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Distribution and drivers of critical hibernacula for the timber rattlesnake *Crotalus horridus* in Illinois, USA

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ABSTRACT: The dependency on hibernacula for extended periods presents terrestrial reptiles with the challenge of locating thermally adequate hibernacula each winter. Defining the habitat characteristics of hibernacula is crucial for understanding the overwintering requirements and distributions of hibernacula-dependent reptiles, alongside identifying habitats which warrant special conservation concern. Our objectives were to identify the overwintering habitat characteristics of the imperiled timber rattlesnake *Crotalus horridus* in Illinois, USA, and to determine the distribution of likely hibernacula habitats throughout the state. Due to the initial sparsity of hibernacula records in Illinois, we adopted an iterative habitat suitability modeling process consisting of 3 distinct rounds of Maxent construction and revision. Each round was informed with updated information from model-guided surveys or by building rapport with in-state naturalists and researchers who knew of additional hibernacula locations. We created our final model using 36 hibernacula and identified slope angle (indicative of rock outcrops and shallow soils), topographical position index, forest patch area, and aspect (decomposed into 2 linearized variables: southness and eastness) as important drivers of *C. horridus* hibernacula habitat in Illinois. Together, the 5 variables and site surveys suggest the suitable overwintering habitat for *C. horridus* in Illinois is located on south- to southwest-facing outcrops on upper slopes and ridges of larger forest patches. Such habitat is distributed primarily in southern Illinois and throughout the Mississippi River and Illinois River border counties. Our study adds to the current understanding of the species' overwintering requirements and provides a foundation for future ecological studies, management, and survey efforts throughout Illinois.

KEY WORDS: Habitat suitability model · *Crotalus horridus* · Hibernacula · Pitviper · Species niche model · Brumation

1. INTRODUCTION

Many terrestrial reptiles depend on thermally adequate hibernacula for overwintering survival. Species unable to create hibernacula often rely on uncommon or patchy landscape features, such as animal burrows or rock crevices, which limit species' dispersal capabilities and subsequent geographic distributions (Gregory 1982), often leading to high fidelity to specific hibernacula. Some taxa — particularly snakes — often travel several kilometers from activity season ranges to return to the same hibernaculum each winter (Brown 1993, Zappalorti et al. 2015). Several high-latitude species also overwinter communally (Ultsch 1989), resulting in large multi-species congregations in a hibernaculum. High fidelity, habitual use, and multi-species residency indicate that such hibernacula have specific habitat characteristics

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required for overwinter survival (Prior & Weatherhead 1996, Keller & Heske 2000, Browning et al. 2005). Defining such characteristics is crucial for understanding the overwintering requirements and distribution of hibernacula-dependent reptiles and can assist in identifying critical habitats which warrant special conservation concern.

The imperilled timber rattlesnake *Crotalus horridus* is a wide-ranging pitviper dependent on hibernacula to survive critically low winter temperatures (Brown 1993, Martin 2002). Despite having the largest geographic range of any rattlesnake, spanning the eastern continental USA from Canada to Florida, information on the overwintering habitat requirements and distribution of *C. horridus* is sparse and predominantly clustered in the northeast of the species range (Martin 1992, Brown 1993, Sealy 2002, but see Browning et al. 2005). Populations throughout such northerly regions use communal hibernacula which typically occur on south- to west-facing rock outcrops, talus slopes, and bluffs throughout upland forests (Martin 1992, Brown 1993). Such hibernacula can occur in both open and shaded locations but are often near exposed basking areas such as prairies, ridgelines, and gaps in the tree canopy (Martin 1992). Basking areas (sensu Brown 1993; 'transient habitat') often share similar habitat characteristics with hibernacula and are used temporarily by individuals, presumably to bask or shelter, before entering the hibernacula in fall (ingress) and immediately after emerging in the spring (egress). Gravid females also use transient habitats during summer gestation (Brown 1991, Gardner-Santana & Beaupre 2009). However, besides anecdotal reports (e.g. Breisch et al. 2021 Bielema 2022), we currently lack information regarding the overwintering characteristics and distribution of hibernacula habitat for *C. horridus* across the rest of the species' northern range.

In the past several decades, *C. horridus* has experienced drastic population declines throughout its range due to habitat loss and human persecution (Brown 1993, Clark et al. 2008). Consequently, the species is considered extirpated in Maine, Rhode Island, and Ontario and is currently threatened or endangered in 14 of the 30 US states within its range (Martin et al. 2008). Despite its status as a threatened species in Illinois, critical hibernacula habitat for *C. horridus* is unknown, severely limiting our understanding of the species' overwintering requirements and restricting effective conservation and management across the state. The species' historical distribution in Illinois spanned the lower southern half of the state and throughout the western Mississippi River border counties (Phillips et al. 2022). However, indiscriminate killing, hibernacula destruction (Warwick et al. 1991, Weir 1992), and landscape conversion (Yadav & Malanson 2008) have led to local extirpations (Foster et al. 2006) and range contraction (Phillips et al. 2022). Anecdotal reports on the distribution of *C. horridus* hibernacula throughout Illinois (Smith 1961, Foster et al. 2006, Bielema 2022) suggest hibernacula are limited by the extent of topographically rugged uplands where outcrops and ridgelines intersect with most of the state's remaining forests. Due to the state's relatively flat topography, such habitat may only exist along the larger river valleys and unglaciated regions in northwestern and southern Illinois.

The objectives of our study were to: (1) identify the overwintering hibernacula characteristics of *C. horridus* in Illinois; and (2) construct a predictive model to determine the distribution of likely hibernacula throughout the state. Such information is vital to further our understanding of the species' overwintering requirements, identify sites for conservation, management, and survey efforts throughout Illinois, and lay the foundation for long-term monitoring regimes.

2. MATERIALS AND METHODS

2.1. Modeling overview

We assessed the habitat requirements and distribution of *Crotalus horridus* overwinter hibernacula in Illinois using habitat suitability models (HSMs). HSMs use occurrence records and environmental variables to predict the geographic distribution of a species' habitat based on its known distribution in environmental space. While there are 2 categories of HSMs based on the type of species occurrence data used (i.e. analyses requiring both presence and absence data versus those using presence-only), absence data for cryptic and imperiled species such as *C. horridus* is sparse due to difficulties in obtaining reliable detection and occupancy estimates. Therefore, we used Maxent (Phillips & Dudik 2008,, 2008) based on the maximum-entropy approach to modeling species distribution, which requires presence-only data. We chose Maxent due to its competitive performance, the ability to handle complex relationships between response and predictor variables, and robustness to small sample sizes (Elith et al. 2011).

2.2. Hibernacula occurrences and model iteration overview

Determining hibernacula locations for enigmatic reptiles is difficult and is particularly challenging for *C. horridus* because of difficult surveying conditions in topographically rugged terrain, the limited window of opportunity to locate snakes before their dispersal to summer habitats (spring egress) or ingress into hibernacula (fall ingress), and low detection rates of snakes, which frequently use inconspicuous locations (e.g. under rocks). Additionally, as a threatened and highly persecuted species, people are secretive in revealing known hibernacula locations to prevent potential poaching or harassment of snakes, an unfortunately common and encouraged practice across the species' range (Brown 1993, Breisch et al. 2021). Consequently, at the beginning of our study, we knew of only 13 hibernacula locations in Illinois. To bolster the sample size, we adopted an iterative HSM approach consisting of 3 rounds of Maxent modeling, revising the model as we determined additional hibernacula via model-guided surveys or as we built rapport with in-state naturalists and researchers who knew of or found additional hibernacula throughout the study period. We also refined our modeling procedures throughout the iterative process as we increased both our sample size and understanding of the species' overwintering requirements.

We briefly explain the data collection and modeling procedures of the first 2 modeling iterations below, but our paper focuses primarily on the final (third) model iteration. The Supplement at www.int-res.com/articles/suppl/m053p467_supp.pdf provides further details regarding modeling and field-survey methods for the first 2 iterations. In all cases, surveyors identified hibernacula via sightings of one or more *C. horridus* entering into, or emerging from, a hole or a crevice during the species' overwintering period (September–May). Most hibernacula were vetted by follow-up visits or further study (e.g. Bielema 2022, Jesper et al. 2023). Hibernacula which were visited only once were all found during the first warm spring days, and consequently we are confident such locations were indeed hibernacula, as snakes would have had limited opportunitity to emerge and diserprse to transient habitats prior to such dates. Surveyors recorded hibernacula locations using GPS receivers with a horizontal accuracy of ≤10 m or marked them on US Geological Survey topographic maps (7.5 min series) before digitizing the locations.

In early 2019 (model round 1), we created an initial Maxent model using 13 hibernacula locations (see Text S1 and Figs. S1–S3), 10 of which were discovered during ongoing research of *C. horridus* in Jersey County, IL, USA, between 2010 and 2018 (S. Eckert unpubl. data), and 3 were found via visual encounter surveys in Jo Daviess County, IL, USA, in 1992 (Bielema 2022). To bolster sample sizes and field-validate the initial model, we conducted model-guided surveys in spring 2019 at 24 sites in Jersey County (Fig. S1). To increase our chances of finding hibernacula, we constrained our survey efforts to areas with a probability ≥50% (as determined by a Maxent-derived C-loglog probability raster) and searched during the species' spring egress period, when snakes were likely to be surface active at hibernacula. Overall, between 6 April and 25 April, 3 surveyors spent 135.34 person-hours across 10 d searching for *C. horridus* (3 sites d^{-1} with repeat site visits), and we identified 2 new hibernacula during our surveys.

In 2022 (model round 2), we created a revised Maxent model using 34 hibernacula locations (21 new hibernacula). Alongside the 2 hibernacula discovered in the first round, we included 8 hibernacula located by Illinois Department of Natural Resources (IDNR) staff and in-state naturalists during (non-model guided) surveys in southern and west–central Illinois in 2020. We also included 11 hibernacula determined via opportunistic information from landowners and in-state naturalists who had located hibernacula in the past 20 yr. As before, to bolster the sample size and to field-validate the revised model, we conducted model-guided surveys in northern Pope County, IL, USA, (Fig. S4) in April 2023. Learning from our previous survey efforts in Jersey County, we conducted surveys only on warmer days (daytime temperatures >20°C) during the spring egress period and made repeat visits to habitat deemed highly suitable (p ≥ 75%) by our HSM to increase the chances of snake detection. Overall, one surveyor searched for 30.22 h over 5 d (mean = 6.04 h d^{-1}) and found 2 new hibernacula.

Thus, we obtained 36 hibernacula occurrences throughout the study period distributed throughout southern, west–central, and northwestern Illinois (Fig. 1). We used all locations to create a final Maxent model (model round 3), our primary focus for the remainder of the manuscript.

2.3. Predictor variables

For the final model, we created 10 predictor variables based on *a priori* knowledge of the determinants of hibernacula distribution (Table 1), several of which we used in previous model iterations. Unless

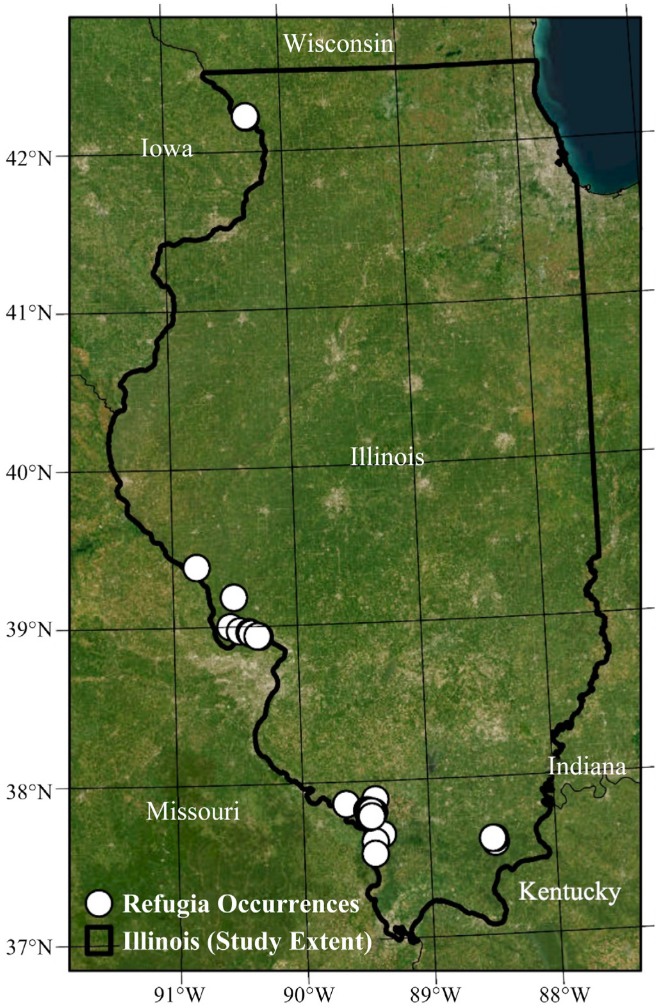

Fig. 1. Locations of 36 *Crotalus horridus* hibernacula occurrences in Illinois used in the final Maxent model. Each point has been enlarged to obscure specific hibernacula locations

specified otherwise, all predictor variables were prepared as ASCII rasters using ArcGIS Pro 3.0 (Esri 2021) with a geographic extent of Illinois and a cell resolution of 10 m. We specifically used a higher resolution (30 m is commonly used; e.g. Browning et al. 2005) to capture finer topographical detail, particularly in the slope raster. To avoid raster 'edge-effects,' or biased values at the edge of a raster due to missing data values from neighborhood analyses, we created all rasters with the extent of a 5 km-buffered Illinois boundary before clipping them to the state boundary.

We prepared several light detection and ranging (LIDAR)-derived predictors using a 10 m resolution digital elevation model (DEM) obtained from the 3D Elevation Program ('3DEP'; USGS 2021). We calculated slope angle (slope; degrees) as the maximum elevation change rate over each DEM cell and its 8 neighbors using the 'surface parameters' tool. Higher slope values represent steeper terrain, which studies frequently use as a proxy for rock outcrops and shallow soils (Browning et al. 2005, Garst 2007, Kakavas & Nikolakopoulos 2021). The topographic position index (TPI; Weiss 2001) measures topographic position with positive TPI values representing upper slopes and ridges and negative TPI values representing lower slopes and ravines. We calculated TPI using a neighborhood window size of 25 m to capture small-scale ridges and valleys throughout Illinois' dendritic drainage system.

We calculated aspect using the 'surface parameters' tool before transforming it into 2 continuous (i.e. removing the circularity of aspect) and linearized variables: eastness, the sine of aspect in radians (gradient between −1 = due west to 1 = due east); and southness, the cosine of aspect in radians (gradient between −1 = due south to 1 = due north). We also calculated insolation (Watt hours per meters squared or Wh m^{-2}) using the 'area solar radiation' tool (Rich et al. 1994, Fu 2000, Fu & Rich 2002), representing the total incoming solar radiation (both direct and diffuse) at a given cell during the species' typical overwinter period in Illinois (1 October–1 May). Higher insolation values represent greater amounts of insolation during the overwintering period. We used the following tool parameters: latitude = 39.7° (mean latitude of Illinois); sky size value = 200; day interval = 14; hour interval = 2.

We also calculated 3 patch-level forest metrics using the software FragStats (McGarigal 1995): forest patch area (f_area), proximity index (f_prox; Gustafson & Parker 1992), and shape index (f_shape). We defined a forest patch as an expanse of forest bounded entirely by non-forest landcover. We determined forest patches using a modified version of the 'WorldCover' landcover dataset (10 m resolution; Zanaga et al. 2022), whereby we added a 'roads' class to the default landcover types using a rasterized road layer of all major and minor roads obtained from OpenStreetMaps (OpenStreetMaps 2015). The inclusion of roads reflected the fragmentation of Illinois forests, which the original landcover raster did not capture, thus more accurately defining individual forest patches. We include the landcover layer and the 3 forest metrics in our initial set of predictor variables. f_area is a forest patch's planimetric area (in ha). f_prox considers the size and proximity of all forest patches whose edges are within a 50 m radius of the focal forest patch. f_prox = 0 if a forest patch has no neighboring forest patches, and f_prox ≥ 0 as the neighborhood is increasingly occupied by patches of the same type

Table 1. Initial set of predictor variables chosen to examine the habitat requirements and distribution of timber rattlesnake *Crotalus horridus* overwinter hibernacula in Illinois using habitat suitability modeling. Predictor variables based on *a priori* hypotheses of the drivers of the hibernacula distribution for *C. horridus*

Variable	Abbrev.	Units	Description
Slope angle	Slope	Degrees	Maximum elevation change rate over each cell and its 8 neighbors; higher slope values represent steeper terrain and can indicate outcrops and shallow soils
Insolation	Insolation	Wh m^{-2}	Sum of direct and diffuse solar radiation during the typical overwinter period of *C. horridus* in Illinois (1 October–1 May) with higher insolation values representing greater amounts of insolation
Proximity index	f_prox	Unitless index	Index considering the size and proximity of all forest patches with edges within a 50 m radius of the focal forest patch (Gustafson & Parker 1992)
Forest patch area	f_area	Hectares (ha)	Planimetric area of a forest patch
Forest shape index	f_shape	Unitless index	Measure of forest patch shape-complexity
Forest cover	f_cov	Percent (%)	Percentage of the forest canopy at a given location derived from 30 m resolution USDM canopy cover data resampled to 10 × 10 m
Topographical position index	TPI	Unitless index	Measure of slope position, positive TPI values represent upper slopes and ridges, while negative TPI values represent lower slopes and valleys/ravines using a neighborhood window size of 25 m to capture small-scale ridge-valley networks throughout Illinois
Aspect southness	Southness	Cos(radians)	Linearization of aspect by taking the cosine of aspect (in radians), resulting in a gradient between 1 (due north) and −1 (due south)
Aspect eastness	Eastness	Sin(radians)	Linearization of aspect by taking the sine of aspect (in radians), resulting in a gradient between 1 (due east) and −1 (due west)

and as those patches become closer and more contiguous or less fragmented in distribution. f_shape is a measure of the shape complexity of a forest patch and is calculated as the forest patch perimeter (m) divided by the square root of forest patch area (m^2), adjusted by a constant to account for square standard (raster cells). Finally, we included percent canopy cover derived from the United States Forest Service (USFS; Coulston et al. 2012), which we resampled from 30 to 10 m resolution. Upscaling from a lower to higher resolution raster should typically be avoided as it can introduce false accuracy, but we made an exception in this instance given the potential importance of canopy cover to hibernacula distribution, and since the USFS raster is the highest resolution and publically available percent canopy cover currently available for Illinois.

2.4. Addressing multicollinearity

Our study objectives were to identify the overwintering hibernacula characteristics of *C. horridus* in Illinois and to determine (predict) the distribution of likely hibernacula throughout the state. Thus, we opted to minimize multicollinearity between predictor variables to increase the interpretation of predictor response and importance. We tested for multicollinearity between all continuous predictor variables by calculating pairwise Pearson's coefficients and variance inflation factor (VIF), retaining only one predictor variable from a set of moderate to strongly correlated variables ($|r| \geq 0.6$ or VIF ≥ 5). Pearson's coefficients also allowed us to interpret the relationship between variables better, even if we did not use them in the final model. Ease of variable interpretation and parsimony (i.e. Occam's razor) are essential for effectively understanding hibernacula habitat drivers and determining likely habitats in the field. Thus, we retained predictor variables with the most biological relevance to the species and ease of interpretation (Merow et al. 2014) and chose not to pursue dimensionality reduction methods (such as principal component analysis) which would complicate variable interpretability.

2.5. Maxent procedures

A critical assumption of Maxent is that the occurrence records used for model building are derived from systematic random sampling; Maxent assumes all locations on the focal landscape are equally likely to be sampled (Elith et al. 2011, Kramer-Schadt et al. 2013). Yet in many cases, including the present study, occurrence data derived from opportunistic observations are not randomly sampled and, therefore, almost always exhibit strong spatial bias and spatial autocorrelation in survey efforts, resulting in biased model predictions (Yackulic et al. 2013). We addressed sampling bias and spatial autocorrelation using a common approach described by Phillips et al. (2009) and Elith et al. (2010), whereby a 'bias layer' is used to manipulate the selection of background data so they reflect the same sample selection bias as the occurrence data. In doing so, the effect of sampling bias/spatial autocorrelation cancels out, allowing Maxent to focus on any differentiation between the distribution of the occurrence and the background. Following Elith et al. (2010), we created a bias layer consisting of a Gaussian kernel density of hibernacula locations rescaled from 1 to 20, where values of 1 reflect no sampling bias and higher values represent increased sampling bias. We used the resulting raster grid as a bias layer in all Maxent runs. Similar to the predictor variables, the background points (n = 10 000 random locations from the predictor rasters) and resulting bias layer were prepared with a geographic extent of the 5 km-buffered Illinois state boundary.

Since feature classes and the L1-regularization multiplier can affect model fit, transferability, and predictive power (Elith et al. 2011, Warren & Seifert 2011, Merow et al. 2013), we compared models with a combination of feature classes and regularization multiplier. To select appropriate Maxent model parameters, we used the corrected Akaike information criterion (AICc) in the R package ENMEval (Muscarella et al. 2014, R Core Team 2021). We omitted product (P) features from our model, and thus compared the linear (L), quadratic (Q), and hinge (H) features using the combinations 'LHQ', 'LH', 'LQ', 'QH', 'L-only', 'Q-only', and 'H-only'. We also examined each combination with regularization multiplier values of 1, 2, 5, 10, 15, and 20 (Warren & Seifert 2011, Shcheglovitova & Anderson 2013), resulting in 42 different model configurations for comparison. We chose the most parsimonious model as determined via AIC_c for further analysis.

We evaluated the relative performance of the most parsimonious model using the area under the curve (AUC) of the receiver operating characteristic (Hanley & McNeil 1982). The resulting AUC performance value ranges from 0–1, with higher values representing better discrimination between presence and background points. Due to our small sample size, we used a bootstrapping approach to resample our data into training and testing datasets. We selected the training data by randomly sampling the occurrence records with replacement, with the number of samples equaling the total number of occurrence records, and then tested the model on the occurrence records not selected. We repeated the bootstrapping procedure for 100 replicate runs and reported the results for an averaged model ±1 SD of the replicate runs.

We also examined model performance by graphing test omission rates as a function of the cumulative threshold averaged over the 100 bootstrap replicate runs (Phillips et al. 2006). If our model was a good fit, we expected the omission rate of training samples to be similar to the predicted omission rate. We avoid threshold-dependent performance statistics for the reasons Merow et al. (2014) outlined. Foremost, background points used by Maxent are not equivalent to absences (a common misconception in the scientific literature; Guillera-Arroita et al. 2014). Thus, many threshold-dependent measures, such as the frequently employed kappa and true skill statistic, are inappropriate for presence-only models and should be avoided.

We examined how each predictor variable affected the probability of suitable hibernacula habitat and model variability using the final averaged model's marginal response curves (holding all other predictor variables at their mean values). Because we omitted the P feature class from our model, the marginal response curves for each predictor completely defined the model as opposed to those depending on the values (interactions) of other predictors (Merow et al. 2013), thus making variable interpretation easier and reliable. Plot data was output by the Maxent software and then imported into R (R Core Team 2021) to create graphs using the package 'ggplot2' (Wickham 2016). We also examined the relative importance of each variable in predicting suitable hibernacula habitat using jackknife tests and variable percent contributions, both output by Maxent.

2.6. Identification of potential hibernacula habita

We generated a Clog-log transformed raster from the final (averaged) model representing the predicted probability of suitable hibernacula habitat across Illinois (hereafter probability raster). The probability raster values ranged from 0–100%, with values closer to 100% indicating highly suitable hibernacula habitat and values closer to 0% indicating lower suitability. The high resolution (10 m) of the probability raster presented difficulties in effectively displaying habitat suitability at the scale of Illinois, so we instead presented example maps for 2 select regions in Jersey and Pope counties, where we conducted surveys using previous model iterations.

We assessed the geographic distribution of potential hibernacula habitat throughout Illinois by calculating each county's total planimetric area (ha) of suitable habitat. It was necessary to make the continuous probability raster binary by choosing a probability value below which we considered habitat unsuitable for hibernacula and above which we considered suitable to calculate area. While thresholding should be avoided where possible (Merow et al. 2013), creating a binary raster, in this instance, allowed for a useful quantitative evaluation of potential hibernacula distribution. We used the 10-percentile training presence threshold of the final averaged model, which retains 90% of the occurrence records while removing extreme outliers. As an administrative division, calculating the area of suitable habitat by county has little ecological relevance but serves as a simple indication of the spatial distribution of potential hibernacula habitat throughout Illinois in relevant spatial units to management and conservation. We present a map detailing the area of suitable hibernacula habitat in each county (see Fig. 5).

3. RESULTS

3.1. Predictor variables

Of the initial 10 continuous predictors (9 continuous and 1 discrete; Table 1), we retained 5 uncorrelated variables for further analysis: slope, f_area, southness, eastness, and TPI (Table 2). The predictor slope was positively correlated with f_cov (r = 0.66), indicating steeper slopes typically had reduced forest canopy cover. We retained slope due to its ecological importance as a proxy for rock outcrops. The predictor variable f_area was positively correlated with f_prox (r = 0.82) and f_shape (r = 0.64), indicating that larger forest patches were in closer proximity to other large forest patches and were less complex in shape (i.e. more contiguous). We retained f_area due to its ease of interpretation over the unitless indices of the other 2 forest patch metrics. The predictor southness was negatively correlated with insolation (r = −0.63), implying southern aspects receive more solar radiation throughout the typical *Crotalus horridus* overwintering period than northern aspects. We retained southness due to its ease of interpretation and calculation over insolation (the computation time to run ArcGIS Pro's solar radiation tool on high-resolution data can be excessive). Preliminary examination of predictor variables also revealed all hibernacula occurrences were within forests, thus rendering the landcover variable obsolete. Consequently, we removed the landcover predictor from our analysis and clipped the final probability raster to forests. The VIF of the remaining predictor variables were < 4.

Table 2. Pairwise Pearson correlation coefficients between the initial set of continuous predictor variables chosen to examine the habitat requirements and distribution of timber rattlesnake *Crotalus horridus* overwinter hibernacula in Illinois. We retained only 1 variable from a set of highly correlated variables (Pearson correlation coefficient (|r|) ≥ 0.6 [**bold** font] or variance inflation factor [VIF] ≥ 5) for subsequent habitat suitability modeling. Definitions of each predictor variable are found in Table 1

	f_area	Eastness	f_cov	Southness	f_prox	Insolation	f_shape	Slope	TPI
f_area	1.00	–	–	–	–	–	–	–	–
Eastness	0.00	1.00	–	–	–	–	–	–	–
f_cov	0.50	0.00	1.00	–	–	–	–	–	–
Southness	0.00	−0.01	0.01	1.00	–	–	–	–	–
f_prox	**0.82**	0.00	0.59	0.01	1.00	–	–	–	–
Insolation	−0.11	0.00	−0.18	−0.63	−0.12	1.00	–	–	–
f_shape	**0.64**	0.00	**0.75**	0.01	**0.62**	−0.16	1.00	–	–
Slope	0.34	0.00	**0.66**	0.02	0.40	−0.28	0.48	1.00	–
TPI	−0.02	0.00	−0.08	0.01	−0.03	0.06	−0.07	−0.01	1.00

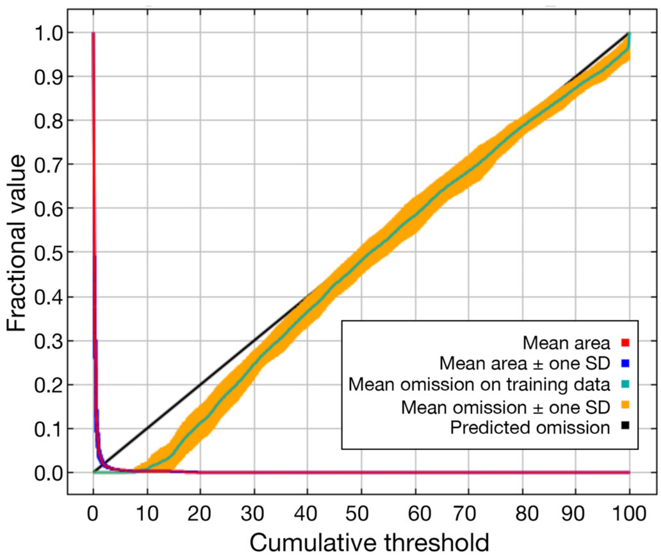

Fig. 2. Test omission rates and predicted area for the final model as a function of the cumulative threshold averaged, over the 100 bootstrap replicate runs. Omission rate of training data should be similar to the predicted omission rate (black line), the definition of the cumulative output format

3.2. Maxent procedures

The best-fit Maxent model, with 100% of the cumulative AIC_c model weight, included the quadratic and hinge feature classes with an L1-regularization multiplier of 1. The bootstrap-averaged top model received a mean AUC performance value of 0.96 (SD = 0.62), and the omission rate of training samples (closely resembled the predicted omission rate (i.e. followed a straight line, Fig. 2), suggesting excellent model fit. Jackknife tests of relative variable importance (Fig. 3) revealed slope was the most important predictor of hibernacula habitat suitability with the highest regularized training gain and percent variable contribution (79.5%; SD = 5.19%), followed by f_area (11.0%; SD = 4.84%), southness (7.52%; SD = 3.05%), eastness (1.12%, SD = 0.65%), and TPI (0.826%; SD = 0.78; although TPI received higher jackknife support).

Examination of marginal plots revealed hibernacula habitat suitability increased with higher slope (Fig. 4A), with all hibernacula occurrences on slope angles between 17 and 47 degrees ($\bar{x}$ = 31.15; SD = 7.72; Table 3). The high slope angle suggested outcrops and shallow soils, as all but one hibernacula were located on or near outcrops and associated talus slopes. Hibernacula were also more likely to occur at higher values of southness (Fig. 4B) or more southerly aspects and higher values of eastness (Fig. 4C) or more westerly aspects. The mean southness and eastness values for all hibernacula occurrences were −0.83 (SD = 0.20) and −0.34 (0.43). When translated to cardinal directions, 34 of the 36 hibernacula records were located on south and southwest slopes, one on a southeastern slope and one on a western slope. No hibernacula were located on northern (NE, N, NW) or due east slopes. Additionally, hibernacula habitat suitability increased with higher TPI (Fig. 4D), with all hibernacula occurrences occurring between TPI values of −7 and 36 ($\bar{x}$ = 10.08; SD = 11.22; Table 3) corresponding to upper slopes and ridges. Hibernacula suitability was also greater with increasing values of f_area (Fig. 4E), corresponding to larger forest patches. The low variance of each marginal plot indicated hibernacula across Illinois share relatively similar characteristics.

3.3. Identification of potential hibernacula habitat

We used the 10-percentile training presence threshold of the final averaged model (p ≥ 52.69%) to create a binary ('suitable' and 'unsuitable') map to quantify the area of potential hibernacula habitat in each county throughout Illinois. In general, suitable hibernacula habitat appears to be distributed across southern Illinois and throughout the Mississippi and Illinois River border counties (Fig. 5). In southern Illinois, Union County appears to have the greatest area of potential habitat (~1139 ha), followed by the neighboring Alexander and Jackson Counties, and extending east through Johnson, Pope, and Hardin Counties (and to a less extent through Williamson, Saline, and Gallatin Counties). Potential habitat continues northward along the Mississippi River to Pike County and then along the Illinois River to LaSalle County. There is a

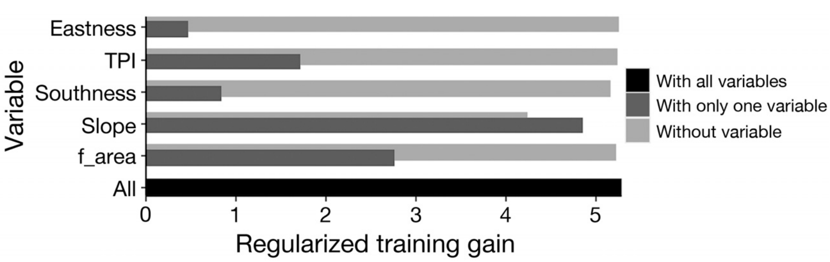

Fig. 3. Jackknife plot of training gain for the final averaged Maxent model of 100 bootstrapped replicate runs. Dark and light gray bars indicate the training gain for a given variable when it was and was not included in the model, respectively. Variables defined in Table 1

noticeable lack of predicted habit along the Mississippi River from Pike County to Carroll and Jo Daviess Counties in northwest Illinois. Several 'outlier' counties in east–central Illinois — primarily Vermilion and Coles Counties — also show a relatively high area of suitable habitat.

Visual examination of the (continuous) probability raster (examples in Fig. 6) reveals highly probable habitat in topographically rugged forested regions, prominently featuring along south-facing outcrops, ridgelines, and bluffs, identified via bands of high probability habitat across the landscape. We provide 2 example maps depicting predicted hibernacula habitat along the Mississippi River bluffs of Jersey County and interior forest outcrops of Pope County (Fig. 6), both of which were the locations of HSM-guided surveys using previous model iterations (see also habitat photos in Fig. S5).

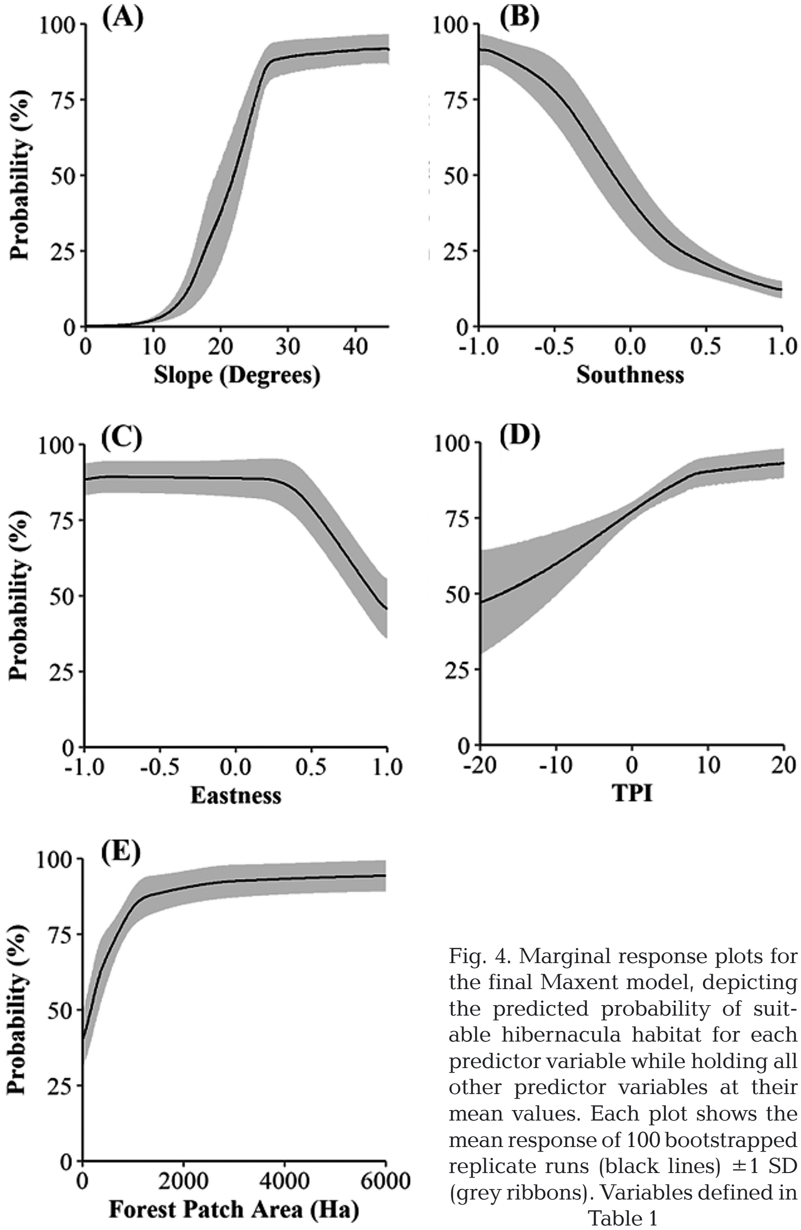

Fig. 4. Marginal response plots for the final Maxent model, depicting the predicted probability of suitable hibernacula habitat for each predictor variable while holding all other predictor variables at their mean values. Each plot shows the mean response of 100 bootstrapped replicate runs (black lines) ±1 SD (grey ribbons). Variables defined in Table 1

4. DISCUSSION

4.1. Overview

Suitable overwintering habitat for *Crotalus horridus* in Illinois appears to be located on south- to southwest-facing outcrops on the upper slopes and ridges of larger forest patches, distributed primarily in southern Illinois and throughout the Mississippi and Illinois River border counties. Our findings are consistent with other reports detailing the species' overwintering requirements across their central to northern range (Martin 1992, 2002, Brown 1993, Browning et al. 2005, Garst 2007) and with anecdotal reports from neighboring states (Breisch et al. 2021). Our HSM's ability to predict such habitat throughout the state is invaluable for guiding survey efforts in finding new *C. horridus* hibernacula and populations, as demonstrated during our iterative model-guided surveys in southern Jersey and Pope counties, increasing the number of known hibernacula throughout the state, as of 2023, by 11%.

Slope was the most important variable in predicting *C. horridus* overwintering habitat, corresponding to

Table 3. Summary statistics of the 5 predictor variables retained for suitability modeling (after removal of multicollinear variables) at 36 *Crotalus horridus* hibernacula locations across Illinois. Data derived from the raster cell values (10 m resolution) in which the hibernacula were located. Definitions of each predictor variable are found in Table 1

Statistic	Predictor variable				
	TPI	Slope	Southness	Eastness	f_area
Mean	10.08	31.15	−0.82	−0.34	1613.36
SD	11.22	7.72	0.20	0.43	1068.96
Min.	−7.00	17.00	−1.00	−0.93	173.21
Max.	36.00	47.00	−0.36	0.39	2829.54

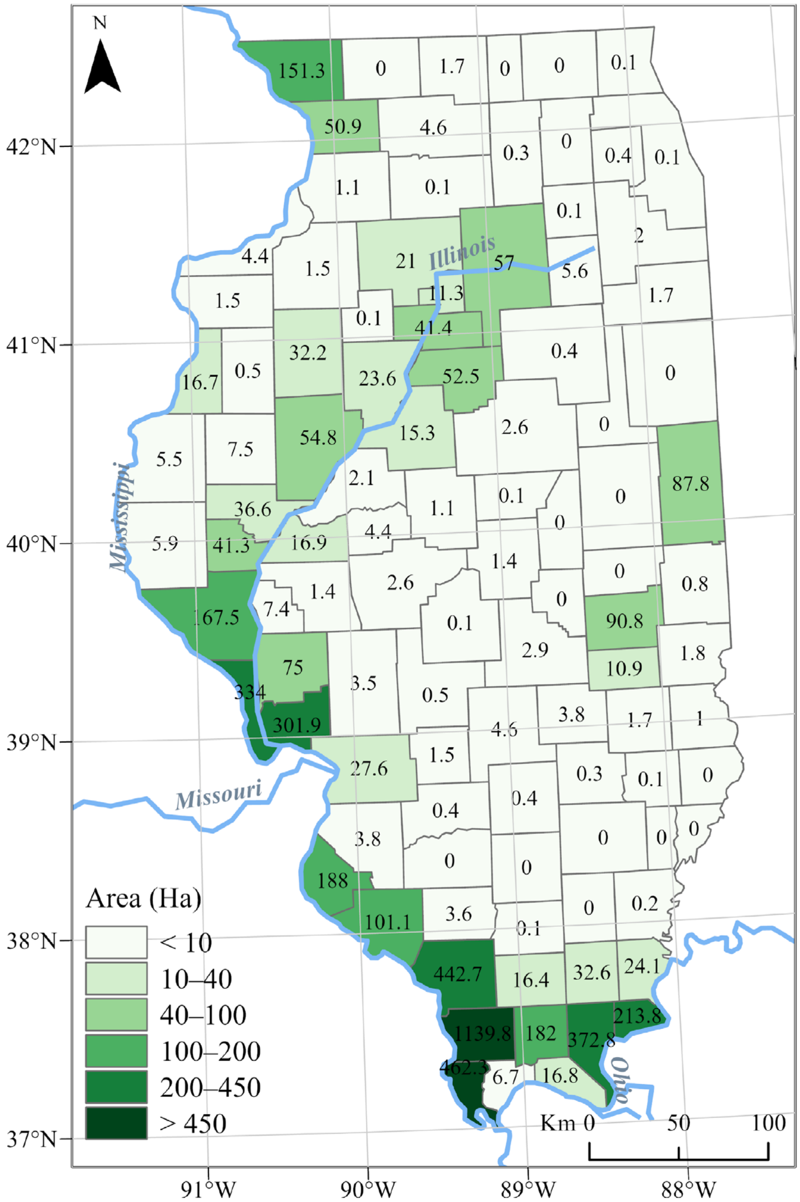

Fig. 5. Map of Illinois detailing the total area (ha) of suitable hibernacula habitat for timber rattlesnakes *Crotalus horridus* in each county, as estimated by the final (averaged) Maxent model. Suitable habitat is defined as locations with a probability value of >52.69%, corresponding with the 10 percentile training presence C-loglog threshold. Legend breaks are colored using natural Jenks to account for unequal data distribution. Major rivers (blue lines) included as a reference

the findings of other reports (Martin 1992, Brown 1993, Browning et al. 2005, Garst 2007). Steep slopes are highly indicative of outcrops and thin soils, and most of the highly suitable areas predicted by our model, similar HSMs (Browning et al. 2005, Garst 2007), and our model-guided surveys appear to be located on rocky habitats (e.g. along river bluffs, forest outcrops). Such habitat is presumably advantageous to *C. horridus*; not only does it provide abundant subterranean access via crevices and cracks at the soil–rock interface, it also provides permanent overwintering sites that are reliably available each winter, as opposed to temporary structures such as animal burrows or root holes that are more ephemeral from year to year. Permanent 'on-demand' hibernacula are desirable for *C. horridus*, particularly northern populations, which do not create their hibernacula and whose survival depends on locating these thermally adequate but geographically limited landscape features.

We suspect reliance on rocky habitats may decrease in more southerly US regions where milder temperatures permit overwintering in temporary structures, including mammal burrows and rootholes (Sealy 2002). Although uncommon, anecdotal reports suggest individuals may use temporary structures as hibernacula in southern Illinois (S. Ballard unpubl. obs., C. Feng pers. comm.); however, such reports might be mistaking hibernacula with nearby transient habitats used by post-emergent individuals before dispersal to summer ranges (Brown 1993). For example, VHF-radiotelemetry of *C. horridus* at Principia College in west–central Illinois revealed post-emergent individuals often retreat into hollow trees, logs, and root holes, particularly during periods of colder temperatures (S. Eckert unpubl. data). It is also possible that such hibernacula are associated with subsurface rock crevices covered by loess (wind-blown silt), thus preventing visual outcrop detection. Further investigation into the significance of non-outcrop hibernacula is warranted.

Outcrops on south- to southwest-facing aspects appear particularly important to *C. horridus*, and the probability of north- or east-facing hibernacula is very low. Other studies support our findings; notably, Browning et al. (2005) found only 2 of 39 confirmed hibernacula in northwest Arkansas occurred on north and northeast-facing slopes. Further, of the 153 hibernacula studied by Martin (1992) in Virginia, only one

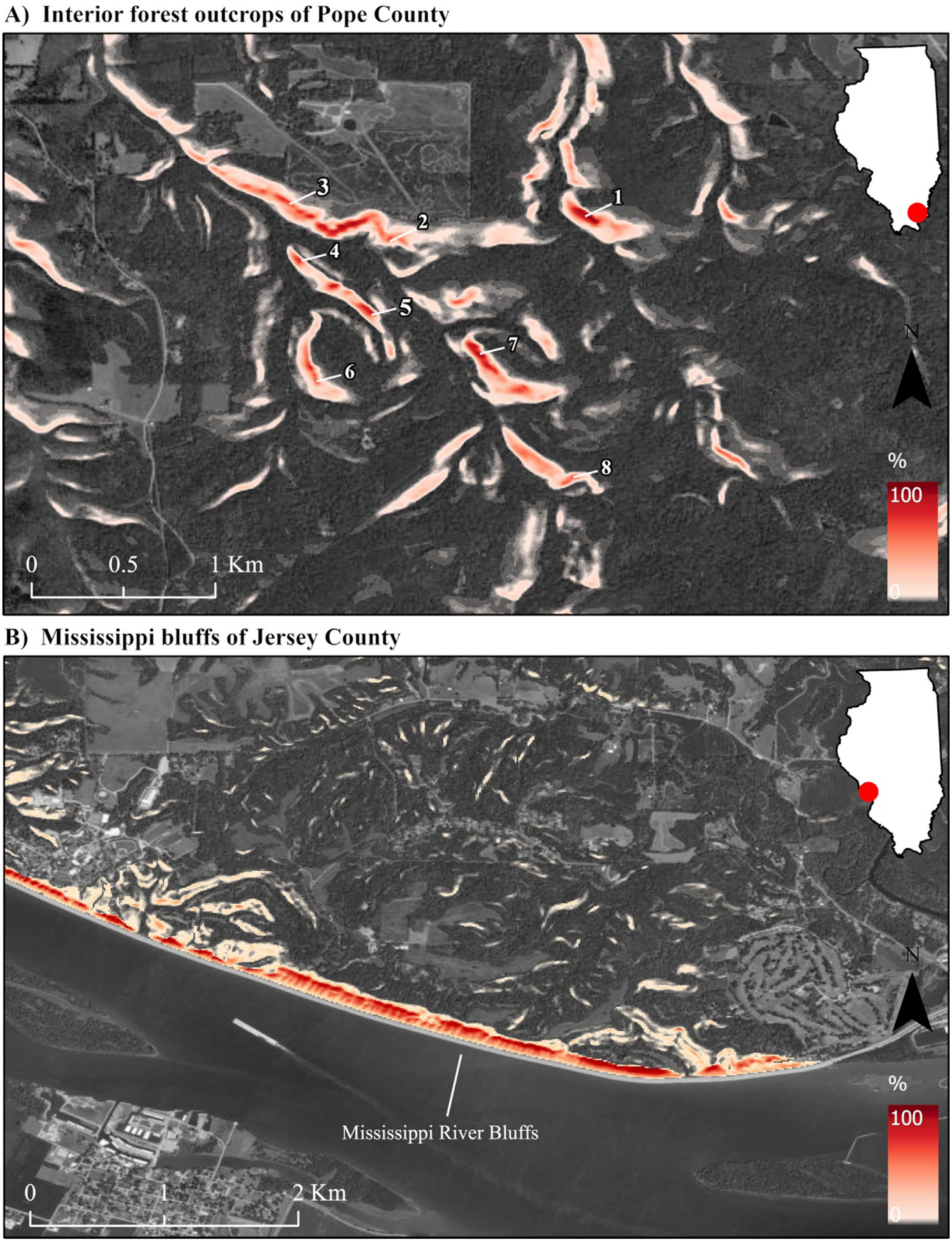

Fig. 6. Hibernacula habitat suitability maps for the timber rattlesnake *Crotalus horridus* across 2 selected regions of Illinois: (A) interior forest outcrops in Pope County (southern Illinois); and (B) Mississippi River bluffs in Jersey County (west–central Illinois). Probability raster was determined using the Clog-log output of the final Maxent model with probability values of 0% made transparent to aid in map interpretation. Number labels in (A) correspond to the locations of photos in Fig. S5, taken during model-guided surveys. The approximate location of each map (red dot) is displayed on an inset map of Illinois (top right of each map)

faced due north, 10 faced northeast, and only 2 faced due east, with the remaining 140 on a south–southwest axis. While the milder winters in more southerly regions such as Virginia and Arkansas may permit overwintering in hibernacula on northern or eastern aspects, it appears rare for individuals to do so.

Southern aspects are superior because they are the warmest, as seen via the correlation between our southness and insolation variables, particularly on steep upland slopes and ridgelines where rocky habitat and shallow soils restrict vegetative growth and canopy cover, as indicated by our correlated slope and forest cover variables. In some cases, such habitat permits the growth of bluff prairies commonly associated with *C. horridus* hibernacula sites (Breisch et al. 2021). South-facing outcrops are, therefore, thermally superior to *C. horridus*, permitting potentially longer activity time and shallower hibernating depths (i.e. more available hibernacula; Martin 1992). Warmer overwintering sites also provide superior thermoregulatory opportunities to pre- and post-emergent snakes, helping prepare individuals for brumation (e.g. purging the gut of food) or 'kick-starting' physiological processes (e.g. metabolic rates) for rapid resumption of active season activities. Such habitat also provides a thermal mosaic of rocky features for enhanced thermoregulation and a protective cover for predator evasion, optimal for use by gravid females during the summer months (Gardner-Santana & Beaupre 2009).

The persistence of *C. horridus* depends on suitable overwintering sites and appropriate surrounding habitats to support active-season activities such as mating and foraging. While our sample size is relatively small, our results suggest smaller forest patches are less suitable as hibernacula habitats (f_area). Since development of the theory of island biogeography (Wilson & MacArthur 2016) and its applications in mainland systems, the effects of small, fragmented forest patches on reptiles have been well-studied (e.g. Michael et al. 2008, Clark et al. 2011) and have far-reaching implications beyond the scope of our study. However, *C. horridus* and other large-bodied snakes appear sensitive to smaller forest patches (Robinson et al. 1992, Kjoss & Litvaitis 2001), thus warranting special mention.

Life history of *C. horridus* necessitates large tracts of forest to accommodate seasonal dispersal movements (of up to 7 km) to and from overwintering sites (Brown 1993) and long-distance mate-searching by males for females (Anderson 2015). Smaller patches of fragmented and increasingly isolated forests, therefore, reduce the ability for *C. horridus* to conduct such vital activities by: (1) creating barriers to movement and isolating populations, causing restricted gene flow and inbreeding (Anderson 2010, Clark et al. 2011); (2) direct mortality via roads (Sealy 2002) or increased human contact (Brown 1993); and/or (3) removal of or restricted access to vital resources (e.g. basking areas, overwintering sites, foraging areas). Thus, while small forest patches might contain a habitat deemed suitable for overwintering, the chance of long-term population viability at such sites is severely reduced; suitable hibernacula habitat for *C. horridus* must have the correct site characteristics and be situated in surrounding forests conducive to active-season activities. Further research into the habitat requirements and spatial ecology of *C. horridus* throughout Illinois is required to elucidate these needs.

4.2. Conservation implications

Determining hibernacula locations for *C. horridus* is challenging. Because of their conservation status range-wide, people are understandably secretive in revealing specific hibernacula locations. In many cases, rapport and trust must be built between researchers, landowners, government/state agencies, and naturalists to collate known locations for a particular region. Surveying for unknown hibernacula is equally difficult because of harsh survey conditions, the limited time to locate snakes during spring egress and fall ingress, and low detection rates of snakes frequently using inconspicuous locations (e.g. under rocks). While we cannot lessen the challenges of secrecy, our results are valuable for identifying new hibernacula by characterizing key habitat characteristics and mapping the distribution of likely hibernacula habitat throughout the state.

We advocate using our results to guide future surveys for new *C. horridus* hibernacula and populations, as demonstrated by our surveys in Pope and Jersey Counties. Surveyors should maximize the chances of detection by using our HSM to constrain survey efforts to areas with a high probability of suitable hibernacula. Additionally, surveys should be conducted on warmer days (daytime temperatures $>15–20°C$) during the fall ingress and spring egress periods, when individuals congregate at or near hibernacula habitat and are more likely to be surface active. Repeated site surveys are likely necessary to determine site occupancy and hibernacula locations (as well as increase the probability of detection). We encourage examination of lower probability areas whenever possible (time and effort permitted) to not bias survey efforts to only the most 'optimal' habitat. While unlikely, hibernacula can occasionally occur on north- or east-facing aspects or the outcrops of mid-lower slopes, given all other suitable habitat characteristics. Additionally, visual encounter surveys of potential hibernacula habitat could also be accompanied by VHF-telemetry of snakes, tracking individuals back to hibernacula in the fall, or deployment of field cameras at suspected hibernacula locations, both of which have been used to locate hibernacula in west—central Illinois (S. Eckert unpubl. data).

We hope future investigators will build on our results by continuing the iterative modeling process to create more robust and informative hibernacula HSMs as new hibernacula locations are located. Future studies should also focus on geographically broader hibernacula HSMs to examine the characteristics and distribution of *C. horridus* hibernacula habitat region-wide, although we acknowledge the logistical challenges in obtaining the number of occurrence records required for such an endeavor and the differences in habitat across their broad geographic range.

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