Research Article

Predicting Minimum Habitat Characteristics for the Indiana Bat in the Champlain Valley

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Abstract

*Predicting potential habitat across a landscape for rare species is extremely challenging. However, partitioned Mahalanobis D^2 methods avoid pitfalls commonly encountered when surveying rare species by using data collected only at known species locations. Minimum habitat requirements are then determined by examining a principal components analysis to find consistent habitat characteristics across known locations. We used partitioned D^2 methods to examine minimum habitat requirements of Indiana bats (*Myotis sodalis*) in the Champlain Valley of Vermont and New York, USA, across 7 spatial scales and map potential habitat for the species throughout the same area. We radiotracked 24 female Indiana bats to their roost trees and across their nighttime foraging areas to collect habitat characteristics at 7 spatial scales: 1) roost trees, 2) 0.1-ha circular plots surrounding the roost trees, 3) home ranges, and 4–7) 0.5-km, 1-km, 2-km, and 3-km buffers surrounding the roost tree. Roost trees (*$n = 50$*) typically were tall, dead, large-diameter trees with exfoliating bark, located at low elevations and close to water. Trees surrounding roosts typically were smaller in diameter and shorter in height, but they had greater soundness than the roost trees. We documented 14 home ranges in areas of diverse, patchy land cover types that were close to water with east-facing aspects. Across all landscape extents, area of forest within roost-tree buffers and the aspect across those buffers were the most consistent features. Predictive maps indicated that suitable habitat ranged from 4.7–8.1% of the area examined within the Champlain Valley. These habitat models further understanding of Indiana bat summer habitat by indicating minimum habitat characteristics at multiple scales and can be used to aid management decisions by highlighting potential habitat. Nonetheless, information on juvenile production and recruitment is lacking; therefore, assessments of Indiana bat habitat quality in the region are still incomplete.*
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Key words

habitat model, Indiana bat, minimum habitat requirements, Myotis sodalis*, New York, partitioned Mahalanobis distance, radiotelemetry, Vermont.*

Predicting potential habitat across a landscape is extremely challenging for rare species. Inherently small population sizes generally result in small sample sizes with low detection probabilities (Thompson 2004). These challenges are exacerbated for species that require distinct habitats for different ecological functions. For instance, migrating species may have landscape-level habitat requirements that vary seasonally, whereas differences in resting and feeding areas can contribute to different small-scale habitat requirements across space.

The natural history of the Indiana bat (*Myotis sodalis*) provides an excellent example of these challenges. Despite being on the United States Endangered Species List from its inception, the population of this small, vespertilionid bat has declined by 57% since 1960 (Clawson 2002). Small local population sizes and difficulty in collecting further complicate the detection of these bats. Habitat requirements vary not only between winter hibernacula and summer maternity sites but also between roosting and feeding habitats and by sex. During the spring and summer, female Indiana bats congregate in large numbers to roost underneath exfoliating bark on dead or dying trees. Maternity colonies typically use multiple trees in an area for roosting and rearing young (Kurta et al. 1996, Callahan et al. 1997, Kurta 2005). Foraging occurs mainly in forested riparian zones and wetlands, and in agricultural areas and upland woods to a lesser extent, within the larger areas surrounding roost trees (Menzel et al. 2001, 2005, Murray and Kurta 2004, Sparks et al. 2005).

Indiana bat summer habitat was only recently documented in the northeastern United States. In 1985 an Indiana bat hibernaculum hosting approximately 5,000 Indiana bats was discovered in Essex County, northeastern New York, USA (Hicks and Novak 2002). Little summer research was done on this population until 2001 and 2002, when radiotracking studies were initiated to determine the location of summer roosting sites for the population. Fifteen of 23 radiotagged females were followed from this hibernaculum near Mineville, New York, to their presumed summer range in the nearby Champlain Valley. Each female bat remained near the area of first discovery over the expected life of the transmitter, and each was observed in roosts with multiple bats (Hicks and Novak 2002, Britzke et al. 2006). Currently, the only known summer maternity colonies within the

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Champlain Valley are those sites to which bats were tracked in 2001 and 2002, and little is known about general habitat requirements and distribution in this region.

To guide conservation efforts for this endangered species in the northeastern United States, managers need to know what type of habitat is important to bats at various spatial scales. For example, it is necessary to identify roost-tree characteristics as well as the landscape configuration surrounding roost trees. Suitable habitat at multiple spatial scales must be considered because a high-quality roost tree located in a poor-quality landscape, or a poor-quality roost tree located in a high-quality landscape, may not be sufficient for use by this species. Traditional approaches to mapping potential wildlife habitat include logistic regression modeling (Mladenoff et al. 1995), discriminant function analyses, and more recently, occupancy modeling (MacKenzie et al. 2002). These methods require that detection–nondetection data be collected across a number of sites, and in the case of occupancy modeling, that surveys be repeatedly conducted at these sites over time (Manly et al. 2002). For rare species, interpretation of nondetection at a site can be difficult because the species may be present but undetected. We used a relatively new approach to address our research goals of documenting minimum habitat requirements of Indiana bats across multiple scales and mapping potential habitat within the Champlain Valley of Vermont and New York, USA. Using partitioned Mahalanobis D^2 based solely on presence data, this approach removes ambiguity associated with absences and has been used successfully by others to predict occupancy and to model future land-use changes on wildlife distribution (Rotenberry et al. 2002, Browning et al. 2005).

Accordingly, our objectives were to 1) identify minimum habitat characteristics of Indiana bat habitat in the Champlain Valley at different scales, and 2) create a predictive map to identify areas that meet the minimum habitat requirements for the species. Specifically, we used partitioned D^2 analyses to identify the minimum habitat requirements at the following scales: 1) roost tree, 2) a 0.1-ha circular plot surrounding the roost tree, 3) home range, and 4) landscape characteristics within 0.5-km, 1-km, 2-km, and 3-km buffers surrounding the roost tree (representing areas of 0.79 km^2, 3.14 km^2, 12.57 km^2, and 28.27 km^2, respectively). We then created a map that identified potentially suitable habitat within the Champlain Valley.

Study Area

The Champlain Valley was a low-elevation area ranging from about 30–<500 m above sea level, bounded to the east by the Green Mountains in Vermont (>1,300 m) and to the west by the Adirondack Mountains in New York (>1,600 m). This area was located in the Champlain section of the St. Lawrence Valley physiographic region and its soil, vegetation, and climate most closely resembled St. Lawrence Valley and United States Great Lakes regions further north and west (Thompson and Sorenson 2000). We used the Champlain Valley biophysical region (Girton and Capen 1997) to delineate study area (Fig. 1). Climate was most influenced by the moderating effects of Lake Champlain (area = 1,130 km^2); both the average July temperature of 21°C and average January temperature of −7°C were warmer than the rest of Vermont. Annual precipitation ranged from 0.71 m near Lake Champlain to 0.97 m at the Green Mountain foothills (Thompson and Sorenson 2000). Landscape was heavily fragmented, consisting primarily of agricultural land, forested areas, wetlands, and developed land. Forested areas were dominated by Northern Hardwood and Valley Clayplain communities, including eastern white pine (*Pinus strobus*), shagbark hickory (*Carya ovata*), white (*Quercus alba*) and red oak (*Q. rubra*), American beech (*Fagus grandifolia*), yellow (*Betula alleghaniensis*) and paper birch (*B. papyrifera*), and sugar (*Acer saccharum*) and red maple (*A. rubrum*). Vermont's largest city, Burlington, dominated the northern part of the Valley (Thompson and Sorenson 2000).

We selected study sites within the Champlain Valley based on occurrence of female Indiana bats during spring emergence radiotracking of 2001 and 2002 by the New York State Department of Environmental Conservation (NYSDEC), United States Fish and Wildlife Service, Vermont Fish and Wildlife Department, and United States Forest Service (A. Hicks, NYSDEC, personal communication). We selected 2 sites in Vermont (VT) and one in New York (NY) from that project: 1) Salisbury, VT; 2) Monkton, VT; and 3) Crown Point, NY (Fig. 1).

Methods

Capture and Telemetry

We used 4-tier, 38-mm nylon mist nets ranging from 6–12 m in length (Avinet, Inc., Dryden, New York) at each of the 3 study sites to capture reproductive female Indiana bats. During each capture night, we arranged mist nets around 2–4 known roosting areas. Once we captured a reproductive female, we clipped a small patch of fur between the shoulder blades and attached a lightweight radiotransmitter (0.4 g; Holohil Systems, Ltd., Carp, Ontario, Canada) with surgical adhesive (Skin Bond Cement; Smith & Nephew, Inc., Largo, Florida). We tracked these marked individuals for the life of the transmitter (14–21 d). We located individuals in their roost trees daily and recorded newly identified roost-tree locations. We used primary roost trees (>30 individuals roosting at one time) and alternate roost trees (<30 individuals; Callahan et al. 1997) for further data collection and analysis. Every other night, we tracked individuals from the time of roost emergence at dusk until they returned to a roost tree in the morning.

We used triangulation methods during nighttime telemetry to estimate location of a bat at a given time by using 2 or more bearings taken from known locations (see White and Garrott 1990). We outfitted 3 vehicles with 3-element Yagi antennas (Wildlife Material, Inc., Carbondale, Illinois) and T-1000 receivers (Communication Specialists, Orange, California). Observers synchronously recorded bearings on a radiotagged individual. Because there were up to 5 bats with

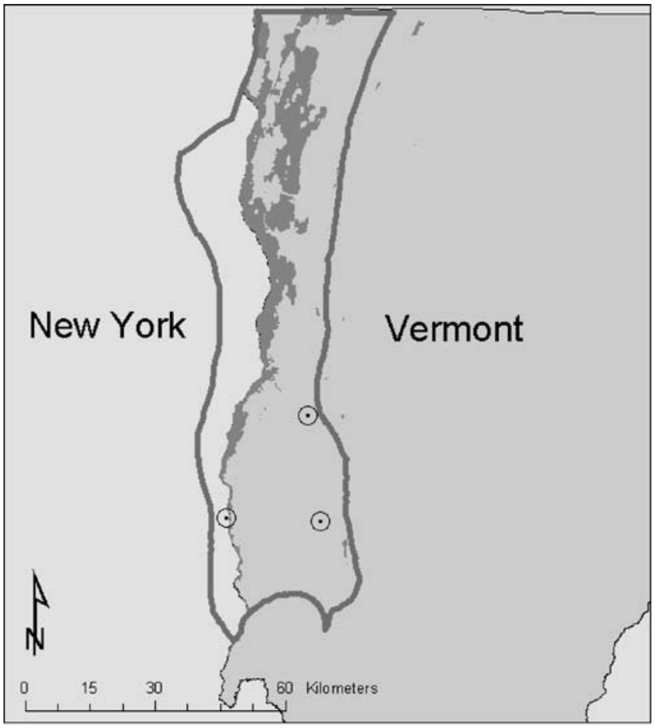

Figure 1. The 195-km^2 Lake Champlain biophysical region, outlined here in black, was used to create maps predicting suitable Indiana bat habitat. Lake Champlain, in dark gray, runs along the border between Vermont and New York, USA. Study sites in 2003 and 2004 are indicated by dots and included Crown Point, New York; Monkton, Vermont; and Salisbury, Vermont.

active transmitters at each site, we randomly chose a focal bat for each half-hour period to concentrate data collection. We recorded triangulations on the focal bat at 5-minute intervals for the half-hour period, at the end of which we chose a new focal bat. Between the 5-minute intervals, we took bearings on other, nonfocal bats in the area in a coordinated manner. We monitored each individual at least once during late night (before 0000 hours), 0000–0300 hours, and early morning periods.

Data Collection at 7 Scales

Roost-tree characteristics.—Previous research has shown that a given tree is considered a suitable roost tree for Indiana bats based on 1) condition (dead or alive), 2) quantity and type of exfoliating bark, 3) solar exposure and location in relation to other trees, 4) spatial relationship to water sources and foraging areas, and 5) size (U.S. Fish and Wildlife Service 1999, Menzel et al. 2001, Kurta et al. 2002, Kurta 2005). To determine if these variables also influenced Indiana bats in the Champlain Valley, we measured the following attributes for each roost tree: species, diameter at breast height (dbh; cm), tree height (m), canopy class (4 categories), decay stage (7 categories), ocular estimation of percent of exfoliating bark left on the tree that is available for roosting, type of roost (Cavity, Bark, Split [i.e., cavities or holes, underneath exfoliating bark, or splits in the trunk]), canopy closure at 4 cardinal directions as measured at the base of the tree by a densitometer, and location (Table 1; Hunter 1990, Menzel et al. 2001, Kurta et al. 2002, Kurta 2005).

We used a version of the 1992 National Land Cover Dataset (Vogelmann et al. 2001) updated to include extent of developed land in Vermont as of 2002 (Spatial Analysis Lab, University of Vermont) to determine distance from each roost tree to nearest water or wetland source (m). We downloaded Digital Elevation Model data (DEM) from United States Geological Survey Seamless Data Distribution System (http://seamless.usgs.gov) for the Champlain Valley and used Geographic Information System (ArcGIS; Environmental Systems Research Institute, Redlands, California) to create aspect and slope data layers. We used these data layers to describe land use, aspect (0–360°), slope (°), and elevation (m) for the 30 × 30-m pixel underlying each roost-tree point (Table 1).

Plot characteristics.—Several metrics may influence the use of roost trees by Indiana bats, including density of suitable roost trees surrounding a known roost tree and canopy structure of those trees (U.S. Fish and Wildlife Service 1999, Menzel et al. 2001, Kurta et al. 2002, Kurta 2005). Therefore, we established one 0.1-ha circular plot around each identified roost tree, and for all trees within this plot with a dbh >10 cm, we recorded the same data collected on the central roost tree except tree height, densiometer reading, and percent exfoliating bark. We averaged metrics collected from all trees within the plot. Because aspect is a circular statistic, we performed a sine and cosine transformation before averaging the values across the plot (Browning et al. 2005).

Home range characteristics.—We used LOCATEIII (Nams 2004) to identify coordinates of individuals during flight using a maximum likelihood estimator (>2 bearings/location) and bi-angulation methods (2 bearings/location). Locations with error ellipses >0.36 km^2 were not used. We imported remaining locations into ArcGIS. We calculated fixed-kernel home ranges using Home Range Extension for ArcGIS (Rodgers and Carr 1998). We only calculated home ranges for those individuals with ≥20 successful locations. We obtained habitat metrics underlying each home range in the same manner as the landscape buffers, described below.

Landscape characteristics.—We used ArcGIS to create 0.5-, 1-, 2-, and 3-km-radius buffers around each roost tree. For each buffer and home range, we used the 1992 National Land Cover Data (NLCD) data layer, FRAGSTATS® (McGarigal et al. 2002), and a batch processor for ArcGIS developed by B. Mitchell (http://arcscripts.esri.com/details.asp?dbid=13839) to describe landscape structure and composition metrics, including area (ha) of forest and wetland patches within each buffer, median forest patch area, median forest patch proximity index, density of patches, and Shannon's diversity index (SHDI). We used DEM, DEM-generated aspect and slope data layers, and 1992 NLCD to describe mean elevation, aspect, slope, and distance to nearest water source for each buffer and home range. As with the plot data, we used sine and cosine of aspect to generate mean aspect.

Table 1. Variable names and units used in partitioned Mahalanobis D^2 model of Indiana bat habitat in the Champlain Valley of Vermont and New York, USA, at each of the 7 different scales, summer 2003 and 2004. Variable abbreviations, when different from the names, are given in italics.

Description	Roost tree	Plot	Home range	0.5 km	1 km	2 km	3 km
Diameter at breast height (dbh; cm)	x	x					
Slope (°)	x	x	x	x	x	x	x
Sine of aspect (*Aspect_sin*; °)	x	x	x	x	x	x	x
Cosine of aspect (*Aspect_cos*; °)	x	x	x	x	x	x	x
Elevation (m)	x	x	x	x	x	x	x
Min. distance to water or wetland (*Dist_water*; m)	x	x	x	x	x	x	x
Height of tree (*Tree_ht*; m)	x						
Average densiometer reading in 4 directions (*Densio*)	x						
Canopy class: 1 (emergent), 2 (dominant), 3 (mid-story), 4 (suppressed; *Can_class*)	x	x					
Decay stage: 1 (alive), 2 (declining), 3 (dead), 4 (loose bark), 5 (no bark), 6 (broken top), 7 (stump; *Decay*)	x	x					
% of exfoliating bark from 1 (0–5%) to 5 (76–100%; *Exfol*)	x						
Presence of cavitites, loose bark, or splits in tree (Y/N; *Cavity, Bark, Split*)	x	x					
Area of forest within buffer (ha; *Area _for*)			x	x	x	x	x
Median forest patch area within buffer (ha; *Area_md*)			x	x	x	x	x
Median forest patch proximity index in buffer (*Prox_md*)			x	x	x	x	x
Area of wetland buffer (ha; *Area_wet*)			x	x	x	x	x
Density of patches in buffer (no. per 1,000 ha; *PD*)			x	x	x	x	x
Shannon's Diversity Index (*SHDI*)			x	x	x	x	x

Statistical Analysis

Partitioned Mahalanobis D^2 technique.—Researchers first used unpartitioned Mahalanobis D^2, as opposed to partitioned Mahalanobis D^2, to overcome challenges created by models requiring detection–nondetection data (Clark et al. 1993, Knick and Dyer 1997, Corsi et al. 1999). This technique determined if an unsampled location could be considered potential habitat by measuring the distance in multivariate space between characteristics of the location and mean characteristics of occupied sites. The smaller the distance, the more similar the unsampled site was to the occupied site and, thus, the more likely to be suitable habitat. In this way, locations that were most similar, in all measured characteristics, to the known habitat were highly probable areas of occurrence. However, this full Mahalanobis D^2 model posed a problem: any deviation from mean characteristics of the occupied sites was considered less-suitable habitat, even if the deviation was in a biologically positive direction (Rotenberry et al. 2002).

To overcome this challenge, we used a partitioned Mahalanobis D^2 analysis which considered only those characteristics that did not deviate across occupied locations (Rotenberry et al. 2002). For instance, if forest patch size was highly variable across the known sample locations, this characteristic may not have been as indicative of high-quality habitat because animals used patches of varying size. Alternatively, if distance to wetland feeding areas did not vary across known locations, this feature was deemed important for the species because all locations shared that same characteristic. Therefore, partitioned Mahalanobis D^2 allowed for more flexibility in defining potential habitat because sites had to share certain vital characteristics with occupied sites instead of having to be identical to them.

Minimum habitat characteristics.—To identify the minimum habitat requirements of Indiana bats at each identified scale, we used a principal components analysis of the standardized variables to identify those habitat characteristics that did not vary across known bat locations. Our analysis first identified the vector of mean habitat characteristics for known locations and then partitioned variation in the mean vector into successive components, each representing a rotation of the original variable axes (Rencher 2002). We were interested in the last principal components that described the least amount of variation among known locations (small eigenvalues) and habitat metrics strongly associated with those components (large eigenvector values). Variables that had the largest eigenvector values within components having small eigenvalues were those that were most consistent across sites, and we considered these to be minimum habitat requirements (Rotenberry et al. 2002).

We conducted principal components analyses including between 8 and 14 variables at each of 7 scales to compare important variables across scales (Table 1). We used SAS procedure PRINCOMP (SAS 9.1; SAS Institute Inc., Cary, North Carolina) to obtain eigenvalues and eigenvectors. At each scale, we identified those last components with the smallest eigenvalues, and we assessed weights associated with individual habitat characteristics within these components. We only considered individual components with eigenvalues <1 (Rencher 2002). We identified the most important habitat characteristics for each component within the reduced set by examining variable weights. We considered the habitat variable that was most heavily weighted to be important for the component, as well as any additional habitat variables that had weights within 0.1 of the most important variable.

To ensure that habitat characteristics varied across known bat locations because they were minimum habitat requirements of the Indiana bat, rather than due to lack of variation in habitat metrics within the Champlain Valley biophysical region, we compared the range of variation in the

Table 2. Means and standard deviations (SD) for general characteristics of habitats known to be used by Indiana bats in the Champlain Valley, Vermont and New York, USA, 2003 and 2004. Variables in bold are either ordinal variables (Can_class, Decay, Exfoliation) or binary variables (Cavity, Bark, Split). See Table 1 for variable abbreviations.

Variable	Roost tree	SD	Plot	SD	Home range	SD	0.5 km	SD	1 km	SD	2 km	SD	3 km	SD
dbh	48.05	20.45	22.89	4.65										
Slope	7.02	6.56	6.51	5.42	4.17	2.46	6.49	3.18	5.64	2.96	5.04	2.63	5.12	2.30
Aspect_sin	−0.12	0.74	−0.01	0.32	0.04	0.09	−0.01	0.05	−0.03	0.07	−0.02	0.07	−0.02	0.05
Aspect_cos	0.28	0.62	−0.12	0.38	−0.03	0.13	−0.01	0.03	0.01	0.04	0.02	0.04	0.02	0.03
Elevation	110.26	50.33	110.2	50.37	99.36	39.34	110.33	43.99	110.68	39.52	111.72	31.08	119.39	27.80
Dist_water	199.21	151.68	199.68	150.51	158.06	88.48	175.21	66.56	175.22	47.83	177.96	68.11	193.36	67.15
Tree_ht	20.7	10.26												
Densio	10.1	17.24												
Can-class	**1.54**	**0.68**	**2.21**	**0.25**										
Decay	**3.18**	**1.44**	**1.78**	**0.45**										
Exfol	**3.16**	**1.7**												
Cavity	**0.08**	**0.28**	**0.02**	**0.03**										
Bark	**0.92**	**0.28**	**0.08**	**0.11**										
Split	**0.15**	**0.36**	**0.02**	**0.04**										
Area_for					22.8	16.81	36.09	12.79	101.3	55.27	322.61	207.18	792.22	370.45
Area_md					2.34	3.83	5.96	12.61	0.21	0.05	0.21	0.05	0.20	0.04
Prox_md					3.91	3.11	23.92	18.04	31.7	34.13	61.59	113.5	58.9	74.59
Area_wet					8.34	13.81	5.01	7.34	24.41	18.14	174.00	84.63	408.58	296.81
PD					58.69	44.38	38.36	14.29	32.38	12.68	29.08	13.18	27.58	11.49
SHDI					1.06	0.35	0.60	0.10	1.17	0.11	1.24	0.06	1.28	0.07

Champlain Valley biophysical region as a whole to that observed at known locations.

Mapping potential habitat in the Champlain Valley.— To create a predictive map that indicated high-probability areas of suitable Indiana bat habitat, we first determined which of the 7 spatial scales to evaluate. This required that the same data used in the principal component analysis be available for all potential locations within the Champlain Valley. Because we did not have access to data about individual tree characteristics across the Champlain Valley, we could not consider the roost tree and plot scales, and we were limited to only evaluating habitat characteristics at the landscape scales. To select among the 5 landscape scales available for mapping (home range, 0.5-km, 1-km, 2-km, and 3-km buffers surrounding roost trees), we first derived a cumulative null chi-square distribution for *n* known roost locations. At each of the 5 landscapes, we computed the full Mahalanobis distance (D^2) for each known location ($n = 50$). We then compared the null chi-square distribution to the distribution of full D^2 values at each scale. We selected the scale that deviated the least from the null chi-square distribution for mapping purposes because it allowed us to convert partitioned D^2 values at any location in the Champlain Valley to a probability score, which indicated probability that the location was suitable habitat (see Browning et al. 2005).

Once we selected the habitat scale, we used the raster calculator in ArcMap to calculate partitioned D^2 scores for each unsampled location at a 30×30-m resolution across the Champlain Valley biophysical region. To do this, we calculated the principal component score of a given unsampled location for each component. We calculated the partitioned distance by squaring the score and dividing by the eigenvalue for the component. We then summed the partitioned distances to create the partitioned Mahalanobis $D^2(k)$ distance, where k is the number of partitioned distances that were summed. We then calculated the χ^2 probability given the $D^2(k)$ value and k degrees of freedom. We used these values in ArcGIS to create a raster map where high χ^2 probabilities indicate areas of suitable habitat for Indiana bats (see Rotenberry et al. 2002, Browning et al. 2005).

Results

Roost-Tree Characteristics

During the summers of 2003 and 2004, we radiotagged 24 reproductive female Indiana bats and tracked them for an average of 4 days per individual (range: 1–7 d). We identified individuals in an average of 3.68 trees (range: 2–8). We identified 50 roost trees comprising 11 tree genera. Shagbark hickory and black locust (*Robinia pseudoacacia*) were most frequently used as roost trees (20% and 18%, respectively). Of roosts occurring in live trees, species used were shagbark hickory, black locust, sugar maple (14%), and butternut (*Juglans cinerea*, 2%). Of roosts occurring in snags, species used included American elm (*Ulmus americana*, 14%), aspen (*Populus* spp., 10%), eastern white pine (10%), and oak (*Quercus* spp., 6%).

Roost-tree characteristics were variable over all known locations (Table 2). The average roost tree was 21 m (SD = 10.26) in height, had a 48-cm (SD = 20.45) dbh, was located at an elevation of 110 m (SD = 50.33), and was 199 m (SD = 151.68) away from the nearest water source. On average, roost trees were emergent in the canopy, had over 50% loose bark and were dead, but they were not in advanced decay stages (Table 2).

Five of the 14 components created in the principal components analysis had eigenvalues >1 and were discarded. These components explained 75% of the variation in the data. The remaining 9 components explained 25% of the variation in the dataset. Taken together, these

Table 3. Minimum habitat requirements at each evaluated scale for Indiana bats in the Champlain Valley, Vermont and New York, USA, 2003 and 2004. Variables are listed in order of importance and only those variables with weights within 0.1 of the most important variable in the component were considered (see Table 1 for variable abbreviations).

Roost tree	Plot	Home range	0.5-km buffer	1.00-km buffer	2.0-km buffer	3.0-km buffer
Elevation[a]	Bark[a]	Aspect_cos[a]	Area_for[a]	Area_for[a]	Aspect_sin[a]	Aspect_sin[a]
Dist_water[a]	Elevation	Aspect_sin[a]	Elevation	Aspect_sin	Aspect_cos[a]	Aspect_cos[a]
Tree_ht	Dist_water	SHDI	Aspect_cos	Aspect_cos	Area_for[a]	PD
Bark	Cavity	PD	Aspect_sin	PD	Dist_water	Dist_water
Can_class	Split	Dist_water	SHDI	SHDI	Slope	Area_for
Exfol	Can_class	Area_for	Area_md	Slope	Elevation	Slope
DBH	Slope	Prox_md	Area_wet	Prox_md	PD	Area_wet
Decay	Decay	Slope	Slope	Dist_water	Area_wet	Prox_md
Densio	Aspect_sin	Elevation	PD	Elevation	Prox_md	SHDI
Cavity	Aspect_cos	Area_md	Dist_water	Area_wet	SHDI	Area_md
Slope	DBH	Area_wet	Prox_md	Area_md	Area_md	Elevation
Aspect_cos						
Aspect_sin						
Split						

[a] Important habitat variables within the last component at each scale.

components revealed that location of the roost tree with respect to elevation and its distance to water were the most important to the last component and, thereby, critical in defining presence of Indiana bats (Table 3). Other important characteristics included physical characteristics of the tree itself, such as height, presence of peeling bark, canopy class, percent exfoliating bark, and dbh (Table 3).

Plot Characteristics

There was an average of 57.7 trees >10-cm dbh (SD = 19.0) within a 0.1-ha (18-m radius) plot centered on each roost tree. These trees were, on average, smaller-diameter trees that were healthier and lower in the canopy than the central roost tree (Table 2). Of the 43 tree species identified in roost plots, the most common species were sugar maple (18.8%), eastern hophornbeam (*Ostrya virginiana*, 9.5%), ash (*Fraxinus* spp., 8.8%), and eastern white pine (7.8%).

Three of 11 principal components had eigenvalues >1 and were not considered. The remaining 8 components together explained 23% of the variation in the data. Physical characteristics of the trees within the plot, including absence of exfoliating bark, cavities, and splits, were important indicators of habitat, along with elevation and distance to water across the plot (Table 3). Of these, absence of trees with exfoliating bark was the least variable metric, indicating that this feature was consistent among known roost trees.

Home Range Characteristics

After eliminating 768 triangulated locations due to high error ellipses, time between locations varied from 2 minutes to 23 hours 48 minutes (mean = 72 min, median = 5 min). Fourteen individuals had sufficient numbers of locations remaining to estimate home range sizes. Average home range size was 0.83 km^2 (SD = 0.82). Home ranges consisted, on average, of 41.4% agricultural areas, 34.3% forested areas, and 22.0% wetland areas (Table 4). The landscape underlying home ranges was diverse (mean SHDI = 1.06, SD = 0.35), indicating that multiple patch types were present within the home range, with an average of 59 (SD = 44.38) unique patches per 1,000 ha (Table 2). Within the average home range, any pixel was an average of 158 m (SD = 88.48) away from a water source (Table 2).

Seven components had eigenvalues <1 and together explained 5% of the variation in the data. Aspect was the most consistent characteristic across home ranges, with home ranges occurring in landscapes with mostly east-facing, low-gradient slopes. Other habitat features at the home range scale that did not considerably vary among the 14 home ranges included land cover diversity, patchiness, and closeness of home ranges to water (Table 3).

Landscape Characteristics

Buffers around roost trees were primarily composed of forest, wetland, and agriculture land use patches (Table 4). Forest cover ranged from 26–47%, wetland cover ranged from 8–14%, and agriculture cover ranged from 35–47% across the 4 landscape scales. Area of forest cover was the most consistent habitat feature at the 0.5-km and 1-km scales, with an average of 36 ha (SD = 12.79) and 101 ha (SD = 55.27) of forest, respectively (Table 2). At the 2-km scale, area of forest and aspect were the most consistent features, and aspect alone was most important at the 3-km scale. Other landscape metrics that varied little among roost

Table 4. A comparison of the average and standard deviation (SD) percent area of forest, wetland, and agriculture within each home range and roost-tree buffer scale measured for Indiana bats in the Champlain Valley, Vermont and New York, USA, in 2003 and 2004.

% area	Home range	SD	0.5 km	SD	1 km	SD	2 km	SD	3 km	SD
Forest	34.3	14.08	45.93	16.28	32.22	17.58	25.67	16.48	28.06	13.14
Westland	22.00	29.28	8.62	9.94	8.18	5.94	13.84	6.73	14.45	10.49
Agriculture	41.41	16.89	34.5	12.90	46.10	15.62	47.13	12.59	44.57	8.68

trees included patch density, diversity of cover type, and slope, but importance of these variables depended on which scale was evaluated (Table 3). Therefore, a typical landscape surrounding a roost tree consisted of small forest patches within a patchy, flat landscape. At the 0.5-km and 1-km buffer scales, the landscape was characterized by diverse land cover types, whereas at the larger 2-km and 3-km scales areas within the landscape were, on average, close to water and also encompassed more wetland patches.

Summary of Minimum Habitat Requirements

Several variables could be considered minimum habitat requirements at each scale (Table 3). Considering only those elements identified in the component explaining the least variation, 4 variables emerged as the most consistent across all known locations: elevation, distance to water, area of forest, and aspect. Elevation and distance to water were consistently important at the small scales of roost tree, plot, and 0.5-km buffer (elevation only) whereas average aspect was most consistent at the home range scale. At the landscape scales, area of forest surrounding the roost tree was most consistent at the 0.5-km and 1-km scales, but aspect became more important as greater spatial scales were considered.

We examined the range of variation in the Champlain Valley as a whole to determine if minimum habitat requirements were just an artifact of homogeneity of the region itself. Our analysis showed that, in fact, the available habitat across the Champlain Valley was more variable than across known Indiana bat maternity colonies (Table 5). Known maternity sites occurred in areas with elevations, slopes, and distances to water sources that were towards the lower end of the range of values across the region. Similarly, although roosting and foraging areas had high patch densities when compared to more contiguous landscapes, these areas actually had fewer patches when compared to the range of patch densities across the Champlain Valley (Table 5). Additionally, Indiana bats seemed to occur in areas with forest patches that were very isolated compared with the range of isolation across the Valley. For known locations, values of mean isolation index across the 5 scales at which it was measured ranged from 3.91–58.9, where values close to zero represented total isolation of a forest patch within the area examined, and isolation decreased as values increased. Across the Champlain Valley, isolation index values ranged from 0–196.95. Finally, these areas of isolated forest patches were also high in diversity of land cover, representing the high end of the range of diversity across the Valley. Indiana bats selected landscapes that had fewer patches compared to the rest of the Valley, but these patches were diverse, and forest patches were isolated from other forest patches (Table 5).

Predictive Map

The 0.5-km buffer was the best-fit landscape scale; therefore, we used it to create the predictive map for the entire Champlain Valley. We calculated probabilities associated with suitable habitat for the Indiana bat in the Champlain Valley based on 2 values of k (no. of partitioned distances used). We generated the first map (Fig. 2A) using the last 3 components at the 0.5-km scale ($k = 3$), which explained 1% of the variation in the data. In this map, 423.9 km^2 out of a total land area of 5,231.1 km^2, or 8.10% of the Champlain Valley, had a probability of suitable habitat >0.05. We created the second map (Fig. 2B) using all 8 components with eigenvalues <1 ($k = 8$), which together explained 13% of the variation in the data. In this map, 245.8 km^2, or 4.70% of the land area within the Champlain Valley, had a probability >0.05.

Table 5. Comparison of the range of habitat values within the 0.5-km roost-tree buffers (Buffer min., max.) to the same habitat variables across the Champlain Valley (Valley min., max.), Vermont and New York, USA, in 2003 and 2004 (see Table 1 for variable abbreviations).

Variable	Buffer min.	Buffer max.	Valley min.	Valley max.
Slope (°)	0.95	13.52	0.0	47.16
Aspect_sin	−0.21	0.04	−0.99	1.0
Aspect_cos	−0.06	0.14	−0.99	1.0
Elevation (m)	35.64	204.1	24.55	1,006.16
Dist_water (m)	55.84	338.86	0.0	1,769.4
Area_for (ha)	10.44	66.69	0.0	71.73
Area_md (ha)	0.09	66.69	0.0	71.73
Prox_md	0.0	93.47	0.0	196.95
Area_wet (ha)	0.09	33.75	0.0	71.73
PD (no. per 1,000 ha)	15.27	68.73	1.39	153.35
SHDI	0.58	1.4	0.0	1.75

As expected, adding components to the model reduced the area of predicted suitable habitat. In the first map (Fig. 2A; $k = 3$), we considered a given location in the Champlain Valley suitable habitat if it was similar to known locations with respect to a few, critical habitat characteristics. We considered other habitat characteristics to be less important and therefore they could vary across identified areas. As we added components, unsampled locations were required to match known locations with respect to more and more habitat characteristics in order to be deemed suitable. Therefore the second map (Fig. 2B; $k = 8$) identified a smaller area of suitable habitat.

Discussion

Partitioned Mahalanobis D^2 techniques allowed us to use habitat characteristics at known Indiana bat maternity colonies and foraging areas to determine 1) minimum habitat requirements, and 2) potential habitat elsewhere in the Champlain Valley. Known Indiana bat roosting habitat occurred in areas of the Champlain Valley that were most fragmented and diverse, and home ranges occurred in areas of high agricultural use that were also characterized by isolated forest patches and patchy, diverse landscapes. Given that the Champlain Valley was located at the northeastern edge of Indiana bat range, it was important to consider whether our results differed from studies conducted in other parts of its distribution. An analysis by Kurta (2005) of Indiana bat roost trees documented across 11 states, including Vermont and New York, found that on average roost trees were 20 m tall, had a 45-cm dbh, and had bark

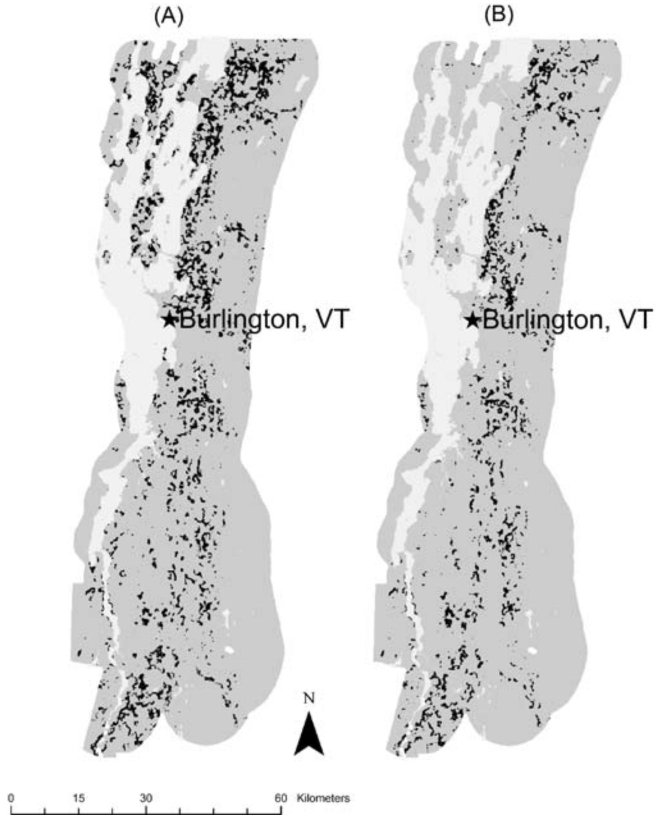

Figure 2. Maps of potential Indiana bat habitat across a 195-km^2 area within the Champlain Valley of Vermont and New York, USA, generated using partitioned Mahalanobis D^2 to determine the suitability of each pixel, in 2003 and 2004. Areas in black indicate a probability of suitable habitat >0.05. Lake Champlain (in light grey) runs down the western length of the Valley. (A) $k = 3$. (B) $k = 8$.

covering 56% of the tree. Thus far, 393 roost trees have been documented range-wide, comprising at least 33 tree species (Menzel et al. 2001, Kurta 2005). Roost trees in the Champlain Valley seemed to mirror these average values in physical attributes. The sheer number of documented roost-tree species both in the Champlain Valley and across the known species range seems to indicate that tree species itself may not be as important as the physical characteristics of the roost tree and its location in the landscape (Menzel et al. 2001, Kurta 2005).

Our average home range size was slightly smaller than that found by Menzel et al. (2005; 1.45 km^2) in the Central Lowland physiographic province of Illinois, USA, and Rommé et al. (2002; 1.13 km^2) in the Interior Highlands physiographic province of Missouri, USA. Differences in sample sizes and the method of calculating home ranges (minimum convex polygons, fixed- or adaptive-kernel estimates) may contribute to these small differences in size. In terms of home range and landscape-scale habitat characteristics, Menzel et al. (2005) found that Indiana bats in the Midwest foraged primarily near forests and riparian habitats, and they seemed to avoid agricultural lands. Indeed, most foraging studies have found either riparian or upland forest patches to be important foraging habitat (Humphrey et al. 1977, LaVal and LaVal 1980, Kessler et al. 1981). We did not determine bat behavior (i.e., foraging vs. traveling) across the nighttime telemetry hours; however, agricultural fields comprised a much greater percentage of home ranges on average than water or wetlands. Further study is needed to determine habitat preference, use, and availability in the northeast to understand any differences across the species' range.

Maps of potential habitat indicated that there are small areas of suitable habitat distributed throughout the Champlain Valley. However, it is important to realize that these maps identify locations that meet landscape requirements only at the 0.5-km buffer scale, and habitat features measured at other scales must also be considered. For instance, high-quality habitat at the 0.5-km scale might be unsuitable if it is devoid of appropriate roost trees or forest patches or if the landscape characteristics at greater scales are not appropriate. To consider multiple scales simultaneously, maps could be generated at each of the scales we assessed and combined through map calculations to locate areas that meet habitat requirements at all scales. We did not analyze whether one scale was more important than others; this is a topic for future research.

Our study contained several caveats that limited our zone of inference. Sample sizes were limited because the Indiana bat was rare and elusive. Therefore, we were required to use fewer locations and larger acceptable location error than is typically suggested to conduct home range analyses (White and Garrott 1990). Moreover, roost samples were not fully independent because Indiana bats are a colonial species. Additionally, our study sites were not determined randomly. This species was only discovered in the Champlain Valley in 2001 and, thereby, there were a limited number of known maternity sites to study. However, we have no reason to believe that the sites studied were not representative, and our results lay the groundwork for future research. Our models can be updated for increased precision as more roost trees and home ranges are found in the Champlain Valley in particular and the Northeast in general.

We caution a strict interpretation of aspect being the most important minimum habitat characteristic in the home range and larger landscape scales because it is measured over a gently rolling topography with very low gradients. For example, a hill with an eastern-facing slope of as little as 1° will still have an aspect around 90°, but the significance that this aspect does not vary across home ranges or landscapes may not have a biological interpretation.

Hibernacula surveys have shown that although the Indiana bat population in the Champlain Valley is small, it appears to be increasing (Hicks and Novak 2002). As populations change in size, habitat characteristics associated with the population may change. For instance, if populations increase, less-optimal habitats may be used by individuals (Fretwell and Lucas 1969, Pulliam 1988, Pulliam and Danielson 1991). Information on Indiana bat habitat quality in the Champlain Valley will further help to predict occupied areas and direct management efforts. Our study found that only a very small area of the Champlain Valley may be suitable habitat for Indiana bats, even when suitable habitat is considered as a proportion of forested area within the region. Although we have no data on actual population metrics of these Indiana bats, this could be an indication that habitat is more limiting to Indiana bats in this region than previously expected. On the other hand, given that a maternity colony could support upwards of 200 bats within a small woodlot, these small percentages of suitable habitat across the region could host a substantial population if Indiana bats inhabited all areas of suitability indicated here.

Management Implications

We encourage the use of modeling techniques presented here to model habitat, particularly in the case of rare or elusive species, for several reasons. Relationships among habitat characteristics are often complex and difficult to model. Multivariate statistical models account for interactions between predictor variables while making no demands on variable distributions. Mahalanobis $D^2(k)$ is a cost-effective approach because there is no need to survey random or unused sites; this also serves to avoid problems with detection. By developing a probability layer, wildlife managers can make better-informed decisions on land management practices. Layers can be made specific or general by adding more or fewer components to fit the needs of the study. Finally, models can be developed in different areas of the species' range to examine if and how habitat requirements vary.

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