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Summer-Habitat Suitability Modeling of *Myotis sodalis* (Indiana Bat) in the Eastern Mountains of West Virginia

Jesse L. De La Cruz[1,*] and Ryan L. Ward[1]

Abstract - Little information exists with regard to suitable summer habitat of *Myotis sodalis* (Indiana Bat) in West Virginia. Our research objectives were to use ultrasonic acoustic equipment and automated identification software to collect presence data for Indiana Bats and to examine habitat characteristics and availability across the local landscape. We used a maximum entropy (MAXENT) approach to determine if the distribution of various ecological factors such as landuse/landcover, forest fragmentation, aspect, area solar radiation, slope, proximity to permanent water, and elevation influenced foraging-habitat suitability of Indiana Bats. We sampled across the 1160-ha Camp Dawson Collective Training Area in Preston County, WV, to determine Indiana Bat presence. We employed the collected presence data to examine habitat suitability within a 16,151-ha study area encompassing the training facility. Based on MAXENT results, we characterized highly suitable Indiana Bat habitat as including large tracts of contiguous forest cover (>200 ha) associated with low to modest slopes (<20°), road corridors, and areas of high solar radiation ($\geq 5.5 \times 10^5$ WH/m^2). High (81–100%) and medium-high (61–80%) suitability classes were uncommon across the landscape (0.6% and 2.7%, respectively), with the broad medium-to-high suitability classes (41–100%) collectively comprising only 11.4% of the study area. Elevation (m) and aspect contributed little to the model and displayed low permutation importance that did not vary notably from the corresponding percent contribution. These variables, along with close proximity to permanent water (≤200 m away), are likely not limiting ecological factors. The results of this study supplement current knowledge of summer habitat of the Indiana Bat and provide land and wildlife managers localized guidance on conservation priorities within the region.

Introduction

It is critical to understand habitat relationships in order to enact effective species management and conservation plans, particularly for endangered, obligate migratory species (Morrison 2001). Knowledge regarding bat habitat in relation to land management is lacking (Keeley et al. 2003). Habitat requirements of *Myotis sodalis* Miller and G.M. Allen (Indiana Bat) are not fully understood, and information is often anecdotal, with only a few studies concentrating their efforts in West Virginia (Ford et al. 2005, Johnson et al. 2010, Weber and Sparks 2013). Science-based conservation of species such as the Indiana Bat is hindered because of the lack of research concerning local resource relationships within the central-Appalachians (Ford et al. 2005). Anthropogenic land use and development-based disturbances have caused extinctions or population declines in numerous wildlife species (Fahrig 1997, Fischer and Lindenmayer 2007, Haila 2002). The Indiana Bat

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has been on the US Endangered Species List since 1967 (USFWS 2013a), and is a focal species for many management efforts. Understanding how landscape-level alterations and forest management potentially affect habitat suitability of the Indiana Bat is important for making informed management decisions. Variation in the scale and intensity of forest-management activity may have wide-ranging effects on bat populations (Britzke et al. 2003, Callahan et al. 1997, Gardner et al. 1991a). Management techniques should attempt to conserve or create suitable maternity habitat (i.e., roost trees; Timpone et al. 2010) and feeding and flyway habitat (e.g., canopy perforations, forested corridors; Hein et al. 2009) across the landscape (Womack et al. 2013). Because the removal of contiguous, mature forest potentially eliminates optimal habitat for Indiana Bats (Britzke et al. 2003, Callahan et al. 1997, Gardner et al. 1991a, Kurta 2005), silvicultural techniques should mimic small-scale natural disturbances, such as those caused by fire, wind, and disease or pests (Womack et al. 2013).

Few studies have described landscape-level summer-habitat suitability and resource selection concerning Indiana Bats in West Virginia. Characterization of roost-tree species and location, particularly in the Midwest, is the primary subject matter of summer research (Britzke et al. 2006, Callahan et al. 1997, Gardner et al. 1991a, Kurta 2005). Furthermore, studies that examine foraging habitat are often inconclusive and qualitative (Murray and Kurta 2004) and relate foraging to a wide variety of habitat types (Brack et al. 2002, Butchkoski and Mehring 2004, Carter 2006, Clark et al. 1987, Gardner et al. 1991b, Humphrey et al. 1977, Jachowski et al. 2014, Kurta and Whitaker 1998, Menzel et al. 2005, Murray and Kurta 2002, Owen et al. 2004, Tuttle et al. 2006). Although Indiana Bat roosts are often described as large snags, a variety of other roosts have also been documented (Battle and Stone 2003, Gardner et al. 1991a, Kurta et al. 2002). Despite discrepancies among studies of foraging- and roosting-habitat use in Indiana Bats, the species shows no selection for early successional forests, old fields, or shrublands in relation to either roosting or foraging habitat (Fuller and DeStefano 2003, Jachowski et al. 2014). Agricultural land is a dominant cover-type throughout much of the Midwestern range of the Indiana Bat; however, these areas are often not selected by the species (Humphrey et al. 1977, Menzel et al. 2005, Murray and Kurta 2004). Furthermore, Indiana Bats do not select large open-water sites or deforested creeks as flyways or feeding areas (Menzel et al. 2005).

In West Virginia, Johnson et al. (2010) found that male Indiana Bats selected roosts in forests with low basal area associated with large canopy perforations, independent of roost-decay class. Weber and Sparks (2013) were unable to draw conclusions on habitat suitability for the species due to an overall lack of occurrence data in the state. Ford et al. (2005) found that foraging activity in West Virginia was associated with small canopy perforations or closed forest-canopy in close proximity to 2nd-order streams. These results contradict those reporting behavior of the species in its Midwestern range, where large, flooded bottomland and forested wetlands are often selected as foraging habitat. Due to this apparent overall plasticity of the species in relation to resource selection, specifically foraging habitat

(Jachowski et al. 2014), research that describes local resource relationships is still needed to enhance the conservation and management of the species, particularly in West Virginia, where research is often localized or inconclusive.

Maximum entropy models use a machine-learning process to assess the probable distribution of a species by evaluating presence data in combination with available ecological resources (Jepsen et al. 2011, Weber and Sparks 2013). Species distribution modeling methods are being used more frequently in ecology (Elith et al. 2006, Peterson 2006) to assess potential relationships between species-presence data and ecological conditions within a study area (Kumar and Stohlgren 2009). Our goal was to identify areas of ecological importance in West Virginia, determine the geographic distribution of suitable Indiana Bat foraging habitat, and describe these resource distributions so that management decisions are specific for the species. Because Indiana Bats have been shown to select foraging areas associated with high canopy-cover, forested streams (Ford et al. 2005), warmer ridges, and bottomlands (Brack et al. 2002, Butchkoski and Mehring 2004), we predicted that suitable habitat would be distributed throughout large tracts of contiguous forest cover that receive high levels of solar radiation and are situated near persistent aquatic resources. We used a geographical distributional approach to evaluate our hypothesis that landuse/landcover, slope, aspect, forest fragmentation, elevation, proximity to permanent water, and solar radiation affect the geographical distribution of suitable Indiana Bat foraging habitat. We fit models based upon population-level observations for the species. In order to better understand and conserve potential summer habitat, we assessed habitat distributions at the local-landscape level in a 16,151-ha study area within a 3.2-km buffer of the surveyed tracts.

Field-site Description

We conducted presence/absence surveys during July and August 2013 at the Camp Dawson Collective Training Area (Camp Dawson) located southeast of Kingwood in central Preston County, WV. We examined habitat suitability across a 16,151-ha study area that encompassed Camp Dawson (Fig. 1). The study area is in the Allegheny Highlands physiographic province of northern West Virginia. Elevation at the site ranges from 360 m to 890 m above sea level (asl) and precipitation averages 89–102 cm annually (Brack et al. 2005). Camp Dawson encompasses 1160 ha of primarily forested land across its 3 main tracts—Pringle, Briery, and Volkstone (Fig. 1). Road construction and creation of roads for training activities disturb vegetation on Camp Dawson and cause the formation of numerous habitat types including: disturbed riparian systems, open meadows, contiguous core-forest, and fragmented forest patches. There are significant edge effects throughout the 3 surveyed tracts (Brack et al. 2005, De La Cruz et al. 2013). Forest types range from mature stands to open, regenerating areas of dense shrub and understory species. Forest types present are Allegheny hardwoods—without *Castanea dentata* (Michx.) Raf. (American Chestnut)—and mixed mesophytic at low elevations and in coves, and Appalachian *Quercus* spp. (oak) on western and southern aspects (Dyer 2006). Forests on undisturbed ridges and upper slopes were dominated by *Acer*

rubrum L. (Red Maple) and various oak species including *Q. alba* L. (White Oak), *Q. prinus* Willd. (Chestnut Oak), and *Q. velutina* Lam. (Black Oak). Undisturbed mesic coves were dominated by *Liriodendron tulipifera* L. (Yellow Poplar), *Q. rubra* L. (Northern Red Oak), *A. sacchrum* Marsh. (Sugar Maple), and *Betula lenta* L. (Black Birch). Disturbed slopes, particularly mined areas on the Pringle Tract, were dominated by *Robinia pseudoacacia* L. (Black Locust), *Pinus strobus* L. (White Pine), and the invasive shrub *Eleagnus umbellata* Thunb. (Autumn Olive). Undisturbed lower slopes and riparian forest near the Cheat River were dominated by *Platanus occidentalis* L. (American Sycamore) and Northern Red Oak, while the forest along Pringle Run contained a *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) and *Rhododendron maximum* L. (Great Rhododendron) community.

Methods

Indiana Bat occurrence data

We derived Indiana Bat occurrence data used for this project from acoustic recordings collected during July–August 2013, at Camp Dawson. Based upon previous acoustic recordings, bat population declines have been observed in the region since the 2010 arrival of white-nose syndrome (Johnson et al. 2013). Our study site was within 15 km of the 668,589-ha Monongahela National Forest and ~10 km from a suitable hibernaculum—potential refugia for the species. We placed Binary Acoustic iFR-IV field recorders (Binary Acoustics Technology, Phoenix, AZ) along suitable flyways, within open feeding areas and canopy perforations, and in close proximity to open aquatic resources in accordance with federal sampling protocols (USFWS 2013b). We programmed recorders to sample from before dusk (1930 h)

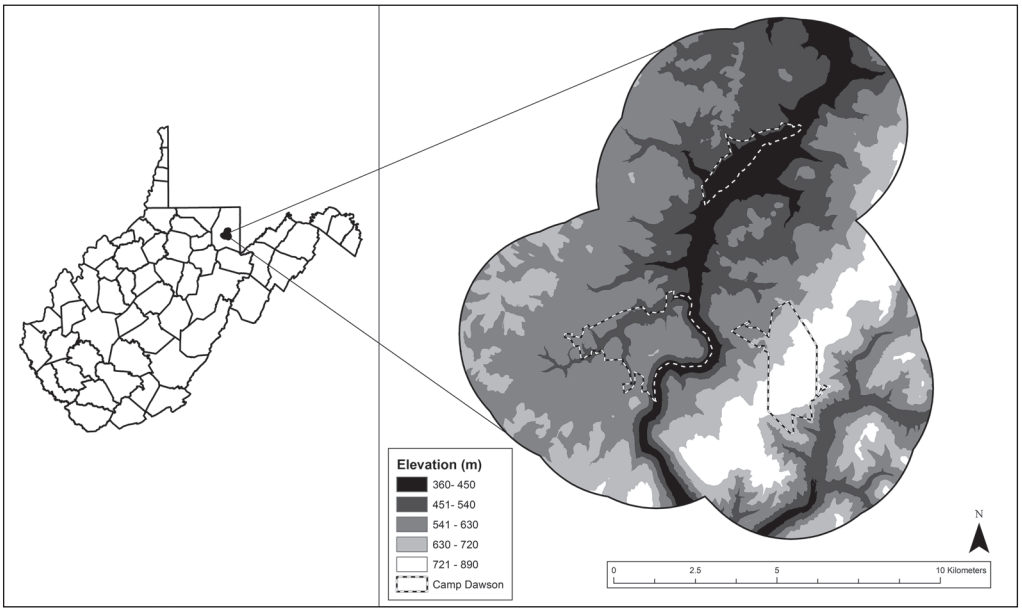

Figure 1. Study area (16,151 ha) and 3 primary tracts of Camp Dawson: Pringle Tract, Briery Tract, and Volkstone, Preston County, WV.

to just before dawn (0530 h). We placed ultrasonic microphones oriented ≥45° from parallel on tripods elevated ~1.5 m above the ground (USFWS 2013b). We recorded data in full-spectrum format at a 10-factor time-expansion rate. We programmed recorders to only activate and record in response to high-frequency sounds ranging from 16 kHz to120 kHz. We used 2 candidate automated identification-software programs to identify any recorded bat-call sequences (USFWS 2013b): Kaleidoscope Pro Version 2.0.4 (Wildlife Acoustics, Inc., Maynard, MA) and Bat Call Identification Version 2.6a (BCID; Bat Call Identification, Kansas City, MO) set on manufacturer defaults to identify bat-call sequences. We used Kaleidoscope to filter all noise and convert the collected full-spectrum data into zero-cross data; we set a division ratio of 8 for the conversion of all full-spectrum data to zero-cross data (Agranat 2012). We made initial Indiana Bat presence determinations via significant ($P < 0.05$) maximum likelihood estimates (MLE; USFWS 2013b). We visually vetted all files identified as Indiana Bats by automated classifiers to verify call quality (e.g., sequences with $n \geq 5$ call pulses) and call characteristics of the species (e.g., high frequency, call duration) in AnalookW 3.9c to help mitigate false-positive/false-negative identification bias (De La Cruz et al. 2013). We recorded all acoustic sampling-site locations with a Trimble Geoexplorer 6000 Series GPS unit capable of sub-meter accuracy.

Habitat data

To characterize Indiana Bat habitat, we assessed landscape-level landuse/landcover, forest fragmentation, slope, area solar radiation, proximity to permanent water, elevation, and aspect. We derived cover classes from the raster dataset Landuse/Landcover of West Virginia 2011 (Strager 2012a). Landuse/landcover data were produced using an object-based image-analysis methodology. Basic landcover classes were extracted from 1-m-cell-size, 4-band, and uncompressed 2011 National Agricultural Imagery Program (NAIP) orthophotography. The analysis produced the following classes: forested, grasslands, barren/developed, open water, mine grass, mine barren, pre-Surface Mining Control and Reclamation Act (Pre-SMCRA) permit forested, Pre-SMCRA grass, Pre-SMCRA barren, herbaceous wetlands, woody wetlands, and census roads 2011 (Strager 2012a). We reviewed the Forest Fragmentation of West Virginia 2011 dataset (Strager 2012b) with ArcGIS (version 10.1; Environmental Systems Research Institute, Inc. Redlands, CA) to examine the differentiated classifications of patch, edge, perforated, core (<100 ha), core (100–200 ha), and core (>200 ha); all non-forest areas were reclassified as a 7th variable within the raster dataset. We derived measures of elevation directly from 3-m–resolution digital elevation model (DEM) raster data (USGS and WVSAMB 2003), made available through the West Virginia GIS Technical Center. We obtained solar radiation, slope, and aspect from DEM raster data using the spatial analyst extension of ArcGIS. Solar radiation represents watt-hours per square meter (WH/m^2); both aspect and slope are reported in degrees. We classified land as either near (≤200 m) or far (>200 m) from permanent water (Humphrey et al. 1977). We determined distance to permanent water by applying a 200-m buffer to perennial streams, open-water resources, and herbaceous and woody wetlands as mapped

in the National Hydrography Dataset (100 k) (NHD; USGS 2002) and extracted from the landuse/landcover raster dataset. We converted NHD stream data to raster data using the polyline to raster tool in ArcGIS. We isolated both NHD streams and landuse/landcover aquatic resources using the reclassification and combined them with the raster calculator spatial analyst tools in ArcGIS. We examined raster data in ArcGIS using the extract by mask and zonal geometry spatial analyst tools.

MAXENT and GIS analysis

We used the machine-learning program MAXENT (version 3.3.3k) that estimates probable species occurrence or habitat suitability of a species based on ecological variables (Phillips et al. 2006). MAXENT operates under the theory of maximum entropy in which the distribution of a population and its habitat will become uniform as ecological variables are taken into consideration (Phillips et al. 2004). MAXENT has been found to perform well in comparison to other modeling methods, particularly when utilizing occurrence data (Dudik et al. 2007, Phillips and Dudik 2008, Phillips et al. 2006), and shows promise even in cases of low ($n < 20$) sample sizes (Hernandez et al. 2006, Kumar and Stohlgren 2009, Papeş and Gaubert 2007, Pearson et al. 2007). Habitat-modeling techniques provide useful tools to relate occurrence data with ecological variables for the creation of detailed maps (Elith et al. 2006). MAXENT measures the statistical relationship between ecological variables at presence locations versus background locations within study areas (Muscarella et al. 2014). MAXENT controls for model overfitting by excluding ecological variables that contribute little or nothing to the model (Merow et al. 2013). Default settings of MAXENT are based on a substantial evaluation study of the program (Phillips and Dudík 2008).

We followed Phillips and Dudík (2008) and analyzed our data by running the program primarily on default settings. We used a random test-percentage of 20% so that each replicate MAXENT model used $n = 9$ observations as training data and $n = 2$ observations to test the model (Jepsen et al. 2011). A single model can show overfitting and bias toward areas around initial training-data points; thus, we followed Jepsen et al. (2011) and used the average area under the curve (AUC) across model replicates to represent our analysis. By measure of standard deviation (SD), mean AUC values have been shown to converge and stabilize with 50 model replicates, with no change in AUC with further replication (Jepsen et al. 2011). We replicated models using a bootstrap run-type, in which replicate sample sets are chosen by sampling with replacement (Phillips and Dudík 2008). The bootstrap run-type requires the use of a random seed, such that the testing and training data used is randomly sampled for each model replicate (Phillips and Dudík 2008). Validation is required to assess the performance of the model (Kumar and Stohlgren 2009). The most common approach is to partition occurrence data into training and test data, thereby creating data for model testing (Fielding and Bell 1997, Guisan and Thuiller 2005). We used a jackknife procedure to assess model performance based on its ability to predict the locality of the training dataset (Pearson et al. 2007). Model AUC values over 0.5 indicate probable occurrence or likely suitable habitat conditions, with increased model

efficiency as AUC approaches 1.0 (Swets 1988).

We used the ENMeval package of the statistical software program R (R Core Team 2015) to construct habitat-suitability models evaluated by Akaike information criterion value corrected for small sample size (AIC_c; Muscarella et al. 2014). The model with the lowest AIC_c value (i.e., $\Delta AIC_c = 0$) reflects both model goodness-of-fit and complexity (Burnham et al. 2010, Warren and Seifert 2010). Models are based on presence locations and 500 randomly selected background locations (Muscarella et al. 2014). Because numerous models evaluated by AIC_c may have substantial support ($\Delta AIC_c < 2$; Burnham and Anderson 2004) and because these models often possess a lower ability to discriminate between testing and background localities (Muscarella et al. 2014), we interpreted this analysis as an additional measure of model validity. We assessed model similarity by measure of spatial correlation between our habitat-suitability model created via 50 model replicates and the model assessed by AIC_c using the band collection statistics spatial analyst tool of ArcGIS. Correlation ranges from +1 to -1, with positive correlation indicating a direct spatial relationship between the 2 models.

We used ArcGIS to analyze the data across the local landscape within specified habitat-suitability classes (Jepsen et al. 2011). Using ArcGIS, we exported the habitat-suitability distribution to raster-data format to create the following classes: low (0–20%), low-medium (21–40%), medium (41–60%), high-medium (61–80%), and high (81–100%). We used these classes to assess the probable availability of suitable habitat within the study area.

Results

Indiana Bat observations

During our acoustic survey at Camp Dawson, we recorded 9200 potential bat-call sequences. From our total dataset, 152 (1.7%) potential Indiana Bat echolocation-call sequences were identified using automated classifiers, with 106 sequences (1.2%) displaying high quality and species-specific call characteristics during qualitative analysis. Initial results indicated recordings of Indiana Bats at 15 (35.7%) acoustic sampling sites; however, after qualitative analysis, we eliminated 4 and used 11 (26.2%) locations in our analysis. The elevation range of observations was from 451 m asl near the Cheat River canyon to 890 m asl near Briery Mountain (Fig. 1).

MAXENT models

The MAXENT model depicting 20% habitat-suitability classes for Indiana Bats within the 16,151-ha study area surrounding Camp Dawson is shown in Figure 2. The average training AUC for 50 model replicates was 0.946 for training data (Fig. 3) and 0.886 with a SD = 0.018 for test points, indicating the stable and robust predictive capabilities of the model. Furthermore, our model constructed via 50 model-replicates displayed a positive spatial correlation (0.71) with the lowest scoring AIC_c model ($\Delta AIC_c = 0$, AUC = 0.74; Fig. 4).

Slope was the variable with the highest percent contribution (30.3%) to the

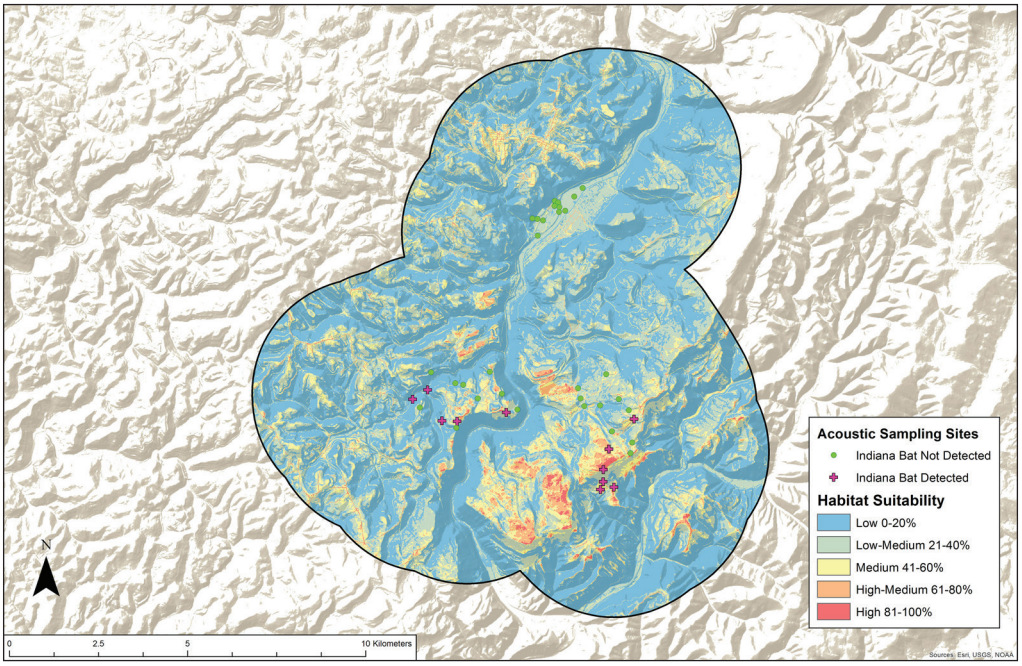

Figure 2. Twenty percent habitat-suitability classes for summering Indiana Bats in Preston County, WV, 2013. Low = 0–20%, medium-low = 21–40%, medium = 41–60%, medium-high = 61–80% and high = 81–100% habitat-suitability classes.

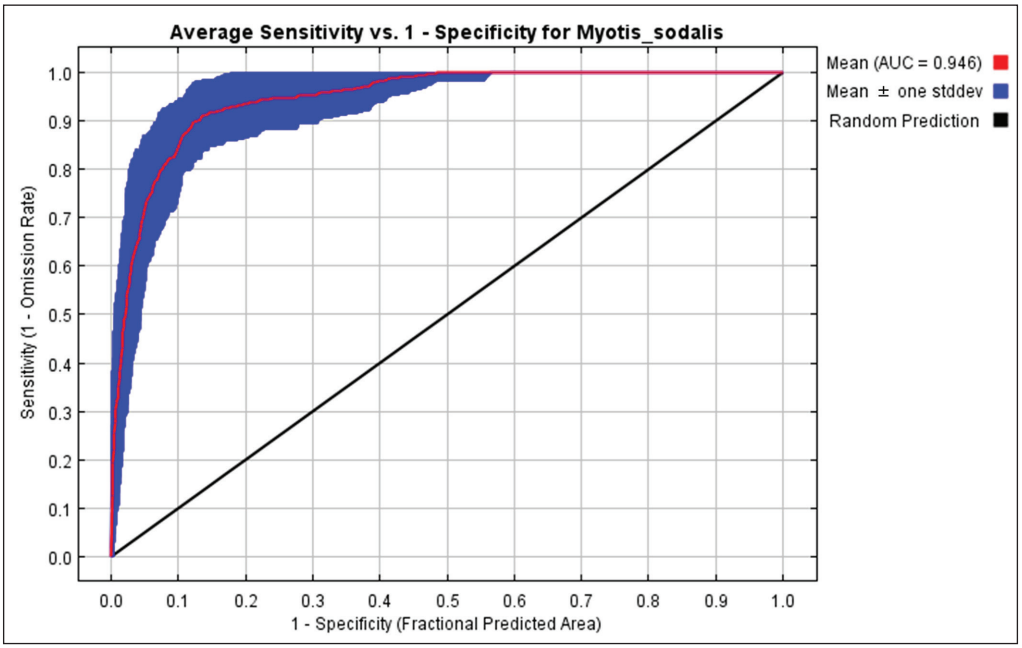

Figure 3. Receiver operating curve (ROC) for 50 MAXENT model replicate runs concerning habitat suitability of Indiana Bat in Preston County, WV, 2013.

model (Table 1). Based upon the marginal response curves, low to modest slopes of 1º–20º were most suitable, and there was a strong negative relationship between bat occurrence and steeper areas. Several other variables contributed positively to the model. Specifically, landuse/landcover contributed 23.2% to the model, with a strong positive correlation between bat occurrence and the presence of roads and barren ground. Forest fragmentation provided a 19.2% contribution to the model. Large tracts (>200 ha) of contiguous forest cover provided the maximum probability of predicting habitat suitability concerning any fragmentation variable, followed by open non-forest areas and isolated forest patches. Area solar radiation contributed 9.9% to the model. Based upon the marginal response curves, areas of $\geq 5.5 \times 10^5$

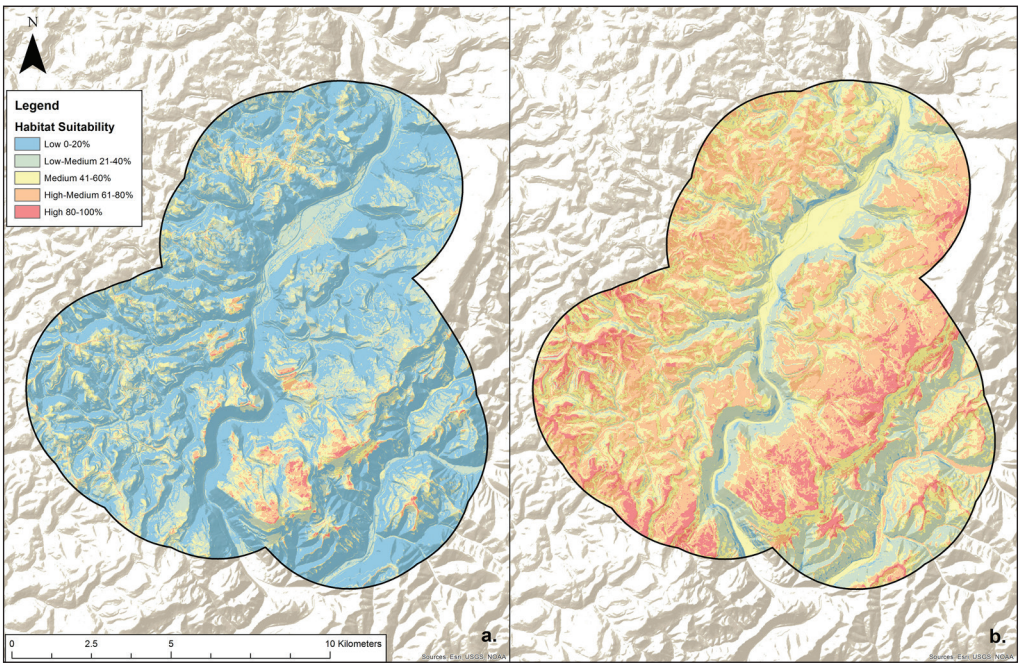

Figure 4. Model comparison of (a) MAXENT averaging based on 50 model replicates (b) MAXENT model having the lowest AIC_c value (i.e., $\Delta AIC_c = 0$) concerning habitat suitability of Indiana Bats in Preston County, WV, 2013.

Table 1. Selected ecological variables and their percent contribution to the MAXENT model for Indiana Bat habitat suitability in Preston County, WV, 2013. DEM = digital elevation-model.

Variable	% Contribution	Permutation importance	Source
Slope	30.3	32.1	Generated in GIS from DEM
Landuse/Landcover of WV	23.2	25.6	Strager 2012a
Forest Fragmentation of WV	19.8	21.5	Strager 2012b
Area solar radiation	9.9	14.1	Generated in GIS from DEM
Proximity to permanent water	9.2	0.7	Generated in GIS
Elevation	6.5	5.1	Generated in GIS from DEM
Aspect	1.1	0.9	Generated in GIS from DEM

WH/m^2 were most suitable for Indiana Bats, with a strong decrease in suitability across areas of lower solar radiation. Proximity to permanent water provided a 9.2% contribution to the model; the absence of permanent water (>200 m away) was a better predictor of habitat suitability. The jackknife procedure indicated that neither elevation (6.5%) nor aspect (1.1%) contributed greatly to the model. Individual-permutation importance of these variables did not vary appreciably from the corresponding percent contribution (Table 1, Fig. 5), further suggesting that these variables are not predictive of suitable Indiana Bat habitat. Solar radiation was the environmental variable with the highest gain when used in isolation, whereas forest fragmentation decreased the gain the most when omitted (Fig. 5).

Distribution of habitat-suitability classes

The geographic analysis of habitat distribution showed that our analysis classified only 0.6% of the study area in the high-suitability class (Table 2, Fig. 2). Furthermore, only 2.7% and 8.1% of the landscape was classified as medium-high and medium, respectively. The low-suitability and low-medium suitability classes accounted for 88.6% of the landscape. Habitat variables within the high-suitability

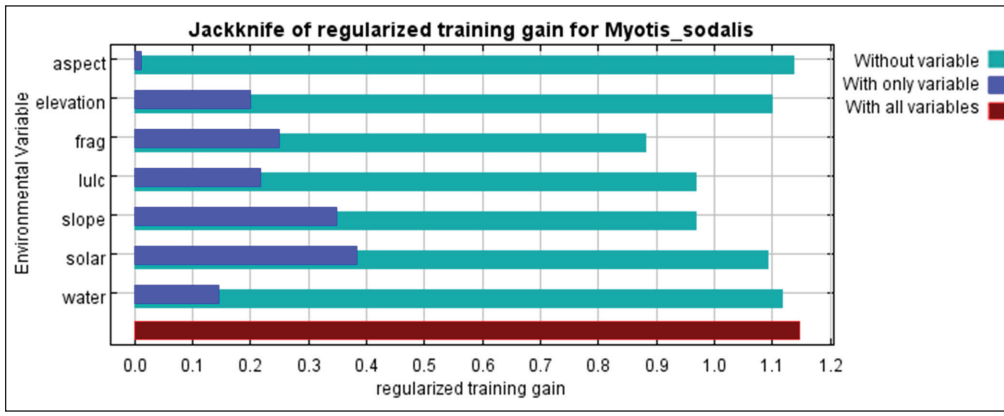

Figure 5. Jackknife evaluation of relative importance of predictor variables for MAXENT habitat-suitability models of Indiana Bats in Preston County, WV, 2013. Aspect = cardinal direction of slope, elevation = height above sea level, frag = Forest Fragmentation of WV value (Strager 2012b), lulc = Landuse/Landcover of WV value (Strager 2012a), slope = degree of land gradient, solar = incoming solar radiation, and water = presence of permanent water within 200 m.

Table 2. Total contribution of 20% habitat-suitability classes for summering Indiana Bats within a study area located in Preston County, WV, 2013.

Habitat suitability class	Total hectares	Present composition
Low (0–20%)	10,021.9	62.0
Low-medium (21–40%)	4292.9	26.6
Medium (41–60%)	1310.7	8.1
High-medium (61–80%)	433.6	2.7
High (81–100%)	92.2	0.6
Total	16,151.3	100.0

class indicate positive influences of contributing variables in the model. Areas within the high-suitability class reflect the presence of large tracts of contiguous forest cover (>200 ha) associated with low to modest slopes (<20°), road corridors, and areas of high solar radiation ($\geq 5.5 \times 10^5$ WH/m^2).

Discussion

Our 11 occurrence observations of Indiana Bats were within the minimum values necessary to effectively model habitat suitability using MAXENT (Kumar and Stohlgren 2009). Our high and stable AUC values across 50 model replicates indicated that the MAXENT model effectively predicted suitable areas of Indiana Bat foraging habitat (Jepsen et al. 2011, Swets 1988). Our results were similar to those of Muscarella et al. (2014) in that our AIC_c model showed an inability to discriminate between testing and background localities when qualitatively compared to the model constructed via 50 model replicates. However, our overall results suggest that large-scale ecological variables are capable of predicting habitat suitability for Indiana Bats at the local-landscape level. Based upon our results, high-suitability areas concerning summer Indiana Bat habitat were rare across the local landscape and accounted for only 0.6% of the study area. Because these highly suitable areas for Indiana Bats are uncommon across the landscape, risks to the species due to land use and development can be addressed within conservation and habitat mitigation efforts on a finer scale. Furthermore, the broader and potentially suboptimal classes of medium to medium-high suitability (41–80%) accounted for only 10.8% of the landscape, which allows for further focus of conservation efforts.

Indiana Bats have been shown to select for highly variable amounts of canopy closure, ranging from <20% to 88% (USFWS 2007). Regional differences in canopy cover have been noted, and cover values are typically higher in areas were live trees such as *Carya ovata* (Mill.) K. Koch (Shagbark Hickory) are used for roosts (Palm 2003). Gardner et al. (1991a) found that a majority of located roost trees were within forests with 80–100% canopy closure, and Carter et al. (2002) found that roosts were surrounded by larger patches of closed-canopy forest than random points. Likewise, Indiana Bats have been shown to forage in areas of high canopy-cover in West Virginia (Ford et al. 2005), while individual roost trees are often located in areas of low basal area and occur within large canopy gaps (Johnson et al. 2010). The importance of large tracts of contiguous forest cover in our model support these earlier findings. The use of larger tracts of forest displaying closed to semi-open canopies likely provides a more diverse range of roost trees (Callahan 1993) and foraging habitat (Brack 1983, Humphrey et al. 1977, Laval and Laval 1980) available to colonies.

Although Indiana Bats have been found in variable canopy conditions, and foraging has been attributed to warmer conditions potentially driven by elevation and aspect (Brack et al. 2002, Butchkoski and Mehring 2004), solar radiation at the larger landscape level has not been addressed. Our results suggest that large tracts of closed canopy forest that receive high levels of solar radiation (with increased ambient temperature) are important foraging habitats for Indiana Bats in West Vir-

ginia. Such areas are likely limited due to highly contrasting topographic features (i.e., slope) that alter available solar radiation, causing variation in the microclimate. Indiana Bats have been shown to select roosting habitats in close proximity to foraging sites (Carter et al. 2002, Kurta et al. 2002, Murray and Kurta 2004, Timpone et al. 2010), suggesting that our results may provide insight into roosting habitat in West Virginia.

Maternity roosts are typically associated with increased solar radiation and are found along forest edges and within canopy perforations (Miller et al. 2002, Whitaker and Brack 2002). Our analysis found that comparable variables were important determinants of foraging activity, particularly the significance of fringe-forest fragments and core forest with high levels of solar radiation. Similar to our results, Gardner and Cook (2002) found a high correlation between occurrence of maternity colonies and areas of non-forested landscape. These areas are generally considered valuable in the production of the insect prey required by actively reproductive females. However, Indiana Bats typically avoid human urbanization and may tend not to utilize such areas due to reduced foraging and roosting habitat (Carter et al. 2002). Similar to our results, Gardner et al. (1991a) found that an Indiana Bat maternity colony was closer to unpaved than paved roads and nearer to intermittent than perennial streams. Such areas likely provide commuting corridors that link various habitats (Carter 2003, Gardner et al. 1991a, Murray and Kurta 2004, Winhold et al. 2005).

Gumbert et al. (2002) suggest that Indiana Bats may be more dependent upon site characteristics than the continued suitability of individual roost trees. Roosts are an ephemeral resource that may quickly become unsuitable due to the loss of exfoliating bark, animal or parasite occupation, or collapse (Belwood 2002, Gardner et al. 1991a, Kurta 1994). Abiotic factors such as slope and solar radiation appear to be limiting ecological factors in the region. Steep slopes may accelerate roost loss, prevent the formation of preferred foraging areas such as wetlands, and alter microclimatic conditions. Our results suggest that solar radiation is the most useful ecological variable for predicting suitable Indiana Bat habitat; however, our results also suggest that solar radiation is potentially correlated with several other variables, while forest fragmentation is likely the least correlated. Variation in solar radiation across the landscape likely limits the suitable foraging range of Indiana Bats in West Virginia. If these abiotic factors affect habitat suitability within the region, Indiana Bats should seek them out annually; similar behavior has been observed throughout the species' range (Gardner et al. 1991a; Kurta et al. 1996, 2002; Murray and Kurta 2002)

The conservation of summer maternity roosts is a cornerstone of Myotine bat management in North America (Brooks and Ford 2005, Jung et al. 2004, Loeb and O'Keefe 2006). Summer maternity roosts are assumed to be critical, limiting resources for bats in both forested and formerly forested environments (Fenton 1997, Kunz and Fenton 2003), and management techniques should attempt to conserve or create suitable maternity habitats (Timpone et al. 2010), with roosts being maintained on the landscape for the long term (Lacki and Schwierjohann

2001, Owens et al. 2004, Perry and Thill 2007) or created through active management (Carter 2006, Johnson et al. 2010). However, management decisions must also consider landscape features such as trails and roads located within intact forests (Palmeirim and Etheridge 1985, Zimmerman and Glanz 2000) and well-defined forest edges and perforations (Grindal 1996, Hogberg et al. 2002). Such landscape structures may be necessary to facilitate foraging success of bats in forests (Lacki et al. 2007). Our results suggest that conservation efforts for the species should be focused within large tracts of contiguous forest cover (≥200 ha) associated with low-to-modest slopes (<20°), road corridors, and, notably, areas of high solar radiation (≥5.5 x 10^5 WH/m^2).

Our results represent a landscape-level analysis conducted to quantify the distribution of suitable Indiana Bat summer habitat. This work can be used to identify candidate areas for conservation planning in West Virginia. Future research should focus on microhabitat features associated with areas of high habitat-suitability for further model validation. For example, small-scale aquatic resources such as wildlife ponds and road ruts are likely valuable to Indiana Bats (USFWS 2007, Wilhide et al. 1998) but were underrepresented in our analysis. However, our results suggest that road corridors are predictive of suitable Indiana Bat habitat and they likely link roosting sites to necessary aquatic resources (Murray and Kurta 2004). Mist netting and radio-telemetry studies will be necessary to investigate microhabitat requirements within the state. Conservation efforts should be based upon information regarding the species at the local level, and our results provide additional data to address conservation priorities of summer foraging habitat. Although we could not determine the sex of bats recorded during this study, our results may still describe resources necessary for the formation of maternity colonies such as access to large tracts of core-forest that display stable thermal conditions and link essential resources. Such areas are potentially critical as summer Indiana Bat habitat and are likely limited across the topographically diverse landscape of West Virginia.

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