status is still precarious, with about 20 individuals in two main population groups (western and central) that are isolated regarding female exchange (Linnell, Salvatori & Boitani 2008). The western subpopulation has contained only males since 2004 and therefore will disappear if females do not arrive naturally or by translocation. A thorough understanding of habitat quality is required to identify and quantify suitable areas to be maintained and/or restored for this critically endangered population, and also areas for potential new releases.

In this study, we aim to provide a spatial description of habitat quality for brown bears in the Pyrenees to locate areas that should be prioritized for management, including increasing their connectivity. We conducted two habitat selection analyses and developed predictive models at two linked spatial scales. First, we quantified the amount of suitable habitat for the Pyrenean population at a large spatial scale (coarse-scale environmental variables and grain to increase the generality of the predictive model). Given the low number of individuals and the limited location data for this population, we used bear presence data from the closest population (Cantabrian Mountains, Spain) to develop this model (aim 1). We used the bidimensional approach from Naves *et al.* (2003), allowing for a coarse inference of the potential demographic properties of a population occupying different areas. Second, we described the ecological niche of bears in the Pyrenees and estimated the amount of suitable habitats at a finer spatial scale (finer resolution and more accurate categories of environmental variables to identify more specific local problems) using Pyrenean bear data (aim 2). Finally, we combined the two predictive models to identify areas that should be prioritized for management, in particular in the area connecting the core areas of this population (aim 3). As for many habitat studies without fitness measurements, we used bear presence and/or abundance as a proxy to assess habitat quality/suitability.

Materials and methods

STUDY AREAS

The Pyrenees Mountains (Fig. 1a) are characterized by alternating large massifs and valleys with relatively steep slopes. Elevations

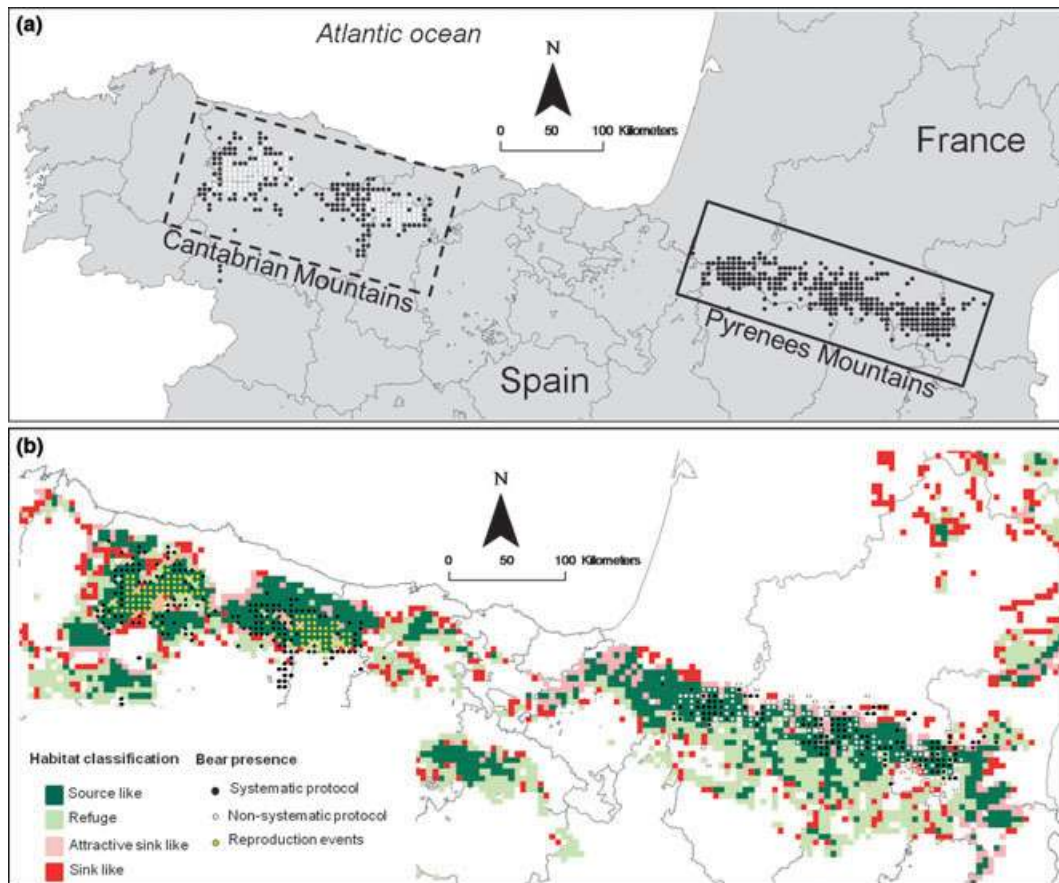


Fig. 1. (a) Location of the study areas in the Pyrenees and Cantabrian Mountains. Black dots represent brown bear presence; white dots reproduction events (for the Cantabrian population only). (b) Map of habitat quality at a coarse scale (5×5 km pixels and global environmental variables) in the Cantabrian and Pyrenees Mountains using the conceptual approach of Naves *et al.* (2003). Dots identify cells with bear presence collected during systematic (black dots) and non-systematic surveys (white dots); yellow dots identify reproduction events.

range from 500 to 3400 m. More than 40% of the area is forested, dominated by beech *Fagus sylvatica*, silver fir *Abies alba* and mixed beech-fir forests. Other dominant deciduous trees include oak (*Quercus robur*, *Quercus pubescens*), chestnut *Castanea sativa*, hazel *Corylus avellana* and gean *Prunus avium*, with common ash *Fraxinus excelsior* and common birch *Betula pubescens* at higher elevations. Common conifers are mountain pine *Pinus uncinata*, Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. Above 1800 m, rhododendron *Rhododendron ferrugineum* and heather *Calluna vulgaris* dominate, with alpine pastures and rocks at the summits. The main human activities are forestry, associated road building and cow and sheep farming. Recreational use, hunting and fishing, hiking, backpacking trips and mushroom picking occur during summer and autumn. Human density averages 5 inhabitants km^{-2} and road density is 1 km km^{-2} .

The Cantabrian Mountains (Fig. 1a) run east–west along the Atlantic coast with a maximum elevation of 2648 m. Vegetation types are similar to the Pyrenees, with forest covering 36% of the study area. North-facing slopes are dominated by oaks (*Quercus petraea*, *Q. pyrenaica* and *Q. rotundifolia*), beech, birch *Betula alba* and chestnuts, whereas south-facing forests are dominated by oaks (*Q. petraea* and *Q. pyrenaica*) and beech. Above 1700–2300 m, subalpine shrubs (*Juniperus communis*, *Vaccinium myrtillus*, *V. uliginosum* and *Arctostaphylos uva-ursi*) dominate. As in the Pyrenees, tourism and livestock (mainly cattle) farming are the main economic activities. Hunting is common, but almost all of the bear range is protected,

mainly as natural parks. Human density is 5.2 inhabitants km^{-2} and road density is 1.2 km km^{-2} .

BEAR DATASETS

The two study areas were defined as the areas surrounding bear presence, allowing random locations (for bear absences) to fall where bears could have visited (15 km from the edge of presence in each population). The Cantabrian Mountains area encompassed approximately 24 300 km^2 and 15 500 km^2 in the Pyrenees. In the Cantabrian Mountains, bear presence was recorded systematically between 1982 and 2004 (see Naves *et al.* 2003). In the Pyrenees, data were collected from 1996 to 2007, both systematically (systematic monitoring of bear presence along transects, e.g. scats) and non-systematically (opportunistic observations by hikers, hunters, foresters, etc., and validated by wildlife technicians). For systematic monitoring, about 45 paths within and around the bear distribution range were visited 2–5 times between April and June, and 2–5 times between July and November.

Coarse-scale study

The two study areas were divided into 5×5 km cells, which approximately corresponds to the size of a bear's seasonal home range (Naves *et al.* 2003). Bear presence was classified as 1 in a cell where at least one observation occurred. There were 321 cells with bear presence in

the Cantabrian Mountains, and we randomly sampled 321 cells without bear presence (classified as 0). The coarse-scale model was fitted using Cantabrian data and validated in both the Cantabrian and Pyrenees areas (see 'Analyses'). To validate the model in the Pyrenees, we used 77 cells classified with bear presence (1) based only on systematic surveys to avoid mixing different types of data. We randomly sampled 77 cells without bear presence (0) in the vicinity of the area with bear presence.

Local-scale study in the Pyrenees

For the finer-grain study, we extended the study area to encompass the entire mountain range (approximately 32 000 km²) and divided it into 200 × 200 m cells. This resolution corresponds to the minimal resolution available for the environmental variables and is a multiple of the resolution of the coarse-scale model, which facilitated the combination of the two scales (see 'Analyses'). To describe the ecological niche of the Pyrenean bears and draw a local Habitat Suitability Map (HSM), we used the data collected systematically (calibration dataset) and the data collected non-systematically to validate the model (validation dataset).

HABITAT VARIABLES

We used large-scale variables expected to be important for bears at the coarse scale: proportion of major vegetation types (forests, forests producing hard mast, shrubs, open areas), topography (terrain ruggedness) and human variables (human density, agriculture areas and roads). We chose coarse vegetation categories to ensure their representativeness in both study areas. For both areas, we calculated an index of terrain ruggedness from a slope layer derived from a 90 m digital elevation model (Consortium for Spatial Information CGIAR-CSI) and vegetation variables derived from Corine Land Cover (CLC00) obtained from the European Environment Agency (EEA, <http://dataservice.eea.europa.eu/dataservice/>) at a 250 × 250 m resolution. The human population density per municipality was derived from the Institut National de la Statistique et des Etudes Economiques (<http://www.insee.fr>) in France and from the Instituto Nacional de Estadística (<http://www.ine.es/>) in Spain. Although the periods of data collection in the Cantabrian Mountains did not exactly correspond to the habitat layers, there were very few changes in this area (see <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-1990>). We are therefore confident of the reliability of our habitat maps.

We also included variables at a larger scale than the map resolution to describe connectivity or diffusion of a given variable. As forest cover is an important habitat feature for bears (Naves *et al.* 2003; Gütthlin *et al.* 2011), we included an index of forest connectivity as the proportion of forest within pixels surrounding each focal pixel at different radii: 5, 10 and 15 km. As the risk of human-induced mortality is high for bears, we included an index of diffusion based on the human population density in the surrounding pixels, at the same radii.

To avoid multicollinearity among explanatory variables, we retained the variables with the greatest explanatory effect on bear presence among those that were strongly correlated (Spearman $r > 0.7$, see Table 1 for the final set of variables) for further analyses. The range of variables in the two areas showed a good overlap (Table 1), indicating that they were similar at this scale and resolution of the variables.

We used finer habitat variables for the local-scale analyses in the Pyrenees (Table 2). The digital elevation model and vegetation types were obtained from the same sources as for the coarse-scale analysis and summarized at the relevant resolution. In this case, collinearity among explanatory variables was not a concern (presence-only method).

ANALYSES

Coarse-scale analysis

Following the approach of Naves *et al.* (2003), we built three logistic regression models of bear presence and absence from the Cantabrian Mountains: a general model (f_g), including all the explanatory variables; a natural model (f_n), including only variables that might affect reproductive rate; and a human model (f_h), including anthropogenic variables that might affect survival (Table 1). We used the Akaike information criterion (AIC) to select the most supported models ($\Delta AIC < 2$) among all possible combinations of variables, but without interactions, selecting the model with fewer variables. We then evaluated the accuracy of the selected general model using area under receiver operating characteristic (AUC; Fielding & Bell 1997), both with the calibration range (Cantabrian Mountains) and outside it (Pyrenees). We then classified habitat quality into five categories within the two-dimensional space using the best natural and survival models (see Naves *et al.* 2003 for a throughout description and validation of this approach). This approach assumes that selection is potentially related to fitness: source-like habitats are good for both

Table 1. Description and units of environmental variables used in the coarse-scale (5 × 5 km cells) models for brown bears in the Cantabrian Mountains (Spain) and the Pyrenean Mountains (France–Spain) study areas

Variables	Label	Type	Description	Cantabrian Mountains	Pyrenean Mountains
Terrain ruggedness	Rugged	Natural	(mean + standard deviation) of slope in degrees	1.25–48.6	2.7–42.8
Shrub cover	Shrub	Natural	% shrub	0–0.90	0–0.57
Open areas	Open	Natural	% natural open areas	0–0.78	0–0.81
Mast tree cover	Mast	Natural	% deciduous and mixed forest cover	0–0.98	0–0.97
Forest connectivity $r = 3$	F_connect_3	Natural	% forest in the pixels up to 15 km surrounding the focal pixel	0.08–0.61	0.17–0.76
Diffusion human population	Diff_Pop	Human	Density of inhabitants in the pixels up to 5 km surrounding the focal pixel	2.1–631	1.4–389
Agricultural areas	Agri	Human	% agricultural area	0–1	0–0.93
Road	Road	Human	Length of roads (km)	0–27.7	0–20.1

Table 2. Description and units of environmental variables used for the local-scale analysis (200 × 200 m cells) of ecological niche of Pyrenean brown bears and the Habitat Suitability Map

Variables	Label	Description
Slope	slope	In degrees
Distance to urban areas	d_urban	Include towns and anthropogenic structures such as building, artificial areas... In metres
Distance to agricultural areas	d_agri	Include arable lands, permanent crops, pastures... In metres
Distance to roads	d_road	Public roads with high traffic. In metres
Distance to deciduous forests	d_decid	Mainly made of European beech <i>Fagus</i> sp., European chestnut <i>Castanea</i> sp., oaks <i>Quercus</i> sp. and birch <i>Betula</i> sp. In metres.
Distance to coniferous forests	d_conif	Mainly made of fir <i>Abies</i> sp. In metres.
Distance to mixed forests	d_mixed	Mixed forests (deciduous and coniferous) In metres.
Distance to shrubs	d_shrub	Vegetation with low and closed cover, dominated by bushes, shrubs and herbaceous plants. In metres.
Distance to regenerating forests	d_regfo	Forest regeneration (after degradation) or colonization. In metres.
Distance to lake	d_lake	In metres.
Distance to natural open areas	d_open	Natural grassland. In metres.

survival and reproduction, refuge-like habitats are good for survival but not reproduction given the low level of natural resources, attractive sink-like habitats are good for reproduction but are dangerous and can be considered as ecological traps and sink-like habitats are poor-quality habitats. No demographic data, apart from presence data, were used in the source-like/sink-like terminology, but we matched the little available demographic data on mortality and reproduction against model output.

Local-scale analyses in the Pyrenees

We used two complementary hindcasting methods to describe the Pyrenean population's ecological niche: the Mahalanobis distance factor analysis (MADIFA, Calenge *et al.* 2008) and the ecological niche factor analysis (ENFA, Hirzel *et al.* 2002; Basille *et al.* 2008). They have the advantage of not requiring absence data and being robust to expanding populations and collinearity among environmental variables. Because we wanted to estimate minimum habitat suitability for the entire Pyrenees, we extended the study area to encompass the entire mountain range.

MADIFA is related to Mahalanobis distances, calculating the departure from the species' niche optimum (centroid of the species distribution) and directions in ecological space where the niche is narrowest compared to the available environment (Calenge *et al.* 2008). The smaller the distance, the more similar the habitat is to the niche. We used this method to compute HSM using approximate Mahalanobis distances (d) from the dominant extracted axes, reducing some of the noise that may be induced when using direct Mahalanobis distances (Calenge *et al.* 2008). To select the axes used in the analyses, we examined the barplot of the eigenvalues and calculated the percentage of variance explained by the first axes.

We measured the goodness-of-fit (G) of the resulting prediction by calculating the area between the empirical cumulative density of the approximate Mahalanobis distances computed for the study area cells, and the calibration and validation datasets, respectively. To provide a standardized measure of the prediction quality, we divided these values by the total area above the empirical cumulative density for all study area cells (Calenge *et al.* 2008). We also computed a continuous Boyce index (Hirzel *et al.* 2006) to classify habitat into three categories (good, suitable and poor) to help interpret the model. We divided d into 10 classes and estimated the predicted-to-expected

ratios (F_i) for each class i , using the validation dataset. F_i are the ratios between proportions of use of class i and the expected frequency based on random use of the study area. We used a bootstrapping procedure to estimate the mean and standard error of F_i , using 100 samples of 500 observed bear locations. $F_i = 1$ indicates random use, $F_i < 1$ indicates poor habitat and $F_i > 1$ indicates selection for the habitat. We then distinguished between suitable and good habitats using the clear break in the slope of the curve relating approximate Mahalanobis distance classes and the F_i (good habitats during the strong decrease, suitable habitats when the slope became less steep, see Fig. 4).

ENFA extracts global marginality (a measure of the difference between what is available and what is used by a population, i.e. a measure of the strength of selection) on the first axis and global specialization, which measures the niche breadth (the ratio between the variance of available conditions and the variance of used conditions) on the other axis. We used the same method as for MADIFA to select which tolerance axes to keep in the analysis. We performed a randomization test to assess the significance of the analysis using 1000 sets of 1529 available random locations. MADIFA and ENFA are complementary analyses to distinguish the parts of the approximate Mahalanobis distances related to marginality or specialization (Calenge *et al.* 2008).

Comparison and combination of scales

Before combining the coarse- and local-scale models, we compared their predictions in terms of habitat quality (e.g. are the best habitat quality cells at large scale, source-like, predicted as good quality at fine scale, low d values?). Then, we classified pixels within each habitat category at the large scale based on habitat quality at the local scale. We calculated the mean and coefficient of variation of d (D and C_v , respectively) of the local-scale cells (200 × 200 m) within each coarse-scale model cell (5 × 5 km). We then calculated the range, mean, standard deviation and median of D for each of the five habitat categories of the coarse-scale model to describe the distribution and variance of D in each category. We focused the combination of models on source-like, attractive sink-like and refuge habitats, as they are optimal or sub-optimal habitats and the potential focus for management actions. Separately for each of the three categories, we ranked the cells based on D and C_v . Highest-ranked cells were those with values

of D lower than the median D of source-like habitats and low dispersion ($C_v < 0.5$). Medium-ranked cells were only those with values of D lower than the median D of source-like cells. All other cells were ranked lowest. Highest- and medium-ranked cells might be more efficiently managed for bears because of higher quality at the fine scale.

Results

COARSE-SCALE ANALYSIS

Model outcomes and evaluation

The best general model contained six variables (Table 3): percentage shrub cover, terrain ruggedness, percentage forest containing hard-mast species, forest connectivity at the 15 km scale, roads and diffusion of human density. The next parsimonious model ($\Delta AIC = 0.30$) included agriculture. The most parsimonious and simple natural model contained the same natural variables as the general model (i.e. shrub cover, masting cover, terrain ruggedness and forest connectivity at 15 km), with the next model ($\Delta AIC = 1.77$) including open areas. The human model we retained contained roads and diffusion of human density, as did the general model, but it also included percentage agricultural areas (ΔAIC with the next model = 4). The general model was reliable in predicting bear presence and absence in the Cantabrian Mountains (calibration dataset, $AUC = 0.77$). In the Pyrenees (outside the calibration range), the model predicted bear presence consistently ($AUC = 0.75$).

Habitat classification

The explained variance of the linear regression between the general model and the average of the natural and human models ($f_n + f_h$)/2 = 0.17 + 0.65 f_g was high: $R^2 = 0.94$. Following Naves *et al.* (2003), the threshold for matrix

habitat was defined, so that only 5% of bear presence was in the matrix (i.e. when $f_n < 0.24$ or $f_h < 0.31$). We then classified a cell as source-like when $f_n > 0.5$ and $f_h > 0.5$; attractive sink-like when $f_n > 0.5$ and $f_h < 0.5$; refuge when $f_n < 0.5$ and $f_h > 0.5$; and sink-like when $f_n < 0.5$ and $f_h < 0.5$. We mapped these categories in both areas (Fig. 1b). The pattern of habitat quality in the Cantabrian Mountains was consistent with Naves *et al.* (2003), but our model classified more cells as source-like habitats. Our model distinguished two core areas of good quality separated by lower-quality areas in both areas.

Most bear presence was found in source-like habitats (66% of bear presence and 78% of reproduction events in Cantabrian Mountains; 61% of bear presence collected systematically and 66% for bear presence collected non-systematically in the Pyrenees). In the Pyrenees, females with cubs were found mainly in source-like habitats (89% of the observations; Table S1, Supporting Information). Between 1997 and 2010, hunter-caused mortality ($n = 2$) occurred in source-like and attractive sink-like habitats, one fatal vehicle collision in a matrix area and natural deaths ($n = 5$) mainly in source-like habitats (Table S1, Supporting Information).

In the Pyrenees, our model classified few areas as attractive sink-like. These were mainly at the periphery of source-like habitats, at low elevations and close to urban areas. However, it identified much refuge habitat, mainly at high elevations in the southern half of the mountain range, which is less forested. Two connected source-like habitat patches were unoccupied. In the Cantabrian Mountains, large and connected areas encompassing source-like habitats are protected (within the European network Natura 2000, Fig. 2), whereas in the Pyrenees, the protected areas are more fragmented and a large area of source habitat with bear presence is outside the network (Fig 2).

LOCAL-SCALE ANALYSIS

Using the broken-stick method (Jackson 1993), we retained one axis of specialization for ENFA (30% of variability) and two axes for MADIFA (42% and 18% of variability). ENFA was highly significant (randomization test, $P < 0.001$) with a marginality of 5.5, meaning that the bears' niche in the bear in Pyrenees was different from the average available condition. The two analyses were consistent, with the first MADIFA axis correlated highly with ENFA marginality ($r = 0.89$) and the second MADIFA axis correlated highly with ENFA specialization ($r = 0.99$). Bears selected steep slopes, forested areas (especially mixed forests) and large distances to agricultural areas, but also open areas (Fig. 3a). Bears selected a small range of medium distances to urban areas (Fig. 3a, specialization axis).

Goodness-of-fit of the HSM computed from the MADIFA axes was high, both for the calibration and validation datasets ($G \geq 97\%$; Fig. S1, Supporting Information). Using the slope of F_i against i (Fig. 4), we classified cells with $d \leq 2.5$ as good quality and cells with $2.5 < d \leq 4.5$ as suitable. We mapped

Table 3. Parameter estimates for the brown bear habitat models selected at coarse scale, based on data from the Cantabrian Mountains (Spain)

Models	Variables	β	SE	P -value
General model	Constant	-3.62	0.53	<0.001
	Shrub	1.78	0.59	0.003
	Rugged	0.08	0.01	<0.001
	Road	-0.07	0.03	0.015
	Masting	1.44	0.55	0.009
	F_connect_3	3.61	1.14	0.002
	Diff_pop	-0.02	0.005	<0.001
Natural model	Constant	-4.28	0.53	<0.001
	Shrub	2.14	0.85	<0.001
	Rugged	0.08	0.01	<0.001
	Masting	1.61	0.55	0.003
	F_connect_3	3.70	1.11	<0.001
Human model	Constant	0.72	0.13	<0.001
	Road	-0.06	0.03	0.016
	Diff_pop	-0.02	0.01	<0.001
	Agri	-3.61	0.72	<0.001

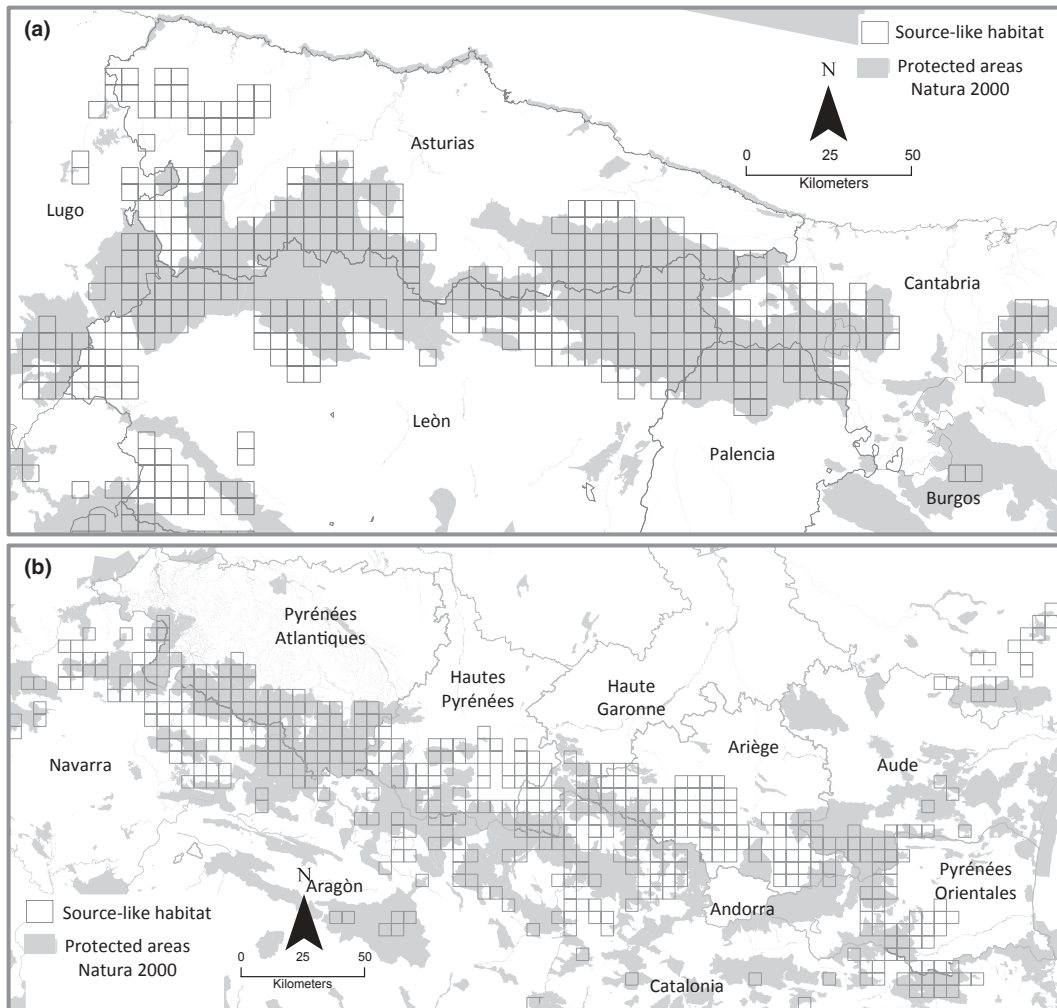


Fig. 2. Map of brown bear habitat quality at a coarse scale (5 × 5 km pixels) in the Cantabrian (a) and Pyrenean mountains (b), and the Natura 2000 network of protected areas (European Directive for Habitat Preservation).

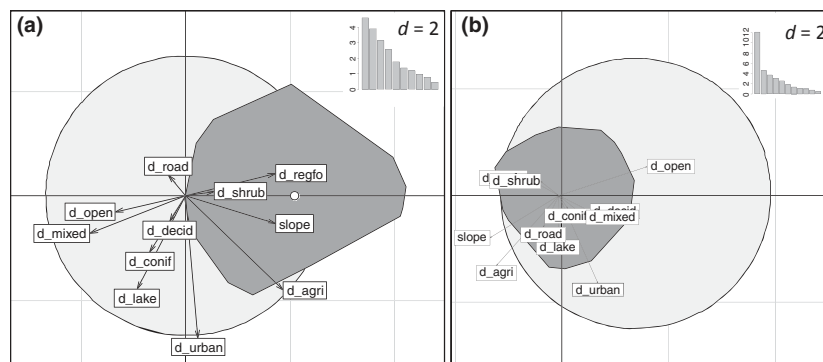


Fig. 3. Biplot of the ecological niche factor analysis (a) and the Mahalanobis distance factor analysis (b) for brown bears in the Pyrenees. (a) The horizontal axis represents the marginality, the vertical axis the first specialization axis and the upper panel is a barplot of eigenvalues of specialization axes. (b) The upper panel is a barplot of eigenvalues of the MADIFA. For both biplots, the light area represents the environmental availability for the bears and the darker area represents the brown bear niche. The arrows represent the correlation of environmental variables to the axis of the analyses.

habitat quality at a fine scale from the model, superimposing source-like habitats from the coarse-scale model to help compare the two models (Fig. 5a).

Females with cubs were observed mainly in good and suitable habitats (80% of the locations). Hunter-caused mortality occurred in suitable habitats, vehicle collision in poor habitat

and natural mortality in all categories (Table S1, Supporting Information).

COMBINATION OF MODELS

Overall, good and suitable habitats predicted at the fine scale were located within source-like habitats predicted by the coarse-scale model (Fig. 5b). Range, mean, standard deviation and median of D for each coarse-scale classification category are provided in Table 4. Source-like habitats had the lowest values of averaged D (Table 4), followed by attractive sink-like habitats, refuge habitats, sink-like habitats and avoided matrix. The median D for source-like habitats was 5.7. High-rank cells of source-like, attractive sink-like and refuges therefore were those having values of $D < 5.7$ with $C_v < 0.5$. Medium-rank cells had values of $D < 5.7$ and $C_v \geq 0.5$. The remaining were low-rank cells (with $D > 5.7$). Among source-like cells, 28% were classified as high rank by the local-scale model, 30% as medium rank and 42% as low rank (Fig. 5b). Among refuge pixels, 18% were high rank, 8% medium rank and 74% low rank. Among attractive sink-like habitats, 8% were high rank, 17% medium rank and 75% low rank.

Discussion

Our model revealed that the underlying processes of habitat selection were similar between the two populations at the coarse scale, as it showed good transferability outside its calibration range. As expected, bears preferred areas with high hard-mast tree cover, sufficient forest connectivity and rugged terrain, which is consistent with the literature (although at different spatial scales, Apps *et al.* 2004; Nellemann *et al.* 2007; Martin *et al.* 2010). Bear presence was negatively correlated with high road density and high human density, and the human model also indicated a negative influence of agricultural areas. Although agricultural areas were not particularly correlated with human density ($r = -0.02$), bears might have perceived them as risky.

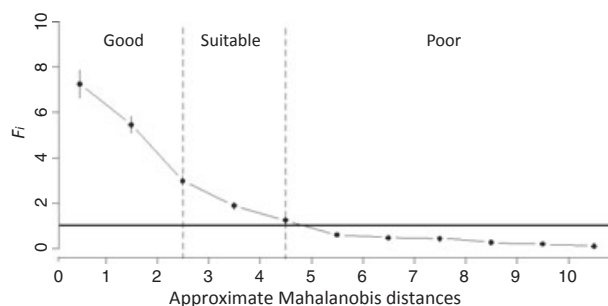


Fig. 4. Plot of average and standard error of predicted-to-expected ratios (F_i) of the validation dataset on 11 classes of approximate Mahalanobis distances from the MADIFA analysis computed for brown bears in the Pyrenees. The solid line corresponds to a random use of the habitat ($F_i = 1$). Below this threshold, the habitat is considered unsuitable or poor; above it the habitat is suitable. We chose 2.5 as the boundary between good habitat and suitable habitat, because of the clear break in the curve.

Attractive sink-like areas corresponded to areas with high resource availability and anthropogenic structures, the very definition of attractive sink habitats for bears (Naves *et al.* 2003). Refuge habitats had few resources, but were in areas far from anthropogenic structures (high elevations). In the Pyrenees, the two core areas of source-like habitats corresponded well to bear presence (Fig. 1b), but our model identified large tracts of source-like habitat that were not occupied. However, these areas were connected via refuge habitats. Because females have a lower dispersal probability than males (Zedrosser *et al.* 2007) and the resource quantity in those areas is low (which might be interpreted as poor habitat for reproduction), the probability of females colonizing those habitats and connecting to the western population segment may be low. Nevertheless, a remnant connection of source habitats between the core areas in the north could represent a potential corridor. At a larger scale, our HSM does not portend an exchange of individuals between the Cantabrian and Pyrenean Mountains, because matrix habitat separates them (Fig. 1b).

We found strong agreement between the patterns at the local and coarse scales; suitable habitats predicted from the local-scale model were located in source-like habitats (Fig. 5a). Bears selected short distances to forested areas that produce hard mast and medium distances to urban areas (Fig. 3). As deciduous forests tend to be close to human infrastructure, we interpreted this behaviour as a trade-off between food resources and security. Bears may seek this type of forest, but try to remain as far as possible from anthropogenic structures. At the coarse scale, brown bears selected areas with low road density, whereas at the local scale, they were unaffected by roads. It should be noted, however, that vehicle collisions are not negligible in the Pyrenees (two collisions in 1997–2010, one fatal; Camarra & Touchet 2009) nor in other brown bear populations (Italy, eight collisions with vehicles in 9 years, C. Groff, personal communication, see also Mertzanis *et al.* 2008).

The combination of models for the attractive sink-like and refuge categories identified several areas that should be higher quality, based on the local-scale model, especially in the northern area connecting the two population segments (Fig. 5b). The management of attractive sink habitats is often difficult because two strategies can be adopted, reducing the risk of mortality or reducing the attractiveness for bears (Nielsen, Stenhouse & Boyce 2006; Falcucci *et al.* 2009). Ranking large-scale attractive sink-like areas using local-scale preferences may facilitate the choice between the two strategies, those with high values based on the local-scale model and located in strategic areas may be more successfully managed to reduce potential mortality risk than those of poorer quality, because they are more similar to source-like habitats. Similarly, refuge habitats with high values based on the local-scale model may be easier to manage (because of their potentially greater resources), for example by increasing forest connectivity/cover in low-elevation areas.

The bear range in the Pyrenees is expanding (in the Cantabrian range, used for the coarse analyses, it has been stable for several decades). Thus, it is impossible to distinguish

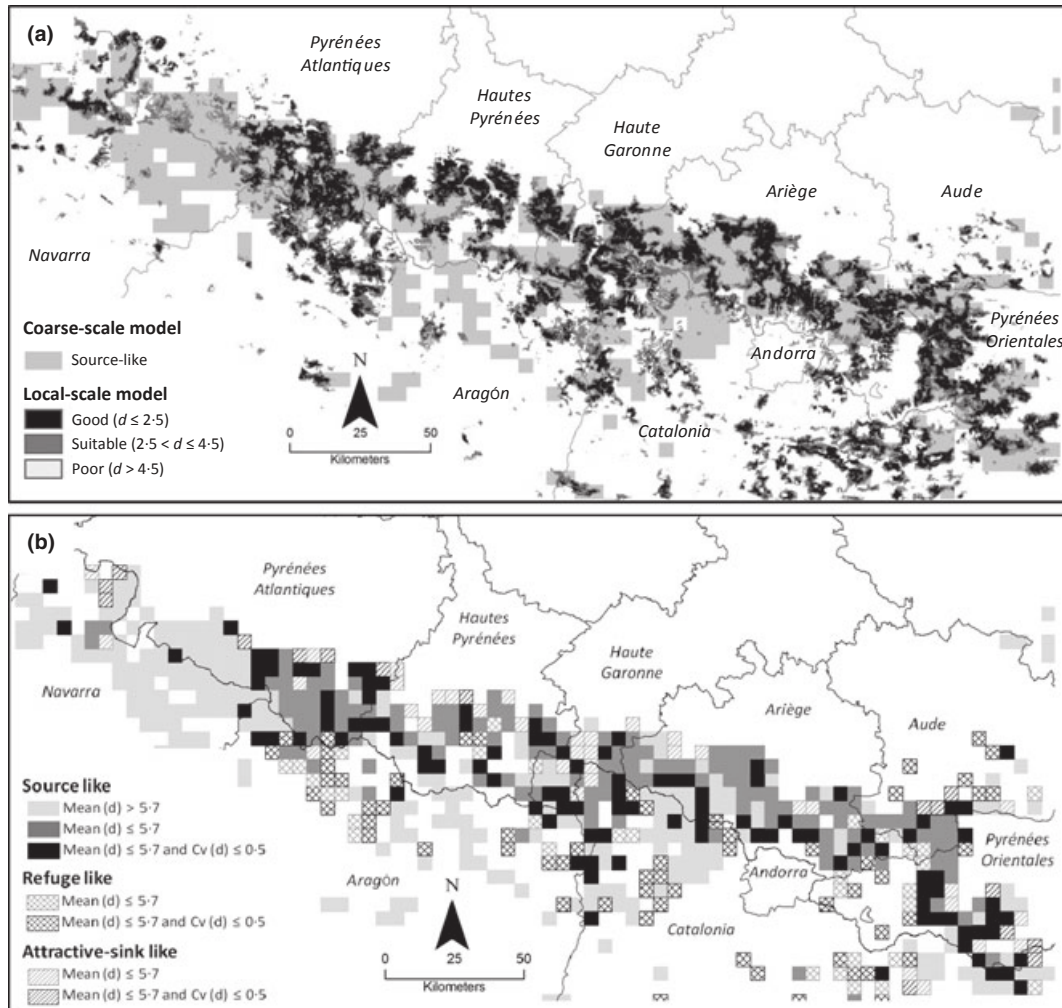


Fig. 5. (a) Habitat suitability map for the brown bear in the Pyrenees, computed from the two-first axes of the MADIFA. Habitat quality was divided into three classes based on the predicted-to-expected ratios; F_i , calculated from the validation dataset. (b) Combination of the coarse and local-scale habitat models for the brown bears in the Pyrenees. Each 5×5 km cell of the coarse-scale model was ranked according to mean values of the approximate Mahalanobis distance (d) on the 625 cells (200×200 m) of the local-scale model composing each large-scale cell and the coefficient of dispersion (C_v) of d . Black colour indicates the highest rank within each category of coarse-scale pixels; dark grey indicates medium rank and light grey indicates lower rank.

Table 4. Summary of the combination of predictive values of coarse and local-scale habitat models for the Pyrenean brown bear population. D corresponds to the average approximate Mahalanobis distances (d) on 200×200 m pixels of the local-scale model within each 5×5 km pixels of the coarse-scale model

Coarse-scale model classification	Local-scale model (D)			
	Range	Mean	SD	Median
Source-like	1.9–14.9	6.2	2.6	5.7
Attractive sink-like	2.6–15.0	6.6	2.4	6.6
Refuge	2.7–18.2	8.4	2.9	8.3
Sink-like	3.5–16.9	8.9	3.1	9.2
Avoided matrix	1.5–22.0	11.3	3.9	11.6

unsuitable areas from those that are suitable but still unoccupied, which underestimates the power of explanatory variables (Boyce & McDonald 1999). High-quality habitats classified by

our fine-scale model are therefore the minimum suitable areas for bears. However, we did not test our coarse-scale model with demographic data *per se*. Nevertheless, almost 80% of the recorded reproduction events in the Cantabrian and Pyrenees Mountains were in source-like habitats. To date, little demographic data are available in the Pyrenees, but more should be obtained in the future to validate the model.

CONSERVATION IMPLICATIONS AND PERSPECTIVES

The Pyrenees apparently provides much good habitat for brown bears much of which remains unpopulated and likely could support additional bears. Although 79% of the source-like habitat is occupied (vs. 86% in the Cantabrian Mountains), the population density is very low (0.28 individuals 100 km^{-2} of source-like habitat vs. 2.1 in the Cantabrian Mountains). Based on the observed density in the Cantabrian

Mountains, we can crudely calculate that the Pyrenees has enough habitat to support more than 110 individuals, which would result in a more favourable conservation status (Chapron *et al.* 2003). If an augmentation programme was planned, individuals should be released into these source-like habitats adjacent to the actual bear distribution to enhance encounters between individuals, especially with the males of the western segment. Chapron *et al.* (2009) suggested that translocating 13 females would be required to ensure population recovery. The western area apparently could support this number, especially in the west. Some males also occur in the very east of the central segment, but there habitat quality probably would not support many additional individuals. However, releasing female bears in the eastern part of the central population segment might encourage contact with males from the east.

We identified only a few attractive sink-like habitats, mainly in the French valleys. Those of higher quality (low *D* values) and between source-like habitats or that connect populations segments (Fig. 1b) should be prioritized in conservation planning to encourage female exchange. Human disturbance should be regulated in these areas (e.g. hunting, resort facilities and forest logging). However, the attractiveness of attractive sink-like areas with lower fine-scale quality and/or located at the periphery of bear presence could be reduced to reduce the risk of human-caused mortality (e.g. increase/start forest logging and electrified barriers near potential food resources, such as beehives or fruit tree plantations and better rubbish management). The best refuge habitats, and especially those located in strategic areas, should also be managed effectively to promote forest cover, especially hard-mast species to increase resource quality. However, refuge habitats are located mainly at high elevation, where ecological conditions are not suitable for those tree species. Thus, these management actions can be applied only at low elevations.

Persecution was the main cause of population decline in the Pyrenees. Today, the demographic parameters of the central segment are similar to other south European populations (Chapron *et al.* 2003), but the recent loss of three adult females (2004–2007) precipitated a low reproductive rate, the most sensitive demographic parameter, explaining the poor population recovery (Chapron *et al.* 2009). Our large-scale model provides a solid basis for habitat management by targeting crucial habitats based on demographic parameters. To reduce mortality, management should be oriented towards mitigating the impact of anthropogenic structures and regulating human access to attractive sink-like habitats. If the main impediment of population recovery is low reproductive rate, management actions should focus on maintaining resource productivity, for example in source habitats. Presently, given the low number of individuals and the abundance of unoccupied source habitats, the most urgent action would be releasing additional females in good habitats, if politically feasible.

These management recommendations are easier to implement and more effective within protected areas. In the Pyrenees, the protected areas defined by the Natura 2000 network are fragmented and much source-like habitat with bear presence is outside the network. Our analyses provide a solid basis

to define where expansion of the Natura 2000 network is desirable for bear conservation and where corridors would enhance connectivity between population segments.

Finally, our spatially explicit tool can be used by managers and decision-makers to identify where the population is likely to expand and to develop appropriate strategies to minimize the future conflicts with human activities (e.g. anticipating social acceptance, one of the main challenges for carnivore conservation).

SYNTHESIS AND APPLICATION

Our study showed how the combination of spatial scales in habitat modelling can be used to develop effective management tools for a small population with little available data. We overcame the problem of overfitting data from too few individuals by using large-scale data from the nearest population and the link with local-scale data improved the reliability of the predictive maps. In addition, this multiscale approach provided an integrated tool for conservation planning for this relict population, as it allowed ranking of habitats that should be prioritized, but also are potentially easier to manage, both technically and economically. If data from another population are available, this approach may be used on any species or population suffering the same data constraints.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Cumulative frequency distribution of the approximate Mahalanobis distances computed using the first and second axis of the MA-DIFA for the brown bears in the Pyrenees Mountains.

Table S1. Location of brown bear mortality and reproduction events in the Pyrenees Mountains for each habitat model.

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