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Brown bear den characteristics and selection in eastern Transylvania, Romania

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Dens are important for species that need to survive and reproduce during harsh winters. Brown bears (*Ursus arctos*) in Romania, listed by the European Union as a population of concern, use dens for several months each year. To date, few quantitative assessments of denning habitat have been carried out for this population or others in Europe. In 2008–2013 and 2015–2017, we used local knowledge and telemetry data from brown bears fitted with GPS collars to identify 115 winter dens and eight open ground nests used by bears in eastern Transylvania, Romania. We located most dens in mountainous areas (64%) and fewer in foothills (36%). Den entrances in mountainous areas were significantly narrower than entrances in foothills, likely due to the need for reduced thermal loss during more severe winters at higher elevations. We selected seven habitat characteristics (abiotic and biotic) and human-related covariates associated with known locations of dens and open nests to identify potential brown bear denning habitat using maximum entropy modeling. We found that terrain ruggedness was the single most important factor when predicting bear denning habitat. The habitat map derived from this study can be used in the future to safeguard bear denning areas from potential human disturbances.

Key words: bear conservation, disturbance ecology, habitat ecology, MaxEnt, topography, Ursidae

Some mammals respond to fluctuations in resource availability by migrating seasonally between wintering and breeding grounds (Fryxell and Sinclair 1988; Alerstam et al. 2003; Avgar et al. 2013), whereas others undergo prolonged hibernation or torpor (e.g., Millesi et al. 1999; Ortmann and Heldmaier 2000; Kryštufek 2010). Decreasing metabolism and sleeping inside a den for the winter allows some mammals to avoid the energetic demands of maintaining high body temperatures in winter, when food often is scarce (Boyer and Barnes 1999). Winter dens also can provide a safe and sheltered environment for giving birth, nursing, and early cub growth, for some bear species (Ursidae—Oli et al. 1997; Seryodkin et al. 2003; Manchi and Swenson 2005; Derocher et al. 2011).

Brown bears (*Ursus arctos*) spend considerable time in their dens (Schoen et al. 1987), especially at northern latitudes (Manchi and Swenson 2005). Winter denning is essential for female brown bears because they use the security of winter dens to give birth to blind cubs that have one of the lowest cub to mother mass ratio of all placental mammals: ~0.5 kg, or < 1% (Huber et al. 1993; Pasitschniak-Arts 1993). During denning, bears do not eat, but instead rely on fat reserves accumulated in the predenning period (Nelson et al. 1983), resulting in the loss of 22–40% of their predenning body weight (Kingsley et al. 1983). Bears also have adapted to winter denning by not drinking water, urinating, or defecating (Linnell et al. 2000), and reducing their metabolism by ~70% (Watts and Jonkel 1988), heart rate from 75 to 26 bpm (Jørgensen et al. 2014), and body temperature from 37°C to 33°C (Hissa et al. 1994).

Flooding, especially following the melting of snow in spring (Schoen et al. 1987; Huber and Roth 1997) and den collapse (Miller 1990) sometimes can affect denning bears. Human disturbances, such as hunting and resource extraction, also

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constitute threats that in some cases result in bears abandoning dens (Swenson et al. 1997). Den abandonment can have potentially lethal effects on litters of cubs (Linnell et al. 2000). Consequently, the selection of a denning site with a low probability of human disturbance is important for winter survival, successful reproduction, and safety from humans (Sahlén et al. 2015). From a management standpoint, educating the public to minimize human–bear interactions during winter denning may promote social acceptance of brown bears, thereby assisting conservation efforts (Sahlén et al. 2015).

Previous studies have documented several den types used by brown bears, including natural rock cavities, excavations in or under live trees or snags, excavations in soil, and surface beds (Schoen et al. 1987; Linnell et al. 2000; Seryodkin et al. 2003). Dens typically consist of a porch, entrance, tunnel, and bedding chamber (Miller 1990; Fig. 1). The porch is defined as the front portion of the den and often is constructed from soil excavated from inside the den. Bears occasionally build a bed on the porch for sunbathing during winter (Harding 1976; Étienne and Lauzet 2009). Within the bedding chamber, bears typically build beds using branches, leaves, grass, and other materials, available in the immediate vicinity (Schoen et al. 1987; Li et al. 1994).

Past studies have identified a variety of factors responsible for brown bears selecting den sites, including land cover, food resources, topography, and anthropogenic features (Petram et al. 2004; Elfström et al. 2008; Libal et al. 2012; Pigeon et al. 2014). The den site selection process occurs at multiple scales. For example, at a broad scale, bears may select areas for denning that are located in alpine or old growth forests (Schoen et al. 1987), and that have abundant and high-quality spring foods in the vicinity (Pigeon et al. 2014). At a more local scale, the presence of stabilizing den material such as large rocks (Ciarniello et al. 2005) and horizontal cover at 1 m (approximate height of walking bears—Libal et al. 2012) positively influence den site selection.

Terrain also is a major factor that contributes to the process of den site selection (Petram et al. 2004; Pigeon et al. 2014), with brown bears in some regions selecting only rugged terrain for denning (Whiteman et al. 2017). Past studies found that extreme ruggedness provides brown bears safety from human disturbance, because such terrain is difficult to access during winter months (Nielsen et al. 2004). Forest cover also provides bears food and refuge to evade people (Pop et al. 2018). In some regions, brown bears select certain slopes to maximize the buildup of snowfall and thermal insulation in the den (Craighead and Craighead 1972; Vroom et al. 1980; Schoen et al. 1987). Distance to roads and agricultural land can have a negative impact on site selection, possibly because brown bear associate roads, infrastructure, and other developed land, with people (Swenson et al. 1997; Sahlén et al. 2011).

To date, most research on brown bear den site selection has been carried out in North America (Ciarniello et al. 2007; Goldstein et al. 2010; Hodder et al. 2014; Pigeon et al. 2014, 2016); few studies in Europe have described brown bear dens and the process of den site selection (Huber and Roth 1997; Petram et al. 2004; Elfström et al. 2008). Despite Romania hosting the largest brown bear population in Europe (> 6,000 individuals), excluding European Russia (Swenson et al. 2000; Chapron et al. 2014), denning of brown bear in Romania has received little attention from researchers over the past 50 years (Almăşan and Vasiliu 1967).

The purpose of this study was to describe brown bear dens and gain an understanding of the factors responsible for selection of den sites by bears in eastern Transylvania, Romania. First, we compared the structure and dimensions of known dens found in the foothills and mountains. We then used these data to test the structural thermal insulation hypothesis, which states that bears construct dens with longer tunnels and smaller entrances in mountainous regions presumably because winters are more severe at higher elevations. We also tested several den site selection hypotheses using data from known den locations: i) the risk minimization hypothesis, which states that terrain ruggedness and forest cover are positively associated with den sites; ii) the snowpack thermal insulation hypothesis, which claims that dens will occur where snow cover is more contiguous, deeper, and longer lasting; and iii) the human avoidance hypothesis, which states that high road density, infrastructure, and human-modified habitats are negatively associated with den sites. Lastly, we used habitat data for confirmed dens and Species Distribution Models (SDMs) to predict the location of sites suitable for denning within the study area.

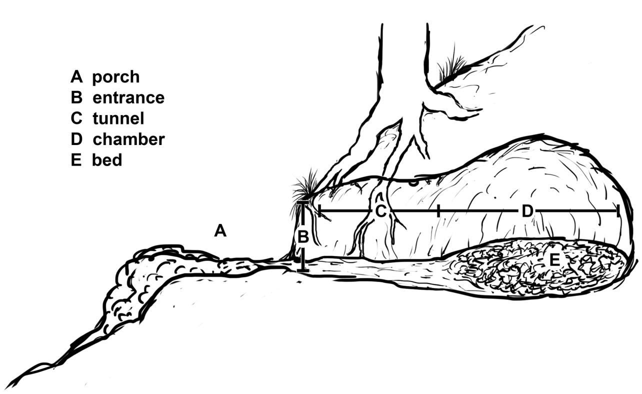

Fig. 1.—Structural components of a typical brown bear den.

Materials and Methods

Study area.—The study was conducted in eastern Transylvania, Romania (Fig. 2). The east section of the study area (1,121 km^2; hereafter, mountains) is mountainous and includes part of Romania's eastern Carpathians (elevation range: 515–1,783 m). More than a third of the eastern study area (35.6%) is protected by the European Union's (EU) Habitats Directive as a Natura 2000 site. Forests account for 68% of total land cover and include: European beech (*Fagus sylvatica*; 25%); Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European larch (*Larix decidua*; jointly 26%); and mixed forests (17%). Approximately 20% of the land is pastureland used to raise livestock from late spring to early autumn. A small portion of the study area (0.5%) also

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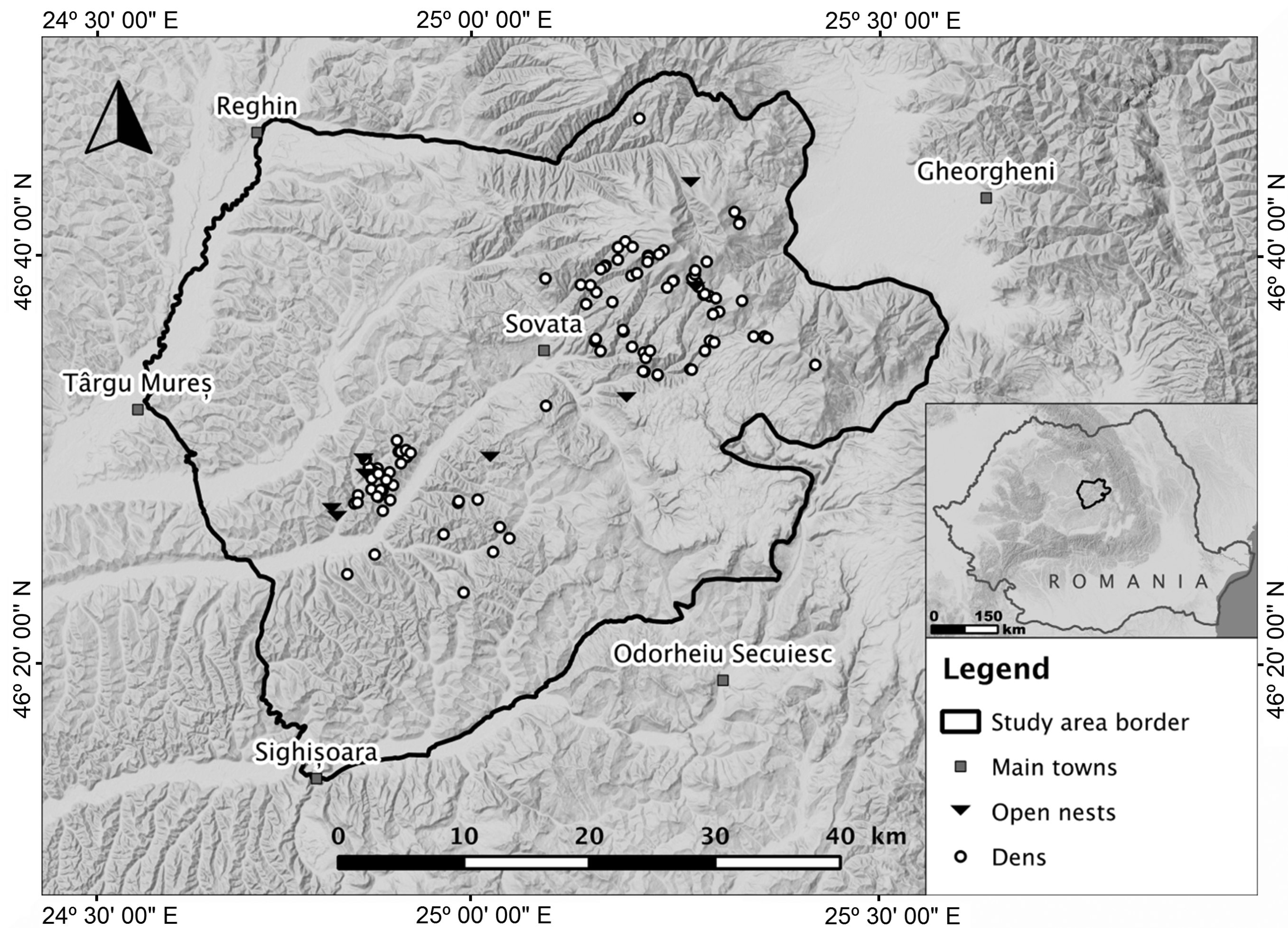

Fig. 2.—A map of the study area (foothills in the West, mountains in the East), known brown bear dens ($n = 115$), and open nests ($n = 8$) in eastern Transylvania, Romania, 2008–2013 and 2015–2017.

includes human settlements, weekend homes, an active stone quarry, and a few small ski resorts (CORINE Land Cover database 2012). The mountainous area has a road density (mean length of roads used by motorized vehicles per km^2) of 0.62 km/km^2. The vast majority of the transportation infrastructure consists of gated roads maintained by local forestry services. Other than a few paved national and county roads and roads leading to forest parcels with active logging operations, the roadways are not cleared of snow during the denning period, making them inaccessible to most vehicles.

The west section of the study area consists mainly of the foothills of the eastern Carpathian Mountains (1,999 km^2; hereafter, foothills), extending west of the Gurghiu Mountains and south of the Gurghiu River (elevation range: 310–1,090 m). A small proportion of the area (< 20%) is part of the Natura 2000 European network of protected areas. The foothills are largely accessible to humans, hosting numerous settlements (7% of the study area—CORINE Land Cover database 2012), ranging from small villages to towns. The main land uses (60%) are arable and pastoral farming. Corn, alfalfa, oat, potato, and wheat croplands occur mainly at lower elevations, and seminatural pastures, hayfields, and orchards at higher elevations. Forest succession occurs in abandoned fields where pioneer species, including blackthorn (*Prunus spinosa*), common hawthorn (*Crataegus monogyna*), and common sea buckthorn (*Hippophae rhamnoides*), form almost impenetrable thickets that develop into deciduous forests (27% of the area) of European hornbeam (*Carpinus betulus*), oak (*Quercus* sp.), European beech, and black locust (*Robinia pseudoacacia*). Plantations of Scots pine (*Pinus sylvestris*; 0.3%) and mixed forests (0.2%) also are present. Forests cover much of the high elevations and narrow valleys, both of which generally are difficult to access by people. The foothills have a road density of 1.2 km/km^2. Major roads are cleared of snow throughout the denning period. Most forestry roads are not gated and, because winters are relatively mild, some roads are periodically accessible to vehicles throughout winter.

Identifying dens.—We located bear dens in 2008–2013 and 2015–2017. In the mountains, we found dens with help from foresters and game managers. In the foothills, we located dens with assistance from game managers, pastoralists, forest owners, mushroom hunters, and berry pickers. In 2015–2017, we identified some dens based on telemetry data from bears fitted with GPS collars.

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We captured bears in cage traps and immobilized them using a dosage of 35 µg Medetomidine and 2–5 mg Zoletil (tiletamine-zolazepam) per estimated body mass (kg) using dart syringes fired from a Dan-Inject CO_2 Injection Rifle (Model J.M.SP; Dan-Inject ApS, Kolding, Denmark). We fitted captured bears with Vectronic Aerospace GPS Pro Light-4 GPS-GSM collars (Vectronic Aerospace, Berlin, Germany). We set collars to record GPS locations of bears every 1 h, including the denning period.

Unless we were absolutely certain that the structure was unoccupied, den visits only occurred outside the denning period, so as to avoid disturbance and prevent potential den abandonment. We carefully inspected each suspected denning structure and identified it as a den only if it contained clearly visible claw marks (e.g., from the digging process, or from usage), bear hair, or clearly recognizable beds. We recorded every den's location, elevation (as determined with a Garmin GPSMAP 60CSx GPS unit; Garmin International, Olathe, Kansas), and land cover type in the immediate vicinity (10-m radius). We only recorded the location of aboveground open nests (excavated, circular, shallow depressions usually containing bedding material) used by wintering bears.

Den characterization.—We described the dimensions of dens (excluding open nests) using the following measurements: height and width of entrance; height, width, and length of tunnel and chamber; and porch length. All measurements were collected by the same person using a measuring tape (cm).

The structural thermal insulation hypothesis predicted that bears would construct dens with longer tunnels and smaller entrances in mountainous regions because winters are more severe. We therefore compared the measurements of dens between the foothills and mountains. Because the data were not normally distributed according to Shapiro–Wilk tests and graphical investigations, we carried out nonparametric Wilcoxon rank sum tests to contrast the den structural metrics. We used R core functions and the dplyr and ggpubr packages in R studio (v 1.1.447—R Development Core Team 2017), and assessed the influence of outliers on our results.

Modeling of Denning Habitat

Modeling method.—Species Distribution Modeling can be used to help predict the distribution or habitat of a species, such as habitat used for denning as we do here, across geographic space and time using environmental data. In brief, we used maximum entropy modeling (MaxEnt) to assess the probability of presence of brown bear dens across the study area based on habitat data collected at known den locations. MaxEnt identifies denning habitat by finding the distribution of maximum entropy (i.e., closest to uniform—Phillips et al. 2006; Elith et al. 2011); where environmental covariates in the predicted extent matched average values recorded at confirmed denning locations. MaxEnt has been shown to be well-adapted to presence-only data and has consistently demonstrated performance that is competitive with other methods, such as generalized linear models, generalized additive models, Genetic Algorithms for Rule-set Prediction (GARP), or bioclimatic envelopes (BIOCLIM—Elith et al. 2006; Phillips et al. 2006).

We fitted models by investigating linear, quadratic, and product feature types and all combinations of those features. The machine learning fitting process was set to end when training gain fell below the threshold value of 0.0001, or after 1,000 iterations. The background data set, which is a random sample of points from the study area (Elith et al. 2011), was set with 10,000 maximum samples within a restricted area defined as the Minimum Convex Polygon of the den occurrences (Webber et al. 2011). The regularization multiplier was set to 1 to minimize the problem of model overfitting, while not producing a widely generalized model (Phillips et al. 2006). A jackknife test also was performed to obtain an estimate of individual variable importance (Elith et al. 2011).

Biased samples can be problematic in distribution modeling. The data collection methods for the den occurrence records could not assure a nonbiased data set. Most dens were discovered opportunistically by people accessing areas throughout the region, including wild boar hunters, shepherds, foresters, mushroom hunters, and berry pickers. At least some of these people likely accessed areas from a nearest road, which could have resulted in spatial distribution of dens concentrated around roadways. To reduce potential spatial autocorrelation caused by proximity to roads, we introduced a bias correction to the models, using background manipulation as described in past studies (Phillips et al. 2009; Kramer-Schadt et al. 2013). We calculated the Euclidean distance to forestry roads, then reversed the distance values and included the final raster as a bias file in MaxEnt.

We fitted six models (features L, Q, LP, LQ, QP, LQP) with and without bias correction, totaling 12 models. We then produced 10 replicates for each feature and condition combination (*k*-fold cross-validation method). For modeling purposes, we reduced the overall data set of 123 known dens to 119 dens. This ensured that each modeling unit (300 m × 300 m) contained one den location only.

Explanatory covariates.—We extracted spatial covariates using ArcGIS (v10.3.1—ESRI 2015) and QGIS software (v2.0.1—QGIS Development Team 2013) at a resolution of a modeling unit (300 m × 300 m). We included as covariates abiotic and biotic habitat characteristics, as well as human-related features. The risk minimization hypothesis predicts that bears should den in rugged terrain and forested areas; we therefore estimated terrain ruggedness (accessibility/disturbance) and forest cover (foraging habitat and refuge). The snowpack thermal insulation hypothesis predicts that dens occur where snow cover is most extreme; to index snow occurrence, we calculated aspect (thermal insulation), assuming that northern and western aspects retain most snow. The human avoidance hypothesis predicts that denning takes place in areas with low densities of roads and infrastructure, and where disturbed habitats are in low occurrence; accordingly, we generated density of roads, percentage of artificial area, and percentage of human-generated open fields (disturbances).

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We estimated ruggedness (*TRugg*) using a terrain ruggedness index (TRI) calculated from a 30-m Digital Elevation Model (DEM) from the GMES RDA project (EU-DEM, https://www.eea.europa.eu/; Supplementary Data SD1). The TRI provides a quantitative measure of topographic heterogeneity, calculating the sum change in elevation between a grid cell and its eight neighboring cells (Riley et al. 1999).

The CORINE Land Cover 2012 polygonal vector layer (CORINE Land Cover database 2012) was used to delineate forest cover percentage (*ForestC*; Supplementary Data SD2). Due to sample size limitations, forest cover pooled conifer, deciduous, and mixed, forests. We undertook calculations with Focal Statistics within a 495-m rectangle buffer around each cell (Elfström et al. 2008).

We derived den aspect from the GMES RDA DEM. Because aspect is a circular variable with values ranging from 1 to 360, it was converted to two continuous aspect-index variables (Northness, *NorthI* [Supplementary Data SD3] and Eastness, *EastI* [Supplementary Data SD4]), using the "*raster*" and "*sp*" packages in RStudio v0.99.4 (R Development Core Team 2017). These aspect indices range from −1 (southern/western aspects) to 1 (northern/eastern aspects).

We exported the linear vector layer of the Romanian road network from the OpenStreetMap (OSM) project database (http://www.openstreetmap.org/; Open Database License [ODbl] v1.0) and used it to calculate the density of paved roads (per 100 km^2) within a 500-m circular buffer (Elfström et al. 2008). The covariate (*RoadD*) included all paved OSM road types, which are used in the study area by cars, horse carts, and pedestrians (Supplementary Data SD5).

We obtained the percentage of artificial area (human infrastructure, *ArtifC*) and percentage of human-generated open fields (crops and pastures, *OpenC*) from the CORINE Land Cover 2012 polygonal vector layer (CORINE Land Cover database 2012). We used Focal Statistics within a 495-m rectangle buffer around each cell to calculate these percentages (Elfström et al. 2008).

We inspected correlations between continuous covariates using ENMTools software (ENMTools 1.4.4 version—Phillips et al. 2006; Warren et al. 2008) and Pearson's correlation tests with 95% confidence intervals. We did not include variables in the same model if correlated $r > |0.65|$ (Kuemmerle et al. 2010). We found *ForestC* and *OpenC* were negatively correlated ($r = -0.82$; Supplementary Data SD6) and *RoadD* was positively correlated with *ArtifC* ($r = 0.71$). For easy interpretation and straightforward applicability to management, *ForestC* and *RoadD* were used to model the distribution of potential denning areas and *OpenC* and *ArtifC* were excluded.

Model selection and projection.—We used the Akaike Information Criterion corrected for small sample sizes (AICc) to select the top model of 12. We calculated the AICc value for each replicate of each feature combination using ENMTools software (Hurvich and Tsai 1995; Warren and Seifert 2011). The most parsimonious model (Mazerolle 2004) was projected over the full study area, with the same parametrization as the one used during the fitting process, excepting the output format that was set to logistic with 10 replicates. The Area Under the receiver operating Curve function (AUC) was used to assess the performance of our top model. The AUC represents the probability of a random presence location to be ranked with a higher value than a random background sample (Fielding and Bell 1997; Merow et al. 2013). We also investigated the degree of model extrapolation by generating a Multivariate Environmental Similarity Surface (MESS; Elith et al. 2010) for brown bear denning, which was spatially constrained to the study area extent. MESS analysis quantified the similarity in covariates between any given location in the projection data set and the locations in the reference (training) data set (Elith et al. 2010).

Results

Den locations.—We identified a total of 115 bear dens and eight open nests. We located 74 dens (60%) and three open nests (2%) in the mountains, and 41 dens (33%) and five open nests (4%) in the foothills. Overall, 10 dens and one open nest were located using telemetry. With the exception of one open nest in the mountains used by a collared male, all open nests were used by females with cubs ($n = 7$), which was confirmed visually by the authors or locals.

Den characterization.—We found that dens were completely dry when inspected, with the exception of four dens in the foothills that were flooded. Most mountain dens (73%; $n = 54$) were excavated (31 under the roots of trees; 23 under rocks), whereas 27% ($n = 20$) were natural cavities located in or under rocks or between large boulders. We identified beds in 80% of the dens ($n = 59$); many dens contained bedding material ($n = 37$). We also documented tunnels in 54% ($n = 40$) of the structures. Elevations of mountain den locations ranged from 486 to 1,607 m ($\bar{x} = 1{,}118$ m; $SD = 249$ m) in different types of forests: 32% ($n = 24$) in deciduous forests, 38% ($n = 28$) in mixed forests, and 30% ($n = 22$) in conifer forests.

A larger proportion of dens in the foothills than in the mountains (95%; $n = 39$) were excavated (24 were dug under the roots of trees, and 15 were dug into the sides of slopes); the remaining two dens in the foothills included one natural cavity in a rock, and one under the roots of a tree. Tunnels were present in 27% of the structures ($n = 11$). We identified beds in 44% of the dens ($n = 18$), and some of the dens ($n = 9$) contained bedding material. Elevations of foothills den locations ranged from 393 to 884 m ($\bar{x} = 491$ m; $SD = 77$ m) in deciduous forests (68%; $n = 28$), thickets on abandoned agricultural land (29%; $n = 12$), and a planted patch of conifer forest (2%; $n = 1$). Elevations of some foothills dens ranged higher than the low range of elevations of mountain dens, because foothills and mountains were delineated by biogeographical region rather than exclusively elevation.

We found some support for the structural thermal insulation hypothesis. Of the nine den structural metrics (Table 2), only entrance width differed significantly between mountains and foothills. Entrances of mountain dens were significantly narrower than those in the foothills ($P = 0.004$). We only discussed our results derived from our full data set because results were

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similar with and without outlying values (Supplementary Data SD7).

Habitat modeling of den sites.—The top two models in the candidate set included linear and quadratic features (LQ) without and with a bias file, respectively (mean AUC = 0.77 ± 0.05; mean AUC = 0.78 ± 0.06; Supplementary Data SD8). The LQ model without the bias file had the lowest AICc score (Supplementary Data SD8) and low standard deviation (Supplementary Data SD9). No other models in the candidate set had an ΔAICc < 2.

Our prediction that bears would den in rugged terrain and forested areas was partially supported. Terrain ruggedness (*TRugg*) was the best predictor of den presence (93.0% of model contribution; Fig. 3). The top model predicted a 0.5 probability of den occurrences at a *TRugg* index value of 21.7, and a maximum probability of presence at a *TRugg* of 41.6 (Fig. 3). The slight decrease in probability of presence with very high *TRugg* suggests that very steep areas are less suitable den sites (Fig. 3). In contrast, forest cover had negligible effect on model predictions (0.8%) (Supplementary Data SD10).

We also found partial support for our prediction that denning would occur where snow cover is most extreme. Aspect contributed relatively little to model predictions (5.9% in total) with slightly higher probabilities on northern- and western-faced slopes (Supplementary Data SD10).

The prediction that bears would den at low densities of human disturbance as indexed by main transportation infrastructure received little support. Only 0.2% of model predictions were explained by paved-road density (*RoadD*; Supplementary Data SD10).

Multivariate Environmental Similarity Surface (MESS) results indicate that there were no overextrapolations of the top model when predicting the presence of dens across the entire area (Supplementary Data SD11). Our model predicted that rugged areas in the Northeast and Southwest sections of the study area were most suitable for brown bear denning and lowlands, plateaus, and river floodplains were the least suitable (Fig. 4).

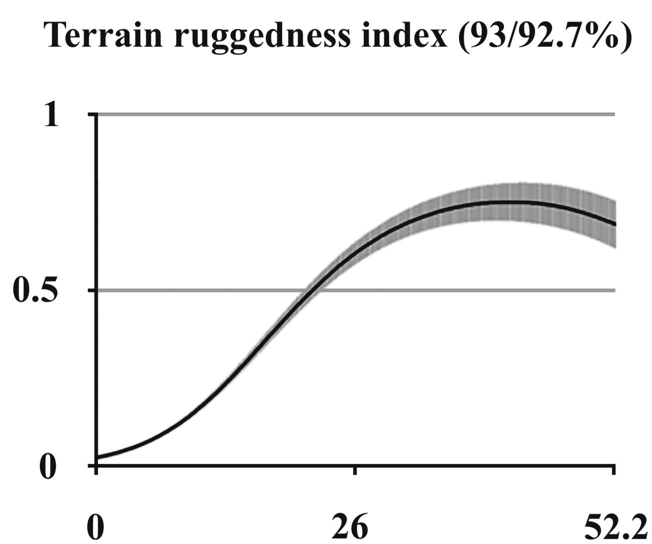

Fig. 3.—Probability of brown bear den presence using data collected from 119 known den sites in eastern Transylvania, Romania. Relative percent contribution of terrain ruggedness to the MaxEnt model is indicated in brackets. Gray area represents the confidence interval for the probability curve among 10 replicates.

Discussion

Habitat modeling aids in landscape-level planning, which in turn can guide the development of conservation and management strategies. Efforts to model brown bear habitat selection in Eastern Europe have lagged compared to similar work ongoing elsewhere in Europe and North America. In eastern Transylvania, Romania, we found that bears mostly excavated their dens (76%) in rugged terrain, which generally has low levels of human activity in winter compared to flatter regions. Areas with high potential for extreme snow conditions, or human disturbance associated with paved roads, may have little influence on the process of den site selection under current study area conditions.

All types of dens (excavations, caves, and nests) that we documented in this study have been described in previous studies (e.g., Ciarniello et al. 2005). Studies in the United States (most of Alaska; Kodiak Island; Montana; Rocky Mountains and Yellowstone National Park), Canada (Banff and Jasper National Parks; the Yukon), and Sweden (Linnell et al. 2000) also found that most dens used by brown bears were excavated. We found that excavated dens were dug into the sides of slopes and often under the roots of trees or under rocks, which presumably decreases the risk of den collapse (Ciarniello et al. 2005). Similar to past studies in the United States (Yellowstone National Park, Admiralty Island, and Chichagof Island—Judd et al. 1986; Schoen et al. 1987), Canada (Vroom et al. 1980; Ciarniello et al. 2005), Croatia (Huber and Roth 1997), and Italy (Groff et al. 1998), we also found that bears used caves in rocks to den for the winter. Denning in caves was much more common in the mountains (20 of 22 caves) than in the foothills (2 of 22). All but one of the natural cavities used by bears were located in or under rocks, or between large boulders. The high frequency of rock formations in the volcanic Gurghiu Mountains (Mason et al. 1995) likely explains the frequent presence of dens excavated under rocks and use of natural cavities in the mountains. A scarcity of rock formations in the foothills also could explain the lack of these den structures in this lower elevation region. Unlike excavated dens, natural cavities do not require energetic investment but may be less insulated.

We located only eight aboveground open nests. In Sweden and Norway, open nests primarily were used by males (Manchi and Swenson 2005; Elfström and Swenson 2009). Manchi and Swenson (2005) found that males that used open nests spent shorter time sleeping than males in other types of dens. The authors concluded that males might be able to use open nests both because of greater fat storage and less weight loss during winter denning compared to females. The need to shelter offspring from environmental conditions also might explain why females did not use open nests in Scandinavia. These open

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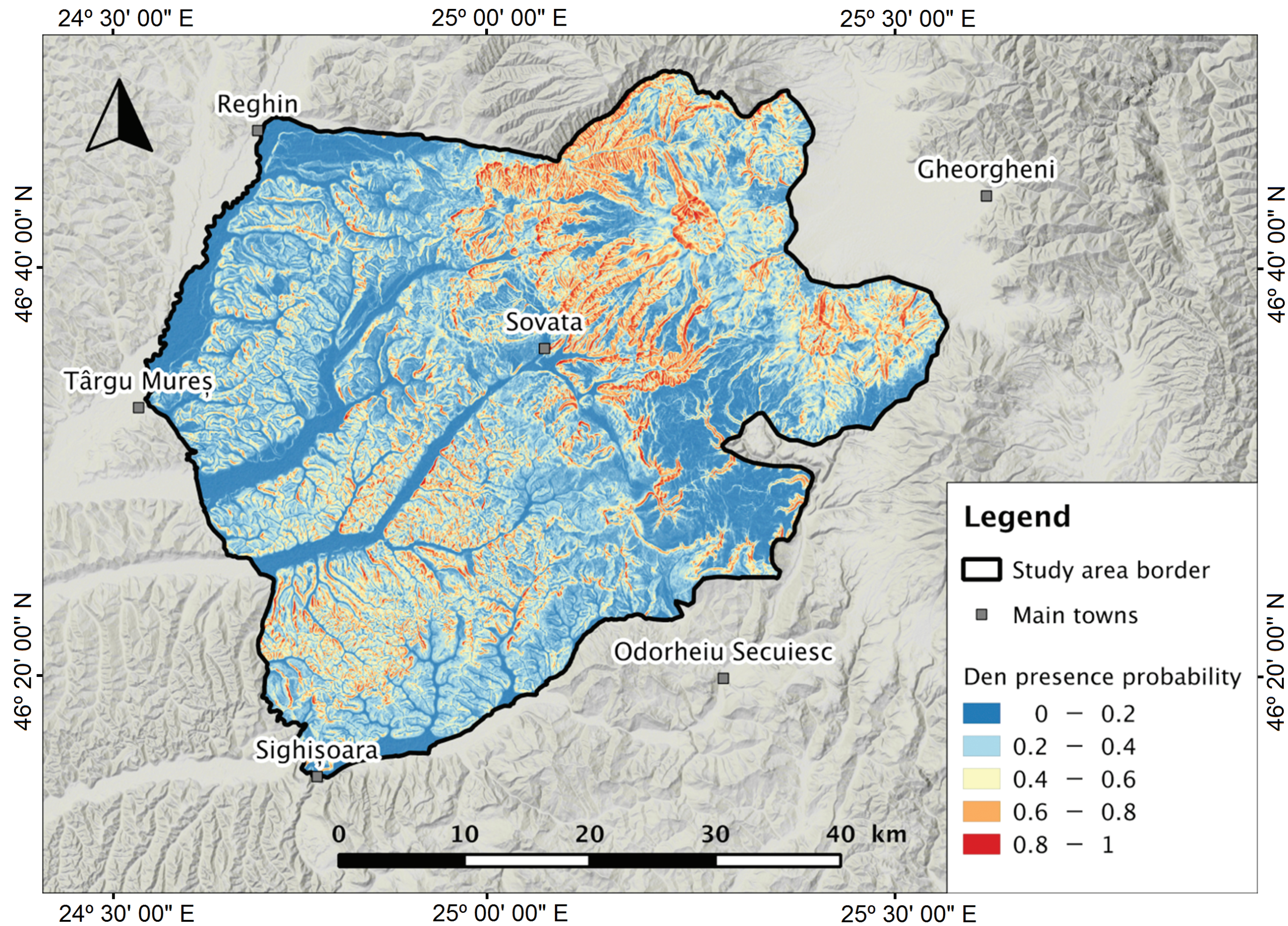

Fig. 4.—Potential areas for brown bear denning in eastern Transylvania, Romania, based on MaxEnt algorithm.

structures probably are less efficient than other den types in terms of reducing energy loss, particularly during periods when there is scant snow cover (Elfström and Swenson 2009). In our study, seven of the eight open nests were used by females that had just given birth, and only one open nest was used by a male. One possible reason for the high use of open nests by females with cubs of the year in our study compared to Manchi and Swenson (2005) was that winters in Romania are less severe than in Sweden.

Bedding material also contributes to thermal insulation in dens (Craighead and Craighead 1972; McLoughlin et al. 2002). Although it is no surprise that we encountered more dens with bedding material in the mountains than in the foothills (50% of the dens versus 22%), we found fewer dens with bedding materials when compared to Croatia (86%—Huber and Roth 1997) and the United States (73%—Servheen and Klaver 1983; 76%—Judd et al. 1986; 76%—Miller 1990). The site level availability of bedding materials might have influenced these findings, but was not quantified in our study.

While den entrance heights and tunnels did not vary between mountains and foothills, entrance widths differed, providing partial support for the structural thermal insulation hypothesis. Mountain den entrances (72.9 ± 29.5 cm) were approximately 10 cm narrower than those in the foothills (82.5 ± 20.3 cm). Results from past studies corroborate these findings, suggesting that bears do not adjust the height of the den entrance, as it is directly proportional to the size of the denning bear (Servheen and Klaver 1983), but instead they modify the width. Given similar den entrance heights, a narrower entrance is more easily obstructed by snow, effectively sealing off the den from the outside weather conditions and increasing thermal insulation (e.g., Craighead and Craighead 1972). Even without a protective snow cover, a narrow entrance likely reduces heat loss (Zhang et al. 2007).

We also found partial evidence toward the risk minimization hypothesis. Similar to other studies (e.g., Sahlén et al. 2011; Smereka et al. 2017; Whiteman et al. 2017), we identified terrain ruggedness as the most important variable for predicting locations where bears would den for the winter. When in proximity of human populated areas, bears may minimize the risk of encounters with humans by using areas of difficult access, including rugged terrain (Martin et al. 2010). Selection of rugged terrain for den sites has also been reported for wolverines (*Gulo gulo*—May et al. 2012), Eurasian lynx (*Lynx lynx*—White et al. 2015), and gray wolves (*Canis lupus*—Ahmadi et al. 2013), and higher terrain ruggedness

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Table 1.—Covariates selected for modeling brown bear den distribution in eastern Transylvania, Romania.

Covariate ID	Description	Covariate type	References
TRugg	Terrain ruggedness index (TRI) based on 30-m DEM[a]	Continuous	Nielsen et al. (2004) Whiteman et al. (2017)
ForestC	Percentage of forest cover within a 495-m rectangle buffer based on CLC[b] 2012	Continuous	Fernández et al. (2012) Pop et al. (2018)
EastI	Easterness-aspect index based on 30-m DEM[a]	Continuous	Craighead and Craighead (1972) Vroom et al. (1980) Schoen et al. (1987)
NorthI	Northerness-aspect index based on 30-m DEM[a]	Continuous	Craighead and Craighead (1972) Vroom et al. (1980) Schoen et al. (1987)
RoadD	Density of paved road within a 500-m circle buffer based on OSM[c] (km^2)	Continuous	Swenson et al. (1997) Sahlén et al. (2011)
ArtifC	Percentage of human infrastructure cover within a 495-m rectangle buffer based on CLC[b] 2012	Continuous	Elfström and Swenson (2009) Fernández et al. (2012)
OpenC	Percentage of open field cover within a 495-m rectangle buffer based on CLC[b] 2012	Continuous	Elfström et al. (2008)

[a]Digital Elevation Model from the GMES RDA project (EU-DEM).
[b]CORINE Land cover 2012.
[c]OpenStreetMap project database.

Table 2.—Measurements for brown bear (*Ursus arctos*) dens in the mountain (n = 74) and foothill (n = 41) regions of the study area in eastern Transylvania, Romania, 2008–2013 and 2015–2017. Height (h), width (w), and length (l) values (cm) represent mean ± *SD*.

	Entrance		Tunnel[a]			Chamber			Porch[b]
	h	*w*	*h*	*w*	*l*	*h*	*w*	*l*	*l*
Mountain dens	62.9 ± 23.8	72.9 ± 29.5	72.0 ± 27.7	87.8 ± 32.7	133.7 ± 69.3	82.1 ± 28.6	118.1 ± 36.1	129.7 ± 34.6	171.9 ± 57.9
Foothill dens	58.3 ± 13.3	82.5 ± 20.3	67.4 ± 15.2	76.5 ± 16.8	112.5 ± 82.4	90.3 ± 29.7	106.5 ± 27.1	129.8 ± 54.1	154.3 ± 62.7

[a]Only for dens with tunnels (tunnel measurements ≠ 0; 40 dens in the mountains and 11 dens in the foothills).
[b]Only for dens with porches (porch length ≠ 0; 51 dens in the mountains and 32 dens in the foothills).

was found to be related to the presence of karstic formations used by denning bears in Croatia (Whiteman et al. 2017). In our study area, brown bears likely prefer rugged terrain because it offers greater availability of potential den sites and potentially because of lower levels of human disturbance in rugged areas (Nielsen et al. 2004; May et al. 2010). Terrain ruggedness at bear den sites was demonstrated to increase with decreasing distance to human presence and activity, such as roads and settlements (Sahlén et al. 2011).

We found unexpected results regarding the relationship between forest cover and suitability for denning. Although all mountain dens and most foothill dens (70%) were located in forests, our model does not support preferential selection of forest habitat for denning (0.8%). Bears that overwinter close to human settlements and activity (as is the case in the foothills region of the study area) need to be concealed, reducing their detectability at den sites (Sahlén et al. 2011). Correspondingly, forest cover provides concealment, which is why forests may be used for denning by many large mammal species, such as Canada lynx (*Lynx canadensis*—Squires et al. 2008) and gray wolves (Norris et al. 2002; Theuerkauf et al. 2003). The surprising lack of association between forest cover and denning in the model results could be due to correlation between forest cover and ruggedness (r = 0.33). Both in the mountains and foothills, rugged areas are predominantly covered with forests. In contrast, woodless, open spaces are located in mostly flat terrain that can be grazed by sheep or cattle, and may be used for haymaking or as arable land. The disproportionately heavy weight of the ruggedness covariate in the model would mask the influence of forest cover, particularly when using a machine-learning algorithm.

We documented partial support for the snowpack thermal insulation hypothesis. The probability of den presence was highest on north- and west-facing slopes. However, the aspect covariate explained only a small percentage of the variability in den distribution in our study area. Previous studies have reported den site associations with all aspects: West (Vroom et al. 1980); North (Craighead and Craighead 1972; Judd et al. 1986); East (Elfström et al. 2008); and South (Schoen et al. 1987; Miller 1990; Groff et al. 1998). Other authors found no preference for a specific aspect at den sites (Huber and Roth 1997; Seryodkin et al. 2003). A review study concluded that aspect selection likely is influenced by the local stability of snow conditions (Linnell et al. 2000). Several studies suggested that bears prefer slope exposures that accumulate the thickest snow cover, insulating the den (Craighead and Craighead 1972; Schoen et al.

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1987). In our study area, west-facing slopes accumulate deeper snow cover due to predominant westerly winds that bring high precipitation, which discharges when encountering the west slopes; whereas slopes with northerly exposures retain snow for longer.

The human avoidance hypothesis as indexed by main transportation infrastructure received scant support. Paved roads did not appear to have an effect on den site selection in our study area. Linnell et al. (2000) suggested that bears den > 1 km from roads, whereas Elfström and Swenson (2009) found that abandoned dens were closer to roads cleared of snow in the winter than successfully used dens. The authors concluded that plowed roads act as a source of disturbance, permitting increased human access to denning areas. Elfström et al. (2008) documented that denning Scandinavian brown bears avoided roads with high disturbance potential, but denned near small roads that were not cleared of snow during winter, and large highways without parking possibilities. We hypothesize that the lack of effect of roads on denning habitat suitability might be due to most roads in our study area being either inaccessible or unused during the denning period. Similarly, Petram et al. (2004) and Whiteman et al. (2017) found that distance to the nearest road had little effect on bear den site selection in Slovenia and Croatia.

Given the complex array of possible human disturbances to bear denning, the map of denning habitat suitability generated in this study is a useful conservation tool to assist in the spatial and temporal planning of human activities in areas exhibiting high probability of den presence, particularly during the denning period. We recommend that forestry management plans include provisions to minimize the amount and duration of forestry operations, or to avoid interventions altogether (road closures—Pigeon et al. 2016) in areas highly suitable for denning, specifically during the denning period. The findings of this study can be used to reduce the negative effects of existing and planned infrastructure development such as the establishment, operation, or extension of ski resorts, quarries, and other tourism- or transport-related infrastructure, including the planned Tîrgu Mureș-Iași [A8] highway. In the foothills, disturbance by pastoralists, villagers, or domestic dogs constitutes additional disruptions that may be harder to regulate, requiring educational programs in local communities.

Lastly, driven hunts for wild boar (*Sus scrofa*) should be avoided altogether in prime brown bear denning habitat during the denning period. Driven hunts present the highest chances for bear dens to be encountered. During these hunts, guides methodically scour forest sections for wild boar on foot, driving (chasing) them toward hunters who lie in wait. Such hunts in winter denning areas may result in den abandonment and threat to human safety.

Given the legal status of brown bears as strictly protected in the EU, through the EU Habitats Directive (Council Directive 92/43/EEC), conferring legal protection to areas highly conducive to bear denning will address current and developing threats associated with this key period in the life cycle of brown bears in Romania.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Spatial distribution of the terrain ruggedness index (TRI) covariate selected for modeling brown bear den distribution in eastern Transylvania, Romania.

Supplementary Data SD2.—Spatial distribution of the forest cover (%) covariate selected for modeling brown bear den distribution in eastern Transylvania, Romania.

Supplementary Data SD3.—Spatial distribution of the Northness index covariate selected for modeling brown bear den distribution in eastern Transylvania, Romania. The covariate ranges from −1 (South exposures) to 1 (North exposures).

Supplementary Data SD4.—Spatial distribution of the Eastness index covariate selected for modeling brown bear den distribution in eastern Transylvania, Romania. The covariate ranges from −1 (West exposures) to 1 (East exposures).

Supplementary Data SD5.—Spatial distribution of the paved-road density covariate selected for modeling brown bear den distribution in eastern Transylvania, Romania.

Supplementary Data SD6.—Pairwise Pearson's correlation coefficients (r) between the seven covariates selected for

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modeling brown bear den distribution in eastern Transylvania, Romania. Covariate details are provided in Table 1.

Supplementary Data SD7.—Structural characteristics of brown bear dens in the mountain versus foothill regions of the study area in eastern Transylvania, Romania, 2008–2013 and 2015–2017. Statistical comparisons of height (*h*), width (*w*), and length (*l*) are presented for the full data set as well as excluding outliers. Wilcoxon rank sum test statistics (*W*) as well as probability values (*P*) are presented. Significant differences (alpha = 0.05) are given in bold.

Supplementary Data SD8.—Ranking of models for brown bear denning habitat distribution in eastern Transylvania, Romania based on ΔAICc. Models were run using MaxEnt and set with and without a bias file as well as linear (L), product (P), and quadratic (Q) features and their combinations.

Supplementary Data SD9.—Model standard deviation for brown bear denning in eastern Transylvania, Romania, based on MaxEnt algorithm, which used data from 119 known den sites.

Supplementary Data SD10.—Probability of brown bear den presence using data collected from 119 known den sites in eastern Transylvania, Romania. Relative percent contributions of four environmental covariates with < 5% individual contributions to the MaxEnt model are indicated in brackets. Gray areas represent the confidence intervals for each probability curve among 10 replicates.

Supplementary Data SD11.—Model Multivariate Environmental Similarity Surface (MESS) for brown bear denning in eastern Transylvania, Romania, based on MaxEnt algorithm fitted using 119 occurrences of wintering structures with linear and quadratic features. MESS map shows areas where covariate values are included inside (dark blue) or outside (dark red) the range of covariate values within the area used to fit the model. The map indicates novelty of the environmental conditions within the projected area, and then the degree of extrapolation of the model.

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