PREDICTING MINIMUM HABITAT CHARACTERISTICS OF THE INDIANA BAT (*MYOTIS SODALIS*) IN THE CHAMPLAIN VALLEY OF VERMONT AND NEW YORK

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Kristen S. Watrous

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Thesis Examination Committee:

____ Advisor
Therese M. Donovan, Ph.D.

____ Chairperson
C. William Kilpatrick, Ph.D.

____
William S. Keeton, Ph.D.

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ABSTRACT

Predicting potential habitat across a landscape is extremely challenging for rare species. Analyzing habitat requirements using partitioned Mahalanobis D^2 methods avoid pitfalls commonly encountered when surveying elusive species that typically have small sample sizes and low detection probabilities because it is based solely on data collected at known species locations. Minimum habitat requirements are determined by examining a principal components analysis to determine habitat characteristics that are consistent across known locations. The goals of this study were to (1) document and compare the minimum habitat requirements of Indiana bats (*Myotis sodalis*) in the Champlain Valley across 7 spatial scales and (2) map potential habitat for the species throughout the same area. We radio-tracked 24 female Indiana bats to their roost trees and across their nighttime foraging areas, and collected 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. Fifty roost trees were identified and found to be tall, large diameter trees with exfoliating bark, located typically at low elevations and close to water. Trees in the plots surrounding roost trees were typically smaller in dbh, shorter in height, and healthier than the central roost trees. Fourteen home ranges were found to be in areas of diverse, patchy land cover types that were close to water, with an east-facing aspect. Across all landscape extents, the total area of forest within roost tree buffers and the aspect across those buffers were the two most consistent features. Predictive maps indicated that suitable habitat ranged from 4.7% to 8.1% of the total area examined depending upon the number of components used, and was distributed throughout the Champlain Valley. However, information is needed on birth and survival rates to assess habitat quality in the region.

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CHAPTER 1. COMPREHENSIVE LITERATURE REVIEW

The Indiana bat

The Indiana bat (*Myotis sodalis*) is a small, 5-11 g vespertilionid bat found in the eastern and midwestern United States. It was first described as a separate species from the morphologically-similar little brown bat (*Myotis lucifugus*) by G.S. Miller and G.M. Allen (1928). Indiana bats characteristically have a distinctly keeled calcar and their hind feet tend to be smaller with fewer, shorter hairs that do not extend beyond the toes. The ears and wing membranes have a dull appearance and flat coloration that does not contrast with the fur. The fur of the chest and belly is lighter than the muted, pinkish-brown fur on the back, but does not contrast as strongly as does that of the little brown or northern long-eared bat (*Myotis septentrionalis*; Whitaker and Hamilton 1998, Menzel et al. 2001). Beyond these differences in appearance, little brown bats exhibit different roosting and hibernating behaviors than Indiana bats. Indiana bats generally roost underneath the exfoliating bark of dead trees, and hibernate in very dense clusters in only a few caves across its range. Little brown bats usually roost in man-made structures such as buildings, and hibernate in less dense clusters in a much larger number of caves (Whitaker and Brack 2002).

The Indiana bat range extends from the Ozark Plateau of Missouri, Arkansas, and Oklahoma in the west to the Florida panhandle and New England in the east, but is absent from the Atlantic Coast (Menzel et al. 2001, Gardner and Cook 2002). In the east, the distribution of Indiana bats is generally associated with the presence of limestone caves

(Menzel et al. 2001). Records of Indiana bat occurrence can be found in 311 counties across 27 states as of 2001 (Gardner and Cook 2002).

Population Status.--In 1960, Indiana bat population size was estimated to be around 880,000 individuals. The estimated population size in 2002 was 380,000 individuals (Clawson 2002). Declining populations led the Indiana bat to be listed as an endangered species on March 11, 1967 under the Endangered Species Preservation Act of October 15, 1966, with legal protection later awarded under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1999). As outlined by the Endangered Species Act, a recovery plan was first approved on October 14, 1983, which guided recovery efforts in the 1980s into the 1990s. Since the majority of the Indiana bat population hibernates in a very small number of caves, conservation efforts initially focused on protecting hibernacula and limiting disturbance to hibernating Indiana bats. Despite these efforts, the species has experienced a 57% decline in total population size since 1960 (Clawson 2002). A revised recovery plan was completed in draft form in October 1996 to address four key areas: (1) an update of the original recovery plan to include information on life history and ecology of the Indiana bat, with emphasis on summer ecology, (2) the continued and accelerated decline of the species, (3) the continued effort to protect and monitor hibernacula, and (4) a new effort towards research on factors causing population declines (U.S. Fish and Wildlife Service 1999).

While the overall population is declining, population trends vary from state to state. Historically, the Indiana bat population was found primarily in the south by a ratio of 3:1, with Kentucky and Missouri alone supporting 73% of the population. Currently, the northern population outnumbers the southern by a ratio of 2:1, primarily as a result of heavy declines in Kentucky and Missouri. In the Northeast, populations of Indiana bats have increased by 30% since the 1960's (Clawson 2002). In 1975, Humphrey (1978) only attributed 500 individuals out of a total population of 459,000 to this area (0.001%), whereas current censuses indicate that ca. 30,000 Indiana bats are present out of a range-wide total of 380,000, or 7.89% of the total population (Hicks and Novak 2002). These increases are not large enough to offset overall population declines; however, it emphasizes the importance of the Northeast for the continued survival of the species.

Natural History

The Indiana bat has a natural history similar to other *Myotis* species. They hibernate in caves or abandoned mines during the winter months. Females emerge from hibernation and travel to summer maternity sites, whereas males either use the hibernacula as a summer roost, or disperse short distances from the hibernacula to roost in trees similar to those chosen by females (Kurta and Rice 2002, Whitaker and Brack 2002). Females give birth to one pup per year, and young stay with the maternity colony throughout most of their first summer (Humphrey et al. 1977, Kunz and Fenton 2003). Migration to the wintering caves usually begins in August and lasts through October (Humphrey 1978).

Hibernation.-- Indiana bats differ from many bat species in the small number of caves used for hibernation. Currently, over 300 hibernacula are known to harbor Indiana bats, but less than 25% of these are classified as Priority One or Two (having over 30,000 bats, or having between 500 and 30,000 bats, respectively). Approximately 50% of the current population hibernates in eight Priority One hibernacula located in Indiana, Kentucky, and Missouri (Clawson 2002). Most hibernacula are located west of the Appalachian Mountains, and are approximately centered on the lower Ohio River Valley (Menzel et al. 2001, Gardner and Cook 2002).

The small number of hibernacula used by Indiana bats is a key limiting factor, and is most likely the result of a narrow range of microhabitat characteristics required by the species. Temperatures inside hibernacula range from -8.3 °C to 13.1 °C, but analyses of population trends within these hibernacula indicated that populations declined when temperatures were outside a range of 3 °C to 7.2 °C (Tuttle and Kennedy 2002). Relative humidity in hibernacula ranges from 70% and 100% (Hall 1962, Humphrey 1978). In hibernacula harboring additional species, Indiana bats occupied areas in the cave with the coldest ambient temperatures, highest humidity, and greatest airflow (Raesly and Gates 1986).

Aboveground activity ends in October for females and November for males (Humphrey 1978, Kiser and Elliot 1996). The inactive hibernation period lasts approximately 190 days (Hall 1962). During hibernation, Indiana bats cluster in groups of up to 3,000 individuals per m^2 (Barbour and Davis 1969) on the walls and ceilings of caves or abandoned mines. Individuals wake up at intervals of 8 to 10 days across the winter months (Hardin and Hassell 1970) and may move to more optimal microclimates within the hibernaculum (Tuttle and Kennedy 2002). These large concentrations of bats make them highly vulnerable to disturbances during the winter. Threats during hibernation include vandalism, improperly designed cave gates which alter airflow, disturbances causing sudden arousal, and natural disturbances such as flooding, unseasonably frigid winter temperatures, or ceiling collapse (Menzel et al. 2001). Arousal following a disturbance can be severely detrimental: agitation and movement can expend 20 - 30 days of stored energy (Daan 1973). The greatest historic losses of Indiana bats were most likely due to events which rendered caves no longer suitable for hibernacula (Tuttle and Kennedy 2002).

Reproduction.-- Indiana bats arrive at hibernation areas from mid-August to October (Kiser and Elliot 1996) and November (Hall 1962, Humphrey 1978). While at the hibernacula bats fly in and around cave entrances throughout the night but usually roost in nearby trees during the day (Cope and Humphrey 1977). During these so-called fall swarms intense foraging ensues, allowing the build-up of fat in preparation for hibernation. Copulation also occurs at this time. Hundreds have been observed copulating on the ceilings just inside cave entrances during late September and early October in Missouri (LaVal and LaVal 1980). Sex ratios change over time from (1) primarily males during the summer, (2) to the first few females arriving in late July, (3) to females making up approximately 47% of the total in early September, (4) to primarily males my late September into October (Cope and Humphrey 1977). This indicates that many females entered hibernation soon after arrival and copulation, while males remained active for longer, presumably to copulate with additional females (Cope and Humphrey 1977).

Indiana bats, like many bat species, exhibit delayed fertilization as a reproductive strategy. After copulation, females store sperm in uteri throughout the winter months until emerging from hibernation in the spring. Only then do ovulation, fertilization, and implantation occur (Thompson 1982). Lactating females have been observed as early as June 11 and as late as July 6 in Missouri (LaVal and LaVal 1980) and parturition was observed between June 25 and July 4 in Indiana with young requiring 25 to 37 days before flying and feeding on their own (Humphrey et al. 1977).

Roosting ecology.--Female Indiana bats gradually emerge from hibernation and migrate to their summer maternity colonies in April and May (Humphrey 1978, LaVal and LaVal 1980). Some males remain in caves over the summer months; others roost solitarily in trees (Hall 1962). A maternity colony is comprised of female Indiana bats that use multiple trees in an area to roost, give birth and raise young. Groups of females congregate in these trees underneath exfoliating bark and in tree crevices (Humphrey et al. 1977, Kurta et al. 1993, Kurta et al. 1996, Callahan et al. 1997, Kurta et al. 2002). Maternity roost trees can be described as "primary" or "alternate" based on the proportion of bats in a colony occupying the roost site. Primary trees consistently harbor greater than 30 bats at a time, while alternate trees harbor less than 30 (Callahan et al. 1997). On a given day the colony is dispersed among both types of trees, with a large number of bats distributed among a few primary trees and the remainder distributed in small numbers among many alternate trees. Across the species range, Indiana bats have used a minimum of 8 - 25 different trees in one season (Humphrey et al. 1977, Garner and Gardner 1992, Kurta et al. 1996, Callahan et al. 1997, Kurta et al. 2002, Kurta 2005). Since individuals change roosts on average every 2 - 3 days, it has been suggested that colonies have a fission-fusion society similar to cetaceans and primates (Kurta et al.

2002, Willis and Brigham 2004, Kurta 2005). Maternity colony characteristics make it difficult to know the number of bats in the population, since it is virtually impossible to identify and census every roost tree the colony is using at a single point in time.

Currently, the list of documented primary and alternate roosts includes over 30 different tree species, and new species are frequently added. At one time there was thought to be regional differences in preferred species, but new work has shown that most documented tree species are used across the entire range. At this time 87% of the tree species used are ash (*Fraxinus sp.*), elm (*Ulmus sp.*), hickory (*Carya sp.*), maple (*Acer sp.*), poplar (*Populus sp.*), or oak (*Quercus sp.;* Kurta 2005). However, the variability in roost tree species suggests that species itself may be less important to Indiana bats than a roost's structure, condition, and location (Callahan et al. 1997, Menzel et al. 2001, Kurta et al. 2002, Whitaker and Brack 2002, Kurta 2005).

Roost trees are typically large-diameter dead or dying trees with exfoliating bark. Living trees, primarily shagbark hickories (*Carya ovata*), are also used as roosts. It is thought that living trees are more often used in times of wet or unusually warm weather; however, it has also been suggested that they are only used when suitable dead trees are not available (Humphrey et al. 1977, Callahan et al. 1997, Kurta 2005). Most roost trees have a diameter at breast height (dbh) greater than 22 cm. Average dbh values for Indiana, Michigan, and Missouri are 62 cm, 55 cm, and 41 cm, respectively (Kurta 2005). It is likely that any differences in the mean across states can be attributed to differences in tree species used. The same can be said for differences in average height, which ranges from 16 m to 26 m across states in the range (Kurta 2005). Roosts are often high in the tree (average height ranges from 7 m to 10 m), likely because bats need to drop from their roost to fill their wings and gain air speed (Kurta 2005).

Primary roosts are often located in open areas, such as open forest, habitat edges, forest gaps, grazed woodlands, or pastures, and are less variable in location and structure than alternate trees (Kurta et al. 1993, Callahan et al. 1997, Kurta 2005). When located in more dense areas, primary roosts often extend above the canopy (Callahan et al. 1997, Kurta 2005). Since common mortality factors such as storms, flooding, or disease tend to affect trees in the same area, roost trees tend to be clustered in space, though there can be more than one cluster in a colony. In a colony in Michigan distances between roost trees used by a colony the same season ranged from 1 m to 8.2 km (Kurta et al. 1996, Kurta et al. 2002).

Maternity colonies were once thought to be exclusively in riparian areas, but no longer. Colonies have been documented in mixed hardwoods, uplands and bottomlands, and wetlands and floodplains as well as riparian areas (Kurta 2005). Three-km areas surrounding maternity colonies are primarily composed of agricultural areas (58-81% in Missouri, 67% in Illinois, 55% in Michigan), forests (19-30% in Missouri, 33% in Illinois, 17% in Michigan), and wetlands (19% in Michigan; Gardner et al. 1991, Callahan 1993, Kurta et al. 2002). At a larger scale, a study examined land cover in 132 couties for which Indiana bat reproduction had been documented. Counties were, on average, 75.7% nonforested habitat (including agriculture), 20.5% deciduous forest, and 3.4% coniferous or mixed coniferous forest (Gardner and Cook 2002).

Foraging ecology.--Indiana bats usually forage and fly from 2 - 30 m above ground level and feed on aquatic and terrestrial insects (Humphrey et al. 1977, LaVal et al. 1977). Five orders of insects (Diptera, Lepidoptera, Coleoptera, Tricoptera, and Hymenoptera) dominate the diet (Kurta and Whitaker 1998, Murray and Kurta 2002). They are habitat generalists and their selection of prey items reflects the environment in which they forage. Diet varies seasonally and among different ages, sexes, and reproductive status groups. Reproductively active females and juveniles exhibit greater dietary diversity than males and non-reproductively active adult females, perhaps due to higher energy demands (Murray and Kurta 2002).

Foraging generally takes place along habitat edges and above, around, and below tree canopies in forested habitats. Foraging areas are generally in riparian zones (Humphrey et al. 1977, LaVal and LaVal 1980), upland forests (LaVal and LaVal 1980, Gardner and Cook 2002), wetlands (Kurta and Rice 2002), or woodlands (Butchkoski and Hassinger 2002, Sparks et al. 2005a).

Literature Review Conclusions

Bats, especially small, tree roosting bats, are difficult to study due to their nocturnal nature and their high degree of vagility. Indiana bat hibernation and hibernacula are well documented, as are the physical characteristics of roost trees themselves. However, less is known about roosting, foraging, and activities pre- and post-hibernation, and very little is known about colony dynamics over the summer months. Furthermore, most of the literature cited in this review is from the core range of the Indiana bat. Little is known about this species at the edge of its range in the

Northeast. Given the increasing importance of this area for the bat population as a whole, more information is needed on all aspects of its life history in this area. In particular, little is known about the maternity habitat requirements during the summer months. In response to this gap, this study was initiated to document the summer habitat used by known maternity colonies within the Champlain Valley of Vermont and New York. Minimum habitat requirements have been determined from data on the habitat characteristics at the roost tree, stand, home range, and landscape scales at known maternity sites. This information will enable wildlife managers to identify critical resource needs throughout the annual cycle, and thus guide them in their conservation efforts.

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Kristen S. Watrous
VT Cooperative Research Unit
University of Vermont
328 Aiken Center
Burlington, VT 05405
802-656-3388; FAX 802-656-8683; E-mail kristen.watrous@uvm.edu

CHAPTER 2. PREDICTING MINIMUM HABITAT CHARACTERISTICS OF THE INDIANA BAT IN THE CHAMPLAIN VALLEY

KRISTEN S. WATROUS, Vermont Cooperative Wildlife Research Unit, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA

THERESE M. DONOVAN, United States Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA

RUTH M. MICKEY, 16 Colchester Avenue, University of Vermont, Burlington, VT 05405, USA

SCOTT R. DARLING, Vermont Department of Fish and Wildlife, 271 North Main Street, Suite 215, Rutland, VT 05701, USA

ALAN C. HICKS, New York State Department of Environmental Conservation, 625 Broadway, 5th Floor, Albany, NY, 12333, USA

SUSANNA L. VON OETTINGEN, United States Fish and Wildlife Service, 70 Commercial Street, Suite 300, Concord, NH 03301, USA

Abstract: Predicting potential habitat across a landscape is extremely challenging for rare species. Analyzing habitat requirements using partitioned Mahalanobis D^2 methods avoid pitfalls commonly encountered when surveying elusive species that typically have small sample sizes and low detection probabilities because it is based solely on data collected at known species locations. Minimum habitat requirements are determined by examining a principal components analysis to determine habitat characteristics that are consistent across known locations. The goals of this study were to (1) document and compare the minimum habitat requirements of Indiana bats (*Myotis sodalis*) in the Champlain Valley across 7 spatial scales and (2) map potential habitat for the species throughout the same area. We radio-tracked 24 female Indiana bats to their roost trees and across their nighttime foraging areas, and collected 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 3km buffers surrounding the roost tree. Fifty roost trees were identified and found to be tall, large diameter trees with exfoliating bark, located typically at low elevations and close to water. Trees in the plots surrounding roost trees were typically smaller in dbh, shorter in height, and healthier than the central roost trees. Fourteen home ranges were found to be in areas of diverse, patchy land cover types that were close to water, with an east-facing aspect. Across all landscape extents, the total area of forest within roost tree buffers and the aspect across those buffers were the two most consistent features. Predictive maps indicated that suitable habitat ranged from 4.7% to 8.1% of the total area examined depending upon the number of components used, and was distributed throughout the Champlain Valley. However, information is needed on birth and survival rates to assess habitat quality in the region.

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Predicting potential habitat across a landscape is extremely challenging for rare species. Inherently small population sizes generally result in small sample sizes, and low detection probabilities (the probability of detecting an individual given it is present; (Thompson 2004). These challenges are exacerbated for species that require different habitats for different ecological functions. For instance, migrating species may have habitat requirements that vary across time, while differences in resting and feeding areas can contribute to different habitat requirements across space.

The natural history of the Indiana bat provides an excellent example of these challenges. Although placed on the Federal Endangered Species List in 1967, the population size of this small, vespertilionid bat has declined by 57% since 1960 (Clawson 2002). Small population sizes further complicate the detection of these nocturnal flyers. Habitat requirements vary not only between winter hibernacula and summer maternity sites, but also between roosting and feeding habitats. During the spring and summer months, female Indiana bats congregate in large numbers to roost underneath the bark of dead or dying trees. These maternity colonies use multiple trees in an area for roosting and rearing young (Kurta et al. 1996, Callahan et al. 1997, Kurta 2005). Foraging, however, is carried out in larger areas surrounding roost trees; these areas are composed of not only forest, but also of wetlands and agricultural areas (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 was discovered in upstate New York, prompting radiotracking studies in 2001 and 2002 to determine summer roosting sites for the population. Spring emergence tracking from this hibernaculum near Mineville NY followed 15 of 23 radio-tagged females to their presumed summer range in the nearby Champlain Valley. Each remained near the area of first discovery over the expected life of the transmitter and each was in at least one roost from which more than one animal was observed exiting (Hicks and Novak 2002, Britzke et al. *in press*). The fact that the majority of radio-tagged bats dispersed to agricultural areas of Vermont and New York suggests that the Champlain Valley provides critical summer roosting habitat. Currently, the only known summer maternity colonies within the 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.

In order to guide conservation efforts for this endangered species, managers first 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. A major goal of this study, therefore, is to document the minimum habitat requirements of the Indiana bat across multiple scales.

A second goal of this study is to map potential habitat for the Indiana bat in the Champlain Valley. 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 collection of detection/nondetection data across a number of sites, and in the case of occupancy modeling, repeated surveys at the same sites. For rare species, interpretation of a nondetection at a site can be difficult. The species may be present but undetected, absent because the habitat is truly unsuitable, or absent because the species was not there at the time of the survey. Only absences due to habitat unsuitability are of interest; the other scenarios simply create noise in the data set. In this paper, we used a relatively new approach to address both research goals. This approach, called partitioned Mahalanobis D^2, is based on presence data only and utilizes theories first described by Pearson in 1901 (Pearson 1901, Rotenberry et al. 2002).

Unpartitioned Mahalanobis D^2, as opposed to partitioned Mahalanobis D^2, was first used to overcome the challenges created by models requiring detection/nondetection data (Clark et al. 1993, Knick and Dyer 1997, Corsi et al. 1999). Because this technique is based solely on data where the species was present and detected, the ambiguity of determining absence is removed. To determine if an unsampled location could be considered potential habitat, the characteristics of the unsampled site are compared to the mean characteristics of the set of occupied sites. The distance between unsampled and occupied sites is calculated in multivariate space. The smaller the distance, the more similar the unsampled site is to the occupied habitat, and thus the more likely it is to be suitable habitat. In this way, locations that are most similar, in all measured characteristics, to the known habitat are areas of highly probable occurrence. However, this full Mahalanobis D^2 model poses a problem: any deviation from mean characteristics of the occupied sites is considered less suitable habitat, even if the deviation is in a biologically positive direction (Rotenberry et al. 2002).

In order to overcome this challenge, we can consider only those characteristics that do not deviate across occupied locations with a partitioned Mahalanobis D^2 analysis. For instance, if forest patch size is highly variable across the known sample locations, this characteristic may not be as indicative of high quality habitat because animals use patches of varying size. Alternatively, if distance to wetland feeding areas does not vary across known locations, this feature is deemed important for the species because all locations share that same characteristic. Thus, partitioned Mahalanobis D^2 allows for more flexibility in defining potential habitat because sites have to share certain vital characteristics with occupied sites instead of having to be identical to them. This approach was used by Rotenberry et al. (2002) to predict how future land use change would affect the distribution of sage sparrows. Browning et al. (Browning et al. 2005) (2005) used the method to estimate occurrence probability for the timber rattlesnake, a state-listed endangered species across most of its range.

The objectives of this study were to (1) identify the minimum habitat characteristics of Indiana bat habitat in the Champlain Valley at different scales, and (2) use these data to create a predictive map that identifies areas that meet the minimum habitat requirements for the species. Specifically, we used partitioned D^2 analysis to identify the minimum habitat requirements at the following seven scales: (1) the roost tree, (2) a 0.1 ha circular plot surrounding the roost tree, (3) the home range, and (4-7) 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 identifies potentially suitable habitat within the Champlain Valley.

STUDY AREA

The Champlain Valley is a low lying area ranging from about 30 m to less than 150 m, surrounded by the Green Mountains in Vermont (maximum elevation = 1,339 m) and the Adirondack Mountains in New York (maximum elevation = 1,629 m). This region is most influenced by Lake Champlain, and its soil, vegetation, and climate closely resemble the lowlands surrounding the Great Lakes. The area is largely agricultural with interspersed woodlots, and Vermont's largest city, Burlington, dominates the northern part of the Valley. Annual precipitation is about 0.75 m (Thompson and Sorenson 2000).

Study sites within the Champlain Valley were chosen based on the spring emergence tracking of 2001 and 2002 by the NYS Department of Environmental Conservation, U.S. Fish and Wildlife Service, VT Fish and Wildlife Department and U.S. Forest Service (A. Hicks, pers. comm.). Two sites in Vermont and one in New York were selected from that project this research: (1) Salisbury, VT, (2) Monkton, VT, and (3) Crown Point, NY (Figure 1).

METHODS

Field Methods

Capture and telemetry.--Mist nets were set up within known roosting areas at each study site in order to capture reproductive female Indiana bats. Females were considered to be pregnant if palpitation of the abdomen by finger indicated that an embryo was present. Once a reproductive female was captured, a small patch of fur between the shoulder blades was clipped and a lightweight radio transmitter (0.4g, Holohil Systems, Ltd., Carp, Ontario, Canada) was attached with surgical adhesive (Skin Bond Cement, Smith & Nephew, Inc., Largo, FL, USA). These marked individuals were tracked for the life of the transmitter. Individuals were located in their roost trees each day, and newly identified roost tree locations were recorded. A tree was considered a roost tree when it was documented harboring a radio-tagged bat in it for at least one day. We used both primary and alternate roost trees for further data collection and analysis. Every other night, individuals were tracked from the time of emergence from the roost tree at dusk until they returned to a roost tree in the morning.

We used triangulation methods during nighttime telemetry to estimate the location of a bat at a given time by using 2 or more bearings taken from known locations. Three vehicles were outfitted with 3-element Yagi antennas (Wildlife Material, Inc., Carbondale, IL, USA) and T-1000 receivers (Communication Specialists, Orange, CA, USA). Observers synchronously recorded bearings on a marked individual. As there were up to 5 bats with active transmitters at each site, a focal bat was chosen for each half-hour period to concentrate data collection. Triangulations on the focal bat were collected at 5 minute intervals for the half-hour period, at the end of which a new focal bat was chosen. Between the 5 minute intervals, bearings on other, non-focal bats in the area were taken in a coordinated manner.

Data Collection at Seven Scales

Roost tree characteristics.--Previous research has shown that a given tree is considered a suitable roost tree for Indiana bats based on (1) its condition (dead or alive), (2) the quantity of loose bark, (3) the tree's solar exposure and location in relation to other trees, (4) the tree's spatial relationship to water sources and foraging areas, and (5) tree size (U.S. Fish and Wildlife Service 1999, Kurta et al. 2002, Kurta 2005). To determine if these variables also influenced Indiana bats in the Champlain Valley, the following attributes were measured for each roost tree: species, diameter at breast height (dbh, in cm), tree height (m), canopy class (4 categories), decay stage (7 categories, adapted from Hunter 1990), percent exfoliating bark left on the tree that is available for roosting, type of roost (i.e., cavities, exfoliating bark, or splits), canopy closure at four cardinal directions as measured by a densiometer, and location. GIS data layers were used to describe the aspect (0-360°), slope (degrees), elevation (m), and distance to the nearest water or wetland source (m) from each roost tree (Table 1).

Plot characteristics.--Several metrics may influence the use of roost trees, including the density of suitable trees surrounding the roost tree and the crown morphology of these trees. One 0.1 ha circular plot was established around each identified roost tree, and all trees within this plot were sampled. Within each plot, we recorded species, dbh, decay stage, and canopy class for each tree with a dbh > 10 cm, and the presence of cavities, loose bark, or splits in the trunk were noted. As with the roost tree data, GIS layers were used to describe the average aspect, slope, elevation, and distance to the nearest water source at each plot.

Home range characteristics.-- We used LOCATEIII (Nams 2004) to identify coordinates of individuals by maximum likelihood estimator (>2 bearings per location) and biangulation methods (2 bearings per location). Locations with error ellipses greater than 0.36 km^2 were not used. Remaining locations were then imported into ArcGIS (ESRI, Redlands, California, USA). Fixed kernel home ranges were calculated using Home Range Extension for ArcGIS (Rodgers and Carr 1998). Home ranges were calculated only for those individuals with 20 or more successful locations. Habitat metrics underlying each home range were obtained 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. Landscape characteristics were described for each of the buffers along with calculated home ranges using a version of the 1992 National Land Cover Dataset (Vogelmann et al. 2001) updated to include the extent of developed land as of 2002 (Spatial Analysis Lab, University of Vermont). We used FRAGSTATS® (McGarigal and Marks 1995) 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 the area of forest and wetland patches within each buffer, the median forest patch area, the median forest patch proximity index, the density of patches, and Shannon's diversity index. GIS data layers were used to describe the average aspect, slope, elevation, and distance to the nearest water source for each buffer and home range.

Statistical Analysis

Minimum habitat characteristics.--Our first goal was to use partitioned Mahalanobis D^2 methods to identify the minimum habitat requirements of Indiana bats at each identified scale. For each of the seven scales, we used a principal components analysis of the standardized variables to identify those habitat characteristics that did not vary across the known bat locations. This analysis first identified the vector of mean habitat characteristics for known locations. It then partitioned variation in the mean vector into successive components, each representing a rotation of the original variable axes. The first component explained the most variation in the data; of the remaining variation, the second component explained the most without being correlated to the first and components were added in this manner until all variation was explained. We were interested in identifying minimum habitat characteristics – those characteristics that did not vary across occupied sites roost trees or their surrounding areas. In other words, we were interested in those principal components that described the least amount of variation among the known locations (i.e., small eigenvalues) and the habitat metrics strongly associated with those components (i.e., large eigenvector values). Variables that had the largest eigenvector values within components having small eigenvalues were those that were most consistent across sites, and were considered minimum habitat requirements.

A principal components analysis including between 8 and 14 variables was conducted at each of the 7 scales in order to compare important variables across scales

(Table 1). We used SAS procedure PRINCOMP (SAS 9.1, SAS Institute Inc., Cary, North Carolina, USA) to obtain eigenvalues and eigenvectors. At each scale, we identified those components with the smallest eigenvalues, and assessed the weights associated with individual habitat characteristics within these components. Only individual components with eigenvalues < 1 were considered. We identified the most important habitat characteristics for each component within the reduced set considered by examining the variable weights. The habitat variable that was most heavily weighted was considered to be important for the component, as well as any additional habitat variables that had weights within 0.1 of the most important variable.

Mapping potential habitat in the Champlain Valley.-- Our second goal was to identify areas in the Champlain Valley that had a high probability of being suitable Indiana bat habitat. To create a predictive map, it was first necessary to determine 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. Thus we were limited to evaluating habitat characteristics at the landscape scales. To select among the five 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 locations. At each of the 5 landscape scales, 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. The scale that deviated the least from the null Chi-square distribution was selected 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 the probability that the location was suitable habitat.

Once the habitat scale was selected, we used the raster calculator in ArcMap to calculate partitioned D^2 scores for each unsampled location at a 30 x 30 meter resolution across the Champlain Valley. To do this, the principal component score of a given, unsampled location was calculated for each component. Only components with eigenvalues < 1 were considered. 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. SAS was then used to calculate the chi probability given the $D^2(k)$ value and k degrees of freedom. The new dataset was then read back into ArcGIS to create a raster map.

RESULTS

Roost tree characteristics.--During the summers of 2003 and 2004, twenty-four reproductive female Indiana bats were radio-tagged and tracked for an average of 4 days per individual (range: 1 - 7 days). Fifty roost trees were identified, comprising 7 tree species. Shagbark hickory (*Carya ovata*) and black locust (*Robinia pseudoacacia*) were most frequently used as roost trees (20% and 18%, respectively), and along with sugar maple (*Acer saccharum*, 14%) and a single butternut (*Juglans cinerea*, 2%) were the only tree species used as roosts while still alive. Other tree genera used included American elm (*Ulmus americana*, 14%), poplar (*Populus spp.,* 10%), eastern white pine (*Pinus strobus,* 10%), and oak (*Quercus spp.*, 6%).

Roost tree characteristics were variable over all known locations (Table 2). The average roost tree was 21 m tall, had a 48 cm dbh, and was located at an elevation of 110 m, 181 meters away from the nearest water source. Roost trees were, on average, emergent trees with loose bark, and dead but not significantly decayed. However, these characteristics were variable among known roost trees, as indicated by their coefficients of variation.

The principal components analysis identified habitat characteristics that were consistent across all known locations. Five of the 14 components created in the principal components analysis had eigenvalues > 1 and thus were discarded. The remaining 9 components explained 25% of the remaining variation in the dataset. Taken together, these 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 thus critical in defining presence of Indiana bats (Table 3). Roost trees were located in elevations ranging from 30 m to 219 m, and were within a range of 30 m to 496 m away from the nearest water source. Other important characteristics included the physical characteristics of the tree itself, such as height, presence of peeling bark, placement in the canopy, degree of exfoliation in the bark, and dbh.

Plot characteristics.--There was an average of 57.7 trees > 10 cm dbh (s.d. = 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 (*Acer saccharum*, 18.8%), eastern hophornbeam (*Ostrya virginiana*, 9.5%), ash (*Fraxinus spp.*, 8.8%), and eastern white pine (*Pinus strobus*, 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 the 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, the 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 = 1:12, median = 0:05). Fourteen individuals had sufficient numbers of locations remaining to estimate home range sizes. Due to the elimination of locations along with the highly vagile nature of bats, we were not concerned with autocorrelation of locations. Average home range size was 0.83 km^2 (s.d. = 0.82). Home ranges consisted, on average, of 41.4% agricultural areas, 34.3% forested areas, and 22.0% wetland areas (Table 4). On average, the landscape underlying home ranges was diverse (SDHI = 1.06), indicating that multiple patch types were present within the home range, with 58 unique patches per 1000 ha (Table 2). Within the average home range, any pixel was an average of 158 m away from a water source. These home range characteristics, however, were variable among the 14 bats, as indicated by the coefficient of variations.

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 most 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 degree of diversity in the land cover, degree of patchiness, and closeness of home ranges to water (Table 3).

Landscape characteristics.--Buffers around roost trees were composed mostly of forest, wetland, and agriculture land use patches (Table 4). Forest cover ranged from 26% to 47%, wetland cover ranged from 8% to 14%, and agriculture cover ranged from 35% to 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 36 ha and 101 ha 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 trees included patch density, diversity of cover type, and slope, but the 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, while at the larger 2 km and 3 km scales areas within the landscape were, on average, close to water, and contained decreasingly isolated forest 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 emerge 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 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.

Predictive Map.-- The 0.5 km buffer was the best-fit landscape scale and was therefore used to create the predictive map. Probabilities associated with suitable habitat for the Indiana bat in the Champlain Valley were calculated based on 2 values of k. The first map (Fig 2A) was generated 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 5231.1 km^2, or 8.10% of the Champlain Valley, had a probability of suitable habitat > 0.05. The second map (Fig 2B) was created using all 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. In order to be considered suitable habitat, a given location in the Champlain Valley had to be more similar to known locations in the map using $k = 8$ components (Fig 2B) than in the previous map using only $k = 3$ components (Fig 2A). This is because more components were used to generate the distance between unsampled and known locations. As components were added, the habitat characteristics at an unsampled location had to match the mean habitat characteristics at known locations in more ways in the Figure 2B map than in the Figure 2A map, thus limiting the area of potential habitat identified.

DISCUSSION

Based on our results, Indiana bats in the Champlain Valley need large, old trees located within younger forest patches embedded in a patchy, diverse landscape. The first goal of our study was to document and compare minimum habitat requirements of Indiana bats in the Champlain Valley across 7 spatial scales. Roost trees were tall, large diameter trees with exfoliating bark, typically at low elevation and close to water. Trees in the plots surrounding roost trees were best described by the absence of physical features that are usually associated with potential roost trees (sloughing bark, cavities or splits), indicating that roost trees were, on average, located in much younger forest. Trees within plots were typically smaller in dbh, shorter, and healthier than the central roost trees. Home ranges were in areas of diverse, patchy land cover types that were close to water, with an east-facing aspect. Across all landscape extents, the total area of forest within roost tree buffers and the aspect across those buffers were the two most consistent features. At smaller landscape scales, elevation and diversity of land cover also were important. Density of patches and distance to the nearest water source increased in importance as larger landscape scales were considered.

These habitat characteristics did not vary across the known bat locations for two alternative reasons: (1) they were minimum habitat requirements of the Indiana bat, and hence bats selected maternity colonies that met these minimum requirements, or (2) there was no opportunity for variation due to lack of variation in habitat metrics within the study area. To differentiate the two, we examined the range of variation in the Champlain Valley as a whole to determine if the 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. Additionally, Indiana bats occurred 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 (Prox_md) across the 5 scales at which it was measured ranged from 3.91 to 58.9, where values close to zero represent total isolation of a forest patch within the area examined, and isolation decreases as values increase. Across the Champlain Valley, isolation index values ranged from 0 to 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. Thus, Indiana bats selected landscapes that had fewer patches compared to the rest of the Valley, but these patches were diverse, and the forest patches were isolated from other forest patches.

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 hills with very low gradients. As an 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. In this study our average slope ranged from 4.1° to 7.0° across the 7 scales investigated.

Given that the Champlain Valley is located at the northeastern edge of Indiana bat's range, it is important to consider whether our results differed from studies conducted in other parts of the range. An analysis 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 covering 56% of the tree. Thus far, 393 roost trees have been documented, comprising at least 33 tree species (Kurta 2005). Roost trees in the Champlain Valley seem to mirror these average values in physical appearance. The shear number of documented roost tree species in the Valley (n = 12) as well as 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.

Our average home range size (0.83 km^2) is slightly smaller than that found by Menzel et al. (2005, 1.45 km^2) (Menzel et al. 2005) and Romme et al. (2002, 1.13 km^2) (Romme et al. 2002). 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 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). Our study did not determine bat behavior, i.e., foraging versus traveling, across the nighttime telemetry hours; however, agricultural fields comprised 40% of home ranges on average, while water or wetlands comprised only 22%. Until we can examine birth and survival rates, we cannot say for sure whether these home range habitat differences reflect a difference in preference, or are a result of the landscape configuration and composition of the Champlain Valley.

The second goal of our study was to map areas in the Champlain Valley that met the minimum habitat requirements of Indiana bats. Maps of potential habitat indicated that there are small areas of suitable habitat distributed throughout the Champlain Valley. However, it is important to keep in mind that these maps identify locations that meet the landscape characteristics only at the 0.5 km buffer scale, and habitat features at other scales must also be considered. For instance, high quality habitat at the 0.5 km scale may not be suitable if it does not contain appropriate roost trees or plots, and if the landscape characteristics at greater scales are not appropriate. To consider multiple scales simultaneously, maps could be generated at each of the scales assessed here and combined through map calculations to locate areas that meet habitat requirements at all scales. Our analysis did not reveal whether one scale was more important than others; this is a topic for future research.

MANAGEMENT IMPLICATIONS

Known Indiana bat roosting habitat occurred in areas of the Champlain Valley that are most fragmented and diverse, and home ranges occurred in areas of high agricultural use which is also characterized by isolated forest patches and patchy, diverse landscapes. However, we caution that our study documented suitable habitat based on habitat characteristics, not on population dynamics. Although the Indiana bat population in the Champlain Valley is small, it appears to be increasing in this area (Hicks and Novak 2002). As populations change in size, the 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).

This study found that only a very small area of the Champlain Valley, ranging from 4.7% to 8.1%, may be suitable habitat for Indiana bats. If suitable area is considered as a proportion of forested area within the region these percentages only rise to between 13.4% and 23.1%. 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 300 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.

The utility of our modeling technique is that it allowed us to be specific or general, depending on the purpose of the map. To identify all possible areas of suitable habitat for conservation purposes, fewer components can be used, which in turn identify more areas as potential habitat. These areas then are similar to the known locations in only a few, key habitat characteristics, while other less-important characteristics are variable. Conversely, if we would like to narrow down the suitable habitat areas identified in order to determine where to begin surveying for new colonies, we can use more components. This subset of areas identified above are further restricted to being more like areas of known Indiana bat habitat as more components are added to the model, and thus may be good starting points for surveys.

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

Description	Roost Tree	Plot	Home range	0.5km	1km	2km	3km
Diameter at breast height (cm) (*DBH*)	x	x					
Slope (degrees)	x	x	x	x	x	x	x
Sine of aspect (degrees) (*Aspect_sin*)	x	x	x	x	x	x	x
Cosine of aspect (degrees) (*Aspect_cos*)	x	x	x	x	x	x	x
Elevation (meters)	x	x	x	x	x	x	x
Minimum distance to water or wetland (meters) (*Dist_water*)	x	x	x	x	x	x	x
Height of tree (meters) (*Tree_ht*)	x						
Average densiometer reading in 4 directions (*Densio*)	x						
Canopy class: 1 (emergent) 2 (dominant) 3 (midstory) 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					
Percent of exfoliating bark from 1 (0-5%) to 5 (76-100%) (*Exfol*)	x						
Presence of cavities, 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 in buffer (ha) (*Area_wet*)			x	x	x	x	x
Density of patches in buffer (number per 1000 hectares) (*PD*)			x	x	x	x	x
Shannon's Diversity Index (*SHDI*)			x	x	x	x	x

Table 2. Means (standard deviations) and coefficients of variation (c.v.) for general characteristics of habitats known to be used by Indiana bats. Variables in bold are either ordinal variables (Can_class, Decay, Exfoliation) or binary variables (Cavity, Bark, Split). Explanations of variable abbreviations and units are given in Table 1.

Variable	Roost Tree	c.v.	Plot	c.v.	Home range	c.v.	0.5km	c.v.	1km	c.v.	2km	c.v.	3km	c.v.
DBH	48.05 (20.45)	0.43	22.89 (4.65)	0.20										
Slope	7.02 (6.56)	0.93	6.51 (5.42)	0.83	4.17 (2.46)	0.59	6.49 (3.18)	0.49	5.64 (2.96)	0.52	5.04 (2.63)	0.52	5.12 (2.30)	0.45
Aspect_sin	-0.12 (0.74)	6.17	-0.01 (0.32)	32.00	0.04 (0.09)	2.25	-0.01 (0.05)	5.00	-0.03 (0.07)	2.33	-0.02 (0.07)	3.50	-0.02 (0.05)	2.50
Aspect_cos	0.28 (0.62)	2.21	-0.12 (0.38)	3.17	-0.03 (0.13)	4.33	-0.01 (0.03)	3.00	0.01 (0.04)	4.00	0.02 (0.04)	2.00	0.02 (0.03)	1.50
Elevation	110.26 (50.33)	0.46	110.20 (50.37)	0.46	99.36 (39.34)	0.40	110.33 (43.99)	0.40	110.68 (39.52)	0.36	111.72 (31.08)	0.28	119.39 (27.80)	0.23
Dist_water	199.21 (151.68)	0.76	199.68 (150.51)	0.75	158.06 (88.48)	0.56	175.21 (66.56)	0.38	175.22 (47.83)	0.27	177.96 (68.11)	0.38	193.36 (67.15)	0.35
Tree_ht	20.70 (10.26)	0.50												
Densio	10.10 (17.24)	1.71												
Can_class	**1.54 (0.68)**	**0.44**	**2.21 (0.25)**	**0.11**										
Decay	**3.18 (1.44)**	**0.45**	**1.78 (0.45)**	**0.25**										
Exfol	**3.16 (1.70)**	**0.54**												
Cavity	**0.08 (0.28)**	**3.50**	**0.02 (0.03)**	**1.50**										
Bark	**0.92 (0.28)**	**0.30**	**0.08 (0.11)**	**1.38**										
Split	**0.15 (0.36)**	**2.40**	**0.02 (0.04)**	**2.00**										
Area_for					22.80 (16.81)	0.74	36.09 (12.79)	0.35	101.30 (55.27)	0.55	322.61 (207.18)	0.64	792.22 (370.45)	0.47
Area_md					2.34 (3.83)	1.64	5.96 (12.61)	2.12	0.21 (0.05)	0.24	0.21 (0.05)	0.24	0.20 (0.04)	0.20
Prox_md					3.91 (3.11)	0.80	23.92 (18.04)	0.75	31.70 (34.13)	1.08	61.59 (113.50)	1.84	58.90 (74.59)	1.27
Area_wet					8.34 (13.81)	1.66	5.01 (7.34)	1.47	24.41 (18.14)	0.74	174.00 (84.63)	0.49	408.58 (296.81)	0.73
PD					58.69 (44.38)	0.76	38.36 (14.29)	0.37	32.38 (12.68)	0.39	29.08 (13.18)	0.45	27.58 (11.49)	0.42
SHDI					1.06 (0.35)	0.33	0.60 (0.10)	0.17	1.17 (0.11)	0.09	1.24 (0.06)	0.05	1.28 (0.07)	0.05

Table 3. Minimum habitat requirements at each evaluated scale. 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. Stars represent important habitat variables within the last component at each scale. Explanations of variable abbreviations are given in Table 1.

Roost tree	Plot	Home range	0.5 km buffer	1.0 km buffer	2.0 km buffer	3.0 km buffer
Elevation*	Bark*	Aspect_cos*	Area_for*	Area_for*	Aspect_sin*	Aspect_sin*
Dist_water*	Elevation	Aspect_sin*	Elevation	Aspect_sin	Aspect_cos*	Aspect_cos*
Tree_ht	Dist_water	SHDI	Aspect_cos	Aspect_cos	Area_for*	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	SHDI
Densio	Aspect_sin	Elevation	PD	Elevation	Prox_md	Prox_md
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						

Table 4. A comparison of the average (s.d.) percent area of forest, wetland, and agriculture within each Indiana bat home range and roost tree buffer scale measured.

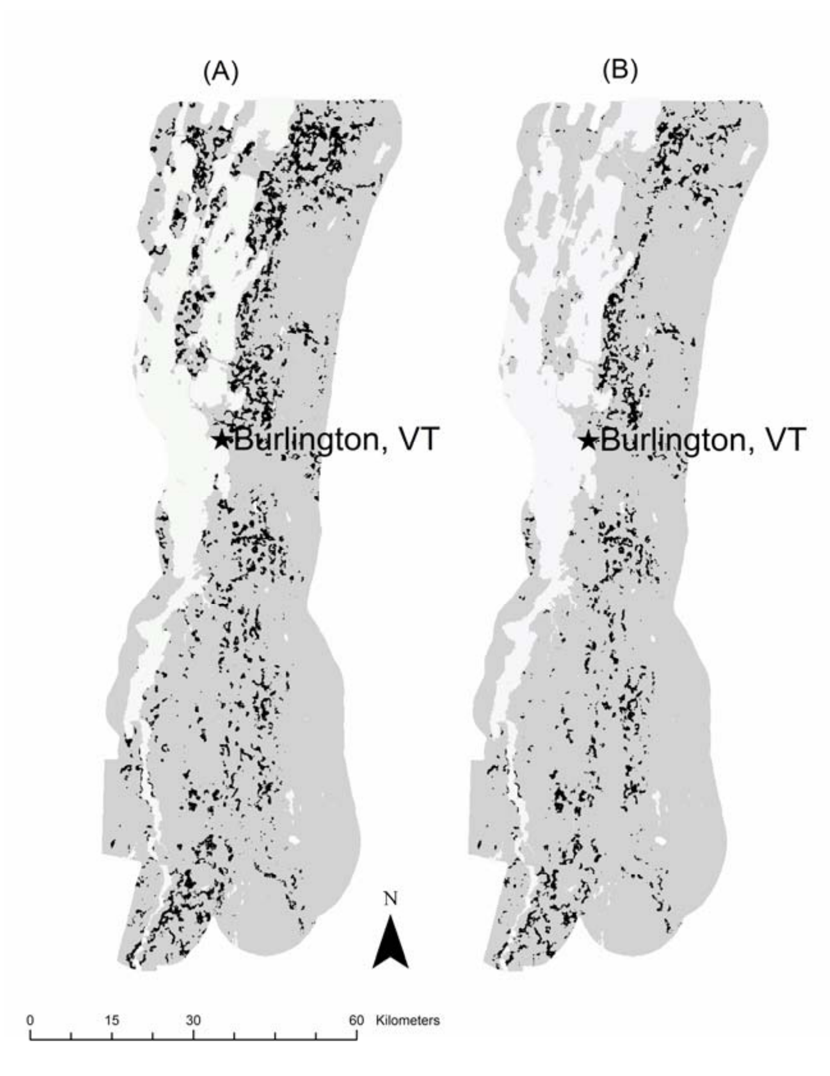
Percent area	Home range	0.5 km	1 km	2 km	3 km
Forest	34.3 (14.08)	45.93 (16.28)	32.22 (17.58)	25.67 (16.48)	28.06 (13.14)
Wetland	22.0 (29.28)	8.62 (9.94)	8.18 (5.94)	13.84 (6.73)	14.45 (10.49)
Agriculture	41.41 (16.89)	34.50 (12.90)	46.10 (15.62)	47.13 (12.59)	44.57 (8.68)

Table 5. Comparison of the range of habitat values within the 0.5 km roost tree buffers to the same habitat variables across the Champlain Valley. Explanations of variable abbreviations are given in Table 1.

Variable	0.5 km buffer		Champlain Valley	
	min	max	min	max
Slope (degrees)	0.95	13.52	0	47.16
Aspect_sin	-0.21	0.04	-0.99	1
Aspect_cos	-0.06	0.14	-0.99	1
Elevation (meters)	35.64	204.1	24.55	1006.16
Dist_water (meters)	55.84	338.86	0	1769.4
Area_for (ha)	10.44	66.69	0	71.73
Area_md (ha)	0.09	66.69	0	71.73
Prox_md	0	93.47	0	196.95
Area_wet (ha)	0.09	33.75	0	71.73
PD (# per 1000 ha)	15.27	68.73	1.39	153.35
SHDI	0.58	1.4	0	1.75

Figure 1. The Lake Champlain watershed straddles the northern borders of New York and Vermont. A 195 km^2 area within this region representing the Champlain Valley itself was used to create predictive maps. Study sites were located in (1) Crown Point, NY, (2) Monkton, VT, and (3) Salisbury, VT.

Figure 2. Maps of potential Indiana bat habitat across a 195 km^2 area within the Champlain Valley of Vermont and New York generated using partitioned Mahalanobis D^2 to determine the suitability of each pixel. 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.



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