

## Wildlife Research

**Title:** Identifying key denning habitat to conserve brown bear *Ursus arctos* in Croatia

**Authors:** Whiteman, A.<sup>a,1\*</sup>, Passoni, G.<sup>b</sup>, Rowcliffe, J.M.<sup>c</sup>, Ugarković, D.<sup>d</sup>, Kusak, J.<sup>e</sup>, Reljić, S.<sup>e</sup>, Huber, D.<sup>e</sup>

a. Faculty of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK, [awhitem1@uncc.edu](mailto:awhitem1@uncc.edu)

b. Faculty of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK, [passonigioele@live.it](mailto:passonigioele@live.it)

c. ZSL Institute of Zoology, Regent's Park, London NW1 4RY, UK, [marcus.rowcliffe@ioz.ac.uk](mailto:marcus.rowcliffe@ioz.ac.uk)

d. Faculty of Forestry, University of Zagreb, Svetošimunska cesta 25, 10000, Zagreb, Croatia, [damir.ugarkovic@gs.htnet.hr](mailto:damir.ugarkovic@gs.htnet.hr)

e. Faculty of Veterinary Medicine, University of Zagreb, Heinzelova 55, 10000 Zagreb, Croatia; [kusak@vef.hr](mailto:kusak@vef.hr), [slaven.reljic@vef.hr](mailto:slaven.reljic@vef.hr), [huber@vef.hr](mailto:huber@vef.hr)

1. Present address: Department of Geography and Earth Sciences, University of North Carolina at Charlotte, 2901 University City Blvd, Charlotte, NC 28223

\*corresponding author: Ari Whiteman, [awhitem1@uncc.edu](mailto:awhitem1@uncc.edu), +1(404)606-2109

## **Abstract**

### *Context*

The preservation of crucial denning habitat is paramount to the recovery of threatened bear populations due to the effect that den site disturbance can have on cub mortality. Understanding habitat suitability for denning can allow management efforts to be directed towards the regions where conservation interventions would be most effective.

### *Aim*

We sought to identify the environmental and anthropogenic habitat variables associated with the presence of Eurasian brown bear *Ursus arctos* den sites in Croatia. Based on these associations, in order to inform future conservation decisions, we also sought to identify regions of high suitability for denning across Croatia.

### *Methods*

Using the location of 91 dens used by bears between 1982 and 2011, we used the presence-only modeling option in software Maxent in order to determine the most important predictors of den presence, and thus predict the distribution of high value denning habitat across Croatia.

### *Key Results*

We found that structural elements were the most important predictors, with ruggedness and elevation both relating positively to den presence. However, distance to nearest settlement was also positively associated with den presence. Highly suitable denning habitat was found both within and outside the current species range.

### *Conclusion*

We determine that there is considerable denning habitat value in areas with high and rugged terrain as well as areas with limited human activity. We suspect that high and rugged terrain contains a greater concentration of the karstic formations used for denning than lower-lying regions.

### *Implications*

Our study presents the first habitat suitability model for brown bears in Croatia, and identifies core areas suitable for denning both within and outside the species' current range. As such, it provides useful evidence for conservation decision making and the development of scientifically-based management plans. Our results also support the need for finer spatial scale studies that can reveal specific denning preferences of sub-populations.

**Keywords:** Habitat use, modelling, conservation, habitat preference

### **Introduction**

After centuries of anthropogenic pressures, the Eurasian brown bear *Ursus arctos* has been extirpated from most of its range. Today about 17,000 bears live in 22 European countries separated in 10 populations. The Dinaric Mountains contain one of the three most abundant populations of bears remaining in Europe (Kaczensky et al. 2012). This particular population has been expanding in recent years, due to favorable management for hunting, and conservation legislation (Huber et al. 2008). Bears are the most abundant large carnivore in Croatia and are protected by both the Nature Protection Act in Croatia as well as the EU Habitats Directive, of which it is a priority species for conservation under Annex II and IV (Kaczensky et al., 2012). Croatia's bears comprise the northwestern portion of the Dinara-Pindos population (Kocijan et al 2011), which reaches further northwest into Slovenia as well as southeast into Bosnia & Herzegovina, eventually reaching all the way to Greece. The permanent bear distribution range in Croatia holds on average at least one individual per 10km<sup>2</sup>, and densities are highest in the intensively managed areas with bear feeding sites (Huber et al. 2008). While Croatia's bear management plan estimates a total capacity of approximately 1100 individuals, the current estimate is at

1000 individuals (Kaczensky et al., 2012). The population expansion relies on young males dispersing to peripheral areas of the range, limiting intraspecific competition and promoting genetic diversity (Kaczensky et al., 2012). Throughout their range in Croatia, bear habitat preferences are highly influenced by human activity (Kusak and Huber, 1995).

As brown bears are especially sensitive to human disturbance during the denning period (Swenson et al., 1997), it is important to understand where highly valued denning habitat is located relative to potential development sites in the region. As such, the conservation of these denning areas is of central concern to the sustainability of Eurasian brown bears (Huber and Roth, 1997). In a review on the consequences of den disturbance, Linnell et al. (2000) explains that brown bears exhibit variable responses to den disturbance, but when human activity of any scale occurs less than 1km away and especially when it occurs less than 200m away, den abandonment increases significantly. This leads to increased rates of cub mortality and can lead to population declines over time if disturbance and den abandonment continues to rise (Swenson et al., 1997; Linnell et al., 2000). While a prior study on den site characteristics in Croatia found that most dens are built in rocky caves, facilitated by the karstic geology of the region (Huber and Roth, 1997), little else is known about the denning preferences of bears in Croatia.

The use of habitat suitability models has become increasingly popular for management purposes in recent years (Elith and Leathwick, 2009; Higgins et al., 2012), and can provide a valuable means of assessing denning habitat requirements for brown bears in Croatia. Recent advances have made it possible to create habitat suitability maps without traditional presence-absence data. This includes the use of presence-only data (Pearce and Boyce, 2006; Tsoar et al., 2007; Aranda and Lobo, 2011), non-point data (Chakraborty et al., 2011; Koreň et al., 2011), and proxy data (Eigenbrod et al., 2010; Feilhauer et al., 2012). Habitat suitability maps from these models indicate the most important zones within species ranges, and also identify high quality areas where the species is absent but that may potentially be recolonized.

Maxent is one habitat suitability modeling method that has exhibited robust performance without the use of known absence points (Saupe et al., 2012; Townsend Peterson, Papeş, & Eaton, 2007; Tsoar et al.,

2007). It has been particularly useful with small sample sizes (Wisz et al., 2008). Thus, it has been used successfully to map habitat suitability for rare large carnivores based on presence-only data in both Asia (Matyukhina et al., 2015), South America (Torres et al., 2013), and Europe (Passoni et al. 2017).

The objective of this study was to identify the environmental and anthropogenic predictors of brown bear denning habitat, and thus to determine the spatial distribution of high quality denning habitat across the species' range in Croatia.

The sustainability of denning habitat is an important driver of long term population stability for bears (Linnell et al., 2000). As such, this study provides information which will help to inform conservation efforts for this protected species. Additionally, it may influence land development plans to reduce the risk of den disturbance.

## **Methods**

### *Study area and den location*

The study area was split between three different regions in central Croatia: Gorski kotar in the north-west, Plitvice in the south-east, and Velebit in the south-west. Thirty-three dens were located between the Gorski kotar and Plitvice regions using data from bears that had been radio-collared between 1982 and 2011. Gorski kotar and Plitvice are both highly forested areas of approximately 70% forest cover, ranging from 417m to 1,528m above sea level. In both Gorski kotar and Plitvice, the primary habitats are a mixture of beech and fir forest. Common beech (*Fagus sylvatica*) and fir (*Abies alba*) are the most abundant tree species, growing in a shallow soil over carbonate bedrock. Terrain in both is typical karst, with an abundance of caves, depressions, and gorges. Mountain peaks and slopes (>60 degrees) are covered in bare rock (Huber et al., 1995; State Institute for Nature Protection, 2015).

The Velebit region bear dens were located using hunting chronicles and forest surveys conducted by the Faculty of Forestry at the University of Zagreb. Maps and chronicles of hunting grounds with bear sighting information were compared with known habitat requirements and local population estimates to locate dens ( Kusak and Huber, 1995; Majnarić, 2002; Huber et al., 2008; Huber and Roth, 2009). Bear

dens were found during detailed searches of terrain during forest inventorying in karst areas, and by backtracking the brown bear tracks in spring following their emergence from the dens. Locations of individual dens were also pointed out by rangers. Dens were confirmed by signs of bear use (including paw prints, scratches by claws and teeth, and rubbing) in the vicinity, beds within the den, and on the basis of ranger observations.

As compared to Gorski kotar and Plitvice, Velebit is less forested. It is the western edge of the Dinaric Mountains and represents the largest, though not the highest, mountain range in Croatia, running north-south along the Adriatic coast. It is a mosaicked landscape, with pockets of forest, grassland, karst canyons, and bare peaks. Above 800m, common beech and fir dominate the forests, especially on the inland side of the range. At higher elevations, subalpine forests give way to rocky plateaus, dry grasslands, and bare jagged karstic rock from 1,100m to 1,650m above sea level. On the Adriatic side, forest cover is low and the habitat is sub-Mediterranean dry grassland and coastal thermophile forest. Gorski kotar, Plitvice, and Velebit are among the least populated regions of Croatia due to their rugged terrain. Furthermore, farm abandonment has been steadily increasing, depopulating the regions for roughly the last forty years (Buršić et al., 2011).

Of the 114 total dens we located across Gorski kotar, Plitvice, and Velebit, three known individuals held multiple dens in the same winter, usually within 70-300m of the others. In the case of a bear utilizing more than one den in the same season, we selected one den from the cluster to be used as the test sample in order to minimize spatial autocorrelation in the model. If multiple dens from the same known individual and year were in the same cell (250m x 250m), we selected the one closest to the center, and if the dens straddled two cells, we selected the one closest to the center of the cell with the majority of dens. While in-situ surveys allowed us to confirm the presence of each den, those located from the hunting chronicles and forest surveys did not maintain details on the individual that used it, and thus all records were treated as independent.

#### *Habitat variables*

The habitat variables we used in the model came from a variety of sources and we chose them to represent a broad spectrum of common habitat features that may influence den site preferences (Table 1). For the structural elements, we used elevation and ruggedness. For the anthropogenic elements, we used human density, landscape heterogeneity, agriculture, grassland, distance to nearest settlement, distance to nearest paved road, and distance to nearest feeding site (where bears are habituated through feeding for the increased ease of hunting). In order to ensure the absence of strong correlations (Pearson Correlation Coefficient > 0.50) between habitat variables, we used the band collection statistics tool in ArcGIS to compute a covariance matrix of each variable (ESRI, 2013). No strong relationships were found and thus no variables were removed from the analysis (Appendix A).

#### *Den habitat suitability model*

In order to determine the drivers of denning habitat suitability, we fitted a presence-only species distribution model into the software Maxent (Phillips et al., 2004). This approach has the advantage that it requires no data on real absences, but at the cost of potentially overestimating species range or ignoring selection bias (Halvorsen, 2013; Yackulic et al., 2013). However, Maxent has been shown to perform relatively well as a model of species habitat suitability rather than distribution modelling, particularly with small sample sizes (Saupe et al. 2012). Hence, Maxent is a widely used tool for mapping habitat suitability when one solely possesses a set of confirmed locations. Instead of providing known absence points, one must provide Maxent with an area known as a bias within which pseudo-absence points are generated for the purposes of model fitting (Phillips, 2008). In this case, we used a minimum convex polygon around all den locations as this method is commonly used when presence points occupy an especially large area (Venette et al., 2010).

#### *Model output*

As an output, Maxent provides suitability maps that can be left in a stretched classification or classified to binary presence-absence maps (Hosseini et al., 2013). As with any ecological modelling, it is essential to validate the results, often using independently gathered test data not used in training the model (Fielding

and Bell, 1997; Phillips and Dudík, 2008). We subsampled 25% of our total data to act as testing data during simulation and used a jackknife as a further method of assessing the influence of each variable on the overall model, as suggested by Verbyla and Litvaitis (1989). Jackknives work by systematically running simulations with each run leaving out one predictor variable, and then running a separate simulation using solely that excluded variable. By doing so, jackknives are able to assess the total gain of the model containing all predictor variables. Subsequently, two variables were chosen as the most essential to the model. The first is the one that most reduces the total gain of the model when it is excluded from simulation and the second is the one that maintains the greatest percent of the maximum gain when the model is run using it alone (Stein, 1981). In order to assess the results of the simulation, we examined the Maxent area under the curve (AUC) of the receiver operating characteristics (ROC) graph.

## **Results**

After removing dens used by single individuals in the same year to avoid spatial autocorrelation, the final dataset used in this model had 91 total dens spanning from 1981-2011. Twenty-six dens were found in the Gorski kotar region, seven in the Plitvice region, and 58 in the Velebit region (fig. 1). The den suitability map indicates that the suitable areas are located in the mountains above the western coast of Croatia, in the Velebit region, as well as north of Velebit, in the Gorski kotar region. The other area with higher suitability relative to the rest of the country is located in the east, along the border of Bosnia & Herzegovina in the Plitvice region (fig. 2). Several additional small pockets of potentially suitable denning habitat occur in the southern arm of Croatia, in the region of Dalmatia, which is outside the current species range. The AUC for the overall model was 0.789.

According to the jackknife results, ruggedness and elevation were the most important predictors of den presence when used individually, followed by distance to settlement and grassland. Ruggedness is clearly the most important variable in predicting den presence, as it maintained the greatest regularized training gain on its own as well as the greatest drop in regularized training gain when removed from the model containing all other variables (fig. 3). Landscape heterogeneity, agriculture, distance to feeding site,



distance to road, and human population density all had minimal effects. These habitat variables individually contain little to no predictive value associated with den presence, with agriculture, distance to feeding site, distance to road, and human density responsible for less than 3% of the regularized training gain when run individually (fig 3).

Den habitat suitability exhibited a positive relationship with distance to settlement, increasing up to a threshold of four kilometers (fig. 4a). Den presence was most likely in cells with little or no grassland (fig. 4b). Dens were most likely to be found at elevations above 800m (fig. 4c) and in highly rugged landscapes (fig. 4d).

## **Discussion**

The AUC for the overall model (AUC=0.789) was ideal considering that brown bears are adaptable to a relatively diverse set of conditions and can be found denning in a variety of habitats in Croatia (Djuro Huber & Roth, 2009). Other models on habitat generalists have also found that accuracy scores are lower than with habitat specialists (Adler & Wilson, 1987; Evangelista et al., 2008; Kumar, Graham, West, & Evangelista, 2014), due to the variety of environments that can be suitable for a generalist.

The two structural variables in the model, elevation and ruggedness, exhibited a stronger effect on den habitat suitability than any of the anthropogenic variables. Following those two variables, the anthropogenic variables seemed to exhibit a relatively minimal effect on den habitat suitability overall. However, two exceptions to this were distance to settlement and grassland. While weaker predictors than elevation and ruggedness, these two variables exhibited far stronger effects on den habitat suitability than all remaining anthropogenic variables, and thus we cannot entirely discount an effect of human activity on den presence. Grasslands, an anthropogenic variable used in this study to denote land used for livestock grazing, were nearly absent in the areas of highest den habitat suitability. However, it is unclear whether this result reflects higher disturbance in areas with more grassland (which are typically used for livestock grazing), or avoidance of the habitat itself by denning bears. In the distance to settlement function (fig. 4a), there is an apparent threshold where den suitability plateaus between 4000m-8000m from a

settlement. At distances greater than 8000m, there are discontinuities in the function and an increase in standard deviation. This can likely be explained by both Maxent's built-in discontinuities at the boundary of the range of predicted values (Stephan, 2014), as well as greater landscape variation at increasing distances from a den. At such distances, multiple interacting factors may lead to discontinuities in niche modelling (Merow et al., 2014).

Our finding of increased den habitat suitability in high rugged terrain is consistent with some findings outside Croatia, including in Canada (Ciarniello et al. 2005) and in Slovenia (Petram et al. 2004).

However, the Slovenian study, which examined an extension of the same population in our study, also found that neither distance to nearest village nor distance to nearest forest road was a significant predictor of den presence across the study range (Petram et al. 2004). Elfström et al. (2008) also found contrasting results for Scandinavia, where brown bear denning sites were more common at lower elevations. Brown bears in the Himalayas provide another counterexample to Croatia, exhibiting strong avoidance of the steepest slopes and highest elevations (Nawaz et al. 2014). In both Sweden and the Himalayas, such avoidance of high rugged terrain is likely due to far more extreme structural and temperature gradients than exhibited in Croatia. However, these contrasts with our results indicate the value of suitability modelling at the sub-population scale, and furthers our knowledge of the spatial scale at which factors influencing bear den habitat suitability operate.

We suspect that the strong effect of ruggedness and elevation in the model can be attributed, at least in part, to those areas containing high concentrations of karstic formations that contain appealing den sites such as caves. A 1997 study found that 78% of Croatian brown bear dens surveyed between 1980-1992 were located in karstic caves (Huber and Roth 1997) and these formations are less likely to occur in low flat regions.

In addition to future studies examining disturbance risk across habitat gradients, we suggest that habitat suitability modelling be extended to locations throughout the rest of the year. Using GPS-collar data, it would be useful to determine if habitat requirements in the denning season are consistent with habitat

requirements throughout other times of the year, or alternatively whether there are other key habitats that are required for population persistence. We also recommend detailed studies of maternal dens, examining the causes and correlates of cub mortality. Since maternal den disturbance can increase the likelihood of cub mortality and affect population levels over time (Swenson et al., 1997; Linnell et al, 2000), it is important to determine the processes that cause these outcomes, as well as the resulting patterns of distribution.

## **Conclusion**

In conclusion, we believe that the increasing suitability of brown bear den habitat in higher, more rugged terrain reflects the appeal of karstic formations for denning. Additionally, we believe that the increased suitability of dens with greater distance to settlement may indicate an avoidance of human activity during the denning season, though this was a weaker effect than the structural elements and more studies will be needed to confirm a causal relationship. Because of the sensitivity of dens to disturbance, and the effects that den disturbance can have on a population, den suitability models are an important tool in determining targets for habitat conservation. They are especially needed at sub-population scales, as bear behavior can vary greatly between regions.

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## References:

- Adler, G. H., & Wilson, M. L. (1987). Demography of a habitat generalist, the white-footed mouse, in a heterogeneous environment. *Ecology*.
- Aranda, S. C., & Lobo, J. M. (2011). How well does presence-only-based species distribution modelling predict assemblage diversity? A case study of the Tenerife flora. *Ecography*, *34*(February 2010), 31–38. <http://doi.org/10.1111/j.1600-0587.2010.06134.x>
- Buršić, I., Lasan, I., Stolnik, G., Miler, V., Miloš, K., & Škrebenc, J. (2011). *Census of Population, Households and Dwellings 2011*. Zagreb.
- Chakraborty, A., Gelfand, A. E., Wilson, A. M., Latimer, A. M., & Silander, J. A. (2011). Point pattern modelling for degraded presence-only data over large regions. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, *60*(5), 757–776. <http://doi.org/10.1111/j.1467-9876.2011.00769.x>
- Ciarniello, L. M., Boyce, M. S., Heard, D. C., & Seip, D. R. (2005). Denning behavior and den site selection of grizzly bears along the Parsnip River, British Columbia, Canada. *Ursus*, *16*(1), 47–58. [http://doi.org/10.2192/1537-6176\(2005\)016\[0047:DBADSS\]2.0.CO;2](http://doi.org/10.2192/1537-6176(2005)016[0047:DBADSS]2.0.CO;2)
- Dečak, Đ., Frković, A., Grubešić, M., Huber, Đ., Iviček, B., Kulić, B., ... Štahan, Ž. (2005). *Brown bear management plan for the Republic of Croatia. Ministry of Agriculture, Forest and Water Management & Ministry of Culture*. Zagreb, Croatia. Retrieved from [http://www1.nina.no/lcie\\_new/pdf/634986164067645008\\_Croatian\\_bear\\_action\\_plan\\_2005.pdf](http://www1.nina.no/lcie_new/pdf/634986164067645008_Croatian_bear_action_plan_2005.pdf)
- Eigenbrod, F., Armsworth, P. R., Anderson, B. J., Heinemeyer, A., Gillings, S., Roy, D. B., ... Gaston, K. J. (2010). The impact of proxy-based methods on mapping the distribution of ecosystem services. *Journal of Applied Ecology*, *47*(2), 377–385. <http://doi.org/10.1111/j.1365-2664.2010.01777.x>
- Elfström, M., Swenson, J. E., & Ball, J. P. (2008). Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology*. <http://doi.org/10.2981/0909->

6396(2008)14[176:SODHBS]2.0.CO;2

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 677–697.

<http://doi.org/10.1146/annurev.ecolsys.110308.120159>

ESRI. (2013). ArcGIS Desktop: Release 10.2. *Redlands CA*.

Evangelista, P. H., Kumar, S., Stohlgren, T. J., Jarnevich, C. S., Crall, A. W., Norman, J. B., & Barnett,

D. T. (2008). Modelling invasion for a habitat generalist and a specialist plant species. *Diversity and Distributions*, 14(5), 808–817. <http://doi.org/10.1111/j.1472-4642.2008.00486.x>

Feilhauer, H., He, K. S., & Rocchini, D. (2012). Modeling Species Distribution Using Niche-Based Proxies Derived from Composite Bioclimatic Variables and MODIS NDVI. *Remote Sensing*, 4(7),

2057–2075. <http://doi.org/10.3390/rs4072057>

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence / absence models. *Environmental Conservation*, 24(1), 38–49.

<http://doi.org/10.1017/S0376892997000088>

Halvorsen, R. (2013). *A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. Sommerfeltia*. <http://doi.org/10.2478/v10208-011-0016-2.SOMMERFELTIA>

Higgins, S. I., O'Hara, R. B., & Römermann, C. (2012). A niche for biology in species distribution models. *Journal of Biogeography*, 39(12), 2091–2095. <http://doi.org/10.1111/jbi.12029>

Hosseini, S. Z., Kappas, M., Zare Chahouki, M. A., Gerold, G., Erasmi, S., & Rafiei Emam, A. (2013). Modelling potential habitats for *Artemisia sieberi* and *Artemisia aucheri* in Poshtkouh area, central

Iran using the maximum entropy model and geostatistics. *Ecological Informatics*, 18, 61–68.

<http://doi.org/10.1016/j.ecoinf.2013.05.002>

Huber, D., Kusak, J., & Frkovic, A. (1995). Traffic Kills Of Brown Bears In Gorski Kotar, Croatia.

*Ursus*, 10, 167–171. <http://doi.org/10.2307/3873124>

Huber, D., Kusak, J., Majić-Skrbinšek, A., Majnarić, D., & Sindičić, M. (2008). A multidimensional approach to managing the European brown bear in Croatia. *Ursus*, 19, 22–32.

[http://doi.org/10.2192/1537-6176\(2008\)19\[22:AMATMT\]2.0.CO;2](http://doi.org/10.2192/1537-6176(2008)19[22:AMATMT]2.0.CO;2)

Huber, D., & Roth, H. U. (2009). Denning of Brown Bears in Croatia. *International Conference on Bear Research and Management*, 9(2), 79–83.

Kaczensky, P., Chapron, G., von Arx, M., Huber, D., Andrén, H., & John, L. (2012). Status, management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe. Retrieved March 23, 2015, from

[http://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/task\\_1\\_part2\\_species\\_countryp\\_reports.pdf](http://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/task_1_part2_species_countryp_reports.pdf)

Kocijan, I., Galov, A., Četković, H., Kusak, J., Gomerčić, T., & Huber, Đ. (2011). Genetic diversity of Dinaric brown bears (*Ursus arctos*) in Croatia with implications for bear conservation in Europe.

*Mammalian Biology - Zeitschrift Für Säugetierkunde*, 76(5), 615–621.

<http://doi.org/10.1016/j.mambio.2010.12.003>

Koreň, M., Find' o, S., Skuban, M., & Kajba, M. (2011). Habitat suitability modelling from non-point data. *Ecological Informatics*, 6(5), 296–302. <http://doi.org/10.1016/j.ecoinf.2011.05.002>

Kumar, S., Graham, J., West, A. M., & Evangelista, P. H. (2014). Using district-level occurrences in MaxEnt for predicting the invasion potential of an exotic insect pest in India. *Computers and Electronics in Agriculture*, 103, 55–62. <http://doi.org/10.1016/j.compag.2014.02.007>

Kusak, J. H. D. (1995). Brown Bear Habitat Quality In Gorski Kotar Croatia. *Ursus*, 10, 281–291.

<http://doi.org/10.2307/3873137>

Linnell, J. D. C., Swenson, J. E., Andersen, R., & Barnes, B. (2000). How vulnerable are denning bears to

disturbance? *Wildlife Society Bulletin*, 28(2), 400–413. Retrieved from

<http://www.jstor.org/stable/10.2307/3783698>  
<http://www.jstor.org/stable/3783698>

Linnell, J. D. C., Swenson, J. E., Andersen, R., & Barnes, B. (2000). How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin*. <http://doi.org/10.2307/3783698>

Lobo, J. M., Jiménez-valverde, A., & Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17(2), 145–151.

<http://doi.org/10.1111/j.1466-8238.2007.00358.x>

Majnarić, D. (2002). Gospodarenje medvjedom kao zadatak državnog šumarstva. *Šumarski List Br.*, 11–12, 601–611.

Matyukhina, D. S., Miquelle, D. G., Murzin, A. A., Pikunov, D. G., Fomenko, P. V., Aramilev, V. V., ...

Marino, J. (2015). Assessing the Influence of Environmental Parameters on Amur Tiger Distribution in the Russian Far East Using a MaxEnt Modeling Approach. *Achievements in the Life Sciences*.

<http://doi.org/10.1016/j.als.2015.01.002>

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., McMahon, S. M., Normand, S., ... Elith, J. (2014).

What do we gain from simplicity versus complexity in species distribution models? *Ecography*, 37(12), 1267–1281. <http://doi.org/10.1111/ecog.00845>

Nawaz, M. A., Martin, J., & Swenson, J. E. (2014). Identifying key habitats to conserve the threatened brown bear in the Himalaya. *Biological Conservation*, 170, 198–206.

<http://doi.org/10.1016/j.biocon.2013.12.031>

Pearce, J. L., & Boyce, M. S. (2006). Modelling distribution and abundance with presence-only data.

*Journal of Applied Ecology*, 43(3), 405–412. <http://doi.org/10.1111/j.1365-2664.2005.01112.x>

Petram, W., Knauer, F., & Kaczensky, P. (2004). Human influence on the choice of winter dens by

European brown bears in Slovenia. *Biological Conservation*, 119(1), 129–136.

<http://doi.org/10.1016/j.biocon.2003.07.021>

Phillips, S. (2008). A Brief Tutorial on Maxent. *AT&T Research*. <http://doi.org/10.4016/33172.01>

Phillips, S., Dudík, M., & Schapire, R. (2004). A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First International Conference on Machine Learning*, 655–662. <http://doi.org/10.1145/1015330.1015412>

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161–175. <http://doi.org/10.1111/j.0906-7590.2008.5203.x>

Saupe, E. E., Barve, V., Myers, C. E., Soberón, J., Barve, N., Hensz, C. M., ... Lira-Noriega, A. (2012). Variation in niche and distribution model performance: The need for a priori assessment of key causal factors. *Ecological Modelling*, *237–238*, 11–22. <http://doi.org/10.1016/j.ecolmodel.2012.04.001>

Stein, B. E. C. (1981). The Jackknife Estimate of Variance. *The Annals of Statistics*, *9*(3), 586–596. <http://doi.org/10.1137/1.9781611970319>

Stephan, W. (2014). Continuity of the Maximum-Entropy Inference. *Communications in Mathematical Physics*, *330*(3), 1263–1292. <http://doi.org/10.1007/s00220-014-2090-1>

Swenson, J. E., Sandegren, F., Brunberg, S., & Wabakken, P. (1997). Winter den abandonment by brown bears *Ursus arctos*: Causes and consequences. *Wildlife Biology*, *3*, 35–38.

Torres, R., Pablo Jayat, J., & Pacheco, S. (2013). Modelling potential impacts of climate change on the bioclimatic envelope and conservation of the Maned Wolf (*Chrysocyon brachyurus*). *Mammalian Biology*, *78*(1), 41–49. <http://doi.org/10.1016/j.mambio.2012.04.008>

Townsend Peterson, A., Papeş, M., & Eaton, M. (2007). Transferability and model evaluation in ecological niche modeling: A comparison of GARP and Maxent. *Ecography*, *30*(4), 550–560.



<http://doi.org/10.1111/j.2007.0906-7590.05102.x>

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., & Kadmon, R. (2007). A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions*, *13*(4), 397–405. <http://doi.org/10.1111/j.1472-4642.2007.00346.x>

Venette, R. C., Kriticos, D. J., Magarey, R. D., Koch, F. H., Baker, R. H., Worner, S. P., ... Pedlar, J. (2010). Pest Risk Maps for Invasive Alien Species: A Roadmap for Improvement. *BioScience*, *60*(5), 349–362. <http://doi.org/10.1525/bio.2010.60.5.5>

Verbyla, D. L., & Litvaitis, J. a. (1989). Resampling methods for evaluating classification accuracy of wildlife habitat models. *Environmental Management*, *13*(6), 783–787.  
<http://doi.org/10.1007/BF01868317>

Vroom, G., William Herrero, S., & Ogilvie, R. T. (1980). The ecology of winter den sites of grizzly bears in Banff National Park, Alberta. *International Conference on Bear Research and Management*, *4*, 321–330.

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, a. T., Graham, C. H., Guisan, a., ... Zimmermann, N. E. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, *14*(5), 763–773. <http://doi.org/10.1111/j.1472-4642.2008.00482.x>

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H., & Veran, S. (2013). Presence-only modelling using MAXENT: When can we trust the inferences? *Methods in Ecology and Evolution*, *4*(3), 236–243. <http://doi.org/10.1111/2041-210x.12004>

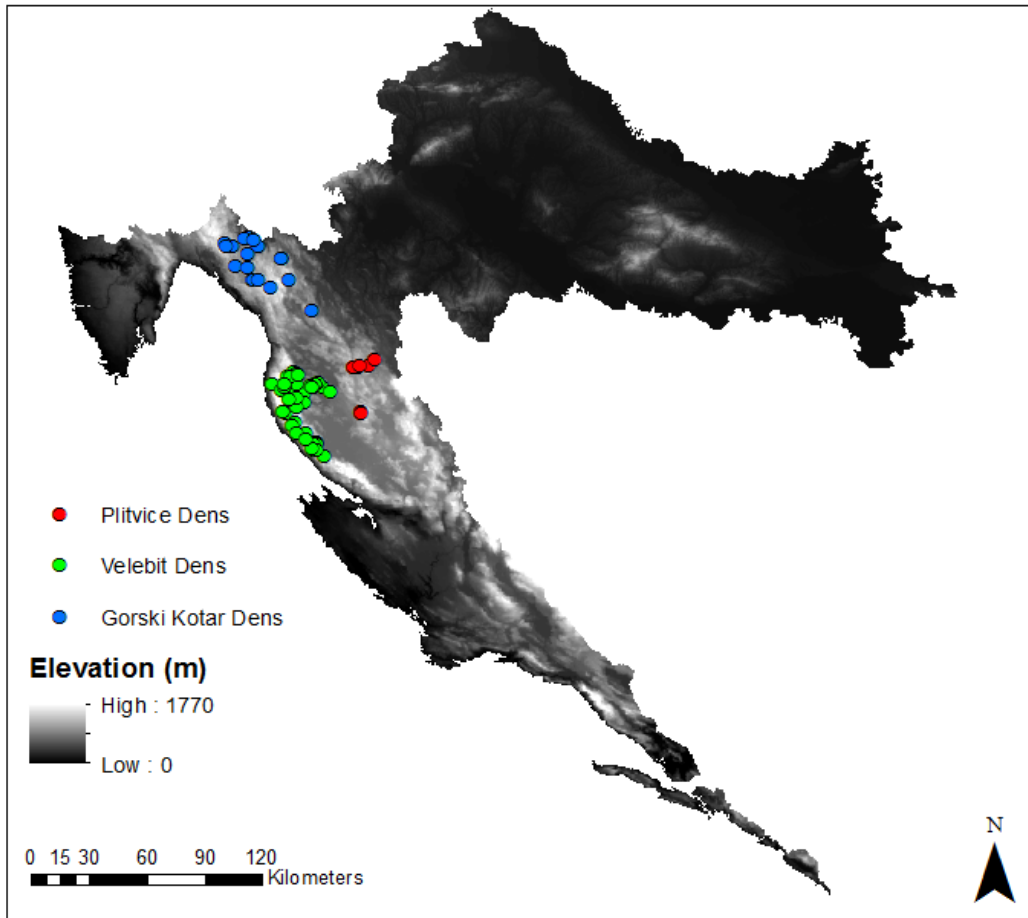


Figure 1. Locations of known den sites used in this study. Ninety-one total dens were located between 1982-2011 in three different regions in Croatia.

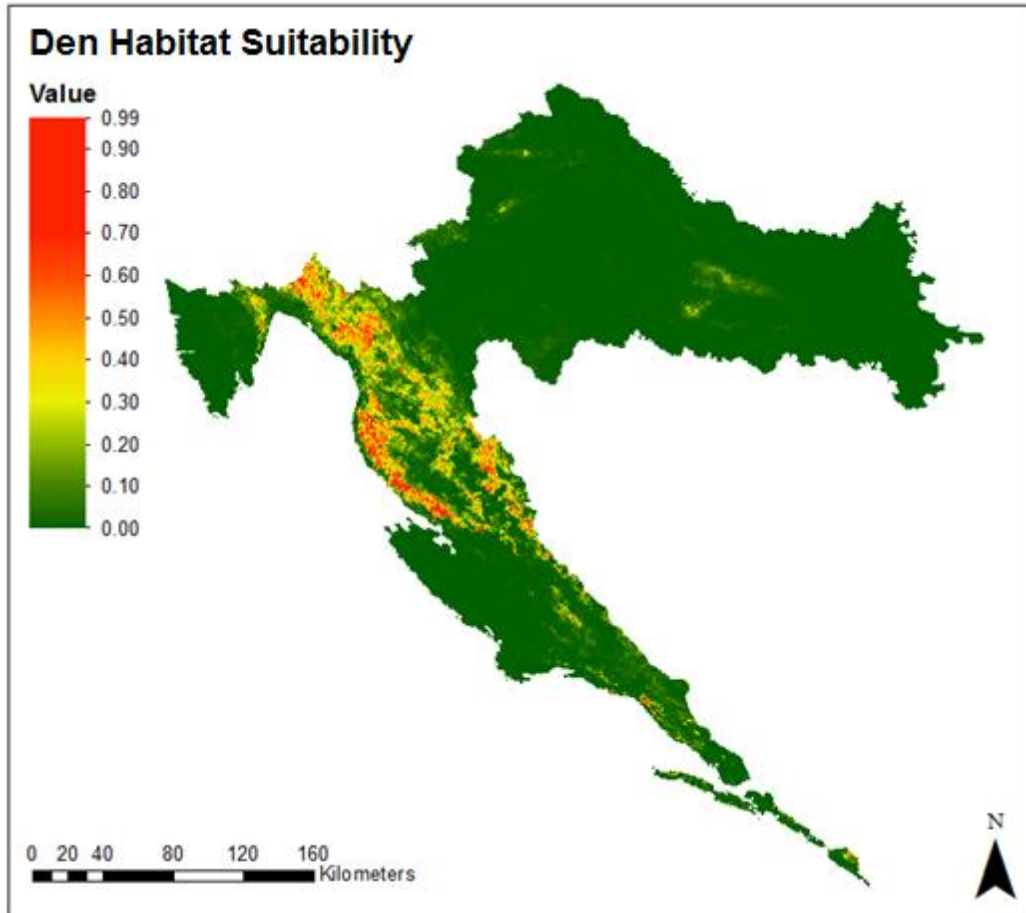


Figure 2. *U. arctos* den habitat relative suitability in Croatia based on modelling ninety-one known den sites using nine habitat variables. Southern Croatia is outside the known range of the species.

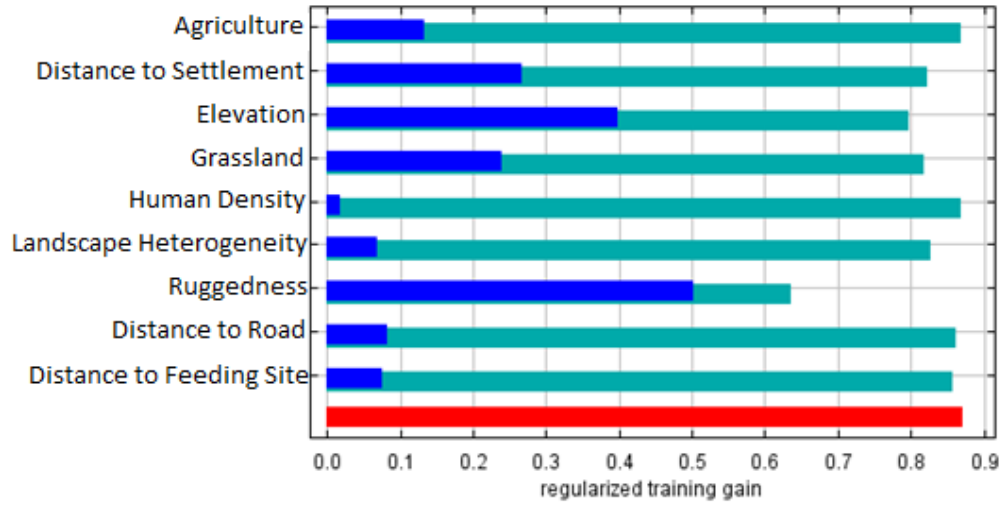


Figure 3. Jackknife test of variable importance. Blue bars indicate the model's regularized training gain using only that particular variable. Teal bars indicate the model's regularized training gain using all variables except that particular variables. The red bar indicates the regularized training gain including all variables.

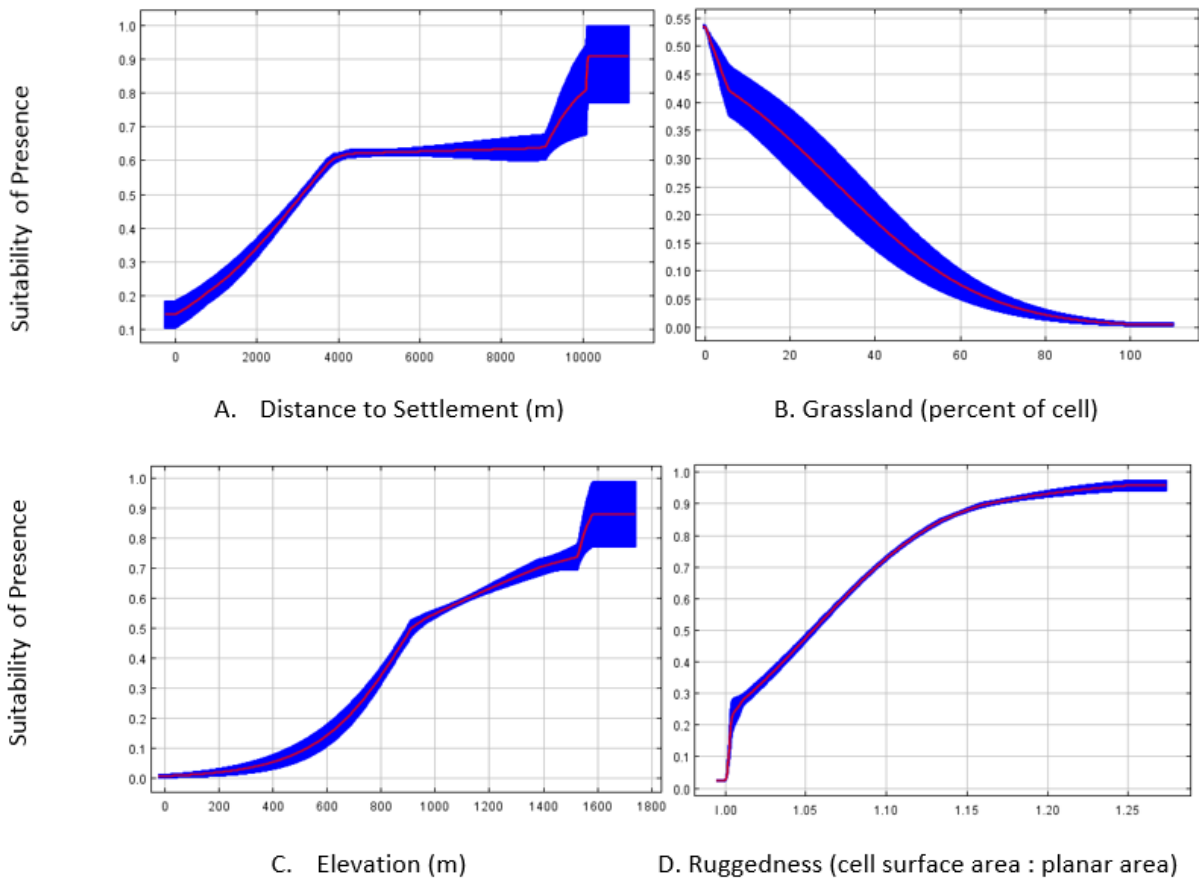


Figure 4. Responses of relative habitat suitability for *U. arcus dens* to A: distance to settlement; B: grassland cover; C: elevation and D: ruggedness (SD in blue).

Table 1.

Description, and source for the habitat variables used in the Maxent model.

Cell size for each layer was 250x250m.

<i>Habitat Variable</i>	<i>Description</i>	<i>Source</i>
<b>Elevation</b>	Average elevation (m) of the total area of the cell	State Institute for Nature Conservation, 2001
<b>Ruggedness</b>	Ratio of surface area (m <sup>2</sup> ) to cell plane area	State Institute for Nature Conservation, 2001
<b>Human density</b>	Number of people per unit area (km <sup>2</sup> )	Croatian Bureau of Statistics, Census of Population, Households, and Dwellings, 1991
<b>Landscape heterogeneity</b>	Shannon diversity index of land cover types per cell	Corine Land Cover Database, 2006
<b>Agriculture</b>	Percent of agricultural land in the cell	State Institute for Nature Conservation, 2005
<b>Grassland</b>	Percent of pastureland in the cell	State Institute for Nature Conservation, 2005
<b>Distance to settlement</b>	Distance from the cell center to the edge of the nearest human settlement of at least five residents	Croatian Bureau of Statistics, Census of Population, Households, and Dwellings, 1991
<b>Distance to road</b>	Distance from the cell center to the nearest paved road	Ministry of Environmental and Nature Protection, 2016
<b>Feeding site</b>	Distance from cell center to the nearest bear feeding site	Ministry of Environmental and Nature Protection, 2016