



Brown bears at the edge: Modeling habitat constrains at the periphery of the Carpathian population

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ABSTRACT

The utility of habitat models for species conservation relies on the integration of ecological knowledge into the modeling process. However, this practice is often limited by incomplete information on the study species requirements and insufficient efforts to adopt robust inference modeling approaches. We developed occurrence and breeding habitat models for the European brown bear *Ursus arctos* in the Northern range of the poorly-known Carpathian population, focusing on the evaluation of a restricted set of hypotheses based on prevailing insights on the species constrains. Hypotheses were confronted using a dataset of 3151 bear observations in Poland for the period 1985–2005. Forest availability was the most important limiting factor, whereas anthropic factors (human density and urban areas) separated between suitable and non-suitable forest-rich areas. Forest composition contributed poorly to predict bear occurrence but was important to differentiate between breeding and non-breeding habitats: breeding females required a larger amount of forest cover, lower human influence and the interspersed of grassland/shrubland patches. Model transfer to the western Carpathian population in Slovakia supported the accuracy of habitat predictions and the robustness of the approach. Results highlight the need to control unplanned urban sprawl to preserve the species habitat and the connectivity between the Western and Eastern segments of the Carpathian population. Predicted but unoccupied habitats in other regions also require consideration, particularly some favorable areas of confluence with other large carnivore habitats. We encourage adopting robust hypothesis testing approaches in habitat modeling in order to support better model transferability and conservation planning.

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1. Introduction

Preserving large mammalian carnivores in human-dominated landscapes remains one of the biggest challenges facing biological conservation (Redford, 2005). In the last two centuries, widespread extinctions of large carnivore populations have occurred in strong association with increasing human density (Woodroffe, 2000). The high vulnerability of these species is explained by a characteristic set of biological traits that complicate their coexistence with humans, including large body size, predatory behavior, high spatial requirements, low fecundity rates and, often, high habitat specificity (Purvis et al., 2000). Moreover, damages caused by large carnivores, such as predation on game and livestock, are often perceived as a threat to economic values, causing negative attitudes against these species conservation efforts (Graham et al., 2005). Far from being mitigated, the frequency of interactions between carnivores and humans is escalating (Treves and Karanth, 2003), not only due

to the continuing expansion of human populations but, paradoxically, also as a consequence of the return of large carnivores to some areas where they had been previously extirpated (Enserink and Vogel, 2006).

Habitat conservation problems faced by populations at risk are being increasingly addressed through the predictive modeling of species-habitat relationships (e.g. Guisan and Thuiller, 2005). These approaches are typically based on the evaluation of species distributions in relation to spatial patterns in resource availability and stressors (Boyce and McDonald, 1999). A relatively good understanding of habitat-related threats has been achieved in this way for many species. In particular, studies in different populations of charismatic carnivores such as the brown bear have allowed an understanding on habitat constrains under a diversity of environmental settings (e.g. Naves et al., 2003; Katajisto, 2006; Falcucci et al., 2009). In principle this should represent an advantage for the conservation planning for less-known populations since inference from other populations would improve habitat predictions. However, the extrapolation of model predictions may be highly problematic due to both methodological and ecological factors

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(Fielding and Haworth, 1995). On the one hand, environmental variables used in habitat modeling may not correlate evenly with the resources and limitations actually affecting the species distribution, implying that the ecological significance of predictions may be compromised. On the other, species may locally respond to habitat constraints through specific behavioral and phenotypic adaptations, making generalizations uncertain. Moreover, different habitat studies have supported contrasting hypotheses on species distribution constraints depending on the study population. For example, Naves et al. (2003) found that brown bears responded differently to human pressure and natural vegetation in two nearby populations in Northern Spain, with bears occupying habitats with low human pressure but suboptimal vegetation structure in one population while showing a higher tolerance to humans in another population with better natural conditions. Potential failures in model extrapolation calls for caution against the temptation of generalizing management guidelines across regions and emphasizing the conservation importance of understanding population-specific responses to environmental constraints (Randin et al., 2006; Whittingham et al., 2007; McAlpine et al., 2008; Rhodes et al., 2008).

Alternatively, previous insights from species-habitat relationships can help to identify the relevant hypotheses, predictors and candidate models and therefore improve habitat predictions. So far, a large amount of species modeling approaches have prioritized practical questions regarding the production of predictive maps while neglecting the ecological theory and implications underneath (Guisan and Thuiller, 2005). A great array of statistical methods has been developed to link species distribution patterns with complex descriptions of the environment (e.g. Elith and Graham, 2009) and our capacity of collecting environmental data to apply these methods is also increasing. However, better modeling resources do not necessarily ensure a deeper understanding on the ecological processes affecting species distributions (Wiens, 2002). The prior generation of biologically realistic hypotheses and the identification of candidate models accordingly is of key importance in the process of ecological inference (Johnson and Omland, 2004), particularly in model applications aimed at improving the conservation status of species and their habitats (Fernández et al., 2003; Vanreusel et al., 2007; Klar et al., 2008).

We studied environmental factors limiting the distribution of the Eurasian brown bear (*Ursus arctos arctos*) in a peripheral population of the Carpathian Mountains evaluating hypotheses derived from habitat studies throughout Europe. Brown bears in Europe have been declining since the 1600s and 1700s and most dramatically during the last 120 years, although in recent decades some populations have slowly recovered (Curry-Lindahl, 1972; Servheen, 1990; Swenson et al., 2000). The Carpathian population is a paradigmatic example: intense persecution and land cover changes led to a dramatic population decline and the fragmentation into two main subpopulations in the early 20th century. Agriculture abandonment, depopulation and the legal protection reversed this trend and favored the population expansion after World War II and until the 1980s (Jakubiec, 2001). However, the population still faces important conservation problems: recent studies suggest that the population retains genetic differentiation between the Western and the Main Carpathian populations despite of the geographic proximity of the subpopulations (Straka et al., 2012), whereas habitat fragmentation and human disturbance are presumed to limit the species distribution nowadays (Koreň et al., 2011).

According to Eurasian brown bear habitat studies in a variety of environments, three general, non-excluding hypotheses can be formulated:

- (1) Individuals are primarily restricted to forest-dominated areas where they find nutritional and refuge resources required for maintenance, hibernation and reproduction

(Naves et al., 2003; Posillico et al., 2004; Katajisto, 2006). Moreover, forest composition is a key determinant of habitat quality due to the high nutritional requirements of the species, its dependence on hard and soft mast during hyperphagia and the need for alternative food resources throughout the year (Preatoni et al., 2005; Moe et al., 2007).

- (2) Landscapes with high topographic complexity are preferred since they provide better sheltering opportunities, denning sites and complementary feeding habitats (Nellemann et al., 2007; May et al., 2008; Guthlin et al., 2011).
- (3) Human activities negatively affect brown bear habitat due to direct disturbance and persecution. These activities may cause bear avoidance and decrease the quality of the species habitat (Wiegand et al., 2003; Nellemann et al., 2007; Ordiz et al., 2011; Martin et al., 2010).

We evaluated these hypotheses through brown bear habitat models developed in Southern Poland, which represents the northernmost limit of the Carpathian population. In addition, we aimed to assess the application of the resulting models to understand the species constraints in other areas, a prerequisite to support the importance of our model results for the population conservation. For this, we evaluated the accuracy of model predictions in the neighboring Slovakia, where >95% of the West-Carpathian population is distributed (Rigg and Adamec, 2007).

Most predictive habitat models exclusively rely on incidence data, however, it is critical to understand how habitat variables are linked to habitat quality and population demographic processes (Naves et al., 2003; Falcucci et al., 2009). Although it is particularly difficult to assess all components of habitat quality in cryptic and rare species, understanding conditions associated with reproduction improves our understanding of the species requirements (Fernández et al., 2003). For the brown bear, it has been shown that reproduction areas coincide with specialized environmental characteristics within the array of conditions where individuals may be found (Naves et al., 2003; Wiegand et al., 2008). Therefore we evaluated occurrence and breeding data separately, expecting that the habitat constraints proposed above would influence reproduction more severely than simple occurrence.

2. Methods

2.1. The Carpathian brown bear population

We evaluated the different hypotheses on brown bear habitat constraints using distribution and breeding data from the Northern Carpathian region in Poland (Fig. 1). The Carpathians, one of the largest mountain ranges in Europe, is characterized by a large amount of forested areas and a highly diverse fauna, being considered a region of special interest for the conservation of large carnivores (Salvatori et al., 2002). The climate is continental with strong altitudinal gradients in precipitation (500–2000 mm) and mean annual temperature ranging from 8 °C in the plains to below 0 °C in the mountains peaks (UNEP, 2007). The Northern Carpathians are dominated by mountains of middle and lower altitude and gentle slopes. Natural vegetation follows an altitudinal gradient: high mountains (>1500 m) are characterized by alpine meadows and dwarf pine *Pinus mugo* forest. The mountain forest zone (between 600 and 1450 m a.s.l) is dominated by beech *Fagus sylvatica* and silver fir *Abies alba* with admixtures of Norway spruce *Picea abies*. Some higher locations are totally dominated by these two conifers. Natural vegetation in the foothills (up to 500–650 m) is characterized by a mixture of deciduous forests of oak *Quercus robur*, lime *Tilia cordata* and hornbeam *Carpinus betulus*, with an admixture of birch *Betula pendula* and Scots pine *Pinus sylvestris*. However,

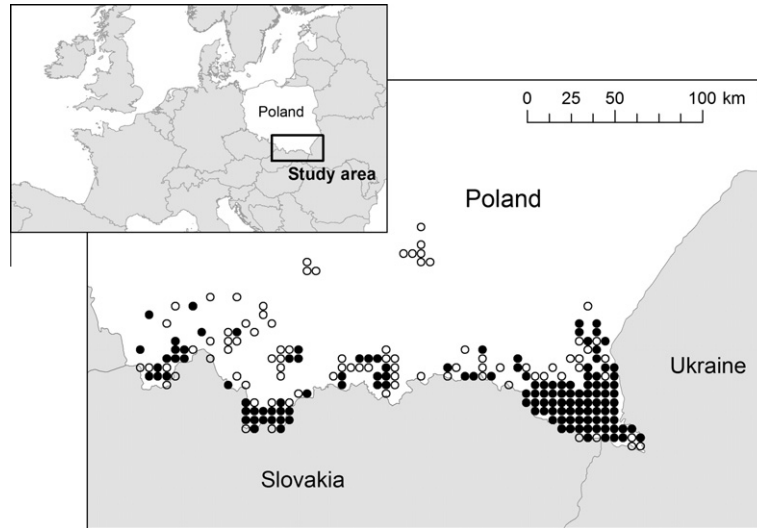


Fig. 1. Map of the study area with the distribution of brown bears (*Ursus arctos*) in Poland assigned from observations of the period 1985–2005. Circles indicate the species presence in 5×5 -km cells including breeding (solid) and non-breeding (open) records.

forest fragmentation is high in this zone and many areas are dominated by agriculture at present, human settlements and artificial lakes (UNEP, 2007).

The Carpathians hold the only persisting brown bears in Poland and constitutes the most Northern limit of a broader Carpathian population estimated in about 8100 individuals, the second largest in Europe (Linnell et al., 2008). After World War I this population was split into a larger segment in the East and a smaller, isolated one in the West. Direct persecution caused a dramatic population decline mostly in the Western segment, leading to nearly extinction with a minimum size of about 40 individuals during the 1930s (Hartl and Hell, 1994). After World War II bears within the new boundaries of Poland were only found in the Tatra and the Bieszczady Mountains (Buchalczyk, 1980; Jakubiec and Buchalczyk, 1987). Nowadays, the Tatra Mountains together with the Central Slovakian Carpathians constitute the so-called Western segment of the Carpathian population, whereas the bear population in Bieszczady is connected to the Eastern segment that inhabits Eastern Slovakia, the Southwest of Ukraine and the rest of the Carpathian chain; however, the degree of connection between both segments remains poorly understood. In the present study we considered the Northern part of both segments and the areas between them (Fig. 1). Bears in Poland are fully protected although they are subject to harvesting and lethal control in Slovakia and Ukraine. A coordinated population management scheme across country borders is still lacking (Selva et al., 2011).

2.2. Bear data

The spatial distribution of bears in southern Poland was estimated for the period between 1985 and 2005 throughout an area of approx. 25,000 km² (Fig. 1). Records of bear presence and reproduction were systematically collected through annual surveys in the framework of the Bear Monitoring Program in Poland (Jakubiec, 2001). Coordinated by the Institute of Nature Conservation of the Polish Academy of Sciences, personnel from Forestry Administration Districts, National Parks and Environmental Protection Agencies, researchers and other organizations recorded systematically all bear observations including information about the type of observation, date, spatial location and, when applicable, number of individuals observed, age class and descriptions of other signs like winter dens and damages (Jakubiec and Buchalczyk, 1987; Jakubiec, 2001). We compiled all this information on a yearly basis

through questionnaires to the people involved in the monitoring program. Some authors have cautioned about potential biases in the estimation of bear numbers and litter sizes from public reports (Swenson et al., 1995; Zedrosser and Swenson, 2005), however, these surveys, especially if aimed at trained personnel, can provide a highly reliable picture of large carnivore distributions (Linnell et al., 1998; Naves et al., 2003). Given the experience and the amount of people involved in data collection, the long-term record and the large number of observations, we are confident that the occurrence data for the period 1985–2005 was reasonably accurate.

A total of 3151 bear records were georeferenced including direct sightings of individual bears, family groups and other unequivocal signs of the species presence (i.e. faces, tracks and winter dens). Observations were finally assigned to 5×5 km squared cells in a grid covering Poland. Breeding cells were similarly assigned on the basis of 1008 observations corresponding to females with cubs and cubs alone. Bear presence was detected in 216 grid cells (i.e. 5400 km²) of which 130 included breeding observations (Fig. 1).

2.3. Habitat modeling

We confronted the different hypotheses using an information-theory approach specifying *a priori* a small number of plausible models and comparing their goodness-of-fit to brown bear data rewarding parsimony (Burnham and Anderson, 1998). Candidate models aimed to capture expectations from each of the three habitat hypotheses independently and combinations of them, in such a way that we could evaluate the combination of potentially influential factors (forest composition, landscape complexity and human influence) with a stronger effect. Based on the existing literature and on our habitat hypotheses we specified a reduced number of 14 candidate models (Appendix, Tables A1 and A2) based on the following criteria:

- Since bear populations in Europe are typically restricted to forested areas we included the proportion of forests within each 5×5 -km grid cell as a predictor in all candidate models, assuming that some amount of forest is required to support individuals regardless of other habitat preferences. In addition, models for the *forest composition* hypothesis included two predictors, the deciduous to total forest ratio and the length of forest ecotones with grasslands and shrubs. In the temperate zone, deciduous forests are dominated by hard mast tree species that

constitute the most critical feeding resource for bears during hyperphagia, allowing them to gain weight and acquiring the physical condition required for hibernation, gestation and lactation. A correlation between the proportion of deciduous and total forest was expected; therefore we calculated the ratio between both to evaluate the pure effect of deciduous forest. Similarly, forest ecotones with pastures and shrubs were included as a measure of patch interspersed with habitats providing herbs, bulks, berries and arthropods on which bears feed after hibernation and during mast shortage (Mattson et al., 1991; Persson et al., 2001; Naves et al., 2006; Bojarska and Selva, 2011).

- The *human influence* hypothesis was tested from the density of inhabitants and of urban areas such as towns, villages and settlements. The first represents an indicator of disturbances associated to a high incidence of humans in the area, whereas the second was used to test the local effects of human proximity independent of their density since many settlements in low-populated areas may also have an important negative effect (Nellemann et al., 2007; Martin et al., 2010).
- *Topographic complexity* models included terrain ruggedness (Riley et al., 1999) and elevation range. Larger differences in elevation are expected to provide more heterogeneous landscapes with a higher diversity of habitats and also a larger variability in vegetation and fruiting phenology, whereas higher ruggedness is usually associated to better sheltering opportunities and protection in winter denning and daily resting sites (Naves et al., 2003; Elfström et al., 2008; Martin et al., 2010).

Vegetation variables were calculated from the Corine Land Cover digital map for Europe of the year 2000 (100-m resolution; CLC2000) and elevation range and ruggedness were calculated from the 1-km resolution Elevation Map of Europe (both are available at <http://www.eea.europa.eu/data-and-maps/data/>). Population and urban data was extracted from a national demography database (Dmochowska, 2007).

Habitat characteristics may influence bear presence and reproduction beyond 25 km² cells e.g. due to the high spatial requirements of the species and the spatial propagation of human impacts (e.g. Naves et al., 2003; Nellemann et al., 2007). Therefore, we preliminarily tested the effect of increasing the scale of influence of environmental variables making similar estimations for areas of $R_1 = 1$, $R_2 = 2$ and $R_3 = 3$ cells around each focal cell, which corresponds with 125, 325 and 750 km² respectively. We used Generalized Linear Models (GLM; McCullagh and Nelder, 1989) with the binomial distribution function and the canonical *logit* link to estimate the strength of association between bear occurrence and reproduction and variables at each scale using AIC_c. For this, we evaluated each variable and scale separately penalizing each scale increase with one additional parameter K . The scale with the lowest AIC_c was retained.

Candidate models were fitted using binomial GLM including cells with bear presence vs. pseudo-absences for the occurrence model. For this we randomly selected 216 cells without bears within a 50-km buffer around breeding cells to guarantee that all studied areas were within the dispersal distance of bears, i.e. they were actually available for selection. This assumption was conservative since studies in other European populations have estimated much greater dispersal and habitat colonization distances (Swenson et al., 1998; Støen et al., 2006). Breeding habitat was studied comparing breeding vs. non-breeding bear cells, i.e. we modeled breeding habitat given bear occurrence.

2.4. Model evaluation

We evaluated model robustness against two potential sources of prediction error: intrinsic model errors and uncertainties

associated to geographic variations in species-habitat relationships. The first may occur if the model structure is inadequate, if important predictors are missing, due to overfitting and due to errors in data collection, all producing inaccurate predictions when the model is applied to independent samples (e.g. Burnham and Anderson, 1998; Fielding, 2002). In addition to those factors, geographic differences in prediction accuracy may occur if the relationships between the species and model predictors change across space, e.g. due to a poor identification of the underlying mechanisms (Miller et al., 2004). Prediction accuracy was evaluated in Poland by comparing classification rates between training and evaluation random subsets of the original data. For this we designed a randomization procedure to calculate the distribution of differences in AUC. In each randomization we performed a stratified 10-fold cross-validation and calculated the AUC from the training and evaluation datasets and the difference between both. Randomization was repeated 100 times resulting in 1000 sub-samples. We finally estimated the mean and the standard deviation from all sub-samples. A non-significant difference between training and evaluation sets supported model predictions whereas the contrary would indicate potentially spurious model relationships.

Predictive accuracy in new areas was assessed using bear distribution data from Slovakia at a resolution of 0.1×0.1 decimal degrees obtained from the National Hunting Database and the State Nature Conservancy as compiled by Rigg and Adamec, 2007. This database contains information on bear presence/absence within the hunting grounds and represents the most comprehensive distribution data available in Slovakia (Koreň et al., 2011). The lower spatial resolution of this data and the origin of bear information may have resulted in a lower data quality as compared with Poland. In this respect, our approach was conservative since a lower quality of the evaluation data would result in poorer classification accuracy rates.

Bear probability of presence was predicted from the best fitted habitat model using habitat information calculated from the CLC2000 map and a geographic database of the 2001 population and housing census of Slovakia (Statistical Office of the Slovak Republic, 2001). Since the spatial resolution of the bear distribution data was coarser than model predictions, we calculated the mean predicted probability at the new scale from the geometric intersection between the coarser and the finer-scale grids. Last, we calculated AUC from the collection of bear presences and absences in Slovakia, including only absences within a 50-km radius from the nearest presence. For comparative purposes we performed the same calculation in Poland after re-scaling the bear distribution accordingly.

A categorical classification of predicted bear habitats vs. non-suitable areas was performed using the probability cut-point providing the best balance between sensitivity and specificity rates (Fielding and Bell, 1997).

3. Results

Univariate statistics resulted in significant differences for nearly all habitat variables and showed that breeding habitats were consistently more distinct than presence-only areas (Table 1). Bears generally occurred in areas with higher forest proportion and a higher density of ecotones with grasslands and shrubs, but only cells with breeding showed a higher deciduous-to-total forest ratio. Terrain ruggedness and elevation range were also higher in areas with bears. Finally, human density and the number of urban areas were lower in bear occurrence cells, especially in breeding areas, although large standard errors indicated a high variability around this general pattern. Analyses of the scale of influence (not shown) resulted in the selection of scales R_2 and R_1 for *percent*

Table 1
Summary and statistical differences of habitat variables measured in 5 × 5-km cells with bear and breeding records and without bears. Values represent means ± SD. P-values are the results from two-sample Wilcoxon tests of differences.

	Bear presence			Absence	P	
	Breeding records	No breeding	All records		Breed vs. no breed	Presence vs. absence
N	130	86	216	791		
Percent forest (%)	69.1 ± 21.5	54.6 ± 22.8	63.3 ± 23.1	28.9 ± 23.3	**	**
Within R ₁	68.0 ± 16.3	51.6 ± 16.2	61.5 ± 18.1	29.4 ± 18.6	**	**
Within R ₂	65.5 ± 15.0	50.7 ± 15.8	59.5 ± 16.9	29.7 ± 16.2	**	**
Percent deciduous forest (%)	24.5 ± 24.3	12.2 ± 9.9	19.6 ± 23.5	7.0 ± 9.9	**	**
Ratio deciduous/total forest	0.31 ± 0.28	0.18 ± 0.24	0.26 ± 0.27	0.27 ± 0.31	**	n.s.
Ecotones forest-grassland (m/ha)	5.11 ± 3.65	2.62 ± 2.75	4.12 ± 3.53	1.12 ± 2.14	**	**
Elevation range (m)	343 ± 175	282 ± 188	319 ± 182	158 ± 123	*	**
Within R ₃	326 ± 119	266 ± 117	302 ± 122	162 ± 98	*	**
Terrain ruggedness	257 ± 127	200 ± 122	234 ± 128	117 ± 84	*	**
Within R ₃	243 ± 82	194 ± 69	224 ± 82	119 ± 69	**	**
Human density (inhabitants/km ²)	59.7 ± 124.2	104.9 ± 104.8	77 ± 119	256 ± 355	**	**
Within R ₃	58.8 ± 63.2	117.6 ± 83.4	82 ± 77	257 ± 238	**	**
Urban areas (n/km ²)	0.03 ± 0.04	0.05 ± 0.05	0.04 ± 0.04	0.07 ± 0.05	**	**
Within R ₃	0.03 ± 0.02	0.05 ± 0.02	0.04 ± 0.02	0.07 ± 0.02	**	**

n.s. = Non-significant differences.

* P < 0.05.

** P < 0.001.

forest in occurrence and breeding habitat models, respectively; R₃ for human density and the number of urban areas in both; and R₃ for elevation range and terrain ruggedness for bear occurrence.

3.1. Bear occurrence model

The best approximating model indicated that, in addition to the percent of forest, brown bear habitat was mostly limited by human population density and the density of urban areas at R₃ (Table 2). This model was clearly better than the nested forest-only model ($\Delta AIC_c = -30.5$; Appendix, Table A1), although scaled model coefficients still showed that forest cover at R₂ had the highest impact on bear presence, followed by the number of urban areas (Table 2). This indicates that forest availability was the most important habitat constrain for bear presence and human factors were important for distinguishing between suitable and non-suitable forest-dominated areas. Two additional models, one including both human and forest-composition variables and the saturated model, were only slightly less supported ($w_i = 0.32$ and 0.21 , respectively; Appendix, Table A1). Although this suggests that some effect of forest composition and topographic complexity cannot be rejected, we based our predictions on the simpler best-approximating model.

Table 2
Best fitting generalized linear models for predicting bear presence and breeding occurrence in the Carpathian Mountains of Southern Poland. Coefficient estimates refer to variables measured in 5 × 5-km squared cells. Variables with correlation >0.6 were not included in the same model.

	Estimate ± SD	Scaled estimate	z	P(> z)	AUC	R ²
<i>Bear occurrence</i>					0.918 ± 0.013	0.644
Intercept	0.070 ± 0.862	0.061	0.08	0.93		
Percent forest at R ₂	0.062 ± 0.011	1.383	5.79	<0.001		
Human density at R ₃	-0.004 ± 0.001	-0.741	-3.09	0.002		
Urban areas at R ₃	-39.21 ± 8.02	-1.003	-4.89	<0.001		
<i>Breeding</i>					0.834 ± 0.031	0.408
Intercept	-1.849 ± 1.011	-2.067	-1.83	0.067		
Percent forest at R ₁	0.043 ± 0.014	0.043	3.15	0.002		
Ratio deciduous/total forest	0.711 ± 0.824	0.192	0.86	0.39		
Ecotones forest-grassland	0.188 ± 0.056	0.663	3.34	<0.001		
Human density at R ₃	0.003 ± 0.003	0.199	0.86	0.390		
Urban areas at R ₃	-32.23 ± 9.46	-0.752	-3.64	<0.001		
<i>Breeding (simplified model)</i>					0.834 ± 0.029	0.405
Intercept	-1.594 ± 0.830	0.570	-1.92	0.055		
Percent forest at R ₁	0.044 ± 0.011	0.795	4.07	<0.001		
Ecotones forest-grassland	0.173 ± 0.053	0.612	3.24	0.001		
Urban areas at R ₃	-31.17 ± 8.709	-0.680	-3.58	<0.001		

3.2. Breeding habitat model

Our results showed that breeding habitats were more specialised: a combination of human and forest composition factors constituted the most parsimonious model to differentiate breeding from non-breeding cells (Table 2). This model included human population density and the number of urban areas at R₃; percent forest at R₁; deciduous to total forest ratio; and the amount of ecotones between forest and grassland and shrubs. A saturated model showed nearly the same selection probability (see Appendix, Table A2) but, as before, we rewarded for simplicity in subsequent analyses. In addition, parameter estimates for deciduous-to-forest ratio and human density were non-significant. Therefore we adjusted a simplified version of the model excluding these two variables. The resulting equation (Table 2) was used to elaborate predictive maps of breeding habitats. According to the scaled coefficients of the simplified model, forest cover, density of ecotones and urban areas had an equivalent impact on breeding habitat probability.

3.3. Model evaluation

Cross-validation supported the robustness of the selected model for estimating bear occurrence probability: the AUC difference

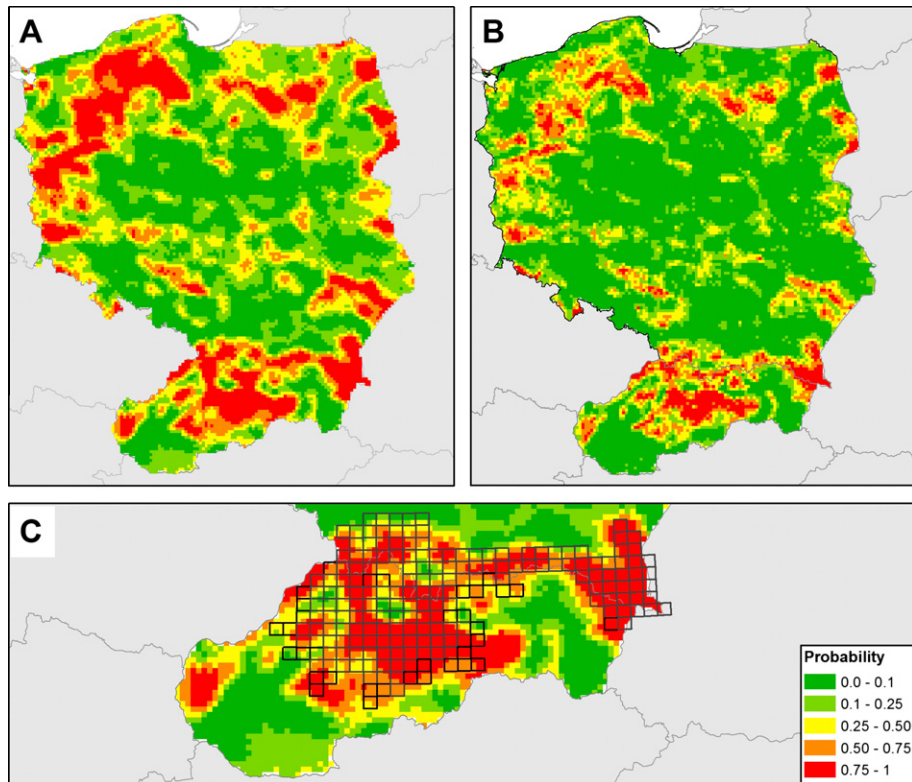


Fig. 2. (A) Bear habitat predictions in Poland and Slovakia estimated from the best approximating occurrence model. (B) Breeding habitat model predictions. (C) Detail of the occurrence-based model predictions in the Carpathian range in Poland and Slovakia with the distribution of brown bears at a spatial scale of 0.1 decimal degrees. Bear occurrence cells were identified by scaling-up our observations in Poland and from the species distribution in Slovakia reported by Riggs and Adamec (2007).

between training and evaluation cross-validation samples was small and with low dispersion ($\bar{X} = 0.002 \pm 0.042$ SD), while sensitivity and specificity rates were moderately high at the best classifying probability (0.844 ± 0.068 and 0.812 ± 0.085 , respectively; P -cutoff = 0.5). A slightly higher discrepancy between training and evaluation data was found for the breeding model, although differences were not important ($\bar{X} = 0.013 \pm 0.097$ SD). Model sensitivity was high (0.830 ± 0.089 ; P -cutoff = 0.5) but specificity rates revealed a greater model uncertainty when classifying non-breeding areas (0.675 ± 0.153). Overall, these results show that models can be reliably used to predict suitable habitats for bear presence and reproduction but they may overestimate the amount of breeding habitat (Fig. 2A and B).

Using independent distribution data from Slovakia (Fig. 2C) we obtained a classification accuracy of $AUC = 0.86$ at 0.1° cell resolution, only slightly lower than the estimated accuracy in Poland at the same resolution ($AUC = 0.90$). In addition, the AUC value that resulted from re-scaling habitat predictions in Poland was very similar to the value obtained at 5-km cells. These results indicated that model extrapolations to a new geographic area were reliable.

3.4. Model predictions

Fig. 3 synthesizes the conditions required for bear presence and reproduction as predicted by the selected models. The vast majority of bear presences ($\sim 80\%$) occurred in areas with urban density of 0.05 nuclei per km^2 at R_3 or below. Up to 40% of non-bear areas coincided with lower urban density, but a minimum amount of 40% forest was needed in bear habitats assuming a moderate human population density of 100 inhabitants per km^2 (Fig. 3A). In contrast, only 23% of all non-bear areas exceed 40% forest cover in our study area (results not shown). These results support the

key role of forest availability limiting bear distribution in the Polish Carpathians. Forest limitation is even stronger in the case of breeding habitats: 75% of breeding observations occurred within cells with a density of urban areas of 0.05 or less but the forest threshold for breeding habitat ranges between 50–70% (Fig. 3B).

Within Poland, a total of 68,790 km^2 and 20% of the country were suitable for bears. Of this area, nearly 29,000 km^2 and about 9% of the total were predicted suitable for reproduction (Fig. 2A and B). In addition to the Carpathian region, these areas were mainly distributed in several patches in the northwestern part of the country and in the northeast near Lithuania and Belarus.

4. Discussion

Habitat models for the brown bear in Europe have used methodological approaches difficult to compare and their extrapolation to new areas have been insufficiently tested or they produced contradictory results (e.g. Kobler and Adamic, 2000; Naves et al., 2003; Posillico et al., 2004; Guthlin et al., 2011; Koreň et al., 2011). These uncertainties limit the use of the existing information for predicting habitat distribution and conservation planning in less-studied populations (Miller et al., 2004; Wilson et al., 2005). Using previous information on bear-habitat relationships, we focused on evaluating a restricted, species-specific set of habitat hypotheses in the less-known Carpathian population to assist habitat predictions and conservation planning.

Forest availability was clearly the most important bear habitat constrain. Moreover, after the species population expansion during the past century (Jakubiec and Buchalczyk, 1987), the current edge of the brown bear distribution seems to be primarily associated to this forest availability. The human influence hypothesis was clearly supported, especially the influence of urban settlements, whereas

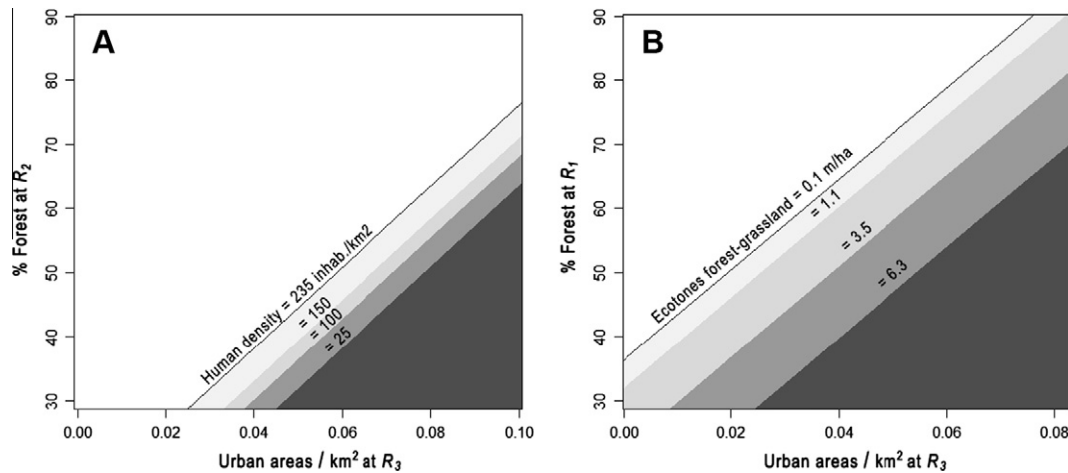


Fig. 3. Predicted habitat thresholds for the brown bear occurrence (A) and breeding habitats (B) in relation to the amount of forests and of urban areas. The solid line and gray transitions separate between parameter combinations that result in suitable predicted habitat (above each line; $P \geq 0.5$) according to the corresponding GLM and under the following boundary conditions: (A) Human density at $R_3 = 236, 152, 98$ and 25 inhabitants/km²; (B) Ecotones forest-grassland = $0, 1.1, 3.5$ and 6.3 m/ha.

the effect of forest composition factors on the species occurrence was less obvious. Habitat use in other European populations is characterized by a clear avoidance of human settlements, infrastructures and disseminated recreational resorts (Clevenger et al., 1997; Preatoni et al., 2005; Nellemann et al., 2007; Martin et al., 2010). Bears may adjust their seasonal and daily use of the habitat according to their perceived risk in relation to human settlements, e.g. influencing resting site selection (Martin et al., 2010; Ordiz et al., 2011); accordingly, behavioral responses to human disturbance would influence the lower probability of bear occurrence in areas with a higher number of urban settlements.

Habitat factors associated to the distribution and availability of natural resources (forest composition and topographic variables) were not selected in the most parsimonious model. Previous studies have found a higher proportion of deciduous forests and terrain ruggedness in bear habitats linking their effects to mast production and to the availability of heterogeneous nutritional resources, respectively (Naves et al., 2003; Preatoni et al., 2005). Although deciduous forests were also more abundant in bear occurrence areas in the Carpathians, their influence was not supported when the confounding effects of the total forest coverage were separated.

Breeding habitats showed more restrictive characteristics: models including the amount of grassland interspersed with forests, a landscape feature clearly associated to nutritional resources, were more parsimonious. Green vegetation and invertebrates may account for 50% or more of the brown bear diet in some populations (Bojarska and Selva, 2011) and, in the Northern Carpathians, grasses and herbs dominate the diet during spring when the forest production of fresh fruits and mast is limited (Frackowiak, 1997; Rigg and Gorman, 2005). Therefore, grasslands and shrublands interspersed with forests provide an important complementary habitat in food shortage periods. A saturated model including human, vegetation composition and topography variables had also a high selection probability, suggesting that these variables may have also a role in determining conditions for breeding.

Differences in habitat characteristics between presence and reproduction areas may be explained by the occurrence of dispersing young males in peripheral habitats, the higher philopatry of females (Swenson et al., 1998) and the stricter habitat requirements for breeding (Wiegand et al., 2008). More generally, concerns are growing about the consequences of relying exclusively on species occurrence models since these ignore differences in habitat quality that may crucially influence the performance of individuals, having serious consequences for the conservation of populations (e.g.

Fernández et al., 2007). Previous studies in Italy and Spain have found an association between different components of bear habitat quality and the proportion of deciduous forest, elevation and ruggedness and human influence (Naves et al., 2003; Falcucci et al., 2009). In addition, Wiegand et al. (2008) found a habitat quality gradient where best conditions for brown bear reproduction coincided with highly specialized habitat characteristics. We observed a similar pattern in the Northern Carpathians, where both human influence and habitat composition variables imposed narrower constraints for breeding habitats within the distribution area. The importance of this distinction becomes clear when comparing predictions from bear occurrence and reproduction models: about 45% of predicted bear habitat showed a low probability of constituting breeding habitat ($P < 0.5$). Moreover, we did not find signs of reproduction in 30% ($n = 27$ cells) of the predicted breeding habitat. The reasons for this discrepancy may be related, among other reasons, to spatial limitations in the access to isolated habitat patches, a miss-detection of breeding areas and to finer-scale habitat constraints not included in our study. Indeed, we relied on broadly defined vegetation types but we did not have information on the vegetation composition, productivity and other important nutritional resources like supplementary feeding (Rigg and Gorman, 2005; Selva et al., 2011). The specific effects of all these factors on bear habitat selection remains unknown. These limitations are intrinsic to most broad-scale habitat models and emphasize the need to complement these approaches with finer-scale investigations (Fernández et al., 2003; Dennis et al., 2006). Last, we identified the most relevant habitat factors differentiating breeding and non-breeding habitat but we did not evaluate mortality. Bears are subject to legal hunting in the neighboring Slovakia and Ukraine and they are also poached in Poland but the specific effect of these activities on the population distribution and demography are unknown. How habitat quality is affected by legal and non-legal human-caused mortality will require further attention in the future.

The present study is unique in transferring European brown bear habitat predictions into new areas with the only exception of Naves et al. (2003), who found a high discrepancy between two neighboring bear subpopulations of Northern Spain. Despite the structural simplicity of our model, the accuracy of extrapolations to a wider test area in Slovakia was satisfactory and encourages the model investigation in the rest of the Carpathian population where the species-habitat relationships remain poorly understood.

Our habitat models were based on broad-scale land cover information and on national urban and human population censuses. Although a debate has raised in past years regarding the need for land cover data to predict species distributions (Thuiller et al., 2004; Luoto et al., 2007), this and many other previous studies have shown the great utility of the European Corine Land Cover project as a basis for conservation-oriented distribution analyses (e.g. Kramer-Schadt et al., 2005; Jedrzejewski et al., 2008; Falcucci et al., 2009). A pan-European initiative to compile urban, infrastructure and population data will have a similar positive impact on habitat analyses and management planning. The conservation of European populations will also require extending this information to limiting non-EU countries such as Ukraine for maintaining the population connectivity (e.g. Kuemmerle et al., 2010).

Habitat predictions have important implications for maintaining a favorable conservation status of the brown bear in Poland and for the management of the trans-boundary population of the Northern Carpathians. The emergence of new urban settlements within the bear distribution range is highly detrimental for the species, especially in Poland, where urban plans are not obligatory and have been developed in only one fourth of the country (Śleszyński et al., 2010). Unplanned urban development probably represents as the main threat for the species conservation in this country, including the construction of single houses and settlements in remote places, ski centers and urban sprawl along roads (Selva et al., 2011). As an example, the built-up area has experienced a twofold increase between 1950 and 1990 in the Bieszczady Mountains (Kozak, 2008), where occurs the highest portion of the Brown bear population occurs in Poland.

Our habitat predictions revealed a linkage zone between the western and eastern segments of the Carpathian bear population through a narrow area in Poland limiting with Slovakia and on which the population connectivity depends. Ongoing genetic and field studies confirm that the connectivity between these two reproductive nuclei is scarce. Therefore, it is critical to pay special attention to the maintenance of forests and the control of urban development in this sensitive area. A coordinated policy between the two countries is deemed necessary to achieve a real trans-boundary management of the species and its habitats in the Northern Carpathians.

Results also indicate that brown bear expansion in Poland beyond the Carpathian region is mainly limited by the availability of connected forest areas. There are, however, other potentially suitable habitats in the country. Some of these coincide with areas where bears were extirpated such as the Białowieża Forest. However, perhaps with the only exception of the Northeastern areas where bears are sporadically observed, unassisted recolonization is unlikely to occur in other potential habitats due to the numerous human infrastructures acting as barriers. We highlight the importance of preserving all these potential habitats and to assess further their value attending to other aspects such as human attitudes and finer-scale habitat characteristics. Moreover, many of these areas coincide with potentially suitable habitats for other large carnivores such as the Eurasian lynx (*Lynx lynx*) and the wolf (*Canis lupus*) (Niedzialkowska et al., 2006; Jedrzejewski et al., 2008). We encourage taking advantage of this agreement to elaborate a joint strategy for large carnivore management and, eventually, for recovering carnivore communities in suitable areas where they were extirpated.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.04.013>.

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