MULTI-SCALE FACTORS INFLUENCING DETECTION, SITE OCCUPANCY AND RESOURCE USE BY FORAGING BATS IN THE OZARK HIGHLANDS OF MISSOURI

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In Partial Fulfillment of the Requirements for the Degree

Doctor of Philosophy

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by

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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

MULTI-SCALE FACTORS INFLUENCING DETECTION, SITE OCCUPANCY AND RESOURCE USE BY FORAGING BATS IN THE OZARK HIGHLANDS OF MISSOURI

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a candidate for the degree of Doctor of Philosophy

and hereby certify that in their opinion it is worthy of acceptance.

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DEDICATION

"The bat is the climax of creation in many things, highly developed in brain, marvelously keen in senses, clad in exquisite fur and equipped, above all, with the crowning glory of flight."

Ernest Thompson Seton: 1913

To Joe and Mom,

Msjc,
Squeak, Pip, Yoda, Chewy, Rosy,
Frog, Tad, and Lutra

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ABSTRACT

The ecological importance of bat populations and their susceptibility to decline emphasizes the need for scientifically rigorous yet economically feasible approaches to assessing bat habitat occupancy patterns, and relative abundance at multiple scales over time. Historically, many such studies have not accounted for imperfect detection probability. Because bats are difficult to detect by either capture or acoustic methods, without consideration of detection probability, inferences for population trends has been problematic. We applied a maximum likelihood approach to estimate probability of site occupancy using acoustic detection data for ten species of forest bats in the Ozark Region of Missouri. We evaluated *a priori* hypotheses relative to both probability of detection and site occupancy using an objective model selection criterion (Akaike's Information Criteria, AIC) to rank the candidate models in terms of their ability to explain the empirical data. Estimated species-specific detection probabilities varied among species. We found support for the effects of time, ambient temperature, days since last rain, vegetative clutter, and date on detection probability. Species responded to landscape pattern at different spatial scales (2, 8, and 16 km). Habitat, patch and landscape characteristics (i.e., terrestrial and aquatic habitat type, composition of non-forest habitat, road density and interspersion of contrasting habitats) were important covariates in estimates of site occupancy by bats; but these characteristics also varied among species.

Key Words: Bats, detection probability, site occupancy, Ozark Region, habitat covariates, landscape scale, acoustic monitoring.

CHAPTER 1

MULTI-SCALE FACTORS AFFECTING PROBABILITY OF DETECTION AND SITE OCCUPANCY OF FOREST BATS IN THE OZARK HIGHLANDS OF MISSOURI

ABSTRACT

The ecological importance of bat populations and their susceptibility to decline emphasizes the need for scientifically rigorous yet economically feasible approaches to assessing bat habitat occupancy patterns and relative abundance at multiple scales over time. Historically, such studies have not accounted for imperfect detection probability. Since bats are difficult to detect by either capture or acoustic methods, without consideration of detection probability, inferences to population trends of bats has been problematic. We applied a maximum likelihood approach to estimate probability of site occupancy using acoustic detection data for ten species of forest bats in the Ozark Region of Missouri. We evaluated *a priori* hypotheses relative to both probability of detection and site occupancy using an objective model selection criterion (Akaike's Information Criteria, AIC) to rank the candidate models in terms of their ability to explain the empirical data. Estimated species specific detection probabilities varied among species. We found support for the effects of time, ambient temperature, days since rain, vegetative clutter and date on detection probability. Species responded to landscape pattern at different spatial scales (2, 8, and 16 km). Habitat, patch and landscape characteristics (i.e.,

terrestrial and aquatic habitat type, composition of non-forest habitat, road density and interspersion of contrasting habitats) were important covariates in estimates of site occupancy but also varied among species.

INTRODUCTION

Bats play a key role in many ecosystems and provide economic benefit as primary predators of nocturnal agricultural and forest insects (Whitaker 1995, McCracken and Westbrook 2002, O'Shea and Bogen 2003, Wickramasinghe 2003). Conservation and management efforts are hampered by lack of information about factors influencing bat distribution and abundance at local and landscape scales. Life history characteristics of bats, such as low reproductive rates and colonial roosting during maternity and hibernation periods, render some populations particularly vulnerable to decline. Declining bat populations are a concern of resource management agencies worldwide (Bat Conservation International 1986, Norberg 1987, Fenton 1997, European Bat Research 1998, Kunz and Racey 1998, Currie 1999). In North America (N. A.), there are neither standardized approaches for inferring species occurrence and distribution over space and time nor for tracking trends in bat populations (Kunz and Kurta 1988, O'Shea and Bogen 2003). The ecological importance and susceptibility to decline of bat populations emphasizes the need for scientifically rigorous yet economically feasible approaches to assessing bat occupancy patterns and relative abundance at multiple scales over time.

The nocturnal, cryptic and largely inaudible nature of insectivorous bats makes them difficult to observe without the aid of acoustic detectors or capture methods. Acoustic monitoring surveys have been conducted to estimate species presence and activity indices (or relative abundance) from counts of calls or counts of calls per time interval (Britzke et al. 1999, Ellison et al. 1999, Erickson and West 1999, Miller et al. 2001, Russ and Montgomery 2001, Broders et al. 2003, Wickramasinghe 2003). Three important sources of variation constrain inferences that can be made from acoustic surveys: spatial variation, temporal variation and variation in detection probability (Hayes 2000, MacKenzie and Kendall 2002, MacKenzie et al. 2002, Pollock et al. 2002, Bailey et al. 2004, Gu and Swihart 2004). Detection probability is the probability of detecting at least one individual of the species during a specific sampling occasion, given the species is present (Boulinier et al. 1998, MacKenzie et al. 2002).

Bat relative abundance studies using acoustic detection rarely state assumptions relative to detectability, or assume all species are detected and are equally likely to be detected at each location, time interval, or date (Hayes 1997, Ballantyne and Sherwin 1999, Arnett and Hayes 2000, Hayes 2000, Russ et al. 2003). Only a few studies have estimated species detection probability for bats (Yates and Muzika 2006). Unadjusted estimates contain an unknown negative bias unless detection probability is equal to one; which is unlikely in field studies. Bat detection probability varies with behavior (Fenton 1981, Aldridge and Rautenbach 1987, Brigham et al. 1989, Britton et al. 1999, Schnitzler and Kalko 2001), morphology (Norberg and Raynor 1987, Andrews 1995), (Obrist et al. 2004), and environment (Griffin 1971, Fenton 1982, Norberg 1994, Barclay et al. 1999b, Broders et al. 2004, Kusch et al. 2004). Differences in types of bat detectors, individual units within a detector type, protective housing, sensitivity settings, microphone orientation and sampling protocols result in additional variability in detection probability (Livengood 2003). Site or landscape specific habitat characteristics influence the distribution and abundance of bat species resulting in patchy distribution of species within and between landscapes (Fenton et al. 1980, van Zyll de Jong and Ahlen 1991, van Zyll de Jong 1995, Ekman and van Zyll de Jong 1996). Cumulatively, these factors make it difficult to compare results between studies using different sampling protocols.

Two processes, occupancy and detection, influence whether or not a species is detected at a site. Occupancy reflects spatial and temporal variation based on differences in behavior and patch or landscape variables. Detection reflects variation based on differences in the ability to detect the species when it is actually present at a site. Occupancy as a metric has been used to quantitatively link key habitat characteristics to the ecological status of a species when detection probabilities are less than one (MacKenzie and Manly 2001, MacKenzie et al. 2002, Pollock et al. 2002, MacKenzie et al. 2003, Bailey et al. 2004) and where it may vary by species and/or habitat (MacKenzie and Kendall 2002, MacKenzie et al. 2002, MacKenzie et al. 2003, Bailey et al. 2004, MacKenzie and Bailey 2004, Royle et al. 2005). Site occupancy (ψ) is the probability that a randomly selected site or sampling unit in an area of interest contains at least one individual of the species of interest (MacKenzie et al. 2006). This approach is based on closed-population capture-recapture methods but uses occupancy (proportion of sites/area occupied) as the status metric. Similar to capture-recapture methods, this method is based on multiple visits to sites of interest within a season. The species is either detected or not-detected and this “detection history” (analogous to a recapture history) is used to estimate the proportion of sites occupied by a species (acknowledging a species may not always be detected even when present). The detection history is used to estimate the detection probability (p) and the probability of occupancy (ψ). On a specific sampling occasion, the species is present and detected (ψ x p), or not detected, which may represent either the species is present and not detected [ψ x (1 - p)], or is not present (1 - ψ).

This study represents one component of a long-term intra-agency cooperative project between the USFS, Northern Research Station (NRS) and the Mark Twain National Forest (MTNF), focused on conservation of forest bats. Our purpose was to (1) evaluate the applicability of site occupancy modeling using acoustic detection for estimating bat species occurrence and distribution over space and time and (2) test a set of *a priori* hypotheses concerning the effects of time-specific sampling covariates and site specific habitat, patch and landscape attributes on the detection probability (p) and probability of site occupancy (ψ) of ten species of forest bats characteristic of the Missouri Ozark Highlands of Missouri during the summer (maternity) season.

METHODS

We studied ten bat species: big brown bat (*Eptesicus fuscus*) (EPFU); eastern red bat (*Lasiurus borealis*) (LABO); hoary bat (*Lasiurus cinereus*) (LACI); silver-haired bat (*Lasionycteris noctivagans*) (LANO); gray bat (*Myotis grisescens*) (MYGR); little brown bat (*M. lucifugus*) (MYLU); northern long eared bat (*M. septentrionalis*) (MYSE); Indiana bat (*M. sodalis*) (MYSO); evening bat (*Nycticeius humeralis*) (NYHU); and eastern pipistrelle bat (*Pipistrellus subflavus*) (PISU). We determined the maternity period (life stage representing period of late pregnancy through volancy of offspring) was the most stable from an occupancy perspective for the bat species occurring in our study area. We developed *a priori* hypotheses, which we expressed as models that could be fit to data collected from sample units and used an objective model selection criterion (Akaike's Information Criteria, AIC) (Burnham and Anderson 2002) to rank the candidate models in terms of their ability to explain the empirical data.

Study Area

Our study was located within the Salem Plateau physiographic region, Ozark Highlands aquatic sub-region of Missouri (Sowa 2005) (Figure 1). We used Missouri's Aquatic GAP Classification system to reflect integration of ecological landtype associations (LTA) and drainage boundaries. Watersheds define interacting systems and act as a distributional constraint for freshwater organisms, including insect prey of insectivorous bats, (Pflieger 1989, Sowa 2005). The Ozark divide, a geographic feature running north and east across the Ozark region, creates north-slope streams that flow to the Missouri River and south-slope streams that flow toward Arkansas and the Mississippi River. This feature was used to subdivide the Ozark region into two subunits based on drainage networks, geology, soils, landform, stream size, gradient and aquatic communities. These characteristics have consistently been shown to be associated with functional, and compositional variation in riverine ecosystems (Jacobsen 1997, Jacobson and Primm 1997, Matthews 1998.). Insect studies suggest the nature of aquatic substrate influences abundance and distribution of insect populations and therefore, may represent landscape differences in food type and abundance for bat species (Pflieger 1989, Jacobsen 1997). Additionally, our pilot studies of animal movements (Amelon 2001) strongly suggest river drainages are used as navigational cues for bats.

Sites located in watersheds draining to the Missouri River, hereafter referred to as "north unit", include sites located on the Houston/Rolla/Cedar Creek, Salem and Potosi Ranger Districts of the Mark Twain National Forest (MTNF) and privately owned lands. Sites located in watersheds draining south to Arkansas and the Mississippi River hereafter referred to as "south unit" include sites located on the Ava/Cassville/Willow Springs, Eleven Point, Fredericktown, and Poplar Bluff Ranger Districts of the MTNF and privately owned lands. The north unit consists of 37,720 square kilometers (km^2), with approximately 1 kilometer (km) of losing stream (discharges water into the groundwater) to 24 km^2 of watershed area and 1 kilometer of permanent stream per every 4 km^2 of drainage area. Average gradients for fifth order and larger streams within the unit range from 1 – 7 meters (m) per km. Historic land cover within the uplands consisted of open woodlands and savannas comprised of post oak (*Quercus stellata* Wang.), black oak (*Q. velutina* Lamark), and white oak (*Q. alba* Linnaeus), with an understory of shrubs and grasses such as big and little bluestem (*Andropogon gerardii* Vitman. and *Schizachyrium scoparium* Michx.) (Missouri Department of Conservation 2006). The southern unit consists of 23,590 km^2 with approximately 1 kilometer of losing stream per 20 km^2 of watershed area and 1 km of permanent stream per every 10 km^2 of drainage area and characterized by rugged, hilly countryside with numerous springs, and clear, fast-flowing streams (Missouri Department of Conservation 2006). Average gradients for fourth order and larger streams within the watershed range from 0.4 – 15.3 m per km. Historic land cover within the uplands primarily consisted of shortleaf pine (*Pinus echinata* Mill.) and mixed shortleaf pine with black oak, scarlet oak (*Q. coccinea* Muenchh.), and white oak with an open understory of grasses and shrubs. Occasional prairie and savanna openings were also common in areas along river bluffs. The north unit is 48.7 percent non-forest and 41.1 percent deciduous forest while the south unit is 37.8 percent non-forest and 49.7 percent deciduous forest with the remainder of both areas consisting of mixed coniferous-deciduous forest and woodland, with small amounts of bottomland hardwood forest and wetland types (Table 1). Distribution of non-forest and coniferous forest was highly variable within each unit primarily based on topographic differences.

Sample Sites

We selected 375 sites for our analysis. Within each study unit, initial focal areas (FA) were selected non-randomly based on management priorities of the

MTNF, land ownership (access permission) and logistical constraints imposed by a collaborative radio-telemetry project (Figure 1, cross hatched areas indicate FA's). A pine-savanna restoration project (Pineknot) encompassing 4,100 hectares served as the initial FA of the southern unit and two oak-savanna restoration projects representing 1,500 hectares served as the initial FA of the north unit. Within each FA, we identified sites that would permit acoustic detection and mist-netting over water sources (for a simultaneous telemetry project). Sites were selected randomly from the set of potential trapping sites within each FA. Potential detection sites were also constrained to a 25,000 m radius of telemetry locations while the telemetry project was active; additional areas not constrained by telemetry locations were included between active telemetry periods (Figure 1; solid dots show general locations).

Acoustic Detection

We collected bat echolocation calls using ANABATII frequency division bat detectors attached to Zero-Crossing Analysis Interface Modules (ZCAIM) with a compact flash card (CF) or laptop as storage (Titley Electronics, Ballina NSW, Australia). For protection, each detector, ZCAIM and 12 volt power source was housed in plastic, waterproof containers. Each container had a four inch opening created using 45^{o} polyvinyl chloride (PVC) elbows oriented upwards. Equipment was placed at ground level and secured in the container with the detector microphone oriented in the middle of the opening. Testing conducted in 2001, indicated detectors in protective housing recorded equivalent numbers of call files as detectors placed without housing. Testing also indicated, for this geographic area and forest types, housed units at ground level recorded similar numbers of call files to those elevated at either 5 or 10 meters above ground (Amelon 2001).

Each season, acoustic equipment was calibrated to minimize variance in zone of detection as described by Livengood (2003) and to standardize area sampled by each detector to reduce bias in estimates (Hayes 2000, Larson and Hayes 2000). Up to 12 sites (habitat patches) were sampled each sampling night from dusk until dawn or during the first five hours past dusk. At aquatic habitats, detectors were placed 2 meters from the edge of the water source with the detector microphone oriented to maximize detection over the source. At terrestrial habitats, detectors were placed 50 meters from a random point at the edge of the patch with the detector microphone oriented in a direction unobstructed by vegetation.

Recorded call sequences for each site and sample period were analyzed using Analook software (http://users.lminet/corben/anabat.htm). We used digital filters to objectively eliminate ambient noise, call sequences with less than 5 call pulses, and low quality sequences prior to identifying sequences to species. We developed a call library of 35,000 known call sequences to characterize the range of call parameters for each bat species by habitat type. Using qualitative examination of call characteristics and sequence patterns with quantitative parameter values associated with each call, we compared calls collected to our call library and published information of call characteristics to identify recorded call sequence to species. Multiple quantitative call characteristics including minimum frequency (minF), duration (dur), characteristic frequency (Fc), initial slope (S1), characteristic slope (Sc), cadence and consistency of call parameters were used to distinguish between species. Each season, and periodically during call analysis processing, observers were tested using known call sequences to determine accuracy rate of species identification. Each of the ten target bat species was detected and captured at sites within the study area.

Probability of Detection and Probability of Occupancy - Estimation and Assumptions

Occupancy modeling is based on the following assumptions: (1) the community is closed to changes in occupancy (immigration or emigration) during the time period (season) studied (2) species identification (presence) is correctly determined and (3) occupancy and detection probabilities are independent between sites (MacKenzie et al. 2002). To meet model assumptions, we used sites sampled between May 15 and August 20 in 2001-2003 because these dates cover the maternity season (closed period for occupancy) for the geographic location and bat species represented. Each call file was identified independently by at least two observers whose accuracy rate in tests using the locally derived call library exceeded 85% (range 86-96%). Habitat patches sampled were constrained to be a minimum of 300 meters apart.

We used one visit per site and divided the night into eight 75 minute intervals (MacKenzie et al. 2002). Multiple sampling occasions (intervals) were used to generate a sequence of detections (1), and non-detections (0) equivalent to capture-recapture histories. One visit from sites with multiple visits was randomly selected using a random number generated in SAS (SAS 2001). This approach allowed us to assume the population was closed to changes in occupancy within a night. Including date as a temporal covariate, allowed us to assume that sites sampled on different days were representative of occupancy patterns for the season of interest.

Formulation of Hypothesized Models

Effects on Probability of Detection (*p*) ***. --*** Prior to conducting the study, we hypothesized (*p*) would be influenced by time based on activity patterns, energetic needs and behavioral characteristics of each species. Additionally, we hypothesized that variation in ambient temperature and precipitation would influence *p* directly based on the physics of sound attenuation and distances that microphones can detect high frequency sounds (Corben 2003, Livengood 2003). These environmental factors were hypothesized to have indirect effects on bat detectability by affecting population dynamics and activity patterns of their insect prey; as well as direct effects based on differences in echolocation intensity and flight behavior characteristic of each bat species (Hayes 1997, 2000). Finally, we hypothesized that density of vegetation (clutter) within the area of the microphone would affect (*p*) (Mackey and Robert 1989, Brigham et al. 1997, Broders et al. 2004).

We selected variables that potentially measured effects of hypothesized factors affecting detection probability. We developed *a priori* models to explain detection probability which included one or more variables based on our generalized hypotheses (Table 2). The attenuation model (ATTEN) included temperature (^{o}C) and days since rain to represent variation in our ability to detect bats with electronic equipment and to account for temperature or moisture related effects on abundance or distribution of insects that may audibly interfere with detection. The vegetative clutter and reflectance model (CLUTTER) included categorical variables to represent 3 classes of potential water surfaces (large water surface, small water surface and no water) and 3 classes of vegetative density (dense forest, open forest, and non-forest).

The time interval model (INTERVAL) included time of night to reflect differences in species behavior, insect availability or other non-measurable factors that vary over time of night. The date model (DATE) included within season variation using Julian date and the year model (YEAR) between year variations using year as covariates. We hypothesized these factors could act in additive combinations so we evaluated all combinations of these models resulting in a total of 31 candidate detection models. We also evaluated a null model with constant detection probability.

***Effects on Probability of Site Occupancy* (ψ). --** We developed five generalized hypotheses to explain ψ for forest bats: "Geography", "Habitat", "Patch-Efficiency", "Landscape-Composition" and "Landscape-Foraging Diversity".

In the Geography hypothesis we hypothesized that bats occupy (use) sites based on geographic distribution within the region. In the Habitat hypothesis, we hypothesized that bats occupy (use) habitats that provide optimal conditions for flight based on each species' size and wing morphology (Freeman 1981, Norberg and Raynor 1987, Norberg 1994, Jacobs 1999b, Fenton and Bogdanowicz 2002). Forests vary in structure and composition with age, productivity, and disturbance history; therefore, the habitats they offer to bats differ in the amount of available clutter. Using multivariate analyses of wing morphology, Norberg (1987) demonstrated that gleaners, or bats that take insect prey from the surface of objects, cluster in different areas of multivariate space than aerial hawkers, or bats that capture insects in flight. Large differences in morphology may restrict individual species to alternate foraging habitats, but small morphological differences influence the realized prey available to bats within a habitat (Barclay 1991; Chruszcz and Barclay 2003; Fenton 1990; Saunders and Barclay 1992). Based on data from Norberg (1987) for the species in our study area, we estimated relative indices of aspect ratio, wing loading, and wing tip shape to classify species as "open-adapted" or "clutter-adapted" (Table 3 and Figure 2). Aspect ratio approximates narrowness of the wing (wingspan (b) divided by mean wing chord (c): $AR=b/c$). Higher aspect ratio reflects aerodynamic efficiency and lower energy loss from flight. Wing tip shape index is determined from the tip length ratio and the tip area ratio. High index values indicate rounded wings. Wing size is described by wing loading (WL), which is mass (M) divided by the wing area (S) expressed in Newton's per square meter ($N \cdot m\text{-}^2$). Characteristic flight speed (V) is proportional to the square root of the wing loading. $V \sim (M/S)^{0.5}$. Slow flying bats have large wings and low wing loadings and bats with smaller wings have to compensate with faster speeds for their body size.

Echolocation design has also been related to foraging strategies (Neuweiler 1989). Bats that use frequency modulated (FM) calls obtain detailed information about target size, shape and distance and are thus adapted for foraging in vegetative clutter. In contrast, bats that use constant frequency (CF) calls obtain information about target distance and speed of prey movement and are thus associated with less cluttered habitats (Fenton 1979).

In the Patch-Efficiency hypothesis, we hypothesized that bats occupy (use) habitats that minimize distances between potential roosting, foraging and watering areas (Kern and Humphrey 1995, Waters 1995, Adams et al. 1999, Rydell et al. 1999, Adams 2000, Luszcz 2001). In the Landscape-Composition hypothesis, we hypothesize that bats occupy (use) habitats based on relative amounts of important habitats available in the landscape (Furlonger et al. 1987, Barclay 1989, Walsh and Brenda 1991, Adam et al. 1994, Barclay and Brigham 1994, Best and Hudson 1996, Catto et al. 1996, Arnett and Hayes 2000, Fenton and Bogdanowicz 2002). In the Landscape-Foraging Diversity hypothesis we hypothesized that bats occupy (use) habitats that provide the best interspersion and diversity of roosting, foraging, commuting and watering opportunities across the landscape (Adam et al. 1994, Whitaker 1994, Best and Hudson 1996, Catto et al. 1996, Wethington et al. 1996, Fenton and Bogdanowicz 2002, Henry et al. 2002).

For each of the two landscape-hypotheses, we hypothesized that each bat species may perceive landscape components at different spatial scales, or that habitat relationships may vary along a range of spatial scales (Manley et al., 1993; Aebisher et al., 1993). Specifically, smaller species with rounder wings adapted to fly within forest canopy may select habitat features based on a smaller spatial scale than larger species with wings adapted for fast, longer distance movements. To evaluate this hypothesis, we evaluated four spatial sizes as radii from the location of the detectors 2, 4, 8, and 16 km. These scales represent reported distances traveled during daily activities for species included in our study.

We developed *a priori* models to explain differences in site occupancy based on each of these hypotheses (Table 4). The variable(s) in each model were evaluated as a group in the model selection process. We evaluated the geography hypothesis with the UNIT model using geographic location as a covariate (north=1 or south=0).

We evaluated the habitat hypothesis with the HABITAT model. We used categorical variables to represent 3 classes of potential water types (pond or stream, road rut, none) using no water as the reference category and 7 habitat type classes using non-forest as the reference category (Table 4). Forested types were categorized to represent composition of vegetation present. For the major forest types (oak-hickory and oak-pine), a measure of patch structure (high versus medium to low basal area) was included to represent differences in the character of the patch relative to the ability of a bat to maneuver within the patch. High or low basal area represent stocking rates greater than 60% and less than 60% respectively. Two forest classes, bottomland hardwood and immature, had consistently high basal area, we therefore used a single category for these types.

We evaluated the patch efficiency hypothesis with the PATCH model. We used distances (km) to important habitat features including water, flight corridor, hard edge and size of patch to explain relationships between water sources, foraging or roosting areas and commuting routes.

We evaluated the landscape composition hypothesis with the LANDSCAPE model. We used composition of non-forest, riparian, oak-pine and water (percent of landscape at given spatial scale). Landscapes in the study area are dominated by oak-hickory forest types. Since this type was not likely to be limiting in either geographic unit, we considered oak-hickory as the matrix type of our landscapes and looked at differences in other types within the landscape. We evaluated our landscape diversity hypothesis with the EDGE model. We used density of roads (m/ha) and edge density (m/ha of forest to open edges), or interspersion and juxtaposition of contrasting vegetation types measured as a relative index between 0 and 100 to describe relative amounts of landscape characteristics

Habitat Types

Sites were classified into seven habitat types, oak-hickory fully stocked (OHM), oak-hickory low to moderately stocked (OHW), oak-pine fully stocked (OPM), oak-pine low to moderately stocked (OPW), bottomland hardwood forest (BLHD), shrub-grass or non-forest (SHG), and immature forest (IMM). We used USFS composition and stocking level guidelines for the Eastern Region (R9) (Gingrich 1967) (USDA 2002) and stand data from the MTNF's combined data system (CDS) database or aerial photography for forest system lands and private lands respectively. Randomly selected patches were validated on site for habitat type designation. To minimize temporal variation, sampling was conducted simultaneously in 4-8 habitat types per sample night.

Since water features serve as centers for bat activity; all ponds, streams and upland roads with standing water (road ruts) on publicly owned lands (or private lands with permission) within a FA were sampled. Additional sample sites, up to a total of 12 per night, were randomly selected from remaining patches within each FA.

Patch, Landscape and Climate Metrics

Landscape metrics were derived from 30-m x 30-m resolution Landsat Thematic Mapper satellite imagery classified into 16 vegetative classes (http://www.cerc.usgs.gov/morap/; (MORAP 2005). Landcover classes were condensed from 16 classes using ArcInfo® (ESRI, 1995) to reflect five habitat classes: (1) deciduous forest and woodland representing oak (*Quercus spp*.), hickory (*Carya spp*.) and mixed hardwood types (2) pine and oak-pine forest and woodland representing shortleaf pine (*Pinus echinata* Miller) and oak-pine (*Quercus spp.-P. echinata*) types (3) bottomland hardwoods representing sycamore (*Platanus occidentalis* Linnaeus), cottonwood (*Populus deltoides* Bartram*),* elm (*Ulmus americana* Linnaeus*, U. rubra* Muhlenberg*)*, ash (*Fraxinus pennsylvanica* Marshall) and mixed hardwood types (4) non-forest representing grassland and shrub types including cool or warm season grassland with forbs and shrubs and (5) water including swamp, marsh, wet herbaceous and open water habitats.

We combined the water class from the landcover classification with the county level perennial stream coverage (MSDIS, 2004) and the MTNF pond and stream coverages to identify as many water sources as possible to calculate patch level distance to water in kilometers (km). Similarly, a county-wide roads and trails layer (MSDIS 2004) was used to calculate distance to nearest flyway (km) and road density (m/ha).

We used FRAGSTATS (McGarigal and Marks 1994) to calculate landscape composition, edge density, interspersion and juxtaposition metrics. We defined edge as the boundary between forest and non-forest types. We used landscape level interspersion and juxtaposition indices for non-forest and pine types to characterize vegetation diversity in a matrix of oak-hickory forest. Landscape level interspersion/juxtaposition is based on patch adjacencies rather than cell adjacencies providing a measure of the interspersion or intermixing of patch types. We used landscape percentages of each class except the oak-hickory matrix in our landscape variables. Since much of the land along streams and rivers in the area has been converted from bottomland hardwoods to pasture, we characterized composition of riparian types using a county-wide hydrography coverage of perennial streams (MSDIS 2004) buffered 30 meters on either side. We combined this class with existing bottomland hardwood to calculate the landscape composition of riparian areas. Each of these landscape factors were evaluated for 2 km, 4 km, 8 km and 16 km radii circles from each detector location. Ranges of landscape metrics by geographic unit and spatial scale are provided in Table 5.

Hourly weather data recorded at Sinkin Experimental Forest (most centrally located National Weather Service station measuring hourly temperature and precipitation) was used to calculate mean temperature (^{o}C) and days since precipitation for each sampling occasion.

Statistical Analysis

We used program PRESENCE (available for download from http://www.proteus.co.nz/) to estimate the probability of detection (*p*) and proportion of sites occupied (ψ) for each bat species. Parameters estimated by PRESENCE include (ψ_i), the probability that a species is present at site $_i$, and p_{it}, the conditional probability that a species is detected at site $_i$ at time $_t$, given it is present (MacKenzie et al. 2002). Both (ψ_i) and (p_{it}) are expressed as a logit-function of site specific covariates; p_{it} may also be expressed as a function of time variable and sample specific variables such as environmental conditions

We evaluated support for our *a priori* hypotheses and associated models using an information-theoretic approach (Burnham and Anderson 2002). This approach to model selection favors models having greater explanatory power and penalizes models based on complexity, helping to identify the most parsimonious model. For comparison, we included a null model (i. e. intercept only) in each set of candidate models. We employed a multi-stage model selection process to reduce the number of potential models and to simplify the model building process as we were primarily interested in the effects of the occupancy covariates. We used Akaike weight (w_i) to estimate the probability that a particular model was the best model in the candidate set (i.e., closest to the "truth", *sensu* Burnham and Anderson 2002) at each stage in the selection process.

In the first stage, we identified the set of sampling covariates that had the most support for estimating probability of detection for each species. Since we were reasonably certain that habitat type affected occupancy, we included covariates from the HABITAT occupancy model in all models we considered for estimating probability of detection. We assessed model fit for the global model (ψ(HABITAT),p(INTERVAL,ATTEN,CLUTTER,YEAR,DATE)) for each species to determine if our data structure was reasonable using Pearson's chi-square statistic and a parametric bootstrap test as described by MacKenzie and Bailey (2004). In this method, if the model is an adequate description of the data, then c-hat should be approximately 1.0. Values greater than 1 suggest more variation in the observed data and values less than 1 suggest less variation than expected. We then fit and ranked candidate (p) models based on AIC values. If model selection uncertainty was present, we model averaged coefficient, model predictions and the associated standard errors and confidence intervals. To estimate the influence of individual explanatory variables we calculated a Relative Importance Value (RIV) for each variable in each model set; RIV's were calculated as the sum of the Akaike weights for all models that included a particular variable (Burnham and Anderson 2002). We examined the effect of explanatory variables by interpreting odds ratios based on magnitude and 95% confidence interval (CI). We used the best supported (p) model (by species) for subsequent stages of occupancy model development. Before finalizing the variables in our set of *a priori* models we examined them for multicolinearity by calculating the tolerance value (PROC REG (SAS 2001)); tolerance values ranged from 0.4 – 0.9.

We estimated the individual covariate effects on probability of detection using the best model set for each species. If model selection uncertainty existed, we model averaged covariate estimates and standard errors (Burnham and Anderson

2002). For each covariate evaluated, we estimated probability of detection over the range of values for that covariate while holding all other covariates at their mean value. The issue of detection probability is very important to future bat research, therefore, we plotted predictions for all covariate effects for each species even though not all effects had strong support for each species (95% odds ratio confidence interval did include one).

Next, we evaluated which spatial scale (2, 4, 8 or 16 km) was best supported for the landscape metrics by species. We used the best supported model for detection from the previous step and the global occupancy model and compared versions of this model with landscape variables calculated at each scale. By evaluating AIC values for these models, we selected the scale that was best supported by the data, and used the landscape metrics generated at this scale in the subsequent site occupancy model selection process for each species.

The occupancy models for each species were based on the best supported detection covariates and spatial scale from the previous steps. We evaluated goodness of fit of the global model for each species based on Pearson's chi-square statistic and a parametric bootstrap test as described by MacKenzie and Bailey (MacKenzie and Bailey 2004). If the global occupancy model fit the data, we proceeded to fit all the candidate occupancy models. We ranked candidate occupancy models using AIC values and calculated the weight of evidence (w_i) for each model. If there was model uncertainty ($w_i < 0.90$) for the best models, we model averaged parameter estimates and model predictions across models with a cumulative $w_i \geq 0.90$. For simplicity, we report only the "best" models (cumulative w_i

$\geq$ 0.90) and the null model. As with sampling covariates, we estimated the influence of covariates on occupancy by calculating a Relative Importance Value (RIV) for each variable in each model set. RIV's were calculated as the sum of the Akaike weights for all models that included a particular variable (Burnham and Anderson 2002). We examined the effect of covariates by interpreting odds ratios based on magnitude and 95% CI. In general, we only discuss covariate effects that had support as indicated by the magnitude of the odds ratio being biologically meaningful and 95% CI that did not overlap 1. In some cases, we mention effects where the odds ratio overlaps one, but we clearly identify this.

We estimated the individual covariate effects on probability of site occupancy using the best site occupancy model set for each species. For each covariate evaluated, we estimated probability of site occupancy over the range of values for that covariate at the representative landscape scale for each species while holding all other covariates at their mean value. If model selection uncertainty existed, we model averaged covariate estimates and standard errors. We plotted predicted occupancy probabilities for the range of observed values in our data for the explanatory variables whose 95% odds ratio confidence interval did not include (or barely included) 1.

Results

We processed 197,078 call files from 375 sites. We detected ten species: *Eptesicus fuscus*, (EPFU); *Lasiurus borealis*, (LABO); *Lasiurus cinereus*, (LACI); *Lasionycteris noctivagans*, (LANO); *Myotis grisescens*, (MYGR); *M. lucifugus*, (MYLU); *M. septentrionalis*, (MYSE); *M. sodalis,* (MYSO); *Nycticeius humeralis*, (NYHU) and *Pipistrellus subflavus*, (PISU). Eight species were detected at 20 percent or more of sampled sites. Two species, *L. noctivagans* and *M. sodalis* were detected at only 4 and 6 percent of sites respectively. Additionally, detection probability for *L. noctivagans* was very low (0.13) and numbers of non-detections for both these species were very high relative to detections; therefore, we did not consider these species in the site occupancy analysis.

General Patterns in Detection (p)

At least one bat species was detected at 342 of the 375 sites on at least one occasion. Mean estimated detection probability ranged from 0.20 (LACI) to 0.64 (LABO) (Table 6). Capture rates for these species determined from mist-net or harp trapping conducted at a subset of acoustic site locations during the same years ranged from 0.05 (LACI) to 0.62 (LABO) and consistently ran 0-25% (mean 11.5%) less than mean acoustic detection rates (Table 6). The capture rates of the four most commonly detected species (LABO, MYSE, PISU, and MYGR) were within the range of observed detection rates; for the less common species, capture rates were lower than the minimum detection rates (Figure 3).

Best supported models for probability of detection varied by species (Table 7); however, several patterns were consistent. INTERVAL effects were consistently represented in best model sets for each species. ATTEN and CLUTTER effects were also well represented in the best model sets for 7 of the 8 species while DATE and YEAR effects were highly variable between species (Table 7). While each of the detection covariates were represented in the best models for at least one species, the magnitude and direction of effect varied by species (Table 8).

General Patterns in Probability of (ψ)

The naïve proportion of sites occupied (number of sites where a species was detected based on assumption of detection probability equaling 1) and the *p*-adjusted proportion of sites occupied (number of sites where a species occurred when accounting for detection probability < 1) varied considerably among species (Table 6). Naïve ψ ranged from 0.20 (MYLU and NYHU) to 0.74 (LABO); *p*-adjusted ψ ranged from 0.24 (MYLU) to 0.75 (LABO). Differences between naïve occupancy and *p*-adjusted occupancy ranged from 0.01 (LABO, MYSO) to 0.13 (LACI). Mean probability of site occupancy for the entire study area compared to unadjusted occupancy based on capture rate over the entire study area suggests two species are captured at a similar rate to sites occupied (MYGR and PISU) and two species are captured at a much lower rate than sites occupied (EPFU and LACI) (Figure 4).

The most supported spatial scale for landscape effects was inconsistent between species; however, larger scales (8 km and 16 km) were supported for 7 of the 8 species examined (Table 9). While three species (*M. grisescens* (16 km), *M. lucifugus* (8 km) and *E. fuscus* (2 km)) were strongly supported at a single scale; there was considerable model uncertainty relative to spatial scale for the other species.

Geographic unit was included in the best model set for each of the eight species (Table 10). Although *E. fuscus*, *N. humeralis* and *M. lucifugus* were positively associated with the northern unit and each of the other five were positively associated with the southern unit, only four species had strong support for a difference in probability of site occupancy associated with geographic location (LABO, MYSE, NYHU, and PISU) (Table 11).

Best supported models for probability of site occupancy varied by species (Table 10). Terrestrial and aquatic habitat effects were important for all species; however, the magnitude and direction of effect varied by species (Table 11). Both landscape diversity and composition had high support for six of the eight species while patch effects had support for only four species (Table 10 and 11).

Eptesicus fuscus

Detection probability.-- *E. fuscus* was detected at 168 sites (45%) and, if present, was detected an average of 2.5 visits per site (range 1-7). The global model, ψ(HABITAT)p($_{\text{global}}$) adequately fit the data with somewhat less variation than expected (c-hat = 0.83; X^2 p=0.59). There was some model selection uncertainty; four models were in the "best" model set representing cumulative w_i > 0.90 (Table 7). INTERVAL, ATTEN, and CLUTTER variables were in each of the top models RIV = 0.998. YEAR and DATE variables had RIV of 0.478 and 0.328 respectively. The null model had no support (w_i=0). Based on magnitude of parameter estimates and 95% CI for variables in these models, sampling occasion, presence of a large water surface, temperature and days since rain had greatest influence on detection probability for this species. Large water surface, increasing temperature and increasing days since rain positively influenced (*p*) . Parameter estimates for year and date indicated little support for these effects (Table 8). Predicted detection probabilities were highest for sampling occasions 3 and 7 (0.47) and lowest for sampling occasions 1 and 8 (0.02, 0.23) (Figure 5).

Predicted probability of detection for *E. fuscus* increased from 0.2 – 0.5 as temperature increased from 8 – 29 ^{o}C (Figure 6) and from 0 – 9 days since rain (Figure 7). Predicted probability of detection was 0.1 greater associated with a large water surface compared to no water and 0.2 greater compared to small water features (Figure 8). There was little effect of vegetative clutter or Julian date on predicted detection probability (Figures 9– 11).

Probability of Site Occupancy. -- The best supported spatial scale for landscape effects was $\psi(2KM_{global})$ (Table 9). This model had very strong support (w_i=0.98). The global model for *E. fuscus*, ($\psi(2KM_{global})p(_{global})$), adequately fit the data with somewhat less variation than expected (c-hat = 0.8; X^2 p=0.58). The most supported site occupancy model was ψ(HABITAT,LANDSCAPE,EDGE) with w_i=0.62; two additional models were in the "best" model set (w_i=0.92) (Table 10). The null model had no support (w_i=0). All three "best" models included HABITAT; two models also included LANDSCAPE and EDGE factors. HABITAT, LANDSCAPE, EDGE and UNIT variables had RIV of 1.0, 0.96, 0.96 and 0.29 respectively. Effect of geographic unit was not supported for this species (Table 11, Figure 12).

HABITAT parameter estimates of each forested terrestrial habitat were negative, suggesting non-forest (the reference category) had a positive effect on ψ (Table 11). Oak-hickory and oak-pine forest with high stocking levels had the largest negative effect on ψ; odds of site occupancy decreased by 93% and 88% for each of these types respectively. Although the odds ratio for bottomland forest was less than 1 (Table 11), the CI included 1 suggesting ψ for bottomland forest may not differ compared to non-forest. Predicted site occupancy for non-forest and bottomland forest was 0.40 – 0.59 higher than other terrestrial habitats (Figure 13). Aquatic habitats had a positive effect on ψ compared to no water (Table 11). Odds of site occupancy increased 1307% if the site had a pond or stream and 632% if there was a road rut compared to a site with no water. Predicted site occupancy for ponds or streams and road ruts was 0.51 and 0.43 greater (respectively) than sites without water (Figure 14).

The LANDSCAPE variables percent oak-pine forest and non-forest had slightly negative effects on occupancy. Odds of site occupancy decreased 2% and 5% respectively as percentages of these types increased in the landscape (Table 11). The odds ratios for both riparian type and water were also less than 1; however, the CI included 1 suggesting effect of these two variables on ψ is lower than either of the other two variables in the landscape composition models. Predicted site occupancy decreased from 0.7 – 0.2 as non-forest increased from 10 – 70 percent and decreased from 0.6 – 0.3 as oak-pine forest increased from 2 – 65 percent in the 2 km landscape (Figures 15 and 16).

The EDGE variables road density and interspersion and juxtaposition of oak-pine types had a positive effect. Odds of site occupancy increased 11% and 5%, respectively, with each unit increase. Interspersion of non-forest had a slightly negative effect; odds of site occupancy decreased 2% with each unit increase

(Table 11). The parameter estimate for edge density was also slightly positive; however, the CI included 1. Predicted site occupancy increased from 0.3 – 0.7 as road density increased from 3 – 20 m/ha, increases were smaller above this level (Figure 17). Predicted site occupancy increased from 0.2 – 0.8 as interspersion of oak-pine forest increased from 40 – 90 (Figure 18) and decreased from 0.7 – 0.3 as interspersion of non-forest increased from 30 – 90 (Figure 19).

Lasiurus borealis

Detection probability. **–** *Lasiurus borealis* was detected at 278 sites (75%) and, if present, was detected an average of 3.9 visits per site (range 1-8). The global model, ψ(HABITAT)$p(_{global})$ adequately fit the data with somewhat more variation than expected (c-hat = 1.53; X^2 p=0.13). There was some model selection uncertainty; three models were in the "best" model set; w_i = 0.94 (Table 7). The null model had no support (w_i=0). INTERVAL, YEAR, and CLUTTER variables were in each of the top models with RIV = 0.998. DATE and ATTEN variables had RIV of 0.37 and 0.18. Presence of a large water surface positively influenced (*p*); odds of detection increased 160% (Table 8). Increasing vegetative clutter and year had a negative influence, odds of detection decreased 50% and 70% respectively (Table 8). There was low support for effects of temperature, rain and date on detectability of *L. borealis*.

This species had the highest overall detection probabilities for each sampling occasion. Predicted detection probabilities were highest for sampling occasions 2 through 4 (0.73, 0.72, and 0.68 respectively) and lowest for sampling occasions 1 and 5 (0.31, 0.56) (Figure 5). Predicted probability of detection was 0.15 greater associated with a large water surface compared to no water and small water features (Figure 8); and decreased 0.15 for both vegetative clutter classes over no vegetative clutter (Figure 9). Detection probability decreased with year (Figure 11).

Probability of Site Occupancy. -- The best supported spatial scale for landscape effects was $\psi(16KM_{global})$ (Table 9). There was model uncertainty between 16KM and 2KM for this species (w_i=0.61 and w_i=0.34; cumulative w_i=0.95); even so, we used the 16KM scale for occupancy analysis. The global model for *L. borealis* adequately fit the data with somewhat more variation than expected (c-hat = 1.5; X^2 p=0.12). The most supported model was the global model, ψ(HABITAT,PATCH,LANDSCAPE,EDGE,UNIT) with w_i=0.534 (Table 10). Two additional models were in the "best" model set; cumulative AIC weight of 0.91. The null model had no support (w_i=0). HABITAT and EDGE variables had strongest support for effect on ψ. HABITAT, EDGE, LANDSCAPE, UNIT and PATCH variables had RIV of 1, 0.96, 0.93, 0.84, and 0.62 respectively. Geographic location affected site occupancy for *L. borealis;* predicted site occupancy was 0.11 greater in the south compared to north units (Figure 12).

HABITAT parameter estimates of each forested terrestrial habitat were negative, suggesting non-forest (reference category) had a positive effect on ψ (Table 11). Oak-hickory forest with high stocking levels and immature forest had the largest negative effect on ψ; odds of site occupancy decreased by 87% for each of these types (Table 11). The 95% CI for bottomland forest included 1 indicating that ψ for bottomland forest was not different compared to non-forest (Table 11).

Predicted site occupancy for non-forest and bottomland forest was 0.01 – 0.13 greater than other terrestrial habitats (Figure 13). Both aquatic habitats had a positive effect on ψ compared to no water, however, the CI for road ruts included 1 (Table 11). Odds of site occupancy increased 2655% if the site had a pond or stream compared to a site with no water. Predicted site occupancy for ponds or streams was 0.16 greater than sites without water (Figure 14).

EDGE variable edge density had a positive effect on ψ; while interspersion of oak-pine or non-forest and road density had negative effect on ψ (Table 11). Odds of site occupancy increased 27% as edge density increased and decreased 20%, 6% and 43% respectively as interspersion of oak-pine, non-forest and road density increased (Table 11). Predicted site occupancy decreased from 0.9 – 0.6 as road density increased from 8 – 16 m/ha (Figure 17); from 0.9 – 0.7 as interspersion of oak-pine forest increased from 50 – 70 (Figure 18); from 0.9 – 0.8 as interspersion of non-forest increased from 50 – 75 (Figure 19) within the 16 km landscape. Predicted site occupancy increased from 0.2 – 0.8 edge density increased from 40 – 52 m/ha then leveled off somewhat (Figure 20).

Each of the LANDSCAPE variables had a positive effect. Odds of site occupancy increased 8% and 1609% respectively as percentages of non-forest and riparian type increased in the landscape (Table 11). Oak-pine and water, while also positive; had CI that included 1 indicating lower support for these variables. Predicted site occupancy increased from 0.6 – 0.8 as non-forest increased from 12 – 30 percent of the landscape then tapered off (Figure 15). Similarly, site occupancy predictions increased from 0.5 – 0.9 as riparian habitat increased from 0.5 – 2.5 percent within the 16 km landscape (Figure 21).

Although PATCH variables were included in the best model set, only distance to water was supported (CI barely included 1) (Table 11); suggesting a slight negative effect. Predicted site occupancy decreased from 0.6 – 0.4 as distance from a water source increased from 0 – 1100 meters (Figure 22).

Lasiurus cinereus

***Detection probability.* –** *Lasiurus cinereus* was detected at 99 sites (26%) and, if present, was detected an average of 1.8 visits per site (range 1-7). The global model, ψ(HABITAT)$p_{(global)}$ adequately fit the data with somewhat less variation than expected (c-hat = 0.79; X^2 p=0.64). There was model selection uncertainty; three models were in the "best" model set with w_i = 0.99 (Table 7). The null model had no support (w_i=0). INTERVAL, ATTEN, and YEAR variables were in all the best models for detection, RIV= .99. CLUTTER and DATE variables had much lower RIV, 0.28 and 0.18 respectively. Covariates positively affecting detectability of this species were large water surface, temperature, days since rain, and year; odds of detecting this species increased 170%, 13%, 8% and 366% respectively (Table 8).

Predicted detection probabilities were highest for sampling occasions 3, 2 and 7 (0.29, 0.27, and 0.23 respectively) and lowest detection for sampling occasions 1 and 8 (0.0, 0.1) (Figure 5). Predicted probability of detection for *L. cinereus* increased from 0.1 – 0.5 as temperature increased from 8 – 29 ^{o}C (Figure

6) and as days since rain increased from 1 – 9 (Figure 7). Predicted probability of detection was 0.06 and 0.08 greater associated with large and small water surface compared to no water (Figure 8). Effects of vegetative clutter and Julian date were not supported for predicting detection probability for this species (Figures 9-10). Detection probability increased with year (Figure 11).

Probability of Site Occupancy. -- The best supported spatial scale for landscape effects was ψ(8KMglobal) with w_i=0.57 (Table 9). There was considerable model uncertainty; other models with support were ψ(16KMglobal), and ψ(4KMglobal) (wi =0.19 and 0.16 respectively). The global model for *L. cinereus* adequately fit the data with somewhat less variation than expected (c-hat = 0.8; X^2 p=0.64). The best supported model for site occupancy was ψ(HABITAT,EDGE) with w_i=0.56; two additional models were in the "best" model set representing cumulative AIC weight of 0.93 (Table 10). The null model had no support (wi=0). All three best models included HABITAT; the two models with most support also included EDGE variables. HABITAT, EDGE, UNIT and LANDSCAPE variables had RIV of 1.0, 0.92, 0.86, and 0.12 respectively. PATCH variables were not included in the best model set. Effect of geographic unit was not supported for this species (Table 11, Figure 12).

HABITAT parameter estimates for forested terrestrial habitat were negative, suggesting non-forest had a positive effect on ψ (Table 11). Oak-hickory and oak-pine forest with high stocking levels had the largest negative effect on ψ; odds of site occupancy decreased by 95% for each of these types (Table 11). Predicted site occupancy for non-forest was 0.28 – 0.64 greater than other terrestrial habitats and bottomland forest was 0.21 – 0.37 greater than other forested terrestrial habitats (Figure 13). Aquatic habitats had a positive effect on ψ compared to no water, however, the CI for road ruts included 1 (Table 11). Odds of site occupancy increased 1679% if the site had a pond compared to a site with no water. Predicted site occupancy for ponds or streams and road ruts was 0.56 and 0.38 greater (respectively) than sites without water (Figure 14).

EDGE and LANDSCAPE variables indicated interspersion of oak-pine forest and non-forest had a positive effect on ψ while road and edge density of non-forest had a negative effect (Table 11). The 95% CI for landscape composition of non-forest only slightly included 1 suggesting a small positive influence from this variable as well. Predicted site occupancy decreased from 0.8 – 0.2 as road density increased above 9 m/ha (Figure 17) and decreased from 0.7 – 0.2 as edge density increased from 40 – 60 m/ha within the 8 km landscape (Figure 20). Predicted site occupancy increased for each incremental increase in interspersion of oak-pine forest or non-forest (Figures 18 and 19).

Myotis grisescens

Detection probability.-- *M. grisescens* was detected at 124 sites (33%) and, if present, was detected an average of 2.7 visits per site (range 1-8). The global model, ψ(HABITAT)p($_{global}$) adequately fit the data (c-hat = 1.03; X^2 p=0.4). Two models had similar support for detection probability, the most supported model was p(INTERVAL,ATTEN, CLUTTER,YEAR) (w_i=0.399) (Table 7). There was model uncertainty; three additional models were included in the model set representing cumulative AIC weight of 0.907. The null model had no support (wi=0). INTERVAL and CLUTTER variables had RIV of 1. YEAR, ATTEN and DATE variables had RIV of 0.86, 0.72 and 0.33 respectively.

Odds of detection increased 135% for high clutter over no clutter (Table 8). Odds of detection decreased with year (Table 8). The 95% confidence interval of estimates for the remaining variables included 1; although temperature, days since rain and Julian date only slightly included 1 (Table 8).

Predicted detection probabilities were highest for sampling occasions 2, 3 and 6 (0.51, 0.47, and 0.46 respectively) and lowest detection for sampling occasions 1 and 8 (0.20, 0.25) (Figure 5). Predicted probability of detection increased for both high and low vegetative clutter classes (0.22 and 0.11, respectively) over no vegetative clutter for this species (Figure 9). Julian date only slightly increased probability of detection for this species (Figure 10). Predicted probability of detection decreased 0.4 – 0.2 as temperature increased from 8 – 29 ^{o}C and from 9 – 1 days since rain (Figures 6 and 7).

Probability of Site Occupancy. -- The best supported spatial scale was $\psi(16KM_{global})$ (Table 9); this model had very strong support (w_i =0.958). The global model, $\psi(16KM_{global})p(_{global})$ adequately fit the data with slightly more variation than expected (c-hat = 1.1; X^2 p=0.43). The best supported site occupancy model was ψ(HABITAT,PATCH,LANDSCAPE,EDGE) with w_i=0.36 (Table 10). There was considerable model uncertainty for this species five additional models were in the "best" model set representing cumulative AIC weight of 0.93. The null model had no support (wi=0). All models in the best model set included HABITAT while other variables were inconsistent. Site occupancy was best explained by HABITAT and LANDSCAPE variables (RIV=1 and 0.96 respectively). PATCH, EDGE and UNIT variables were much lower (RIV=0.72, 0.58, and 0.49 respectively). Effect of geographic unit was not supported for this species.

HABITAT parameter estimates indicated bottomland forest of the terrestrial habitats most positively influenced ψ compared to non-forest habitat. Immature forest and oak-pine forest with high stocking levels had the largest negative effect on ψ. Odds of site occupancy increased 95% and decreased by 93% and 88%, respectively, for these types (Table 11). Predicted site occupancy for bottomland forest was 0.10 – 0.30 greater than other terrestrial habitats (Figure 13). Both aquatic habitats had a positive effect on ψ compared to no water (Table 11). Odds of site occupancy increased at sites with ponds (492%) or road ruts (928%) compared to sites with no water. Predicted site occupancy for ponds or streams and road ruts was 0.16 and 0.09 greater (respectively) than sites without water (Figure 14).

Each LANDSCAPE variable had a positive effect on ψ. Odds of site occupancy increased 8, 114 and 3275% respectively as percentages of non-forest, water and riparian type increased (Table 11). While the CI for percentage of water in the landscape did include 1, the odds ratio was not centered within the range. Predicted site occupancy increased 0.1 – 0.3 as landscape percentage of water increased (Figure 23). Predicted site occupancy increased 0.4 as percent riparian increased from 0.5 – 2.5 (Figure 21) and 0.2 as percent non-forest increased from 35 – 55 in the landscape (Figure 15).

Although EDGE and UNIT variables were included in the best model set, only edge density was supported by odds ratio (Table 11). Edge density, interspersion of non-forest and oak-pine had negative effects while road density had a positive effect on ψ. Odds of site occupancy decreased 18% as density of non-forest edge increased. Predicted site occupancy decreased 0.5 – 0.3 as edge density increased from 35 – 55 m/ha within the 16 km landscape (Figure 20).

Although PATCH variables were included in the best model set, odds ratio confidence intervals for each of these variables included 1. Predicted site occupancy increased 0.1 – 0.3 as distance from a road increased (Figure 24).

Myotis lucifugus

Detection probability. -- *M. lucifugus* was detected at 77 sites (21%) and, if present, was detected an average of 2.2 visits per site (range 1-6). The global model, ψ(HABITAT)p($_{global}$) adequately fit the data with somewhat less variation than expected (c-hat = 0.82; X^2 p=0.79). The most supported model was ψ(HABITAT)p(INTERVAL,DATE) with w_i=0.23. There was some model uncertainty; three additional models were included in the model set representing cumulative AIC weight of 0.92 (Table 7). The null model had no support (w_i=0). INTERVAL and DATE had the highest support for influence on detectability of this species (RIV=1 and 0.44 respectively). Temperature, rain and date parameter coefficients were positive; however, there was low support for these effects (Table 8).

Sampling occasion had strong support; predicted detection probabilities were highest for sampling occasions 3 and 2 (0.39 and 0.37) and lowest for sampling occasions 1 and 8 (0.02, 0.19) (Figure 5). Predicted detection probability increased very slightly with Julian date (Figure 10).

Probability of Site Occupancy. -- The best supported spatial scale was $\psi(8KM_{global})$ (Table 9). This model had very strong support (w_i =0.99). The global model, $\psi(8KM_{global})p(_{global})$ adequately fit the data with slightly less variation than expected (c-hat = 0.95; X^2 p=0.83). The best supported model was ψ(PATCH,LANDSCAPE,EDGE) (w_i=0.47) (Table 10). Three additional models were in the "best" model set (w_i=0.92). The null model had no support (w_i=0). All models in the best model set included PATCH, LANDSCAPE, and EDGE variables (RIV=0.99). RIV of HABITAT and UNIT variables were 0.28. Although UNIT was included in the best model set, differences between north and south units were not supported by model averaged odds ratios (Table 11).

Although HABITAT was not strongly supported for this species, among the terrestrial habitats, bottomland forest most positively influenced ψ compared to non-forest habitat. Predicted site occupancy for bottomland forest was 0.20 – 0.25 greater than other terrestrial habitats (Figure 13). Predicted site occupancy for ponds or streams and road ruts was 0.17 and 0.09 greater (respectively) than sites without water (Figure 14).

PATCH variables indicated distance to road had a positive effect on ψ while distance to water and distance to edge had a negative effect (Table11). Predicted site occupancy decreased from 0.25 – 0.1 as distance from a water source increased from 0 – 400 meters (Figure 22) and increased by 0.2 – 0.9 as distance to a road increased from 0 – 600 meters (Figure 24).

LANDSCAPE variables had a positive effect on ψ. Odds of site occupancy increased 37% and 29% respectively as percentages of riparian and water increased in the landscape (Table 11). Predicted site occupancy increased from 0.2 – 0.3 as riparian increased from 2 – 4 percent of the 8 km landscape (Figure 21); increased from 0.2 – 0.5 as water increased from 3 – 8 percent (Figure 23); and increased from 0.1 – 0.4 as percent non-forest increased from 20 – 50 percent (Figure 15).

EDGE variables had a negative effect on ψ; however, the CI for edge density included 1 (Table 11). Predicted site occupancy decreased from 0.8 – 0.2 with road densities from 8 – 12 m/ha (Figure 17). Predicted site occupancy gradually decreased for each incremental increase in interspersion of oak-pine forest and sharply decreased from 0.7 – 0.2 as interspersion of non-forest increased from 50 – 65 within the 8 km landscape (Figures 18 and 19).

Myotis septentrionalis

Detection probability. -- *M. septentrionalis* was detected at 264 sites (70%) and, if present, was detected an average of 3.1 visits per site (range 1 – 8). The global model, ψ(HABITAT)$p(_{global})$ adequately fit the data with slightly more variation than expected (c-hat = 1.1; X^2 p=0.24). The most supported model was *p*(INTERVAL,ATTEN,CLUTTER,YEAR,DATE) with w_i=0.57. There was some model uncertainty; four additional models were included in the model set (w_i=0.92) (Table 6). The null model had no support (w_i=0). INTERVAL and CLUTTER variables were strongly supported (RIV=1). ATTEN, YEAR and DATE variables had RIV of 0.75, 0.72 and 0.72, respectively.

CLUTTER variables, Julian date and days since rain had a positive influence on (*p*) while temperature and year had a negative influence (Table 8). Odds of detecting *M. septentrionalis* were 108 – 160% greater with low to high basal area than for non-forest types. Odds of detecting this species were 122% greater with larger water surfaces compared to no water. Predicted probability of detection was 0.25 and 0.11 greater for low and high vegetative clutter classes, respectively, over no vegetative clutter (Figure 9). Predicted probability of detection was 0.27 and 0.11 greater associated with large and small water surfaces, respectively, compared to no water feature (Figure 8). Odds of detection decreased 5% with increasing ambient temperature while odds of detection increased 7% with days since rain (Table 8). Predicted probability of detection decreased by 0.07 for each 10^{o}C increase in ambient temperature and increased 0.01 for each day since rain for this species (Figures 6 and 7). Probability of detection increased very slightly with Julian date (Figure 10). Predicted detection probabilities were highest for sampling occasions 3 and 2 (0.64 and 0.56) and lowest for sampling occasions 1 and 8 (0.2 and 0.25) (Figure 5).

Probability of Site Occupancy. – . The best supported spatial scale for landscape effects was $\psi(16KM_{global})$ with w_i =0.72 (Table 9). There was some model uncertainty; one additional model (8 KM) was in the best supported model set (cumulative w_i =0.93). The global model, $\psi(16KM_{global})p(_{global})$ adequately fit the data (c-hat = 1.03; X^2 p=0.31). The best supported model was

ψ(HABITAT,PATCH,EDGE,UNIT) with w_i=0.73 (Table 10). Model uncertainty resulted in four additional models in the "best" model set representing cumulative AIC weight of 0.91. The null model had no support (w_i=0). HABITAT and EDGE variables had highest support for effect on site occupancy for *M. septentrionalis* (RIV=1.0, 0.96, respectively). PATCH and UNIT variables had RIV of 0.91 and 0.81 respectively. LANDSCAPE variables were not in best model set (RIV=0.08). Geographic location influenced site occupancy for *M. septentrionalis;* predicted site occupancy was 0.13 greater in the south compared to north units (Figure 12).

HABITAT parameter estimates indicated forested habitats had a positive effect on ψ compared to non-forest, except immature forest which had a negative effect (Table 11). Among terrestrial habitats, bottomland forest and forests with low stocking rates had the strongest positive effect on ψ (Table 11). Predicted site occupancy for bottomland hardwood and open oak-hickory forest was 0.04 – 0.37 greater than other terrestrial habitats (Figure 13). Odds of site occupancy increased 37% and 7% if the site had a pond or road rut compared to a site with no water (Table 11). Ponds or streams and road ruts increased predicted occupancy by 0.05 and 0.11 (respectively) over sites without water (Figure 14).

The PATCH variables distance to road and distance to edge had a positive effect on ψ while distance to water had a negative effect (lcl=1) (Table 11). Predicted site occupancy decreased by 0.2 as distance to water increased from 0 – 1100 meters (Figure 22). Predicted site occupancy increased slightly (0.1) as distance increased from a road or from an edge between forest and non-forest (Figures 24 and 25).

The EDGE variables non-forest edge density and road density had a positive effect on *ψ;* while interspersion of oak-pine or non-forest types had a negative effect on *ψ* (Table 11). Predicted site occupancy increased from 0.6 – 0.9 as road density increased from 8 – 14 m/ha (Figure 17) or edge density increased from 40 – 65 m/ha (Figure 20) within 16 km. Predicted site occupancy decreased 0.4 as interspersion of oak-pine forest increased from 50 – 70 (Figure 18) and decreased slightly as interspersion of non-forest increased from 55 – 75 (Figure 19).

Nycticeius humeralis

Detection probability. – *N. humeralis* was detected at 75 sites (20%); and if present, was detected an average of 2.8 visits per site (range 1 – 7). The global model, ψ(HABITAT)$p(_{global})$ adequately fit the data with slightly less variation than expected (c-hat = 0.7; X^2 p=0.94). The most supported model was *p*(INTERVAL,ATTEN,CLUTTER,YEAR) with w_i=0.64. There was some model uncertainty resulting in two additional models in the best model set (cumulative w_i=0.94). The null model had no support (w_i=0). CLUTTER, YEAR and ATTEN were important detection variables RIV=1.0, 1.0 and 0.97. Sampling occasion had less support for this species (RIV=.91) and DATE had fairly low support (RIV=.28).

CLUTTER variable large water surface positively influenced (*p*) (Table 8). Odds of detecting *N. humeralis* were 133% greater over a large water surface and 93% lower over a small water surface compared with no water. Support for vegetative clutter over no clutter was low as the CI included 1 (Table 8). Temperature, days since rain and year each had a positive influence on (*p*) ; odds of detecting *N. humeralis* were 9% and 10% greater as temperature and days since rain increased. YEAR had a positive influence with 2003 having greater odds of detection than either other year (Table 8).

Predicted probability of detection was highest for sampling occasions 3 and 8 (0.40, and 0.38 respectively) and lowest detection for sampling occasions 1 and 5 (0.2, 0.23) (Figure 5). Predicted probability of detection increased from 0.2 – 0.6 as temperature increased from 8 – 29°C (Figure 6) and from 0.3 – 0.5 as days since rain increased from 0 – 9 (Figure 7). Predicted probability of detection was 0.1 greater associated with a large water surface compared to no water and 0.2 greater compared to small water features (Figure 8) and 0.3 – 0.5 greater for low or no vegetative clutter over high clutter (Figure 9). Julian date had very little effect on predicted detectability (Figure 10) and 2003 had greater predicted detectability than either 2002 or 2001 for this species (Figure 11).

Probability of Site Occupancy. – The best supported spatial scale for landscape effects was $\psi(8KM_{global})$ with w_i=0.52 (Table 9). There was some model uncertainty; two additional models were represented in the best model set (cumulative w_i=0.99) (Table 9). The global model, $\psi(8KM_{global})p(_{global})$ adequately fit the data with somewhat less variation than expected (c-hat = 0.9; X^2 p=0.57). The best supported model was ψ(HABITAT,LANDSCAPE,EDGE,UNIT) with w_i=0.31 (Table 10); three additional models were in the "best" model set (cumulative w_i=0.93) (Table 10). The null model had no support (w_i=0). Site occupancy was best explained by HABITAT and LANDSCAPE variables (RIV=1.0, 0.92, respectively). EDGE and UNIT variables had RIV of 0.59 and 0.45 respectively, while PATCH was much lower (RIV=0.01). Geographic location influenced site occupancy for *N. humeralis;* predicted site occupancy was 0.15 greater in the north compared to south units (Figure 12).

HABITAT parameter estimates of each forested terrestrial habitat were negative compared to non-forest, except bottomland forest which had an odds ratio of 1; however, each CI overlapped 1 (Table 11). Predicted site occupancy was highest for non-forest, bottomland forest and oak-hickory forest with low stocking (Figure 13). Aquatic habitats had a positive influence over no water. Odds of site occupancy increased with ponds (715%) compared to sites with no water (Table 11). No site in the southern unit with a road rut had a detection of this species (detection matrix included only zeros), therefore, maximum likelihood calculations behaved erratically.

LANDSCAPE variables had a positive effect on ψ. Odds of site occupancy increased 7% and 4% respectively as percent non-forest and oak-pine forest increased in the landscape (Table 11). Predicted site occupancy increased by 0.8 as percent oak-pine forest increased from 2 – 44 within the 8 km landscape (Figure 16).

EDGE variables, except interspersion of non-forest, had a negative effect on ψ; however, the support for these variables was low (Table 11). Predicted site occupancy was highest for low road density and decreased by 0.2 as road density increased from 6 – 14 m/ha (Figure 17). Predicted site occupancy gradually decreased as interspersion of oak-pine forest increased and slightly increased as interspersion of non-forest increased within the landscape (Figures 18 and 19). PATCH variables were not supported in the best model set for this species.

Pipistrellus subflavus

Detection probability. -- *P. subflavus* was detected at 112 sites (32%) and, if present, was detected an average of 2.5 visits per site (range 1 – 7). The global model, ψ(HABITAT)$p(_{global})$ adequately fit the data with slightly less variation than expected (c-hat = 0.74; X^2 p=0.74). The most supported model was *p*(INTERVAL,ATTEN,CLUTTER,YEAR,DATE) with w_i=0.31 (Table 7). There was considerable model uncertainty; four additional models were included in the best model set (cumulative w_i=0.94). The null model had no support (w_i=0). INTERVAL and CLUTTER variables were most supported (RIV=1). DATE, YEAR and ATTEN variables had RIV of 0.67, 0.50 and 0.37, respectively. CLUTTER variable parameter estimates except small water surface were positive (Table 7); however, small water surface and low vegetative clutter had low support. Odds of detecting *P. subflavus* were 190% greater for larger water surfaces compared to no water and 148% greater for sites with high basal area compared to no clutter (Table 8). Days since rain and date positively influenced detection while temperature negatively influenced detection; YEAR had low support (Table 8).

Predicted detection probabilities were highest for sampling occasions 7 and 2 (0.44) and lowest for sampling occasions 1 and 8 (0.21 and 0.20 respectively) (Figure 5). Predicted probability of detection decreased as temperature and days since rain increased (Figures 6 and 7). Predicted probability of detection was 0.2

greater associated with a large water surface compared to no water or small water features (Figure 8). Predicted probability of detection was greater for both classes of vegetative clutter than no vegetative clutter (Figure 9). Predicted probability of detection increased by 0.3 as date increased from May 25 – August 25 (Figure 10).

Probability of Site Occupancy. -- The best supported spatial scale for landscape effects was $\psi(16KM_{global})$ with w_i =0.40. There was considerable model uncertainty; two additional scales (8KM and 4KM) were included in the best model set (cumulative w_i=0.96) (Table 9). The trend in model support was from larger to smaller spatial scale. The global model, $\psi(16KM_{global})p(_{global})$ adequately fit the data with somewhat less variation than expected (c-hat = 0.8; X^2 p=0.73). The best supported model evaluated at the 16KM spatial scale was ψ(HABITAT,UNIT) with w_i=0.69; two additional models were in the "best" model set (cumulative w_i=0.94) (Table 10). The null model had no support (w_i=0). Site occupancy was best explained by HABITAT and UNIT variables (RIV=1.0, 0.78, respectively). LANDSCAPE, EDGE and PATCH variables had RIV of 0.1, 0.04 and 0.02 respectively. Geographic location influenced site occupancy for *P. subflavus;* predicted site occupancy was 0.15 greater in the south compared to the north unit (Figure 12).

HABITAT parameter estimates of each forested terrestrial habitat were negative compared to non-forest; however, bottomland forest CI included 1 (Table 11). Oak-hickory forest with high stocking levels and immature forest had the largest negative effect on ψ; odds of site occupancy decreased by 87% for each of these types (Table 11). Predicted site occupancy for non-forest and bottomland forest was 0.06 – 0.36 larger than other terrestrial habitats (Figure 13). Both aquatic habitats had positive parameter estimates; predicted site occupancy for ponds or streams was 0.53 greater than sites without water; CI for road ruts included 1 (Figure 14).

There was little support for the effect of LANDSCAPE variables. However, the CI for odds ratio of percent non-forest barely included 1 and predicted site occupancy increased by 0.6 as percent non-forest increased from 10 – 55 within the 16 km landscape (Figure 15).

DISCUSSION

Applicability of Site Occupancy Modeling

We demonstrated that relationships between habitat covariates and bat occupancy can be described when detection probability is less than 1 through the use of occupancy modeling. Bat detectors and mist nets have traditionally been used to determine indices of abundance or activity for forest bat species based on relative numbers of captures or relative number of detections and comparing that status spatially or temporally without a means of accounting for detection probability (Hayes 2000). Without a means to quantify detection probabilities, it has not been possible to account for bias associated with non-constant detection across species, time, or space; therefore, accuracy of these indices is unknown. We estimated realistic values of (p) and (ψ) for eight of ten species commonly occurring in the Ozark region of Missouri.

An important advantage of the likelihood based method of MacKenzie et al.(2002) is its ability to model both detection probability and occupancy as functions of habitat covariates. Mackenzie et al., (2002) determined by simulation when detection probability is low (<0.15) estimates of ψ that approach 1 should be viewed cautiously. For all species except *L. noctivagans* and *L. cinereus* our estimated mean probability of detection was > 0.26. Estimates of ψ are reasonably unbiased when number of sites are between 20 and 60, detection probability is $\geq$ 0.3 and number of sampling occasions is $\geq$5 (MacKenzie et al. 2002). None of the species we evaluated were detected at less than 75 sites during 8 sampling occasions. Therefore, our estimates of probability of detection should be relatively unbiased. The precision of our estimates ([$SE_{estimate}$/estimate]) did not exceed 30% for any of the species included.

Of the eight species evaluated for site occupancy, only *L. cinereus* had a mean detection probability below 0.30 (p=0.20). Naive ψ for this species was 0.26 and p-adjusted ψ was 0.39. While this estimate may be slightly inflated due to the relatively low detection probability (MacKenzie and Bailey 2004); estimated ψ did not approach 1. We view the values for *L. cinereus* cautiously; however, this estimate of ψ may be a reasonable value considering the distribution of this species is patchy and this species is rarely captured in the study area (naïve capture rate = 0.05). This species usually forages above the canopy and is a fast flying species (Barclay 1985); characteristics that would reduce detection by either capture or detection methods when the species is actually present. In South Carolina, Menzel et al.(2000), found *L. cinereus* was detected about 20% more often than it was captured, which is very similar to the relative proportions we observed.

Local density and variation in behavior realistically affects the detection probability and site occupancy estimates for most species (Royle and Nichols 2003). Theoretically, as the population density of a specific species increases, so does the probability of detecting a single individual of that species. Species-specific detection probabilities were highly consistent for each species across sampling occasions within sites. Even greater consistency was observed when site covariates were included. Even with missing observations resulting from unequal numbers of sampling occasions for some sites, this method appeared to be robust in estimation of both p and ψ.

The highest detection probabilities were for *L. borealis, M. septentrionalis*, and *M. grisescens;* the same species captured most frequently in the study area (Amelon et al. 2000) (Figure 3). Two additional species, *E. fuscus*, which is locally abundant near more developed areas, and *P. subflavus* also had relatively high detection probabilities. The most rarely captured species, *M. sodalis, L. noctivagans* and *L. cinereus* also had the lowest detection probabilities. While additional investigation comparing within night sampling occasions to between night sampling occasions is warranted, the trade-off between temporal variation and increased detection probability may not yield improved results. Tyre et al., (2003), found maximum likelihood estimates of detection and the associated parameter coefficients of occupancy covariates will converge to their true values as numbers of sites increase. Additional investigation will be needed to determine whether it is better to increase the number of visits to a site at the expense of number of sites or vice versa when using acoustic surveys. Calculating optimum combinations of visits and sites will be the focus of future studies with the rarer species in our area.

Factors Affecting Detection Probability

Time and sample-specific covariates clearly influenced detection probability for each of the bat species evaluated. Sampling occasion was consistently important; this covariate had a RIV of 1.0 for 7 of the 8 species evaluated (NYHU, RIV=0.92). Temporal variation has been identified as an important factor in other habitat studies of bats (Kunz 1973, Hayes 1997, Elangovan et al. 2001, Broders et al. 2003). By including time-specific covariates in our estimates of detection probability, we were able to examine the patterns of species specific detection probability within a night (interval covariate) as well as within the season (date covariates).

A number of processes are likely involved with the temporal variation observed. Bats are highly mobile and can quickly move from one area to another during foraging activities. Bats use vocalizations for prey location and navigation; therefore, relative periods during the night when bats are actively feeding would strongly influence detection probability. Feeding activities for most species are highest early in the evening and in association with high levels of insect activity (Fenton 1979, Whitaker 1994, Catto et al. 1996, Lee and McCracken 2002, Agosta et al. 2003). Following feeding, many species spend various periods of time night roosting (low acoustic activity) (Anthony et al. 1981, Finn 2001, Kiser et al. 2001, Murray and Kurta 2004). Some species aerial-hawk, and may vocalize less while engaged in this activity (Fenton 1972, Wethington 1994, Mora et al. 2004). Temporal variation may be related to spatial variation in habitat patch distribution for some species (Arditi and Dacorogna 1988, van Zyll de Jong 1995, Swihart et al. 2003). Several species in this study have specialized roosting requirements, for example *M. grisescens* roosts only in caves and *E. fuscus* routinely roosts in buildings, these species must travel from these roost sites to foraging locations that may be some distance from the roost, affecting the time these species might be detected in particular locations (Tuttle 1974, Best and Hudson 1996, Wethington et al. 1996, Rabe et al. 1998, Henry et al. 2002). During the summer in Missouri, daytime (roosting) temperatures can be quite high, for species that roost in exposed locations, this may result in a negative water balance (Kunz 1980, Thomas and Cloutier 1992, Limpert and Bounds 1999, Adams 2000, Luszcz 2001), prompting species such as *L. borealis* and *P. subflavus* to seek sites with water features as soon as they become active. Sites with water features had the highest detection in the first sampling interval. Other factors that may have influenced temporal variation in detection include prey availability, weather conditions, and potentially interactions between species (Bell 1980, Zinn and Humphrey 1981, Barclay 1985, Callahan et al. 1997, Verts et al. 1999, Agosta et al. 2003, Ratcliffe and Dawson 2003, Sendor and Simon 2003, Carter et al. 2004).

While time was universally important among species as a detection covariate, other covariates varied in their importance by species, largely related to habitat adaptation as predicted by echolocation call structure. Echolocation call characteristics provide insight into associations between bat species adaptations and associated habitats (as described by species in subsequent sections). Bat echolocation calls consist of combinations of audio components. The two most common are frequency modulated (FM components), and constant frequency (CF components). Frequency modulated sounds sweep through a range of frequencies in a very short time, usually in just 1 – 5 milliseconds (ms). Calls that have low characteristic frequency, constant-frequency or quasi-constant-frequency components, and relatively long call duration are associated with bats that forage in open habitats (Fenton 1982, Norberg 1987, Kalko and Schnitzler 1993). Conversely, bats using FM produce about 10 calls per second. These bats process the returning echo of each call before sending the next one using the time delay between sound emission and the return of an echo to gain information about the target. High characteristic frequency, frequency modulated components and short duration is associated with species adapted to forage in cluttered habitats.

Covariates representing effects of clutter (reflecting or damping surfaces to sound) were important covariates for 6 of the 8 species, only *L. cinereus* and *M. lucifugus* had RIV less than 1 (0.32 and 0.03) for these covariates. While from the perspective of echolocation characteristics these two species are very different, from the perspective of relative detectability they similarly had the lowest mean detection rates (0.20, 0.31) of the eight species evaluated. In this analysis, the clutter covariates were represented by categorical variables requiring 2 covariates for reflecting surface and 2 covariates to represent damping surface. The lower importance of these covariates for these species may reflect lower amounts of information available requiring more parsimonious models (MacKenzie et al. 2006), particularly for *M. lucifugus*, a species often associated with cluttered habitats (Adams 1992). In the case of *L. cinereus*, low importance of clutter may actually reflect differences in behavior, specifically, this species forages above the canopy and in open areas (Barclay 1985), conditions that are low in clutter suggesting this covariate is less important acoustically to this species.

Of the clutter variables, presence of a large water surface positively influenced *p* for all eight species. Presence of a smaller water surface also positively affected six species (*E. fuscus, L. borealis, L. cinereus, M. septentrionalis, N. humeralis* and *P. subflavus, M. septentrionalis*). One important source of heterogeneity in detection probability, is variation in animal abundance among sites (Royle 2004). Water features are attractants for bat species for water, feeding activity and social interactions (Rydell et al. 1999, Adams et al. 2003). Water features are frequently targeted for detection of bats using both acoustic and capture methods based on similar assumptions of increased local density resulting in increased probability of detecting a single individual of that species as noted earlier (Royle and Nichols 2003). We know of no studies that have examined the relationship between bat population density and area of influence for water features. This factor clearly was an important factor in detection probability. We incorporated this variation as a covariate as described by MacKenzie et al., (2006) and Royle et al., (2005); *p* served as a random variable with heterogeneity averaged over possible values of abundance.

Effects of vegetative density on *p* were lower than expected; this may in part be due to using a categorical rather than continuous measure of vegetative density. Our classes of vegetative density had wider ranges of basal area than specific measurements; this may have resulted in higher standard errors and therefore, confidence intervals for odds ratios that included 1. However, as indicated by results for *M. septentrionalis*, a species that characteristically is associated with habitats with high levels of clutter, increased probability of detection may indicate a different relationship. While increased levels of vegetation would be expected to reduce distances that echolocation calls would be detectable (Schnitzler and Kalko 2001, Dennya 2004), the foraging behavior of this species within the vegetation may compensate for the reduction by either increased occupancy or increased duration of occupancy, and therefore, increased probability that an individual will be detected. The only species indicating negative influence on *p* from vegetative clutter (over no-clutter) was *L. borealis*. This was as expected as this species has long narrow wings adapted for flight in more open habitats rather than within dense stands. Vegetation influences were observed on *ψ* for *L. borealis* and other species not adapted for foraging in highly cluttered habitats.

Variables affecting attenuation of sound had high importance (RIV $\geq$ 0.75) for *E. fuscus, L. cinereus, M. septentrionalis,* and *N. humeralis*. These variables had less importance but measurable influence on *M. grisescens* and *P. subflavus* as well. Days since rain, a surrogate variable for relative humidity, had a positive influence on these species, while influence of temperature varied. We believe time since rain was important because it is negatively correlated with relative humidity, and relative humidity has been shown to affect the distance sound carries through air (Livengood 2003, Dennya 2004). Increasing time since rain, may arguably also influence *p* in that species may be more likely to be using sites with water features during drier periods. In the Pacific Northwest, bat detections were highest in areas of low precipitation and high temperatures (Erickson 1998). Species positively influenced by drier conditions were inconsistent in their response to influence of water features. *E. fuscus, L. cinereus* and *N. humeralis* detection probabilities were positively influenced by increasing temperature while *M. septentrionalis, M. grisescens*, and *P. subflavus* were negatively influenced. Increasing temperature has also been shown to reduce sound wave transmission (Dennya 2004). The three species positively affected by increasing temperature and *P. subflavus* each have high intensity, quasi-constant frequency echolocation calls; while the two *Myotis* species have low intensity, frequency modulated echolocation calls. The intensity of echolocation calls decreases with increasing distance because of geometric and atmospheric attenuation of sound (Schnitzler and Kalko 2001). Low intensity calls would be more attenuated at higher temperatures leading to a reduction in number of calls that would be recorded by the electronic equipment. Additionally, high attenuation would yield call files for these species that would be of poorer quality and more likely to be eliminated for identification. The higher intensity species would be less affected by attenuation of their calls. Potentially, since several species with constant frequency type calls had similar positive responses to increasing temperature, an indirect relationship, such as increased insect activity with temperature may be reflected by increase *p* (Woodson and Ellsbury 1994, Coxwell and Bock 1995, Smith and Ward 1995).

Detection probabilities for *L. borealis* and *M. grisescens* were negatively influenced over the years of the study while *L. cinereus* and *N. humeralis* were positively influenced. Influence on detection probability by year may reflect either changes in density or distribution of sampling sites (Gu and Swihart 2004, MacKenzie et al. 2006). While numbers of *L. borealis* captured in the area decreased during the period, the opposite has been observed for *M. grisescens* and *N. humeralis* (Amelon, unpublished data). Bats follow a 'K-strategy' life history (Gaisler, 1989). For long-lived species with low reproductive rates such as bats, changes over a relatively short time span (3 years) large enough to influence detectability at the population level for fairly common species would not be expected, (with the possible exception of catastrophic loss of large colonies of colonial species) (Royle and Nichols 2003). Influence by year may reflect distribution differences either from weather, study related factors of an environmental effect we did not measure. Insect populations may vary by year which may influence local distribution of bat species (Paige 1995, McCracken 1996, Turner 2001). Sites sampled in each year of this study varied to some extent by geographic location which may be reflected in the year covariate. Sites in 2001 centered on the initial focal areas while sites in subsequent years also included the expanded focal areas. Additional investigations with data from additional years may help to sort out the influence of this covariate.

Julian dates had a positive influence on *M. lucifugus* and *P. subflavus*. As with the year covariate, this may be related to differences in sampling locations based on date of sampling occasion related to sampling scheme constraints associated with simultaneous telemetry activities. *P. subflavus* was also positively influenced by days since precipitation which may reflect some relationship between precipitation and date. The slight negative influence from temperature is inconsistent with increasing detectability by date further suggesting the influence may reflect distributional differences related to sampling scheme. Yates and Muzika (2006) also found an increase in detection probability for *P. subflavus* after July 20, in a similar area of Missouri.

Spatial Scale Effects on Site Occupancy

It is well documented that factors operating at multiple scales influence habitat patterns of many wildlife species (Johnson 1980, Moilanen 1999, Manly et al. 2002, Scott et al. 2002). While studies addressing effects of landscape heterogeneity on other groups of vertebrates indicate that "area-sensitive" species may be affected by habitat patchiness (MacArthur and Wilson 1967, Aebischer et al. 1993, USFWS 1996, Donovan et al. 1997, Rushton et al. 1997, McLean et al. 1998, Orrock et al. 2000, Pollock et al. 2002). Few studies have evaluated the influence of landscape scale patterns on the abundance and distribution of highly mobile species, such as bats (Hayes 1997, Erickson 1998, O'Shea and Bogen 2003). Our results demonstrate the importance of spatial scale and landscape context as well as local site factors when evaluating forest bat habitat associations.

The most supported spatial scale varied among species; however, larger scales (8 km and 16 km) were supported for 7 of the 8 species examined. While three species (*M. grisescens* (16 km), *M. lucifugus*(8 km) and *E. fuscus* (2 km)) were strongly supported at a single scale; there was considerable model uncertainty relative to spatial scale for the other species, suggesting fairly complex processes between local and landscape factors may be involved in habitat selection of forest bat species.

Occupancy was best explained by a smaller scale (2 km) only for *E. fuscus*. While this species is well adapted to fly long distances (Lausen and Barclay 2003), it is frequently the most abundant bat near urban areas (Geggie and Fenton 1985, O'Shea et al. 1999) and is a habitat generalist (Brigham 1987, O'Shea et al. 1999, Solberg et al. 1999). While we did not identify distance to human development as a factor in our study area, highest road densities and higher percentages of non-forested habitats are associated with small rural communities in both study units. This species' occupancy associated with a relatively small landscape scale is consistent with its ability to utilize resources available within relatively short distances of their roost sites in man-made structures.

Larger spatial scales were important to *M. grisescens*, *P. subflavus*, *M. septentrionalis*, and *L. borealis*. While only *M. grisescens* was strongly supported at the 16 km scale, both *M. septentrionalis* and *P. subflavus* had considerable support for 16 km and 8 km scales. *Lasiurus borealis* had considerable support for 16 km and 2 km. Landscape selection at larger scales is consistent with known behavior of both *M. grisescens* and *L. borealis*. *M. grisescens* is a colonial species roosting in either fairly large maternity or bachelor colonies in caves along rivers in the study area. Although fairly small (8 – 11 grams) at least some individuals have been found to forage at fairly long distances from roost sites (Tuttle 1976, Grigsby 1980, Rueter et al. 1992, Best and Hudson 1996, Amelon et al. 2003). This species is associated with riverine habitats but has also been found using roads, ponds and road ruts in uplands within 5 km of rivers (LaVal and Clawson 1977, Best and Hudson 1996, Rabe et al. 1999, Amelon et al. 2003).

Geographic Effects on Site Occupancy

Geographic unit (north versus south) had some influence on each of the eight species and strongly influenced four species. All species except *N. humeralis* and *M. lucifugus* were positively associated with the southern unit. This may be related to geographic range for *M. lucifugus* but is inconsistent with range of *N. humeralis*. Additional analysis will be necessary to isolate the principal factors responsible for this as several fairly complex differences are indicated in the landscape metrics relative to geographic differences in amount and distribution of non-forested habitat and riverine systems. We suggest that spatial scale and landscape context are strongly supported as important components in evaluation of site occupancy by bats. By evaluating landscape covariates and geographic location based on the spatial scale that best fits the data we have accounted for species specific differences in selection of landscape characteristics across spatial scales and geographic locations.

Habitat Effects on Site Occupancy

HABITAT was consistently important for all species; this covariate had a RIV of 1.0 for 7 of the 8 species evaluated (MYLU, RIV=0.3). Habitat effects were consistent with morphological, behavioral and echolocation characteristics of the species we evaluated (specifics are included in subsequent sections). Differing wing structures are required by bats with different foraging behavior to minimize energetic costs. Slow flying bats have large wings and low wing loadings and bats with smaller wings have to compensate with faster speeds for their body size (Aldridge 1986, Aldridge and Rautenbach 1987). Higher aspect ratios are associated with aerodynamic efficiency and lower energy losses; species with high wing loading and low wing aspect ratio are associated with less maneuverable and more energetically expensive flight (Norberg and Raynor 1987, Norberg 1994, Norberg 1998).

Of the terrestrial habitats evaluated, bottomland forest was an important habitat for all species. Bottomland forest and aquatic habitats were associated with highest overall occupancy predictions. Predicted occupancy in bottomland forest was greatest for *M. grisescens, M. septentrionalis, M. lucifugus* and *N. humeralis* (Figure 13). Bottomland forest was second to non-forest for *L. borealis, L. cinereus, P. subflavus* and *E. fuscus*. High relative activity levels based on numbers of call files recorded have been reported for bottomland forest and aquatic habitats from the Northeast (Hart et al. 1993) (Krusic et al. 1996), Southeast (Carter et al. 1999, Menzel and Menzel 2000, Ford et al. 2005), and Northwest (Erickson and West 1999, Kalcounis and Hobson 1999, Hayes and Gruver 2000).

Occupancy estimates for *M. grisescens* were positively affected by bottomland forest, riparian and non-forest habitats. Foraging habitat for this species includes riparian areas where they fly over the water and in the protection of forest canopy (Tuttle 1974), in fact, *M. grisescens* may competitively exclude *M. sodalis* from river areas (LaVal and Clawson 1977). Throughout large portions of the Midwest, as well as in the study area, large percentages of bottomland forests have been converted to agriculture either as crop or pastureland (Hefner and Brown 1985). We included riparian type regardless of land cover type as a covariate to isolate whether the topographic association with streams or association with bottomland forest was more important. The correlation between riparian type and non-forest habitat in both units of this study ranges from 0.42 – 0.61 suggesting that this relationship may explain the higher than expected association between this species and non-forest. Many non-forested sites along riparian zones have overflow channels, fencerows or other features that retain large trees providing commuting corridors between forested areas allowing these sites to be occupied even if in lower proportions than they would be with native vegetation. While other forested and non-forest habitats were used by this species they were consistently associated with bottomland forests. Among the other forest types, no trend between forest density versus composition was clear for this species, but occupancy of immature forest was low (Figure 26).

M. septentrionalis forage opportunistically (Kunz 1973) on species of lepidopterans, coleopterans, trichopterans, and dipterans (Brack and Whitaker 2001) beneath the canopy level in forested habitats (LaVal and Clawson 1977). This species had the highest site occupancy in forested habitats, with slightly higher occupancy in bottomland forest and low to moderately stocked oak-hickory or oak-pine forests. The trend for this species suggested density rather than composition was important for this species (Figure 26). *M. septentrionalis* have short, broad wings and high maneuverability enabling them to hover and carry prey from surfaces. They are relatively slow flyers that are well adapted to hunting in cluttered environments where they often glean insects directly from foliage (Tuttle 2001).

As hypothesized, *M. lucifugus* had highest site occupancy in bottomland forest (Figure 13). In contrast to *M. grisescens*, *M. lucifugus* did not frequently occupy non-forest habitats (i.e., those associated with riparian types). *M. lucifugus* feed on aquatic insects, but may vary their foraging habits from along the edge of water sites to directly over the water sites (Belwood and Fenton 1976, Anthony et al. 1981). *M. lucifugus,* as with other *Myotis* species use FM calls and have wing morphology suggestive of a species adapted for foraging in cluttered habitats (Figure 2); however, studies have indicated this species frequently forages in more open habitats often associated with open water (Fenton 1979) and may suggest other morphological or diet based habitat selection (Patriquin and Barclay 2003). The percentage of sites where this species was present was fairly low (21%); patchy distribution of this species in our study area may in part explain lower occupancy in habitats other than bottomland forest.

N. humeralis have been found foraging in association with their roosts in bottom-land forests in Indiana (Duchamp 2000) and over riparian zones, beaver ponds, and bottomland hardwood or swamp forests in South Carolina (Menzel et al.

2001). Our results are consistent with studies of this species from other areas; bottomland forest and non-forest habitats had highest occupancy for this species followed closely by oak-hickory low density forest (Figure 13). In open habitats, *N. humeralis* produce 7 ms, FM/CF echolocation calls and they have wing morphology consistent with a species that is somewhat more adapted to flight in open habitats (Figure 2). Their high occupancy in bottomland forest and open habitats, is consistent with their morphology.

E. fuscus, *L. cinereus*, *L. borealis*, and *P. subflavus* had the highest occupancy in non-forested habitats. These species have echolocation call characteristics that include both FM and CF components; indicating they are adaptable to using cluttered and open habitats. *E. fuscus* and *P. subflavus* also exhibit wing characteristics that can be classed as intermediate between cluttered and open habitats (Figure 2).

P. subflavus had highest occupancy in bottomland forest and non-forest habitats. Among the other terrestrial habitats, occupancy was fairly consistent with somewhat increased occupancy in lower density habitats (Figure 13). *P. subflavus* frequently alternate echolocation signals depending on the level of clutter encountered. In open habitats, *P. subflavus* produces 5 ms frequency modulated-constant frequency (FM/CF) echolocation calls. Our results are consistent with other authors who have described *P. subflavus* associated with varying habitats including watercourses, (Davis and Mumford 1962), water and forest edges (Barley 1923, Blair 1935, Bowles 1975, LaVal and Clawson 1977, Schmidly et al. 1977), and foraging activity just over the top of streamside vegetation and taller streamside trees (Caire et al. 1984).

E. fuscus had highest occupancy in bottomland forest and non-forest; other terrestrial habitats had fairly similar occupancy (Figure 13). *E fuscus* are habitat generalists, foraging over land, water, edge, non-edge, open or closed canopy forest and urban or rural areas (Geggie and Fenton 1985, Furlonger et al. 1987). This species frequently uses human-made structures for roosting and may therefore, be able to exploit a variety of foraging habitats and human-induced prey concentrations (Fenton 1997). *E fuscus* produces 3 – 4.2 ms FM/CF echolocation calls typically sweeping from 48 through 27 kHz (Brigham et al. 1989); characteristics consistent with our findings of open habitat foraging.

Our results for *L. borealis* are consistent with other studies and their morphology. *Lasiurus borealis* have long narrow wings adapted for rapid, poorly maneuverable flight associated with edge habitats along fields, streams, and other openings associated with deciduous forests or park-like stands (Hickey 1987, Hickey and Fenton 1990, Acharya and Fenton 1992, Salcedo et al. 1995) *Lasiurus borealis* have preference for open stands (Thomas 1988, Sealander and Heidt 1990, Humes et al. 1999, Jung et al. 1999, Elmore et al. 2004) and areas with water (Furlonger et al. 1987, Salcedo et al. 1995, Hutchinson and Lacki 2001). *Lasiurus borealis* use long, frequency-modulated calls when hunting in open areas and short ones for close-range hunting in small forest openings (Barclay 1984, 1985, Aldridge and Brigham 1988, Brigham et al. 1989, Brigham et al. 1997, Barclay et al. 1999b, Barclay et al. 1999a).

Lasiurus cinereus had highest occupancy in non-forest. Bottomland forest was second most important; however, this species was fairly consistent in occupancy among all forested terrestrial habitats. This is consistent with findings of Menzel (2000) in Georgia where this species was found to forage above the canopy. This species was the most strongly associated with open habitats of the species we studied. *Lasiurus cinereus* primarily forages in open habitats due in part to the high wing loading and low maneuverability (Barclay 1985, 1989). As with other *Lasiurines,* wing morphology strongly places this species in the open space foraging group (Figure 2).

Aquatic habitats had a strong positive influence on occupancy. Ponds had greater influence than road ruts for all species except for *M. septentrionalis* (Figure 14). This species has been noted to drink from small water sources (Kunz 1973, Kiser 1996).

Patch and Landscape Effects on Site Occupancy

While habitat scale occupancy strongly supported importance of bottomland forest and aquatic habitats to all species; landscape scale composition of water or riparian type, while positive, was not strongly indicated. As hypothesized, site occupancy by *M. grisescens* and *M lucifugus* increased with landscape percentages of water or riparian type and bottomland forest habitat. Both local and landscape factors are important. *Lasiurus borealis* also showed a strong positive relationship to landscape percentage of riparian type but not to habitat type. Landscape or landform factors may be more important to this species than local habitat factors.

The overall percentages of water and riparian types are very low in each of these landscapes relative to the other landscape components. The low availability of this type may explain the lower magnitude of influence associated with these factors. Additionally, many areas in close proximity to streams have been cleared for pasture and are represented in the non-forest vegetative percentages. Of particular note with reference to this issue, is *M. grisescens*, a bat associated with karst regions for appropriate cave roosts and known to forage in close proximity to rivers (Tuttle 1974, 1976, LaVal and Clawson 1977, Best and Hudson 1996). Despite the land use changes in the area, we found strong support for riparian areas for this species.

Of the species we hypothesized to be "open" adapted (Figure 2, Table 3) *L. cinereus* and *L. borealis* had strong positive relationships to landscape percentages of non-forest and non-forest habitat. *N. humeralis*, while positively affected by non-forest at the habitat scale, indicated no effect at the landscape scale. *E. fuscus*, also had a strong positive effect at the local scale, but had a negative relationship with non-forest at the 2KM landscape scale. While the results for the Lasiurines suggest the importance of both local and landscape factors; the results for *N. humeralis* and *E. fuscus* suggest more complicated relationships. The lack of strong influence at the landscape level for *N. humeralis* likely relates to the difference in distribution of this species between the units and the relatively low percentage of sites occupied by this species. For *E. fuscus*, the lack of landscape effects may be explained by the difference in landscape attributes associated with the best supported spatial scale. This was the only species whose occupancy was be supported by the 2 km landscape scale. In some areas this scale had higher percentages of non-forest than the larger landscape scales. While this species may be associated with more open landscapes due to proximity of roosting sites in human-built structures, our predicted occupancy suggest there is an upper limit to the amount of non-forest in the overall landscape they will occupy (Figure 18).

Three species had a strong positive relationship to landscape percentage of pine or oak-pine forest (LACI, NYHU, and MYLU) and one a strong negative relationship (EPFU). Of these species, *L. cinereus* and *M. lucifugus* also indicated a positive relationship to pine at the site scale; suggesting the importance of a pine component at both site and landscape scales. These species have been associated with pine forest in South Carolina (Menzel et al. 2005) and Canada (Broders and Forbes 2005) *N. humeralis*, while positively affected by pine at the landscape scale, indicated a neutral effect at the site scale. In contrast, *E. fuscus*, indicated a positive effect at the site scale and a negative relationship at the landscape scale; supporting the premise they are locally generalists but may be more selective at the landscape scale.

The effect of edge factors varied considerably among species. Of the four species positively associated with increasing road density, densities up to approximately 20 m/ha had the strongest positive influence. Of the species negatively associated, densities above 10 – 15 m/ha had the strongest negative influence. The strong positive relationship observed for *E. fuscus* supports the relationship between urban or at least areas of increased human influence and their use of human-made structures. In the case of *M. septentrionalis* the positive relationship may be related to the type of road. In heavily forested landscapes, roads are primarily unpaved and often include high canopy coverage. This type of road may actually provide foraging areas for this species. The species negatively influenced by road density, with the possible exception of *M. lucifugus*, are associated with landscapes that have higher percentages of non-forest habitat. The strong decrease in occupancy around 10 m/ha may reflect the landscape association between percent of non-forest area and increased road density associated with human development and/or an increase in amount of paved roads which may not be as good as unpaved roads for foraging.

Of the four species influenced by edge density, the strong positive relationship observed for *M. septentrionalis*, as with road density, may reflect the use of canopy gaps associated with unimproved roads in an otherwise heavily forested landscape. The negative relationship with edge for *L. cinereus* may reflect use of large non-forest areas with less total edge or use of areas above the canopy.

Relationships with landscape interspersion were complex and varied by spatial scale and composition of the landscapes. Three species were negatively influenced by both interspersion of non-forest and pine forest (LABO, MYLU, MYSE); one was positively influenced by both (LACI); and the other two were inversely influenced by these factors (EPFU, NYHU). To help interpret these effects, we examined sites from the appropriate landscape scale at upper and lower ends of the range in values. Both *L. borealis* and *M. septentrionalis* (16 KM scale) declined slightly in site occupancy as interspersion/juxtaposition of non-forest increased (Figure 18); however, *L. borealis* was also influenced by higher landscape percentages of non-forest (Figures 15). While *L. borealis* declined sharply as interspersion of pine increased above 60, *M. septentrionalis* was affected only slightly (Figure 19). Site occupancy of *L. borealis* was most associated with many, well interspersed patches of non-forest and pine (Figure 27). In contrast, *M. septentrionalis* was associated with landscapes with fewer, yet still well interspersed patches of these types (Figure 28). *M. lucifugus* (8KM) while declining with increasing interspersion of both non-forest and pine; increased as landscape percentages of these types increased, particularly pine (Figures, 18, 19, 15 and 16). Considering these aspects simultaneously, *M. lucifugus* had greatest occupancy in landscapes with at least moderate amounts of pine and with non-forest in larger more contiguous patches (Figure 29).

Site occupancy of *L. cinereus* increased as interspersion/juxtaposition of non-forest and pine increased (Figures 18 and 19); and similarly increased with higher landscape percentages of non-forest and pine (Figures 15 and 16). In contrast, site occupancy decreased with non-forest edge density. We suggest *L. cinereus* is associated with landscapes with relatively high percentages of non-forest and pine where the forest patches are fairly large and well interspersed (Figure 30).

Sites occupied by *N. humeralis* increased slightly with interspersion/juxtaposition of non-forest and decreased as pine interspersion increased (Figures 18 and 19). In contrast, occupancy increased as percentage pine increased but was not changed with changes in percent non-forest or edge density (Figures 15, 20 and 16). We suggest *N. humeralis* is associated with landscapes with relatively high percentages of pine in large patches (Figure 31). Site occupancy of *E. fuscus* increased with interspersion/juxtaposition of pine and decreased as interspersion of non-forest increased (Figures 18 and 19). However, occupancy decreased as both percentage of non-forest and pine increased (Figures 15 and 16). This species was evaluated at a much smaller (2 km) scale which in part accounts for these relationships. In a reduced area, increases in non-forest and pine quickly reduce the amount of deciduous forest available. We suggest *E. fuscus* is associated with diverse landscapes of non-forest and forest types, where patches of pine forest are well interspersed and patches of non-forest are relatively large and contiguous (Figure 32).

We did not find as strong support for patch characteristics as for habitat and landscape characteristics. All of the bats species that occur within the Central Hardwood region move large distances seasonally as well as daily. We suggest patch characteristics were not important because accessibility was not constrained; specifically, water and commuting routes were easily accessible.

Implications for Conservation and Management

Effective bat conservation requires understanding the relationships among individual bat species, their environment and humans. Land managers are repeatedly faced with evaluating complex conservation issues relative to forest bat populations. These issues relate to questions involving either presence or abundance/density such as: a) is the species present (or how many individuals are present) in a management area, b) if present, what habitats are important to the species' presence (or abundance) and how does this differ between management areas and c) does management effect the presence (or abundance) of the species and if so, what is the magnitude and direction of the effect. O'Shea and Bogan (2003) identified bat conservation issues including limitations imposed by un-calibrated indices (lack of methods to estimate detection probability), the need to determine the appropriate spatial scale, and the need to consider alternatives to sampling abundance directly. Not dealing with these issues requires accepting results that are biased estimates and which may lead to erroneous inferences (Tyre et al. 2003, Gu and Swihart 2004, MacKenzie et al. 2005). Effective management requires population information to identify changes of conservation concern at a sufficiently early stage. The approach we report can be used directly to address issues and questions relating to presence of a species in an area of interest (Royle and Nichols 2003, Royle et al. 2005). By incorporating detection probability into the occupancy estimate, a measure of certainty can be associated with estimates of abundance.

The concept of area occupied by a species estimated by repeated visits and adjusted for detection probability dates back at least two decades (Gessler and Fuller 1987, Azuma et al. 1990, Zielinski and Stauffer 1996, Vojta 2005). However, it has only recently been demonstrated that presence-absence data can be used in a maximum likelihood approach to simultaneously estimate probability of detection and proportion of area occupied (Bailey et al. 2004, Royle et al. 2005, MacKenzie et al. 2006). We demonstrated that detection probabilities for forest bats in the Ozark region were consistently above 0.3 for most species. Our results were similar to those found in simulation studies and studies from other cryptic and elusive species (MacKenzie et al. 2002, Bailey et al. 2004, Wintle et al. 2004, Pellet and Schmidt

2005, MacKenzie et al. 2006). We suggest acoustic detection with adequate sampling intensity provides an unbiased estimate of site occupancy (a population metric) for forest bat species.

We view our results as a step towards a feasible and statistically rigorous option for managers and researchers to assess forest bat populations. Additional evaluation is needed relative to trade-offs between more sites or more sampling occasions, differences due to geographic area, and relationships between relative density and detection probability to improve estimates of site occupancy (particularly for species detected at levels below 0.3). With additional work and evaluation of the newest modeling approaches that incorporate changes in vital rates (local extinction and colonization probabilities)(MacKenzie et al. 2003), multiple season models (MacKenzie et al. 2006), and false positive or negative errors (Royle and Link 2006), this approach may provide a means to compare results between studies both spatially and temporally.

We have demonstrated that estimates of detection probability and site occupancy can be obtained using relatively inexpensive methods within the constraints of the model assumptions. By using an acoustic detection approach for area assessments of forest bat presence and habitat use, funds saved can be directed towards more expensive methods (capture or radiotelemetry) and important demographic questions in specific locations where rare or endangered species are detected.

Information gained from this research highlights several important considerations for bat conservation and landscape management. Landscape scales important to habitat use by temperate bat species are relatively large; this emphasizes the need to evaluate habitat factors and management effects in a broader context even if roosting factors are evaluated at a smaller scale. The importance of habitat type to both detection probability and occupancy indicates the importance of simultaneously accounting for both processes when assessing distribution or impacts from management activities. Land managers should employ carefully designed monitoring approaches to evaluate the effects of management activities at appropriate spatial and temporal scales.

The importance of riparian features, aquatic habitats and bottomland forests to the entire community of bat species suggests the importance of maintaining these habitats and restoring forested corridors associated with streams and rivers. Landscape context is an important management consideration, even species adapted to non-forest habitats and anthropogenic roosts use landscapes with high percentages of forest. In increasingly human-dominated landscapes, maintaining a forested canopy over large portions of the landscape may be important to conservation of bat populations. While no single forest structure or composition was optimal for all species; each species used forested habitats and each species represented in this study were individually associated with habitats for which they are best adapted. Most species consistently occupied forests with lower basal area over those with higher basal area; indicating land management practices that maintain a forested canopy while decreasing basal area (such as thinning, uneven-aged management, savanna restoration and prescribed fire) are important to bat conservation. In areas of contiguous, mature canopy, land management practices including individual tree or small group selection would reduce understory and create a mosaic of edge thus enhancing foraging habitat. Savanna and woodland habitats would have historically supplied this type of habitat; management activities that restore or enhance these habitats would provide important foraging locations.

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Table 1: Landscape characteristics of Southern and Northern units included in a study of habitat occupancy by forest bats in the Ozark Highlands of Missouri 2001-2003.

	South Unit[a]	North Unit[b]
Drainage area	23,590 km2	37,720 km^2
<u>Percent Landscape Composition:</u>		
Non-forest	37.8	48.7
Deciduous Forest and Woodland	49.7	41.1
Mixed Deciduous/Coniferous Forest and Woodland	11.2	8.8
Bottomland Hardwood Forest	0.2	0.5
Water, Marsh, Swamp	1.2	0.9

a - South Unit refers to watersheds south of Ozark Divide draining towards Mississippi River and Arkansas

b - North Unit refers to watersheds north of Ozark Divide draining towards Missouri River

Table 2: Generalized hypotheses, model names, variables, and variable descriptions for factors affecting the probability of detecting bat species with acoustic detectors in the Missouri Ozark Highlands 2001-2003.

Probability of Detection (*p*)			
Generalized Hypothesis	Model	Variables	Description
Attenuation	ATTEN	tc	Mean temperature in Celcius recorded during sampling interval
		rain	Days since precipitation event
Vegetative Clutter	CLUTTER	cl1	Clutter classification for water as a reflecting surface (large surface)
		cl2	Clutter classification for water as a reflecting surface (small surface)
		cl3	Clutter classification for vegetation density as damping surface (low basal area)
		cl4	Clutter classification for vegetation density as damping surface (high basal area)
Time	INTERVAL	v1	Sampling occasion 1: 18:45 – 20:14
		v2	Sampling occasion 2: 20:15 – 21:44
		v3	Sampling occasion 3: 21:45 – 23:14
		v4	Sampling occasion 4: 23:15 – 00:44
		v5	Sampling occasion 5: 00:45 – 02:14
		v6	Sampling occasion 6: 02:15 – 03:44
		v7	Sampling occasion 7: 03:45 – 05:14
		v8	Sampling occasion 8: 05:15 – 06:44
	DATE	jul	Julian date
	YEAR	year	Year of study

Table 3: Wing morphological characteristics for species likely to be encountered in Central Hardwood Region of Missouri arranged from species adapted for cluttered habitats to species adapted for open habitats. From: Norberg and Raynor, 1987.

							AR	WL	SI	Call Type
Species	Mass (kg)	wingspan	wing area	aspect ratio	wing loading	tip shape				
myso	0.0068	0.234	0.0102	5.4	6.5	5.56	--	-	++	FM
myse	0.0070	0.241	0.0101	5.8	6.8	2.24	-	-	.	FM
mylu	0.0071	0.237	0.0093	6.0	7.5	3.20	-	.	+	FM
pisu	0.0051	0.237	0.0090	6.2	5.6	2.05	-	--	.	FM/QCF
mygr	0.0104	0.281	0.0124	6.4	8.2	1.79	.	.	.	FM/QCF/FM
lano	0.0106	0.289	0.0127	6.6	8.2	1.68	.	.	.	FM/CF(QCF)
epfu	0.0159	0.325	0.0166	6.4	9.4	1.09	.	.	-	FM/CF(QCF)
nyhu	0.0096	0.244	0.0088	6.8	10.7	1.01	+	+	--	FM/CF(QCF)
labo	0.0167	0.281	0.0117	6.7	14.0	1.26	+	++	-	FM/CF(QCF)
laci	0.0330	0.398	0.0196	8.1	16.5	1.60	++	++	.	FM/CF

(myso = *Myotis sodalis*; myse = *Myotis septentrionalis*; mylu = *Myotis lucifugus*; myle = *Myotis leibii*; pisu = *Pipistrellus subflavus*; mygr = *Myotis grisescens*; epfu = *Eptesicus fuscus*; lano = *Lasionycteris noctivagans*; labo = *Lasiurus borealis*; nyhu = *Nycticeius humeralis*; laci = *Lasiurus cinereus*. AR=aspect ratio relative index, WL=wingloading relative index and SI=wing tip shape relative index; - = low, . = neutral, + = high).

Table 4: Generalized hypotheses, model names, variables and variable descriptions representing covariates affecting probability of site occupancy with hypothesized ranks of categorical effects or direction of continuous variable effects for 10 bat species in the Ozark Highlands of Missouri.

Probability of Site Occupancy (ψ)

				Species									
Generalized Hypothesis	Model	Variables	Description	EP FU	LA BO	LA CI	LA NO	MY GR	MY LU	MY SE	MY SO	NY HU	PI SU
Geography Hypothesis	UNIT	unit	Geographic location relative to Ozark Divide within study area; North=N South=S; .= neutral	.	.	.	S	.	.	S	N	.	S
Habitat Characteristics Hypothesis	HABITAT	opm	Pine and Oak/Pine: > 75% stocking; > 30% pine	5	5	5	4	6	4	4	4	5	6
		opw	Pine and Oak/Pine: < 75% stocking; > 30% pine	3	4	3	3	3	2	3	2	3	3
		ohm	Oak and Oak/Hickory: >75% stocking	6	6	7	6	5	5	5	5	6	5
	(terrestrial)	ohw	Oak and Oak/Hickory: <75% stocking	4	3	4	5	2	3	2	3	4	4
		blhd	Mixed hardwoods + lowland topographic position	2	2	2	2	1	1	1	1	1	1
		imm	Immature forest less than 20 yrs old	7	7	6	7	7	7	7	7	7	7
		shg	Non-forest: open grasslands of warm or cool season grass; shrubland with less than 30% woody vegetation	1	1	1	1	4	6	6	6	2	2
		pond	Pond or large body of water	+	+	+	+	+	+	+	+	+	+
	(aquatic)	rr	Standing water along road or trail	.	.	.	.	+	+	+	+	.	.
		noh2o	No water feature	-	-	-	-	-	-	-	-	-	-
Patch Characteristics Hypothesis	PATCH	dh2o	Distance to nearest permanent water source (km)	.	.	.	.	–	–	.	.	.	-
		droad	Distance to nearest road or trail (km)	–	–	–	.	+	+	+	+	.	.
		dedge	Distance to nearest edge between forested stand and opening (km)	–	–	–	.	.	.	.	.	-	-
		patcharea	Patchsize (km2)	.	.	.	.	.	+	+	+	.	.

Table 4: continued

Probability of Site Occupancy (ψ)

				Species									
Generalized Hypothesis	Model	Variables	Description	EP FU	LA BO	LA CI	LA NO	MY GR	MY LU	MY SE	MY SO	NY HU	PIS U
Landscape Composition Hypothesis	LAND-SCAPE	%op	Percent of landscape in pine or oak/pine vegetation types	.	.	+	+	.	.	+	+	+	.
		%open	Percent of landscape in non-forested vegetation types	+	+	+	.	.	–	–	–	+	+
		%ripar	Percent of landscape within 30 meters of permanent streams	.	+	+	.	+	.	.	+	.	+
		%water	Percent of landscape in stream, lake, pond, marsh or wetland types	.	+	.	.	+	+	.	+	.	+
Landscape Diversity Hypothesis	EDGE	rdden	Road density in meters per hectare	+	+	+	.	.	–	–	–	.	.
		ijioak-pine	Interspersion/juxtaposition of pine and oak/pine types	+	+	+	+	.	+	+	+	+	.
		ijiopen	Interspersion/juxtaposition of non-forest types	+	+	+	.	.	–	–	–	+	+
		cwed-open	Contrast weighted edge of non-forest	+	+	+	.	.	–	–	–	+	+

Ranks: 1 = Most likely occupied; + = positive; - = negative; . = neutral.;

Table 5: Minimum (MIN), maximum (MAX) mean (MEAN) and standard error (SE) values of landscape metrics for northern and southern units by spatial scale. dh2o= distance to water (m), droad=distance to road or trail (m), dedge=distance to hard edge (m), patcharea= size of patch (ha), k2-k16 indicates 2 km – 16 km radius spatial scale, rdden= road density (m/ha), iji= interspersion juxtaposition, cwedopen = contrast weighted edge of non-forest

	South				North			
VARIABLE CODE	MIN	MAX	MEAN	SE	MIN	MAX	MEAN	SE
dh2o	0.2	1111.1	178.0	214.9	0.1	857.0	211.0	190.0
droad	0.3	292.2	46.8	56.7	0.1	913.5	56.6	100.0
dedge	0.5	2389.4	374.8	512.8	0.0	2642.5	114.5	249.8
patcharea	0.0	2751.5	589.9	780.4	0.0	3000.0	1547.5	1370.5
k16 %oakpine	2.1	28.8	13.4	7.7	2.5	16.4	11.6	3.3
k16 %open	12.2	41.1	26.7	7.8	26.0	57.4	41.8	9.2
k16 %riparian	0.6	2.2	1.4	0.4	1.0	2.0	1.4	0.2
k16 %water	3.4	6.1	4.0	0.6	3.2	4.8	3.6	0.4
rdden16k	7.5	13.5	10.6	1.2	11.4	16.4	13.7	0.9
k16 ijioakpine	49.3	71.0	63.0	7.2	59.2	70.4	64.3	3.5
k16 ijiopen	53.3	77.7	68.8	4.2	55.2	70.4	64.7	2.4
k16 cwedopen	38.5	55.3	46.2	4.2	49.3	58.5	53.4	1.8
k8 %oakpine	3.4	44.4	17.4	9.2	1.6	32.8	12.9	7.3
k8 %open	10.5	42.7	23.5	7.5	21.4	64.5	35.8	9.4
k8 %riparian	0.7	3.8	1.8	0.7	0.6	3.1	2.1	0.5
k8 %water	3.1	8.3	4.2	1.2	2.9	5.1	3.9	0.4
rdden8k	5.3	12.6	9.5	1.5	10.3	17.6	13.9	1.9
k8 ijioakpine	46.9	74.6	65.2	7.3	52.8	75.4	61.9	6.8
k8 ijiopen	57.4	77.9	70.9	5.0	56.1	75.1	63.6	4.5
k8 cwedopen	39.3	60.6	46.7	3.8	47.7	60.8	55.6	3.5
k4 %oakpine	3.5	50.2	20.4	11.1	1.2	50.0	14.2	9.9
k4 %open	8.8	48.1	21.3	8.7	14.3	64.7	31.5	10.7
k4 %riparian	0.0	4.7	2.0	1.3	0.3	3.6	2.3	0.8
k4 %water	2.9	14.5	4.6	2.6	2.5	6.2	3.9	0.6
rdden4k	6.1	13.6	9.0	1.9	9.5	24.8	14.1	3.9
k4 ijioakpine	46.8	80.3	66.1	6.9	50.9	78.0	62.0	8.0
k4 ijiopen	54.5	84.7	70.2	7.9	43.3	86.2	61.1	8.1
k4 cwedopen	32.1	67.1	47.5	5.6	41.5	72.7	60.4	8.1
k2 %oakpine	2.3	65.4	23.9	14.1	0.8	57.4	16.7	11.2
k2 %open	5.9	49.6	17.8	8.8	6.7	67.3	26.7	11.2
k2 %riparian	0.0	7.3	2.5	1.8	0.0	7.4	2.9	1.6
k2 %water	1.6	31.6	5.3	5.2	1.7	8.3	4.3	0.9
rdden2k	2.6	18.3	9.1	2.7	4.3	43.9	11.8	5.4
k2 ijioakpine	40.4	93.1	69.5	9.6	41.8	89.3	63.5	9.1
k2 ijiopen	52.0	90.9	71.5	11.2	32.5	94.5	61.3	9.7
k2 cwedopen	26.1	69.1	47.9	8.9	31.1	87.6	64.4	14.7

Table 6: Mean detection probability (*p*), naïve site occupancy estimate, *p*-adjusted site occupancy with associated standard error (SE), and capture rate for sites also sampled with mist nets.

Species[a]	Estimated Detection Probability (*p*) (Mean)	Naïve Site Occupancy	*p*-adjusted Site Occupancy	SE *p*-adjusted Site Occupancy	Capture Rate[b]
EPFU	0.36	0.45	0.51	0.05	0.20
LABO	0.64	0.74	0.75	0.02	0.62
LACI	0.20	0.26	0.39	0.03	0.05
LANO	0.13	0.04	0.11	0.03	0.04
MYGR	0.41	0.33	0.36	0.02	0.29
MYLU	0.31	0.20	0.24	0.06	0.10
MYSE	0.48	0.70	0.73	0.03	0.60
MYSO	0.26	0.06	0.07	0.02	0.03
NYHU	0.35	0.20	0.27	0.02	0.10
PISU	0.35	0.32	0.35	0.03	0.29

a –Species: *Eptesicus fuscus*, EPFU; *Lasiurus borealis,* LABO; *Lasiurus cinerius*, LACI; *Lasionycteris noctivagans*, LANO; *Myotis grisescens*, MYGR; *M. lucifugus,* MYLU; *M. septentrionali*s, MYSE; *M. sodalis*, MYSO; *Nycticeius humeralis*, NYHU; and *Pipistrellus subflavus*, PISU.

b - Based on unpublished capture data collected 1997 to 2004. Amelon, North Central Research Station

Table 7. Probability of detection (p) best model set (Akaike weight ≥ 0.90 in descending order) including number of parameters (NP) and selection criteria for 8 species of forest bats in the Ozark Region of Missouri, 2001-2003.

Model by species	NP	AIC	Model Likeli-hood	delta AIC	AIC wgt
Eptesicus fuscus					
p(INTERVAL + ATTEN + CLUTTER + YEAR)	24	1732.55	0.1132	0	0.337
p(INTERVAL + ATTEN + CLUTTER)	23	1732.57	0.1121	0.02	0.333
p(INTERVAL + ATTEN + CLUTTER + JUL)	24	1733.73	0.0628	1.18	0.187
p(INTERVAL + ATTEN + CLUTTER + YEAR + JUL)	25	1734.28	0.0477	1.73	0.142
cumulative model weight					0.998
Lasiurus borealis					
p(INTERVAL + CLUTTER + YEAR)	22	2336.32	0.2655	0	0.515
p(INTERVAL + CLUTTER + YEAR + JUL)	23	2337.34	0.1594	1.02	0.309
p(INTERVAL + ATTEN + CLUTTER + YEAR)	24	2339.24	0.0617	2.92	0.120
cumulative model weight					0.944
Lasiurus cinerius					
p(INTERVAL + ATTEN + YEAR)	20	1054.06	0.517	0	0.719
p(INTERVAL + ATTEN + CLUTTER + YEAR + JUL)	25	1056.9	0.125	2.84	0.174
p(INTERVAL + ATTEN + CLUTTER + YEAR)	24	1057.89	0.0762	3.83	0.106
cumulative model weight					0.999
Myotis grisescens					
p(INTERVAL + ATTEN + CLUTTER + YEAR)	24	1397.16	0.1593	0	0.399
p(INTERVAL + ATTEN + CLUTTER + YEAR + JUL)	25	1397.91	0.1095	0.75	0.274
p(INTERVAL + CLUTTER + YEAR)	22	1398.85	0.0684	1.69	0.172
p(INTERVAL + CLUTTER)	21	1400.88	0.0248	3.72	0.062
cumulative model weight					0.907
Myotis lucifugus					
p(INTERVAL + JUL)	18	963.01	0.0532	0	0.231
p(INTERVAL)	17	963.68	0.0381	0.67	0.165
p(INTERVAL + ATTEN)	19	963.97	0.0329	0.96	0.143
p(INTERVAL + YEAR)	18	964.29	0.0281	1.28	0.122
p(INTERVAL + ATTEN + JUL)	20	964.59	0.0241	1.58	0.105
p(INTERVAL + YEAR + JUL)	19	965.01	0.0196	2	0.085
p(INTERVAL + ATTEN + YEAR)	20	965.23	0.0175	2.22	0.076
cumulative model weight					0.927

Table 7. Model Selection (*p*) (continued)

Model	NP	AIC	Model Likeli-hood	delta AIC	AIC wgt
Myotis septentrionalis					
p(INTERVAL + ATTEN + CLUTTER + YEAR + JUL)	25	2429.73	0.3213	0	0.567
p(INTERVAL + ATTEN + CLUTTER)	23	2432.97	0.0636	3.24	0.112
p(INTERVAL + CLUTTER + JUL)	22	2433	0.0626	3.27	0.111
p(INTERVAL + ATTEN + CLUTTER + YEAR)	24	2433.78	0.0424	4.05	0.075
p(INTERVAL + CLUTTER)	21	2434.28	0.033	4.55	0.058
cumulative model weight					0.923
Nycticeius humeralis					
p(INTERVAL + ATTEN + CLUTTER + YEAR)	24	949.31	0.4156	0	0.645
p(INTERVAL + ATTEN + CLUTTER + YEAR + JUL)	25	951.27	0.156	1.96	0.242
p(ATTEN + CLUTTER + YEAR)	17	954.26	0.035	4.95	0.054
cumulative model weight					0.941
Pipistrellus subflavus					
p(INTERVAL + ATTEN + CLUTTER + YEAR + JUL)	25	1236.49	0.9052	0	0.951
cumulative model weight					0.951

Table 8: Model-averaged parameter estimates, odds ratios with unconditional standard error (SE), and 95% confidence interval for factors explaining probability of detection of forest bats in the Ozark Region of Missouri, 2001-2003. UCL= Odds ratio upper confidence limit LCL= lower confidence limit)

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Eptesicus fuscus 2 KM	V 1	-6.828	1.260	0.001	0.000	0.013
	V 2	-2.949	0.721	0.052	0.013	0.215
	V 3	-2.486	0.701	0.083	0.021	0.329
	V 4	-2.936	0.697	0.053	0.014	0.208
	V 5	-3.119	0.690	0.044	0.011	0.171
	V 6	-3.212	0.690	0.040	0.010	0.156
	V 7	-2.305	0.683	0.100	0.026	0.381
	V 8	-3.507	0.704	0.030	0.008	0.119
	tc	0.070	0.020	1.072	1.031	1.114
	rain	0.077	0.033	1.080	1.011	1.153
	cl1	0.721	0.166	2.057	1.486	2.847
	cl2	-0.403	0.430	0.668	0.288	1.553
	cl3	-0.225	0.222	0.799	0.517	1.234
	cl4	0.083	0.177	1.087	0.768	1.537
	year	0.244	0.160	1.276	0.933	1.746
	date	-0.001	0.001	0.999	0.997	1.002
Lasiurus borealis 16 KM	V 1	1.916	6.791	0.499	2.551	18.075
	V 2	4.484	88.593	0.466	35.519	220.972
	V 3	4.425	83.473	0.465	33.525	207.838
	V 4	4.223	68.228	0.463	27.549	168.972
	V 5	3.667	39.118	0.458	15.941	95.994
	V 6	3.838	46.426	0.463	18.726	115.103
	V 7	3.792	44.349	0.463	17.905	109.847
	V 8	3.707	40.735	0.463	16.444	100.913
	tc	0.001	0.004	1.001	0.994	1.009
	rain	-0.004	0.009	0.996	0.979	1.014
	cl1	0.950	0.148	2.586	1.933	3.46
	cl2	0.056	0.258	1.057	0.638	1.752
	cl3	-0.727	0.177	0.483	0.342	0.684
	cl4	-0.644	0.154	0.525	0.388	0.71
	year	-1.029	0.153	0.357	0.265	0.482
	date	0.001	0.001	1.001	0.999	1.003

Table 8: continued.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Lasiurus cinerius 8 KM	V 1	-33.930	0	0	0	0
	V 2	-7.411	1.245	0.001	0	0.007
	V 3	-7.181	1.224	0.001	0	0.008
	V 4	-7.693	1.228	0	0	0.005
	V 5	-7.928	1.23	0	0	0.004
	V 6	-7.850	1.227	0	0	0.004
	V 7	-7.342	1.215	0.001	0	0.007
	V 8	-8.407	1.253	0	0	0.003
	tc	0.122	0.050	1.129	1.024	1.246
	rain	0.078	0.027	1.081	1.025	1.141
	cl1	1.548	0.352	2.703	1.358	4.384
	cl2	-0.150	0.427	0.861	0.373	1.986
	cl3	0.004	0.093	1.004	0.836	1.205
	cl4	0.089	0.162	1.093	0.796	1.502
	year	1.657	0.352	4.664	2.336	9.314
	date	-0.002	0.003	0.998	0.992	1.004
Myotis griscesens 16 KM	V 1	-1.100	0.969	0.333	0.050	2.227
	V 2	1.644	0.758	5.178	1.171	22.895
	V 3	1.396	0.737	4.039	0.953	17.117
	V 4	1.101	0.732	3.008	0.716	12.636
	V 5	1.073	0.725	2.924	0.706	12.114
	V 6	1.304	0.720	3.682	0.898	15.093
	V 7	0.814	0.719	2.256	0.551	9.240
	V 8	0.329	0.741	1.390	0.325	5.943
	tc	-0.032	0.021	0.968	0.929	1.009
	rain	-0.070	0.042	0.932	0.859	1.012
	cl1	0.115	0.207	1.121	0.747	1.683
	cl2	-1.125	0.615	0.325	0.097	1.084
	cl3	0.481	0.284	1.618	0.927	2.824
	cl4	0.858	0.226	2.358	1.513	3.676
	year	-0.457	0.177	0.633	0.447	0.896
	date	0.002	0.003	1.002	0.997	1.007

Table 8: continued.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Myotis lucifugus 8 KM	V 1	-28.945	0	5574821.2	0	.
	V 2	-1.344	0.261	25111.756	0	.
	V 3	-1.219	0.296	0.947	0.046	1.890
	V 4	-1.440	0.237	0.944	0.037	1.507
	V 5	-1.624	0.197	0.943	0.031	1.252
	V 6	-1.522	0.218	0.946	0.034	1.393
	V 7	-1.543	0.214	0.956	0.033	1.393
	V 8	-2.264	0.104	0.996	0.015	0.732
	tc	0.013	1.013	0.099	0.834	1.229
	rain	0.021	1.021	0.036	0.951	1.096
	cl1	0	1	0	1	1
	cl2	0	1	0	1	1
	cl3	0	1	0	1	1
	cl4	0	1	0	1	1
	year	-0.071	0.931	0.121	0.735	1.180
	date	0.003	1.003	0.021	0.963	1.045
Myotis septentrionalis 16 KM	V 1	-4.447	0.786	0.012	0.003	0.055
	V 2	-1.060	0.575	0.346	0.112	1.070
	V 3	-0.763	0.563	0.466	0.155	1.406
	V 4	-1.294	0.555	0.274	0.092	0.813
	V 5	-1.556	0.550	0.211	0.072	0.620
	V 6	-1.477	0.552	0.228	0.077	0.674
	V 7	-1.765	0.553	0.171	0.058	0.506
	V 8	-2.489	0.570	0.083	0.027	0.254
	tc	-0.043	0.015	0.957	0.930	0.986
	rain	0.076	0.027	1.078	1.023	1.137
	cl1	0.796	0.142	2.217	1.678	2.929
	cl2	0.294	0.303	1.342	0.741	2.429
	cl3	0.736	0.221	2.088	1.355	3.219
	cl4	0.958	0.211	2.608	1.723	3.946
	year	-0.056	0.131	0.945	0.731	1.222
	date	0.007	0.001	1.007	1.006	1.008

Table 8: continued.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Nycticeius humeralis 8 KM	V 1	-7.865	1.510	0	0	0.007
	V 2	-5.940	1.639	0.003	0	0.065
	V 3	-5.737	1.604	0.003	0	0.075
	V 4	-5.840	1.610	0.003	0	0.068
	V 5	-6.431	1.655	0.002	0	0.041
	V 6	-6.087	1.624	0.002	0	0.055
	V 7	-5.780	1.593	0.003	0	0.070
	V 8	-5.681	1.594	0.003	0	0.078
	tc	0.083	0.030	1.087	1.025	1.153
	rain	0.085	0.053	1.089	1	1.209
	cl1	0.849	0.258	2.337	1.410	3.872
	cl2	-2.689	0.627	0.068	0.020	0.232
	cl3	0.100	0.345	1.105	0.562	2.175
	cl4	0.145	0.271	1.156	0.680	1.967
	year	1.296	0.353	3.656	1.829	7.308
	date	0	0.001	1	0.998	1.001
Pipistrellus subflavus 16 KM	V 1	-5.982	1.049	0.003	0	0.020
	V 2	-3.346	0.822	0.035	0.007	0.176
	V 3	-3.617	0.801	0.027	0.006	0.129
	V 4	-4.172	0.802	0.015	0.003	0.074
	V 5	-4.240	0.799	0.014	0.003	0.069
	V 6	-4.266	0.798	0.014	0.003	0.067
	V 7	-3.636	0.788	0.026	0.006	0.123
	V 8	-4.825	0.820	0.008	0.002	0.040
	tc	-0.081	0.024	0.922	0.879	0.968
	rain	0.118	0.045	1.125	1.029	1.229
	cl1	1.084	0.206	2.957	1.974	4.430
	cl2	-0.186	0.901	0.830	0.142	4.851
	cl3	0.454	0.305	1.574	0.866	2.862
	cl4	0.879	0.237	2.407	1.513	3.829
	year	0.210	0.187	1.234	0.856	1.778
	date	0.017	0.001	1.017	1.015	1.019

Table 9. Spatial scale model selection criteria including number of parameters (NP) and selection criteria for 2 kilometer (2KM), 4 kilometer (4KM), 8 kilometer (8KM), and 16 kilometer (16KM) spatial scales for 8 species of forest bats in the Ozark Region of Missouri, 2001-2003.

Model	NP	AIC	Model Likeli-hood	delta AIC	AIC wgt
E. fuscus					
ψ(2KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1733.24	0.957	0.00	0.978
ψ(4KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1741.00	0.020	7.76	0.020
ψ(16KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1746.16	0.002	12.92	0.002
ψ(8KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1752.23	0.000	18.99	0.000
ψ(.),*p*(.)	2	1899.68	0.000	166.44	0.000
***L. boreali*s**					
ψ(16KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,YEAR)	34	2332.70	0.373	0.00	0.611
ψ(2KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,YEAR)	34	2333.88	0.207	1.18	0.339
ψ(4KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,YEAR)	34	2337.71	0.031	5.01	0.050
ψ(8KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,YEAR)	34	2345.39	0.001	12.69	0.001
ψ(.),*p*(.)	2	2564.65	0.000	231.95	0.000
L. cinerius					
ψ(8KM$_{\text{GLOBAL}}$),*p*(INTERVAL,ATTEN,YEAR)	32	1061.57	0.321	0.00	0.567
ψ(16KM$_{\text{GLOBAL}}$),*p*(INTERVAL,ATTEN,YEAR)	32	1063.76	0.108	2.19	0.190
ψ(4KM$_{\text{GLOBAL}}$),*p*(INTERVAL,ATTEN,YEAR)	32	1064.08	0.092	2.51	0.162
ψ(2KM$_{\text{GLOBAL}}$),*p*(INTERVAL,ATTEN,YEAR)	32	1065.44	0.046	3.87	0.082
ψ(.),*p*(.)	2	1149.47	0.000	87.90	0.000
***M. grisescen*s**					
ψ(16KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1387.55	0.918	0.00	0.958
ψ(8KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1393.95	0.037	6.40	0.039
ψ(2KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1399.58	0.002	12.03	0.002
ψ(4KM$_{\text{GLOBAL}}$),*p*(INTERVAL,CLUTTER,ATTEN,YEAR)	36	1402.75	0.001	15.20	0.001
ψ(.),*p*(.)	2	1512.02	0.000	124.47	0.000
M. lucifugus					
ψ(8KM$_{\text{GLOBAL}}$),*p*(INTERVAL,YEAR)	30	954.52	0.996	0.00	0.998
ψ(4KM$_{\text{GLOBAL}}$),*p*(INTERVAL,YEAR)	30	968.39	0.001	13.87	0.001
ψ(2KM$_{\text{GLOBAL}}$),*p*(INTERVAL,YEAR)	30	969.01	0.001	14.49	0.001
ψ(16KM$_{\text{GLOBAL}}$),*p*(INTERVAL,YEAR)	30	972.46	0.000	17.94	0.000
ψ(.),*p*(.)	2	985.42	0.000	30.90	0.000
M. septentrionalis					
ψ(16KM$_{\text{GLOBAL}}$),*p*(GLOBAL)	37	2422.95	0.498	0.00	0.706
ψ(8KM$_{\text{GLOBAL}}$),*p*(GLOBAL)	37	2425.42	0.145	2.47	0.205
ψ(4KM$_{\text{GLOBAL}}$),*p*(GLOBAL)	37	2428.17	0.037	5.22	0.052
ψ(2KM$_{\text{GLOBAL}}$),*p*(GLOBAL)	37	2428.84	0.026	5.89	0.037
ψ(.),*p*(.)	2	2647.96	0.000	225.01	0.000

Table 9 (con't). Model Selection for Spatial Scale Models

Model	NP	AIC	Model Likeli-hood	delta AIC	AIC wgt
N. humeralis					
$\psi(8KM_{GLOBAL}),p(INTERVAL,CLUTTER,ATTEN,YEAR)$	36	950.78	0.269	0.00	0.519
$\psi(2KM_{GLOBAL}),p(INTERVAL,CLUTTER,ATTEN,YEAR)$	36	952.25	0.129	1.47	0.249
$\psi(16KM_{GLOBAL}),p(INTERVAL,CLUTTER,ATTEN,YEAR)$	36	953.18	0.081	2.40	0.156
$\psi(4KM_{GLOBAL}),p(INTERVAL,CLUTTER,ATTEN,YEAR)$	36	954.62	0.040	3.84	0.076
$\psi(.),p(.)$	2	1030.21	0.000	79.43	0.000
P. subflavus					
$\psi(16KM_{GLOBAL}),p(GLOBAL)$	37	1245.34	0.156	0.00	0.395
$\psi(8KM_{GLOBAL}),p(_{GLOBAL})$	37	1245.43	0.149	0.09	0.378
$\psi(4KM_{GLOBAL}),p(_{GLOBAL})$	37	1246.93	0.071	1.59	0.178
$\psi(2KM_{GLOBAL}),p(_{GLOBAL})$	37	1249.52	0.019	4.18	0.049
$\psi(.),p(.)$	2	1357.41	0.000	112.07	0.000

Table 10. Probability of site occupancy (ψ) best model set (Akaike weight $\geq$ 0.90 in descending order) including number of parameters (NP) and selection criteria for 8 species of forest bats in the Ozark Region of Missouri, 2001-2003. Each model includes $p(_{\text{BEST}})$ for the specified species and spatial scale.

Model	NP	AIC	Model Likelihood	delta AIC	AIC wgt
***Eptesicus fuscus* 2K**					
ψ(HABITAT + LANDSCAPE+ EDGE)	32	1727.65	0.38	0	0.619
ψ(HABITAT + LANDSCAPE+ EDGE + UNIT)	33	1729.44	0.16	1.79	0.253
ψ(HABITAT)	24	1732.55	0.03	4.9	0.053
Cumulative AIC weight					0.920
***Lasiurus borealis* 16K**					
ψ(HABITAT + PATCH + LANDSCAPE + EDGE + UNIT)	35	2326.82	0.28	0	0.534
ψ(HABITAT + LANDSCAPE + EDGE + UNIT)	31	2328	0.16	1.18	0.309
ψ(HABITAT + PATCH + LANDSCAPE + EDGE)	34	2331.14	0.03	4.32	0.067
Cumulative AIC weight					0.920
***Lasiurus cinerius* 8K**					
ψ(HABITAT + EDGE)	24	1067.72	0.31	0	0.555
ψ(HABITAT + EDGE + UNIT)	25	1069.71	0.11	1.99	0.229
ψ(HABITAT + LANDSCAPE)	28	1071.87	0.04	4.15	0.145
Cumulative AIC weight					0.930
***Myotis grisescens* 16k**					
ψ(HABITAT + PATCH + LANDSCAPE + EDGE)	36	1385.55	0.13	0	0.360
ψ(HABITAT + PATCH + LANDSCAPE + EDGE + UNIT)	37	1386.69	0.07	1.14	0.200
ψ(HABITAT + PATCH + LANDSCAPE + UNIT)	33	1387.56	0.05	2.01	0.130
ψ(HABITAT + LANDSCAPE + EDGE)	31	1388.24	0.03	2.69	0.090
ψ(HABITAT + LANDSCAPE + UNIT)	29	1388.59	0.03	3.04	0.080
ψ(HABITAT + LANDSCAPE + EDGE + UNIT)	32	1389.12	0.02	3.57	0.060
Cumulative AIC weight					0.920
***Myotis lucifugus* 8k**					
ψ(PATCH + LANDSCAPE + EDGE) +	22	952.83	0.22	0	0.470
ψ(HABITAT + PATCH + LANDSCAPE + EDGE)	30	954.52	0.09	1.69	0.200
ψ(PATCH + LANDSCAPE + EDGE + UNIT)	23	954.8	0.08	1.97	0.170
ψ(HABITAT + PATCH + LANDSCAPE + EDGE + UNIT)	31	956.48	0.04	3.65	0.080
Cumulative AIC weight					0.920

Table 10. Probability of site occupancy (ψ) best model set (continued)

Model	NP	AIC	Model Likelihood	delta AIC	AIC wgt
Myotis septentrionalis 16k					
ψ(HABITAT + PATCH + EDGE + UNIT)	34	2415.28	0.527	0	0.726
ψ(HABITAT + PATCH + EDGE)	32	2419.04	0.081	3.76	0.111
ψ(HABITAT + EDGE + UNIT)	29	2420.79	0.034	5.51	0.046
ψ(HABITAT + EDGE)	28	2422.22	0.016	6.94	0.023
Cumulative AIC weight					0.906
Nycticeius humeralis 8k					
ψ(HABITAT + LANDSCAPE + EDGE + UNIT)	32	945.15	0.096	0	0.309
ψ(HABITAT + LANDSCAPE + EDGE)	31	945.43	0.083	0.28	0.269
ψ(HABITAT + LANDSCAPE)	28	945.67	0.074	0.52	0.238
ψ(HABITAT + LANDSCAPE + UNIT)	29	947.27	0.033	2.12	0.107
Cumulative AIC weight					0.923
Pipistrellus subflavus 16k					
ψ(HABITAT + UNIT)	26	1233.77	0.48	0	0.690
ψ(HABITAT)	25	1236.49	0.12	2.72	0.180
ψ(HABITAT + LANDSCAPE + UNIT)	30	1238.49	0.05	4.72	0.070
Cumulative AIC weight					0.940

Table 11: Model-averaged parameter estimates, odds ratios with unconditional standard error (SE), 95% confidence interval for factors explaining probability of site occupancy of forest bats in the Ozark Region of Missouri, 2001-2003. UCL= Odds ratio upper confidence limit LCL= lower confidence limit.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Eptesicus fuscus 2 KM	intercept	-0.71	1.169	0.492	0.05	4.866
	pond	2.645	0.519	14.078	5.086	38.963
	rr	1.991	0.772	7.323	1.611	33.284
	opm	-2.13	0.566	0.119	0.039	0.361
	opw	-1.885	0.63	0.152	0.044	0.522
	ohw	-2.022	0.574	0.132	0.043	0.408
	ohm	-2.761	0.595	0.063	0.02	0.203
	blhd	-0.415	0.488	0.66	0.254	1.719
	imm	-1.948	0.621	0.143	0.042	0.482
	dh2okm	0	0	1	1	1
	droadkm	0	0	1	1	1
	dedgekm	0	0	1	1	1
	patcharea	0	0	1	1	1
	%oakpine	-0.02	0.013	0.98	0.956	1.005
	%open	-0.047	0.019	0.954	0.92	0.989
	%riparian	-0.014	0.093	0.986	0.823	1.183
	%water	-0.027	0.05	0.973	0.882	1.074
	rdden	0.11	0.051	1.116	1.01	1.234
	ijioakpine	0.052	0.012	1.054	1.029	1.079
	ijiopen	-0.021	0.009	0.979	0.962	0.997
	cwedopen	0.002	0.008	1.002	0.986	1.018
	unit	0.049	0.141	1.05	0.796	1.385
Lasiurus borealis 16 KM	intercept	8.354	2.706	4245.938	21.096	854550.9
	pond	3.316	1.101	27.558	3.185	238.445
	rr	0.514	0.664	1.672	0.455	6.142
	opm	-1.614	0.606	0.199	0.061	0.653
	opw	-1.745	0.637	0.175	0.05	0.608
	ohw	-1.415	0.618	0.243	0.072	0.816
	ohm	-2.064	0.613	0.127	0.038	0.422
	blhd	-0.9	0.656	0.407	0.112	1.472
	imm	-1.992	0.648	0.136	0.038	0.486
	dh2okm	-0.001	0.001	0.999	0.997	1.001
	droadkm	0.003	0.003	1.003	0.997	1.009
	dedgekm	0	0.001	1	0.999	1.002
	patcharea	0	0	1	1	1
	%oakpine	0.007	0.04	1.007	0.931	1.09
	%open	0.078	0.025	1.081	1.029	1.136
	%riparian	2.825	0.955	17.094	2.595	109.484
	%water	0.337	0.532	1.401	0.494	3.975
	rdden	-0.57	0.145	0.565	0.426	0.751
	ijioakpine	-0.222	0.022	0.801	0.767	0.835
	ijiopen	-0.061	0.011	0.941	0.92	0.962
	cwedopen	0.246	0.044	1.279	1.174	1.394
	unit	-1.791	0.703	0.167	0.042	0.662

Table 11: continued.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Lasiurus cinerius 8 KM	intercept	-4.134	3.304	0.016	0	10.405
	pond	2.879	0.663	17.794	4.851	65.272
	rr	1.356	0.833	3.879	0.758	19.839
	opm	-3.057	0.749	0.047	0.011	0.204
	opw	-2.096	0.709	0.123	0.031	0.493
	ohw	-3.054	0.746	0.057	0.011	0.204
	ohm	-3.151	0.727	0.043	0.010	0.178
	blhd	-1.379	0.584	0.252	0.080	0.792
	imm	-2.410	0.743	0.090	0.021	0.385
	dh2okm	0	0	1	1	1
	droadkm	0	0	1	1	1
	dedgekm	0	0	1	1	1
	patcharea	0	0	1	1	1
	%oakpine	0.015	0.024	1.015	0.968	1.065
	%open	0.002	0.007	1.002	0.988	1.017
	%riparian	-0.028	0.119	0.973	0.771	1.228
	%water	-0.057	0.133	0.945	0.727	1.227
	rdden	-0.121	0.101	0.886	0.727	0.944
	ijioakpine	0.013	0.013	1.01	1.005	1.04
	ijiopen	0.036	0.017	1.043	0.995	1.071
	cwedopen	0.096	0.026	1.101	1.046	1.158
	unit	-0.007	0.127	0.993	0.774	1.273
Myotis griscesens 16 KM	intercept	-5.146	2.58	0.006	0	0.915
	pond	1.779	0.458	5.922	2.414	14.53
	rr	2.331	1.143	10.287	1.094	96.677
	opm	-2.126	0.704	0.119	0.03	0.474
	opw	-1.091	0.526	0.336	0.12	0.941
	ohw	-1.214	0.534	0.297	0.104	0.846
	ohm	-1.624	0.567	0.197	0.065	0.599
	blhd	0.669	0.354	1.952	1.007	3.306
	imm	-2.617	0.904	0.073	0.012	0.43
	dh2okm	-0.001	0.001	0.999	0.998	1.001
	droadkm	0.004	0.003	1.004	0.999	1.01
	dedgekm	0.0001	0.001	1	0.998	1.001
	patcharea	0.0001	0.0001	1	0.999	1
	% oakpine	0.078	0.045	1.081	0.989	1.181
	%open	0.076	0.021	1.079	1.035	1.125
	%riparian	3.519	0.934	33.751	5.408	210.659
	%water	0.762	0.502	2.143	0.802	5.731
	rdden	0.337	0.157	1.401	0.998	1.907
	ijioakpine	-0.012	0.019	0.988	0.952	1.025
	ijiopen	-0.001	0.002	0.999	0.996	1.003
	cwedopen	-0.196	0.068	0.822	0.719	0.94
	unit	-0.432	0.585	0.649	0.206	2.044

Table 11: continued.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Myotis lucifugus 8 KM	intercept	18.218	1.76	.	.	.
	pond	0.319	0.479	1.376	0.538	3.516
	rr	0.065	0.283	1.068	0.613	1.858
	opm	0.029	0.191	1.029	0.708	1.497
	opw	0.124	0.295	1.133	0.635	2.02
	ohw	0.01	0.179	1.01	0.711	1.435
	ohm	-0.045	0.204	0.956	0.641	1.427
	blhd	0.427	0.637	1.533	0.44	5.341
	imm	-0.099	0.311	0.906	0.492	1.668
	dh2okm	-0.002	0.001	0.998	0.996	1
	droadkm	0.005	0.002	1.005	1.001	1.008
	dedgekm	-0.002	0.001	0.998	0.997	1
	patcharea	0	0	1	0.999	1.001
	%oakpine	0.13	0.021	1.139	1.093	1.186
	%open	0.074	0.024	1.077	1.028	1.128
	%riparian	0.317	0.299	1.373	0.764	2.468
	%water	0.254	0.259	1.289	0.776	2.143
	rdden	-0.561	0.098	0.571	0.471	0.692
	ijioakpine	-0.025	0.012	0.975	0.952	0.999
	ijiopen	-0.242	0.021	0.785	0.753	0.818
	cwedopen	-0.013	0.024	0.987	0.942	1.034
	unit	0.033	0.161	1.033	0.754	1.416
Myotis septentrionalis 16 KM	intercept	-7.762	3.47	0	0	0.383
	pond	1.568	0.566	4.796	1.383	11.328
	rr	1.918	1.137	6.806	1.609	67.021
	opm	1.008	0.496	2.741	1.036	7.25
	opw	1.352	0.568	3.863	1.27	11.752
	ohw	2.187	0.612	8.906	2.684	29.55
	ohm	0.726	0.507	2.067	0.765	5.587
	blhd	2.212	0.57	9.131	2.989	27.897
	imm	-0.507	0.544	0.602	0.207	1.75
	dh2okm	-0.001	0.001	0.999	0.997	1
	droadkm	0.006	0.003	1.006	1	1.013
	dedgekm	0.001	0.001	1.001	1	1.002
	patcharea	0	0	1	1	1
	%oakpine	0	0	1	1	1
	%open	0	0	1	1	1
	%riparian	0	0	1	1	1
	%water	0	0	1	1	1
	rdden	0.369	0.155	1.446	1.066	1.961
	ijioakpine	-0.055	0.017	0.947	0.916	0.978
	ijiopen	-0.031	0.027	0.969	0.92	1.021
	cwedopen	0.201	0.039	1.223	1.134	1.32
	unit	-1.627	0.786	0.197	0.042	0.918

Table 11: continued.

SPECIES	PARA-METER	PARAMETER COEFFICIENT	SE	ODDS RATIO	LCL	UCL
Nycticeius humeralis 8 KM	intercept	-1.99	3.607	0.137	0	160.869
	pond	2.103	0.391	8.157	3.787	17.569
	rr	19.421	.	.	.	.
	opm	-1.314	0.692	0.269	0.069	1.043
	opw	-0.756	0.687	0.47	0.122	1.806
	ohw	-0.319	0.539	0.727	0.252	2.092
	ohm	-1.086	0.582	0.337	0.108	1.056
	blhd	0.001	0.503	1.001	0.374	2.68
	imm	-0.849	0.582	0.428	0.137	1.34
	dh2okm	0	0	1	1	1
	droadkm	0	0	1	1	1
	dedgekm	0	0	1	1	1
	patcharea	0	0	1	1	1
	%oakpine	0.059	0.036	1.077	1.018	1.139
	%open	0.045	0.037	1.046	0.972	1.126
	%riparian	0.184	0.329	1.083	0.843	1.585
	%water	0.247	0.245	1.281	0.792	2.072
	rdden	-0.116	0.172	0.89	0.635	1.247
	ijioakpine	-0.042	0.041	0.959	0.886	1.039
	ijiopen	0.036	0.037	1.037	0.963	1.116
	cwedopen	-0.012	0.024	0.988	0.943	1.034
	unit	0.879	0.329	2.415	1.246	4.679
Pipistrellus subflavus 16 KM	intercept	0.312	0.847	1.366	0.26	7.183
	pond	2.195	0.403	8.98	4.077	19.781
	rr	0.169	0.809	1.184	0.243	5.781
	opm	-2.076	0.599	0.125	0.039	0.406
	opw	-1.424	0.62	0.241	0.071	0.811
	ohw	-1.768	0.575	0.171	0.055	0.527
	ohm	-2.612	0.63	0.073	0.021	0.253
	blhd	-0.637	0.505	0.529	0.196	1.423
	imm	-1.844	0.663	0.158	0.043	0.58
	dh2okm	0	0	1	1	1
	droadkm	0	0	1	1	1
	dedgekm	0	0	1	1	1
	patcharea	0	0	1	1	1
	%oakpine	0.004	0.008	1.004	0.988	1.02
	%open	0.002	0.004	1.002	0.994	1.009
	%riparian	0.061	0.127	1.062	0.828	1.364
	%water	0.023	0.053	1.023	0.922	1.135
	rdden	0	0	1	1	1
	ijioakpine	0	0	1	1	1
	ijiopen	0	0	1	1	1
	cwedOpen	0	0	1	1	1
	unit	-0.669	0.309	0.512	0.28	0.937

Figure 1. Study Areas in Missouri surveyed for bats, 2001-2003. Lines indicate Mark Twain National Forest Ranger Districts, North and South Units (South Unit bold), initial focal areas with cross hatch, supplemental sampling areas with solid dots.

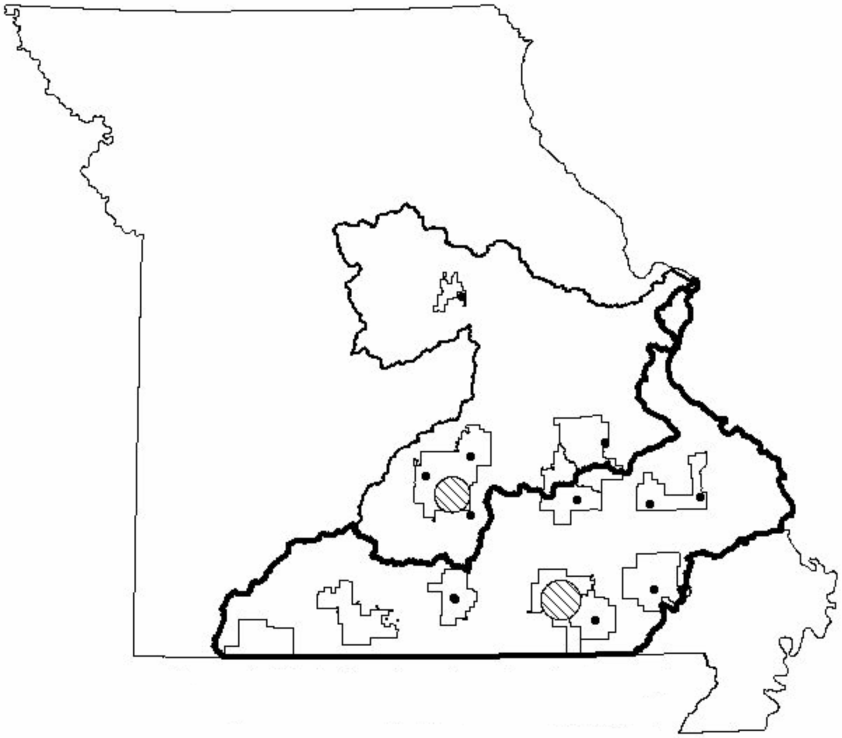
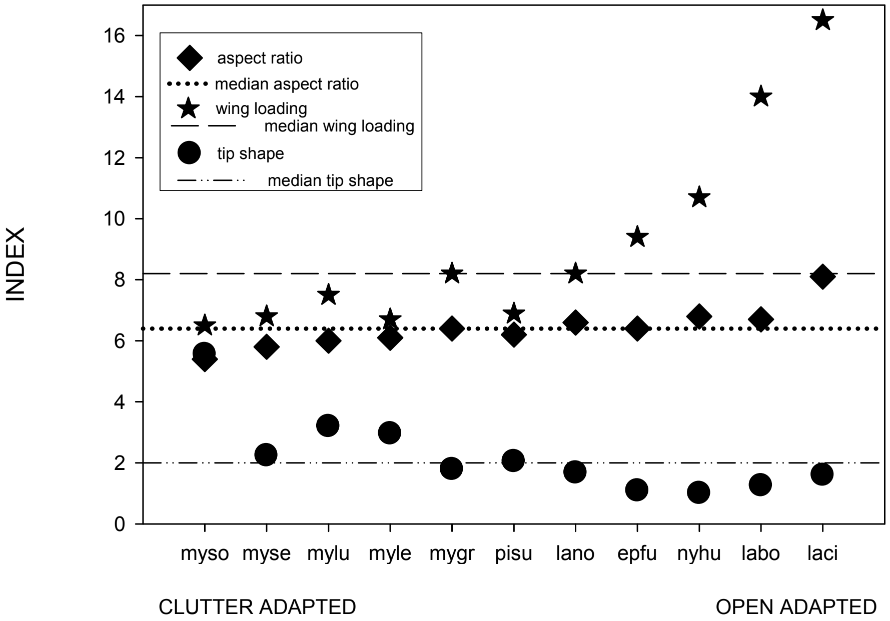
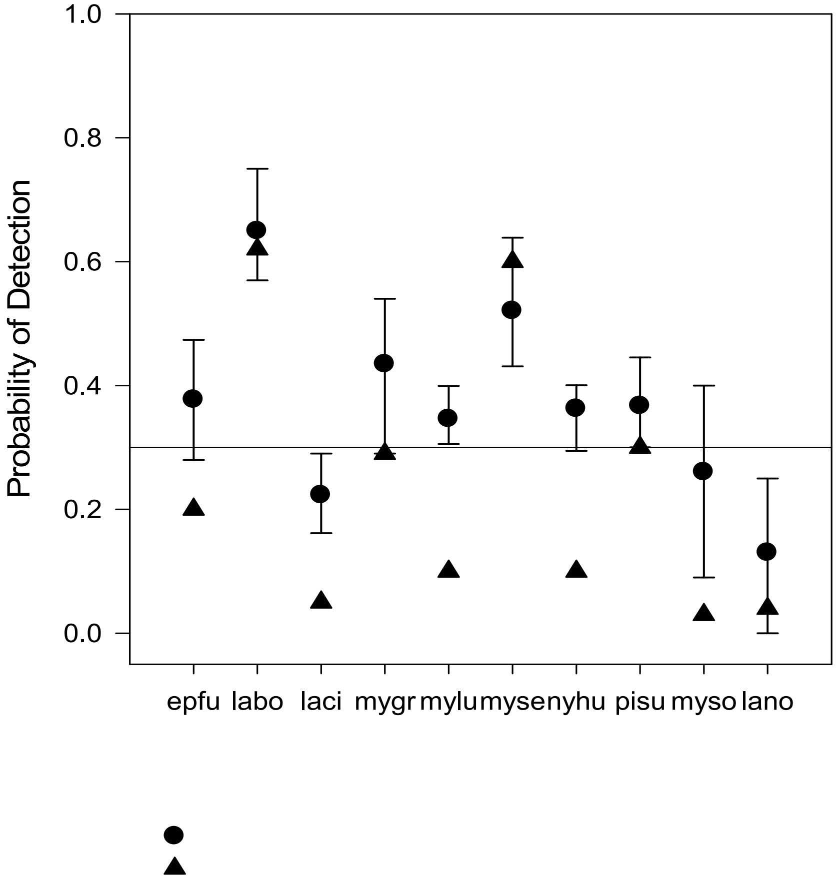


Figure 2. Wing morphology of ten bat species commonly found in Missouri illustrating relative adaptation of each species to foraging in "open" or "cluttered" habitats. See text for description of aspect ratio, wing tip shape index, and wing loading. For details of calculations, see Norberg and Raynor (1987).



myso= *Myotis sodalis*, myse=*M. septentrionalis*, mylu=*M. lucifugus*, myle=M. leibii, mygr=*M. grisescens*, pisu=*Pipistrellus subflavus*, lano=Lasionycteris noctivagans, epfu=*Eptesicus fuscus*, nyhu=*Nycticeius humeralis*, labo=*Lasiurus borealis*, laci=*L. cinereus*

Figure 3. Mean, minimum, and maximum probability of detection based on acoustic detection and occupancy models (closed circles) compared to capture rate (closed triangles) for ten species of bats in the Ozark Region of Missouri (2001-2003). Reference line indicates 0.3 probability of detection. Probability of detection and capture rate represent pooled data of entire study area.



myso= *Myotis sodalis*, myse=*M. septentrionalis*, mylu=*M. lucifugus,* myle=*M. leibii*, mygr=*M. grisescens*, pisu=*Pipistrellus subflavus*, lano=*Lasionycteris noctivagans*, epfu=*Eptesicus fuscus,* nyhu=*Nycticeius humeralis*, labo=*Lasiurus borealis,* laci=*L. cinereus*

Figure 4. Mean (± 95% CI) for probability of site occupancy based on acoustic detection and occupancy models (closed circles) compared to capture rate (closed triangles) for ten species of bats in the Ozark Region of Missouri (2001-2003). Mean probability of occupancy and capture rate represent pooled data of entire study area. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus*, MYGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, PISU=*Pipistrellus subflavus*, NYHU=*Nycticeius humeralis*.

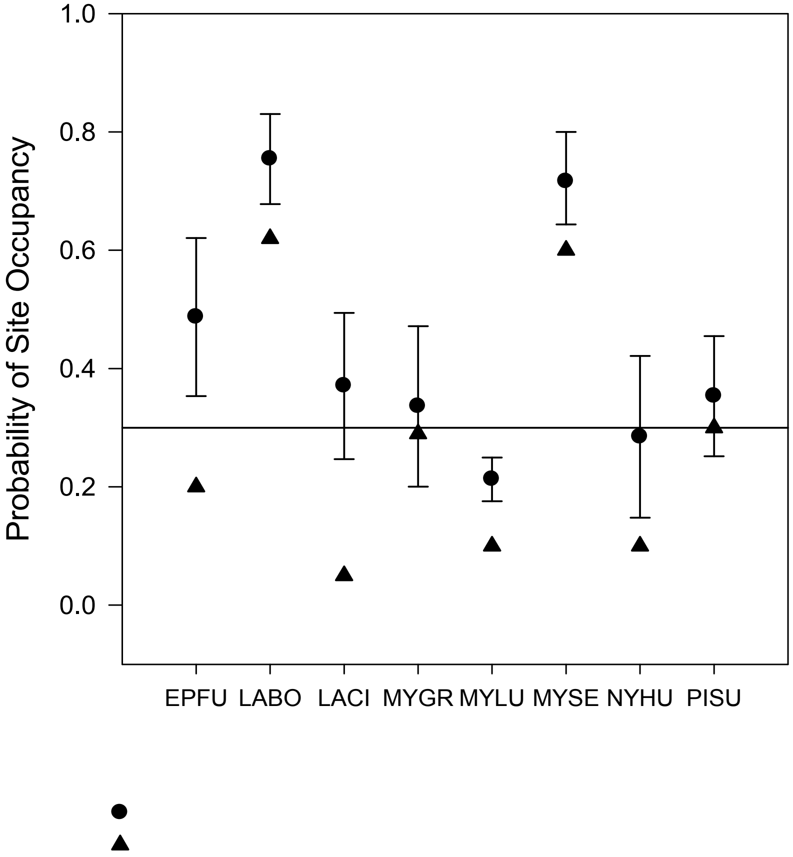


Figure 5. Predicted probability of detection by sampling occasion (time of night) for ten species of bats in the Ozark Region of Missouri 2001-2003. (For details of time intervals refer to Table 2). EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus*, MYGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, PISU=*Pipistrellus subflavus*, NYHU=*Nycticeius humeralis*.

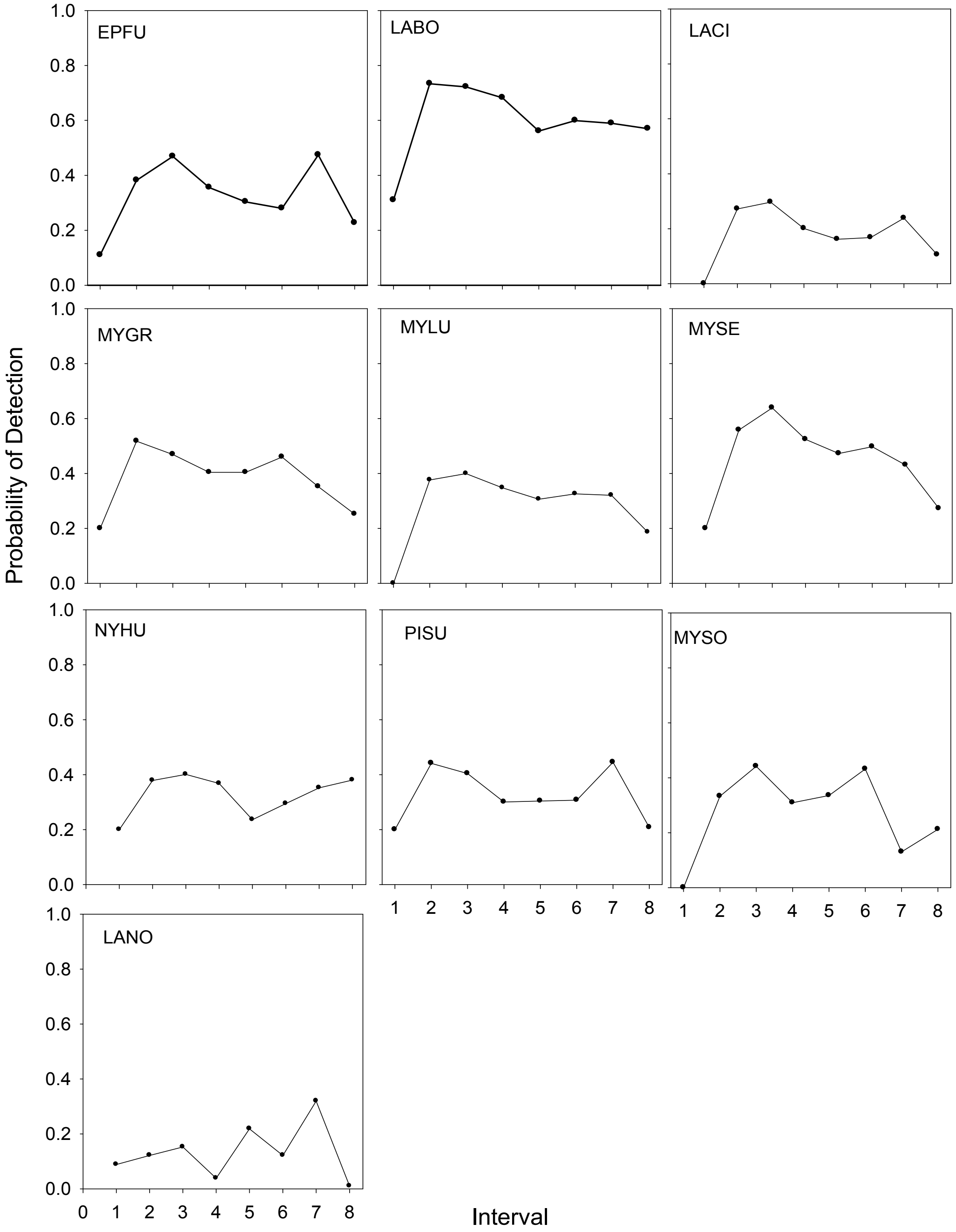


Figure 6. Predicted mean (+ 95% CI) probability of detection for eight species of bats in relation to ambient temperature in the Ozark Region of Missouri 2001-2003. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus*, MYGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

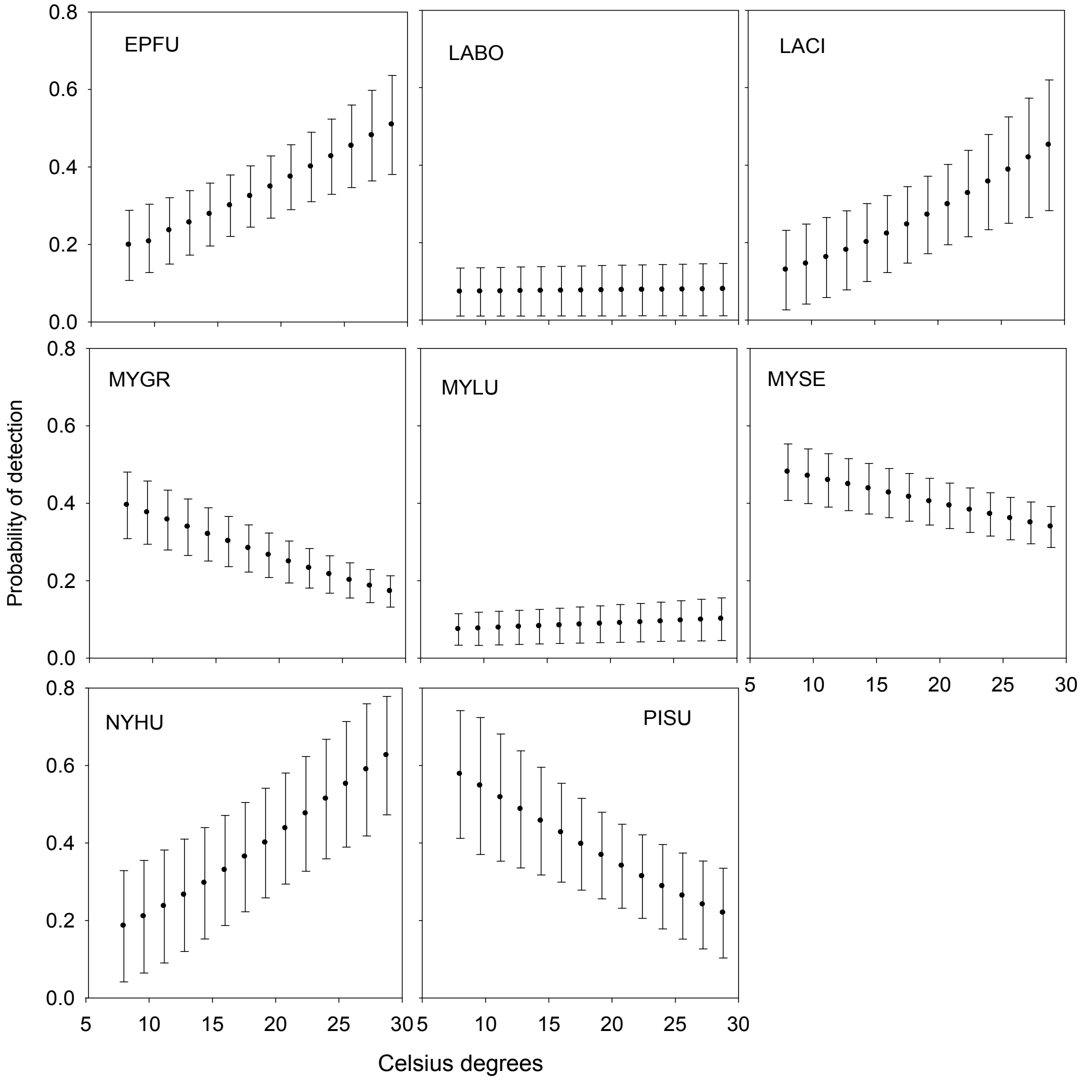


Figure 7. Predicted mean (+ 95% CI) probability of detection for eight species of bats in relation to days since rain in the Ozark Region of Missouri 2001-2003. PFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus,* MYGR=*M. grisescens,* MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*

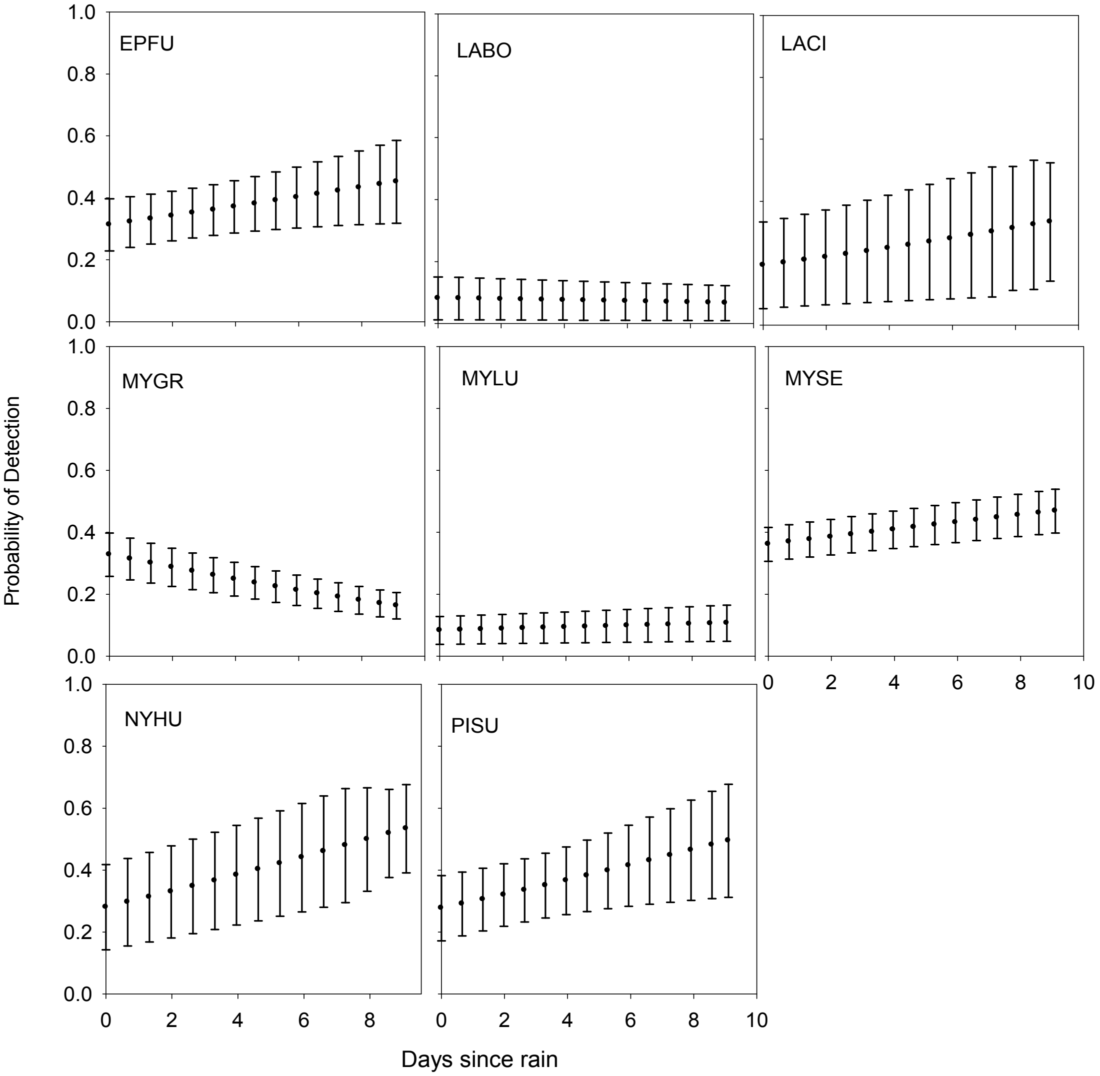


Figure 8. Predicted mean (+ 95% CI) probability of detection for eight species of bats in relation presence or absence of a water surface that would reflect echolocation calls and relative size of that feature if present in the Ozark Region of Missouri 2001-2003. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

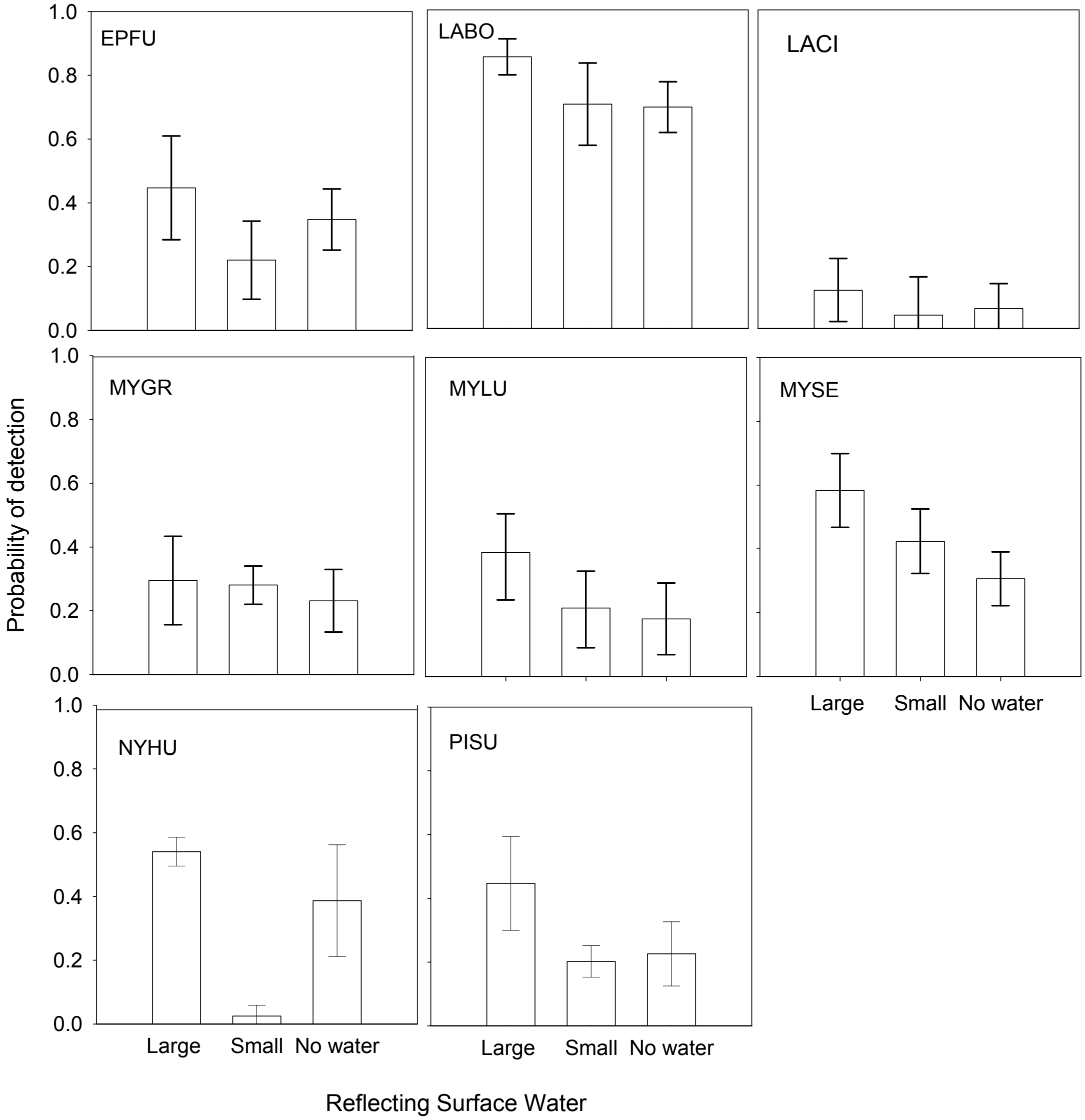


Figure 9. Predicted mean (+ 95% CI) probability of detection for eight species of bats in relation to vegetative clutter (forest density) that would damp echolocation calls in the Ozark Region of Missouri 2001-2003. (Density refers to percent stocking. High is greater than or equal to 60%, Low is less than 60%). EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

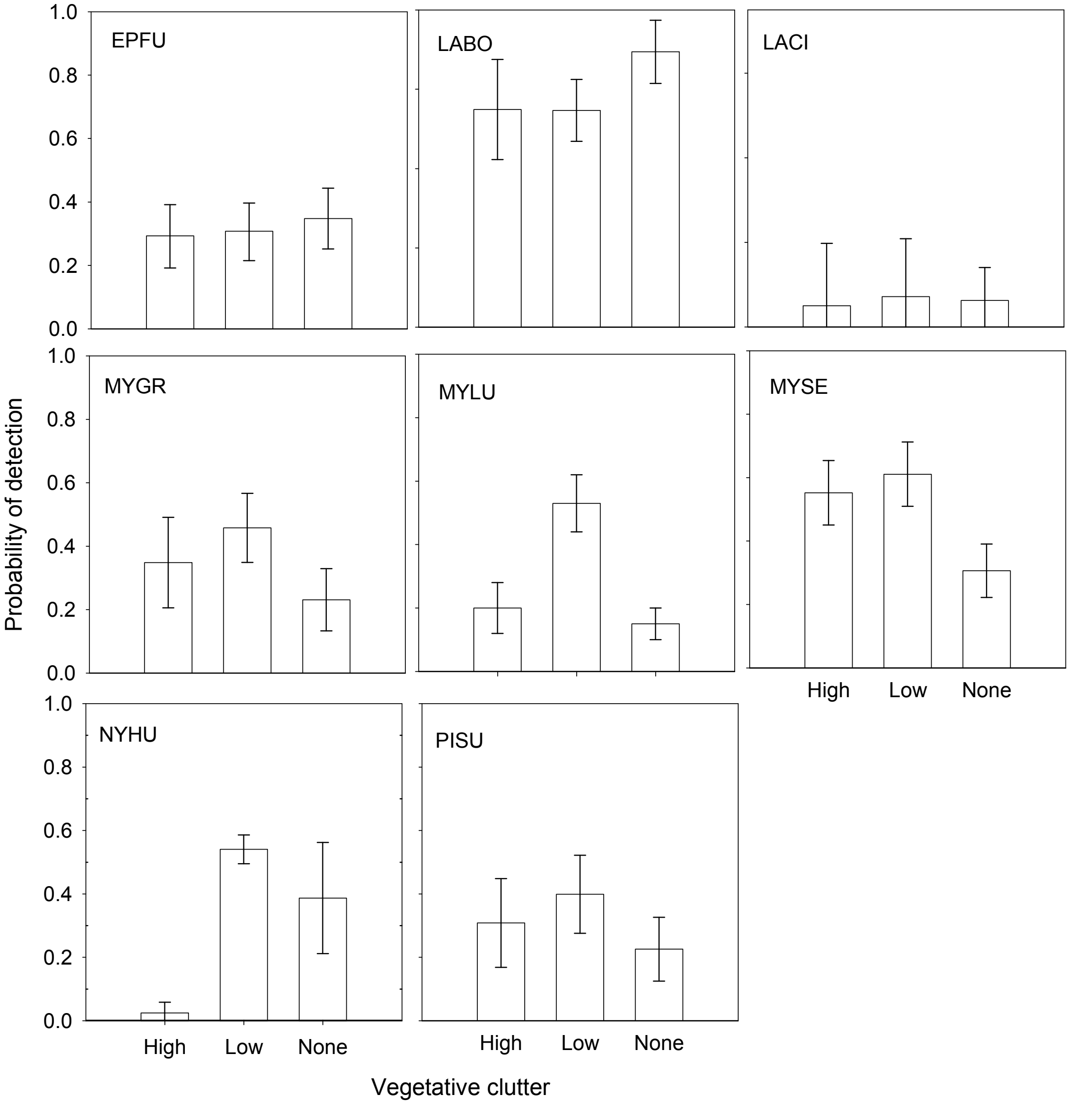


Figure 10. Predicted mean (+ 95% CI) probability of detection for eight species of bats in relation to Julian date in the Ozark Region of Missouri 2001-2003. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus,* *M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

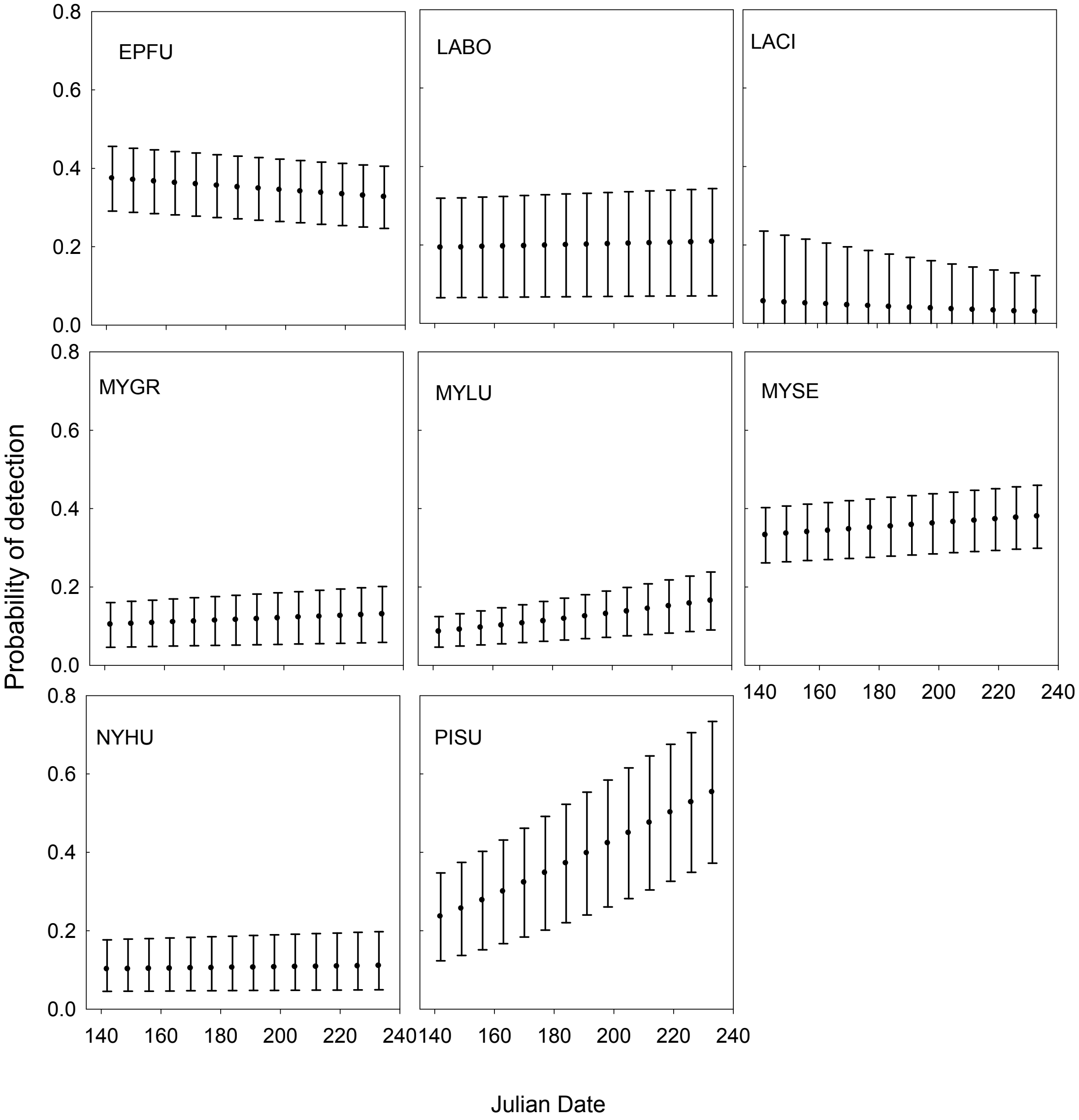


Figure 11. Predicted mean (± 95% CI) probability of detection for eight species of bats in relation to year in the Ozark Region of Missouri 2001-2003. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

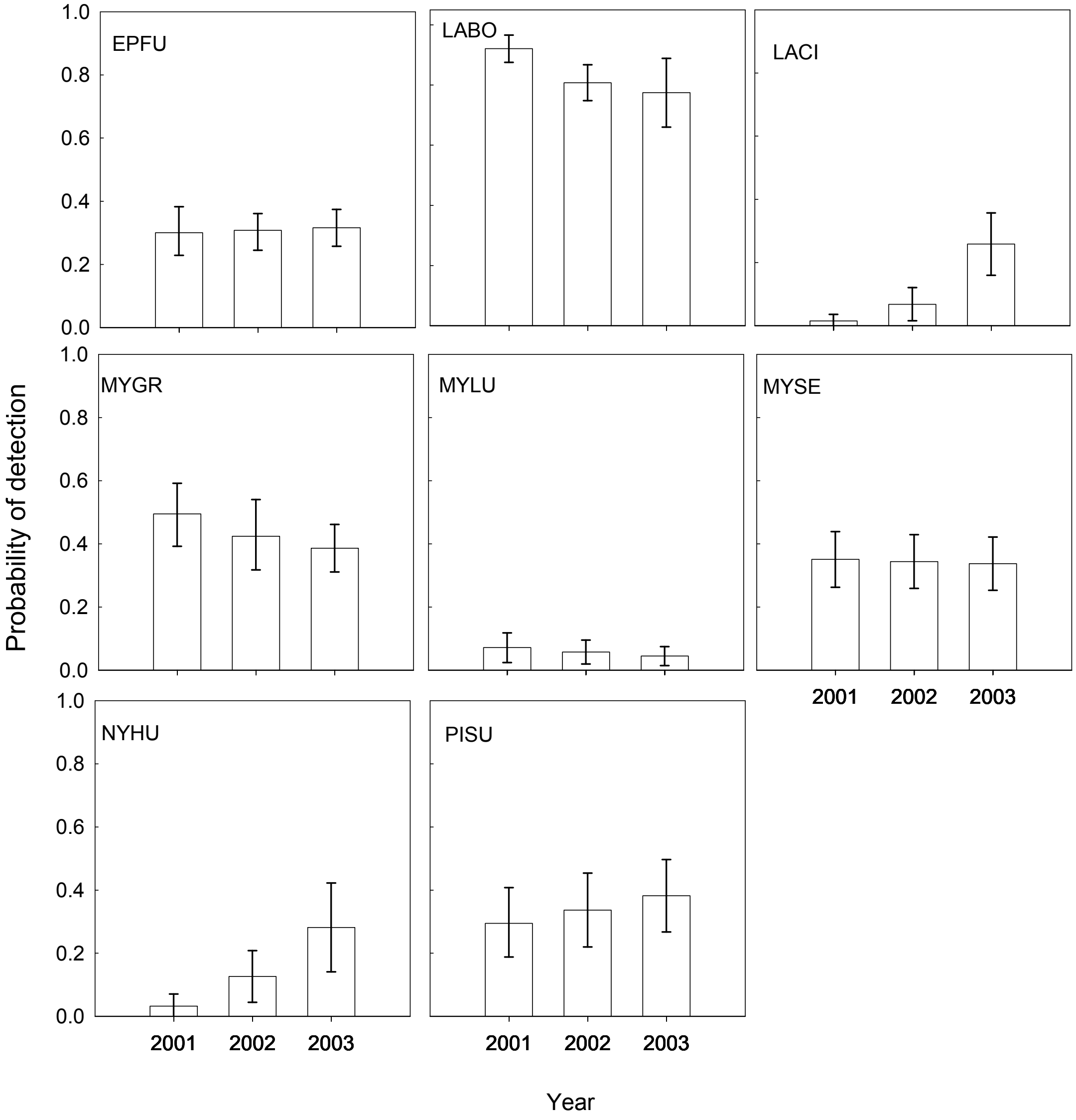


Figure 12. Predicted mean (+ 95% CI) probability of site occupancy for four bat species affected by geographic location in the Ozark Region of Missouri 2001-2003. Left bar = north unit and right bar = south unit). LABO=*Lasiurus borealis*, MYSE=*M. septentrionalis*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*,

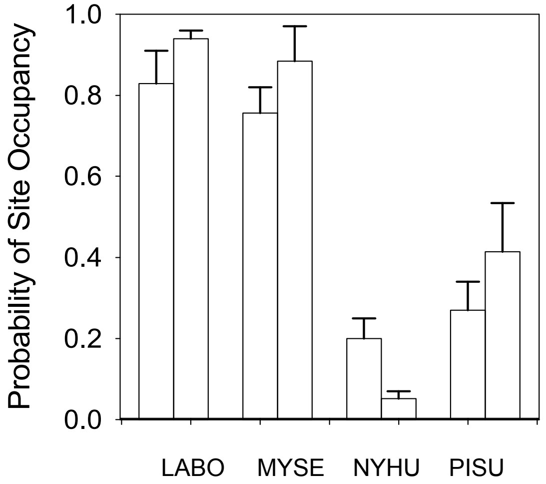


Figure 13. Predicted mean (± 95% CI) probability of site occupancy based on effect of terrestrial habitat type for eight bat species in the Ozark Region of Missouri 2001-2003. OPM= Pine or Oak-Pine fully stocked forest, OPW = Pine or Oak-Pine low to moderately stocked forest, OHM = Oak-Hickory fully stocked forest, OHW = Oak-Hickory low to moderately stocked forest, BLHD = Deciduous lowland forest, IMM = Forest less than 20 years old, NF = Non-forest. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

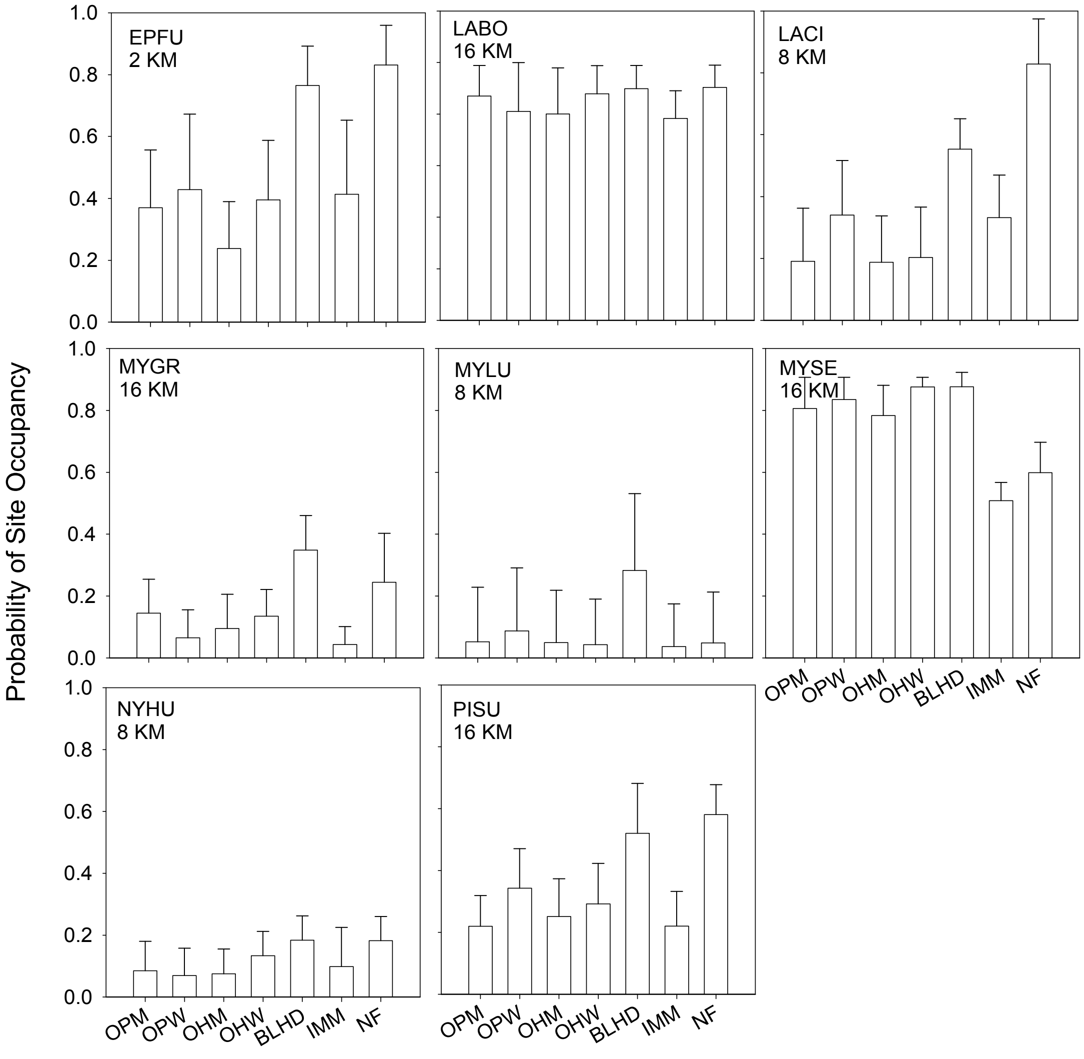


Figure 14. Predicted mean (± 95% CI) probability of site occupancy based on effect of aquatic habitat type for eight bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

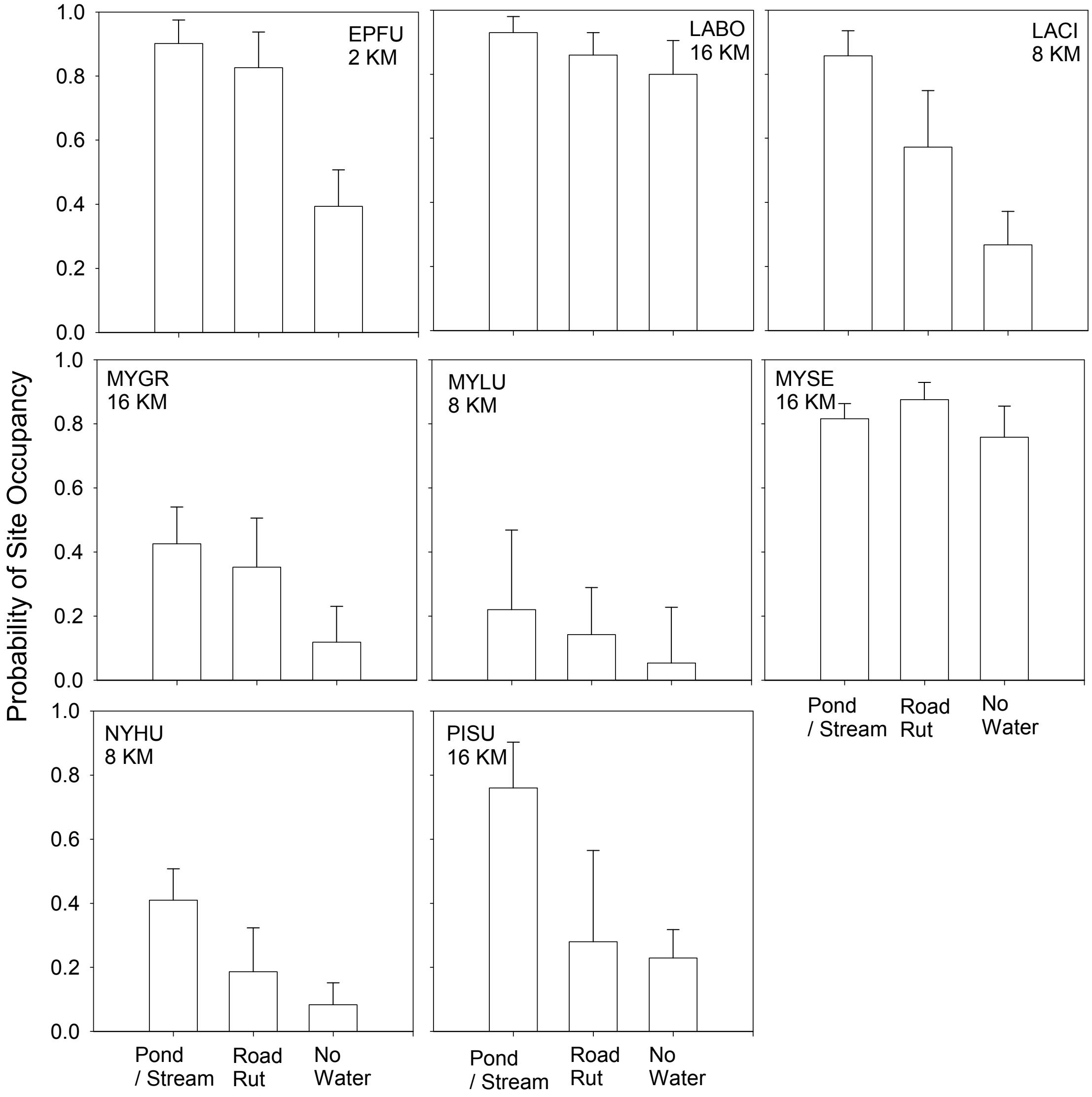


Figure 15. Predicted mean (± 95% CI) probability of site occupancy based on landscape percent of non-forest for six bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

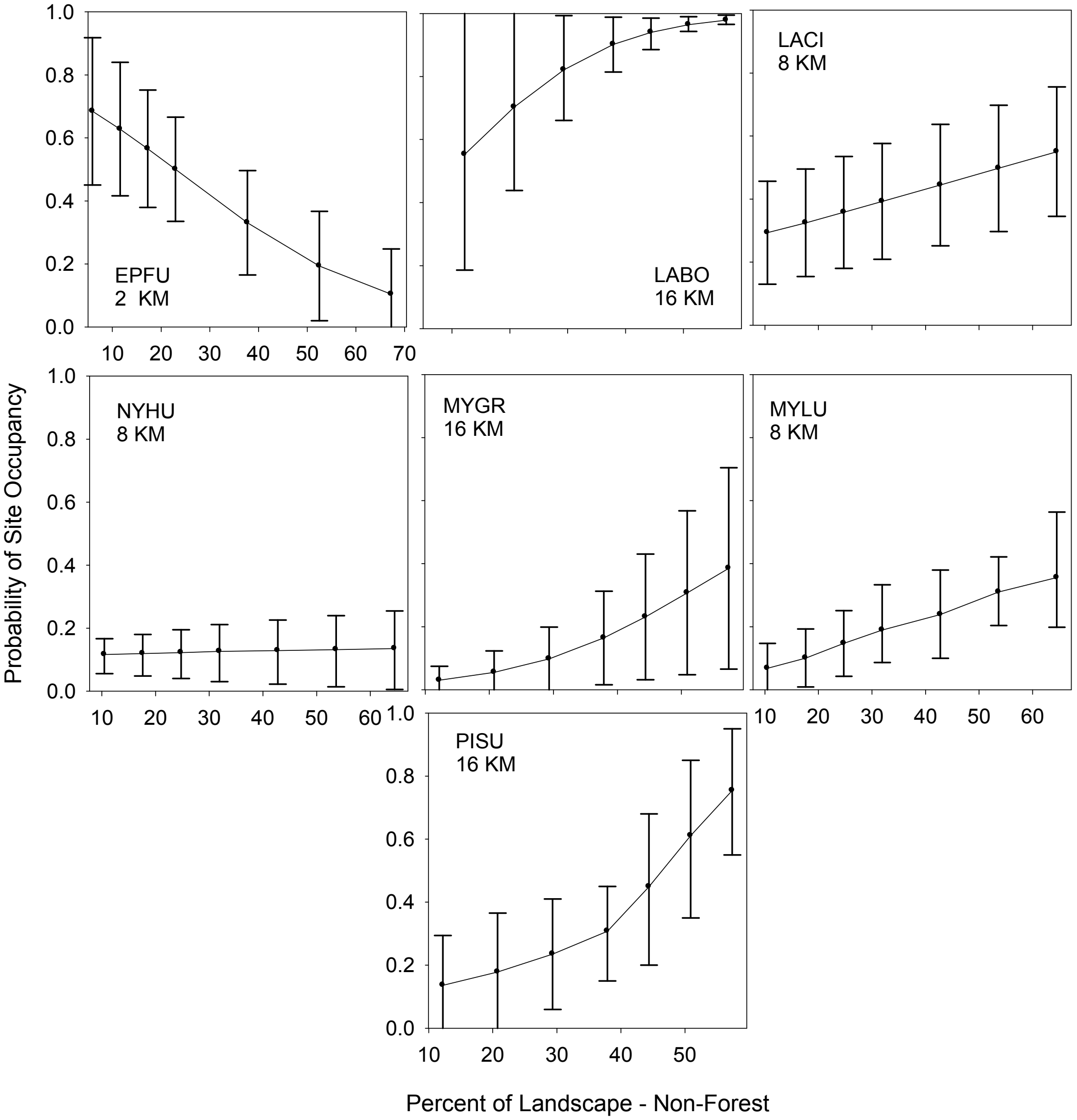


Figure 16. Predicted mean (± 95% CI) probability of site occupancy based on landscape percent of oak-pine or pine forest types for five bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative $w_i >$ 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

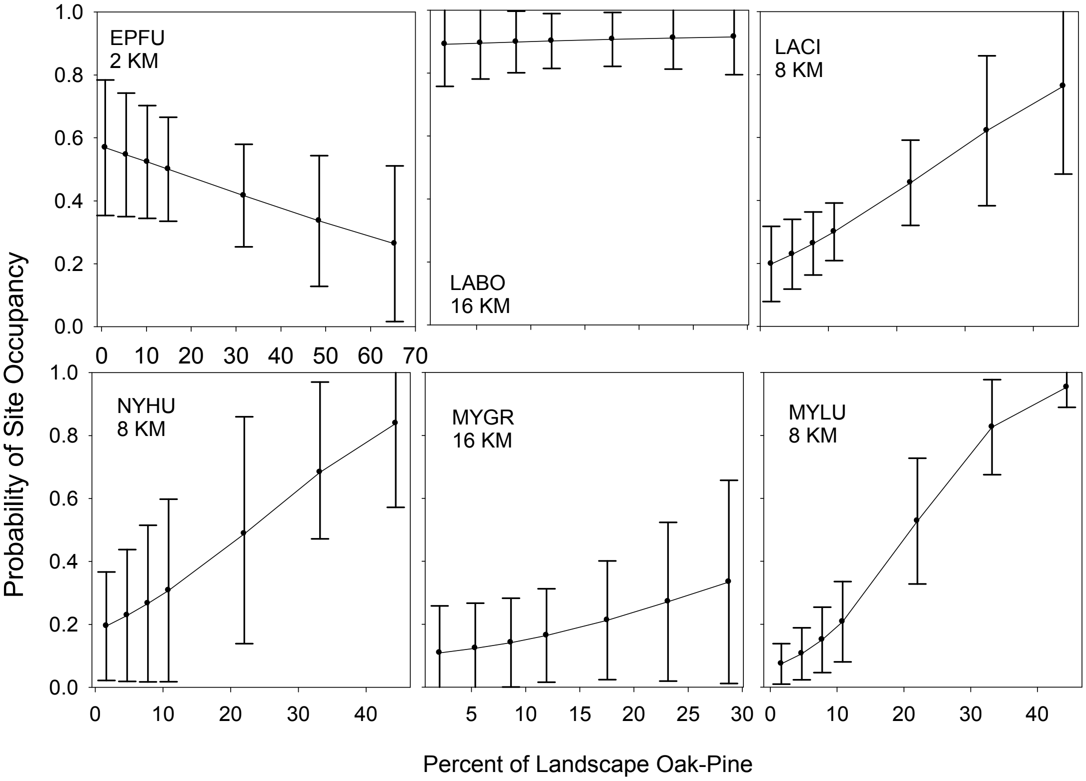


Figure 17. Predicted mean (+ 95% CI) probability of site occupancy based on effect of roa density (m/ha) for six bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

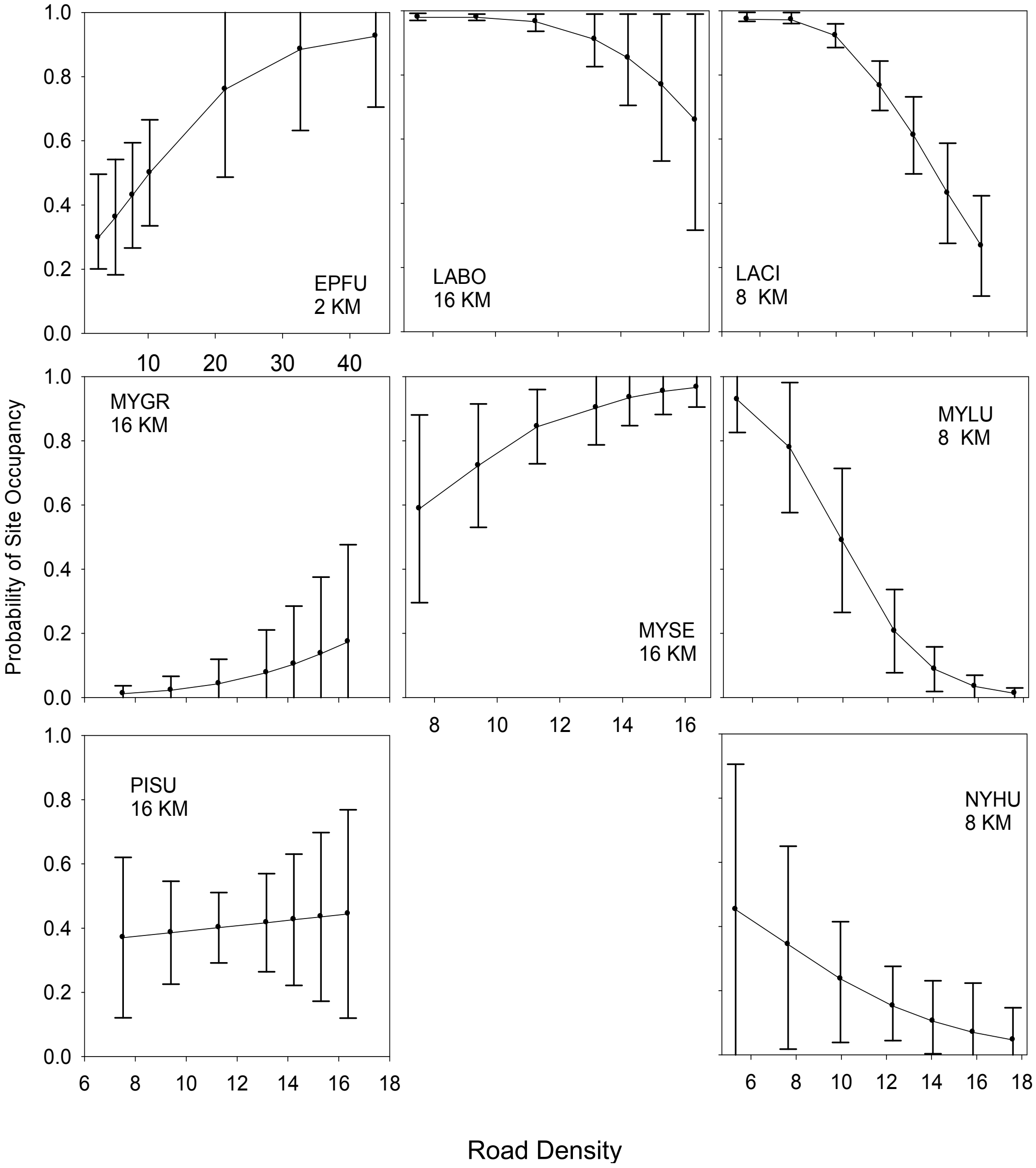


Figure 18. Predicted mean (± 95% CI) probability of site occupancy based on effect of landscape interspersion and juxtaposition of oak-pine and pine forest patches for five bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus*, MYGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

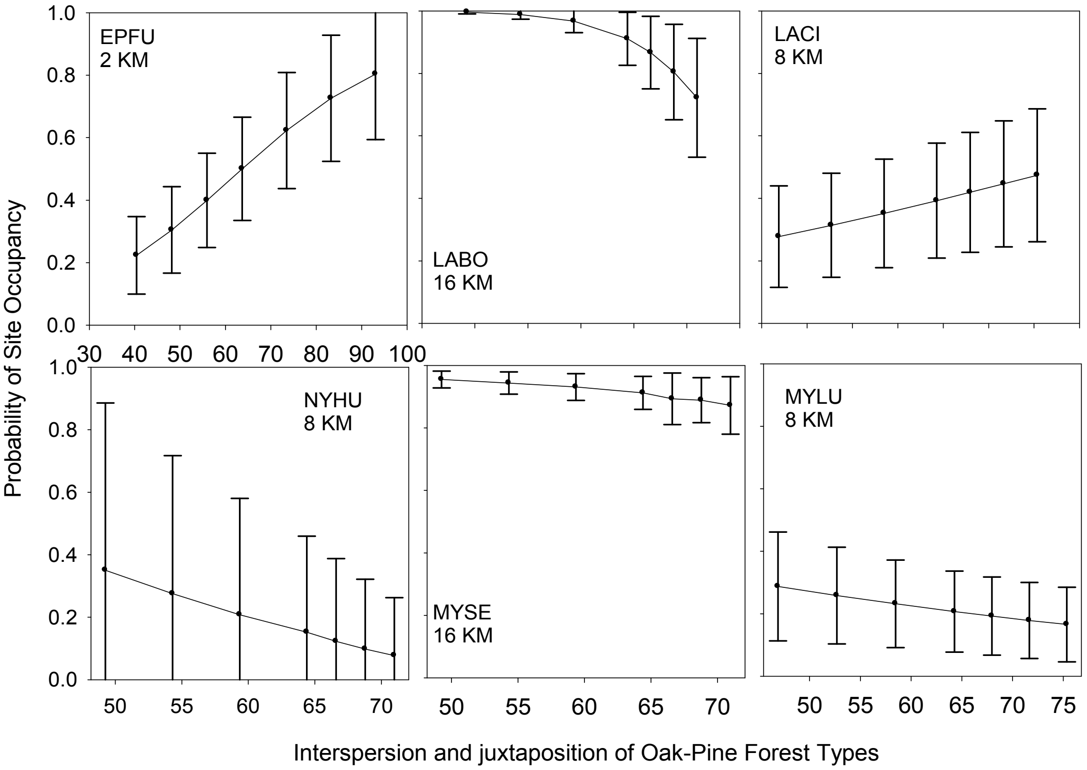


Figure 19. Predicted mean (± 95% CI) probability of site occupancy based on effect of landscape interspersion and juxtaposition of non-forest patches for three bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

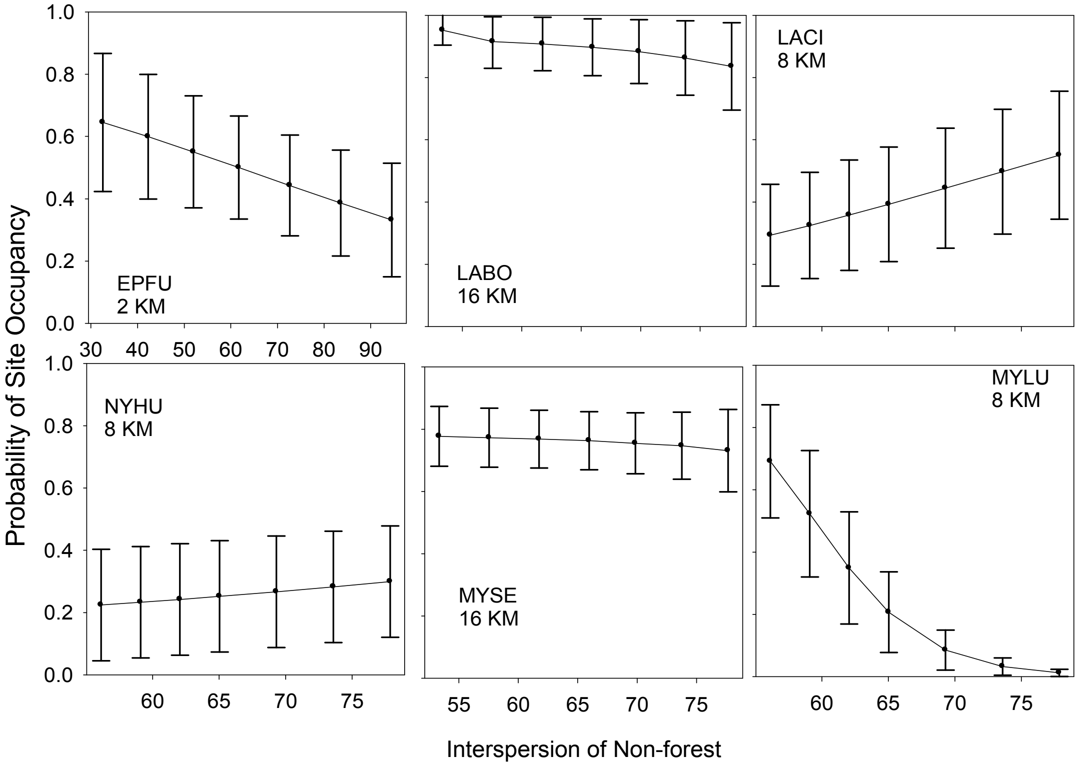


Figure 20. Predicted mean (± 95% CI) probability of site occupancy based on effect of edge density of non-forest to forest (m/ha) for three bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i> 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus,* MYGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

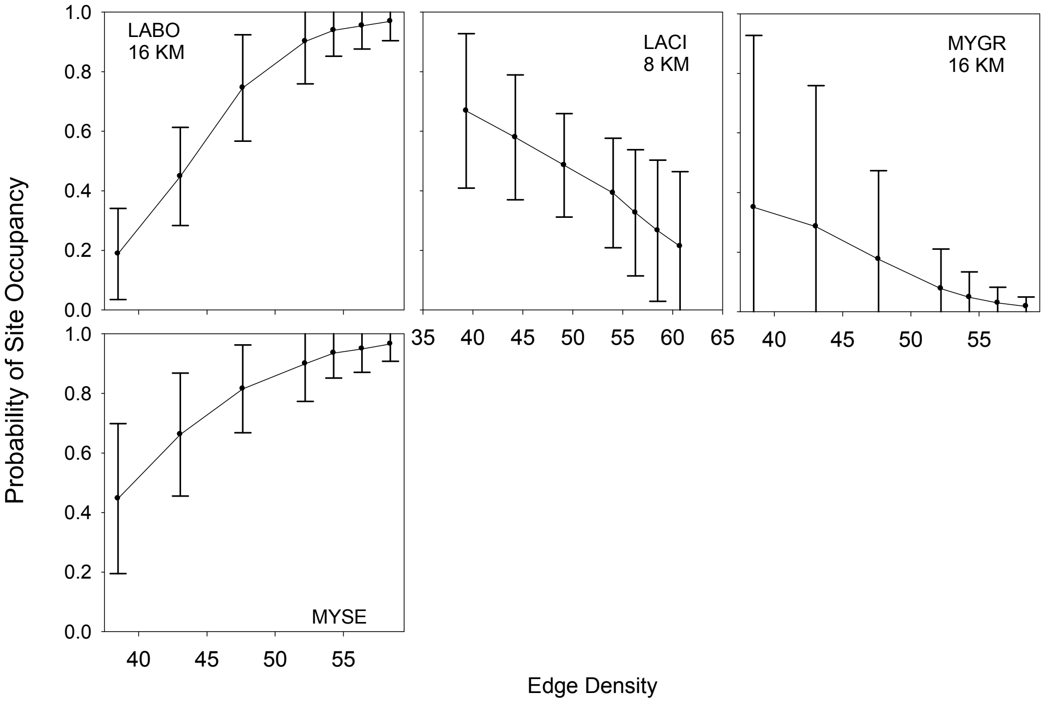


Figure 21. Predicted mean (± 95% CI) probability of site occupancy based on landscape percent of riparian types for three bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

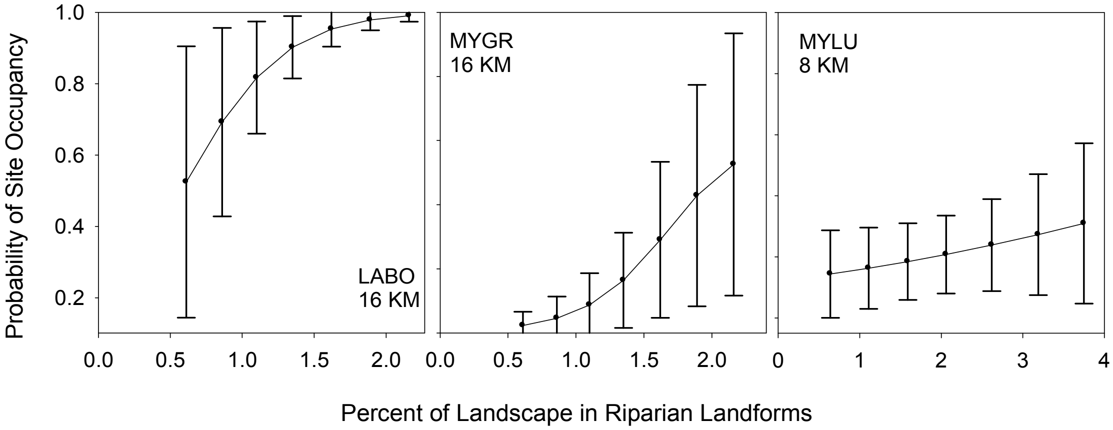


Figure 22. Predicted mean (± 95% CI) probability of site occupancy based on effect of distance to water (meters) for four bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

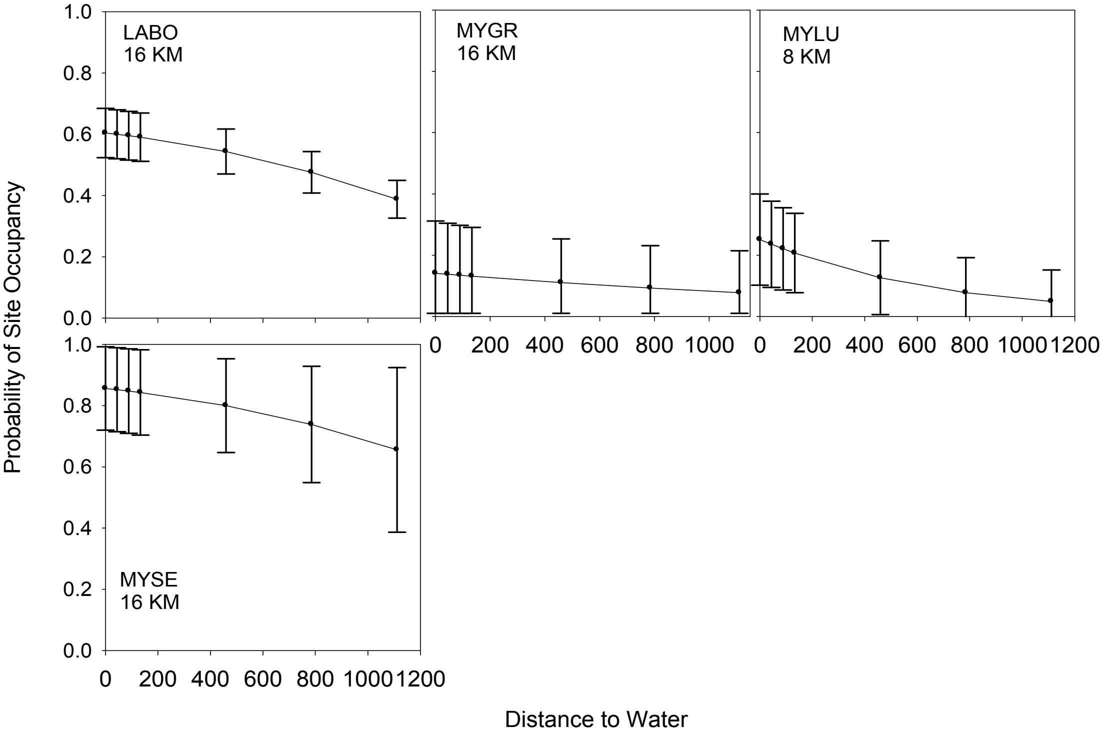


Figure 23. Predicted mean (± 95% CI) probability of site occupancy based on landscape percent of water in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy at16 kilometer spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

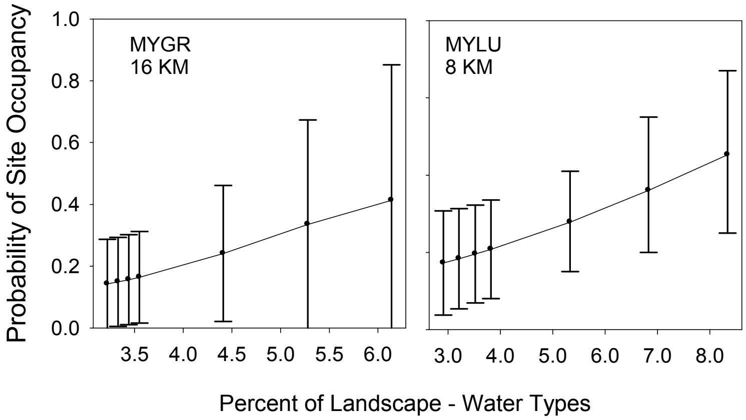


Figure 24. Predicted mean (± 95% CI) probability of site occupancy based on effect of distance to roads (meters) for three bat species in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative w_i > 90%) for site occupancy for each species at best spatial scale. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

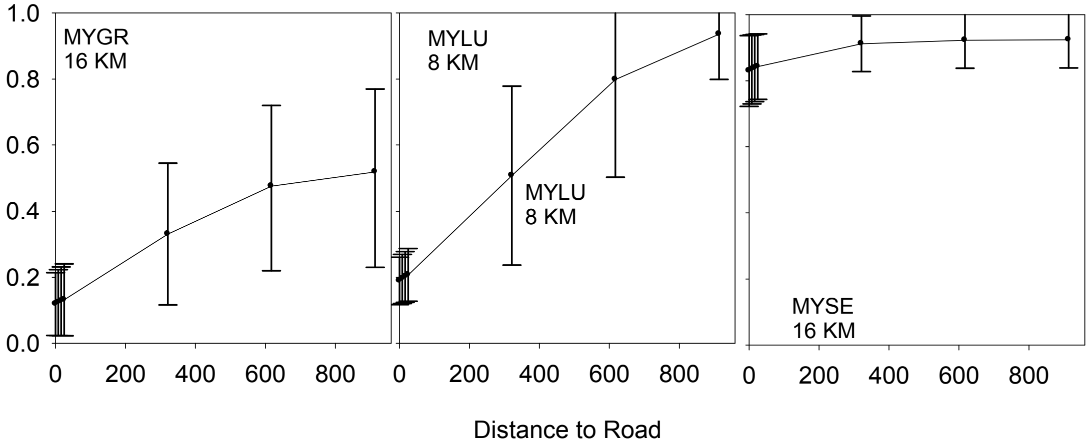


Figure 25. Predicted mean (± 95% CI) probability of site occupancy based on effect of distance to non-forest edge (meters) for *M. septentrionalis* in the Ozark Region of Missouri 2001-2003. Predicted effects are model averaged over the best model set (cumulative $w_i >$ 90%) for site occupancy at 16 kilometer spatial scale.

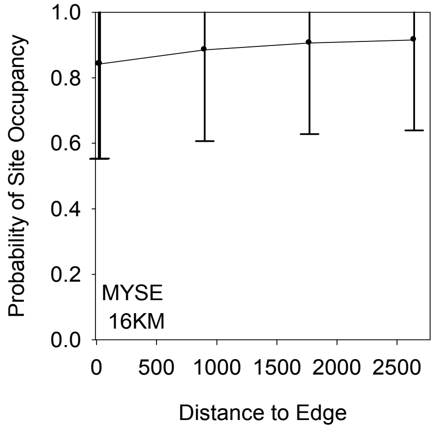


Figure 26. Predicted probability of site occupancy by terrestrial habitat for eight species of bat in the Missouri Ozark Region. Oak-hickory forest high stocking (OHM), oak-pine/pine forest high stocking (OPM), oak-hickory forest low stocking (OHW), and oak-pine/pine forest low stocking (OPW) are shown as a line representing a continuum from densest to most open forest conditions; bottomland hardwood forest (BLHD), non-forest (NF) and immature forest (IMM) are shown as bars for relative comparison. EPFU=*Eptesicus fuscus*, LABO=*Lasiurus borealis*, LACI=*L. cinereus, M*YGR=*M. grisescens*, MYSE=*M. septentrionalis*, MYLU=*M. lucifugus*, NYHU=*Nycticeius humeralis*, PISU=*Pipistrellus subflavus*.

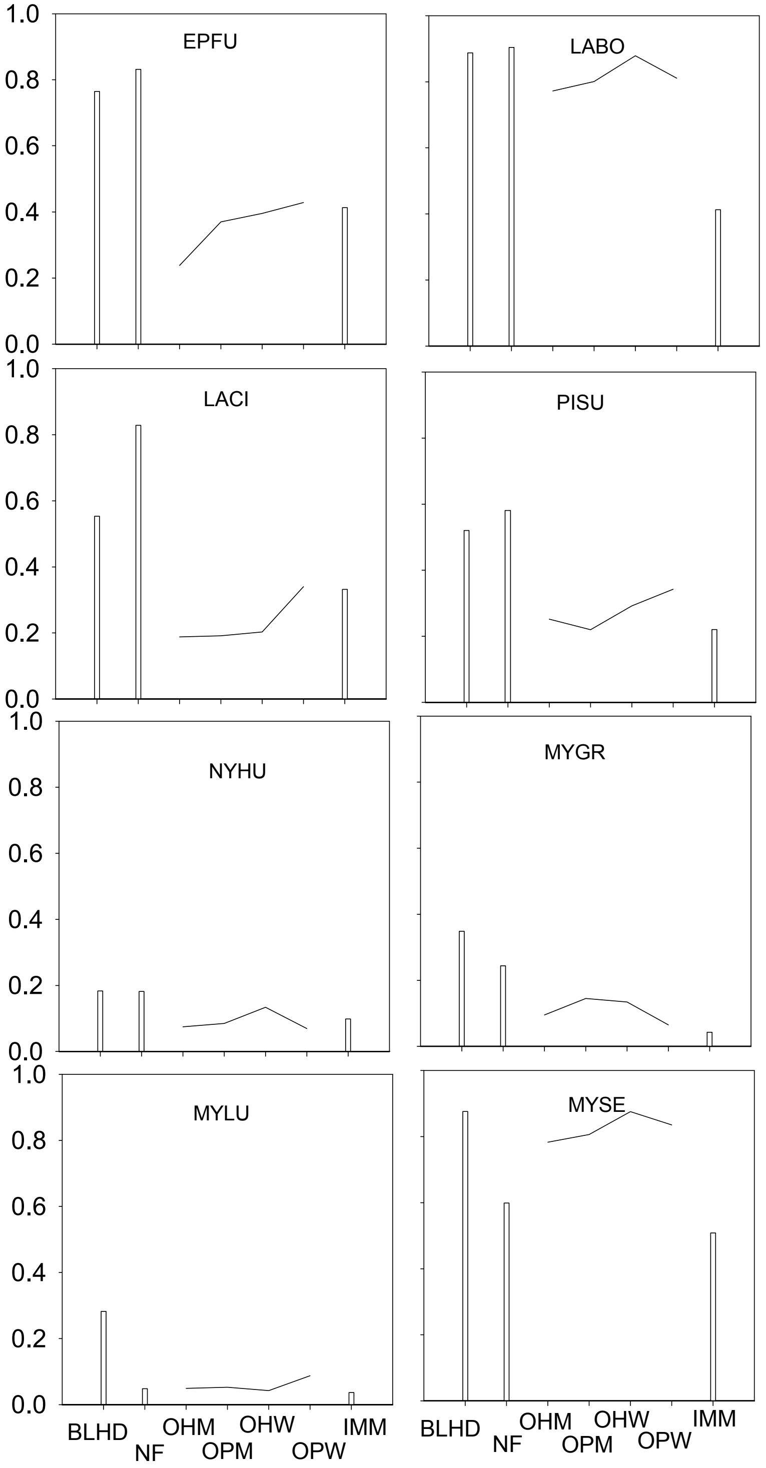

EPFU
LABO
LACI
PISU
NYHU
MYGR
MYLU
MYSE
1.0
0.8
0.6
0.4
0.2
0.0
BLHD
NF
OHM
OPM
OHW
OPW
IMM

Figure 27. Examples of landscape patterns affecting predicted site occupancy of *L. borealis* at 16 km landscape scale. Occupancy in (a) is 0.9 as a result of moderate levels of non-forest (25–35%) with interspersion below 60. Occupancy in (b) is 0.5 as a result of higher levels of non-forest (>45%) and interspersion of non-forest above 60. (White=water, light gray=non-forest, dark gray=deciduous forest, black=pine or mixed pine forest).

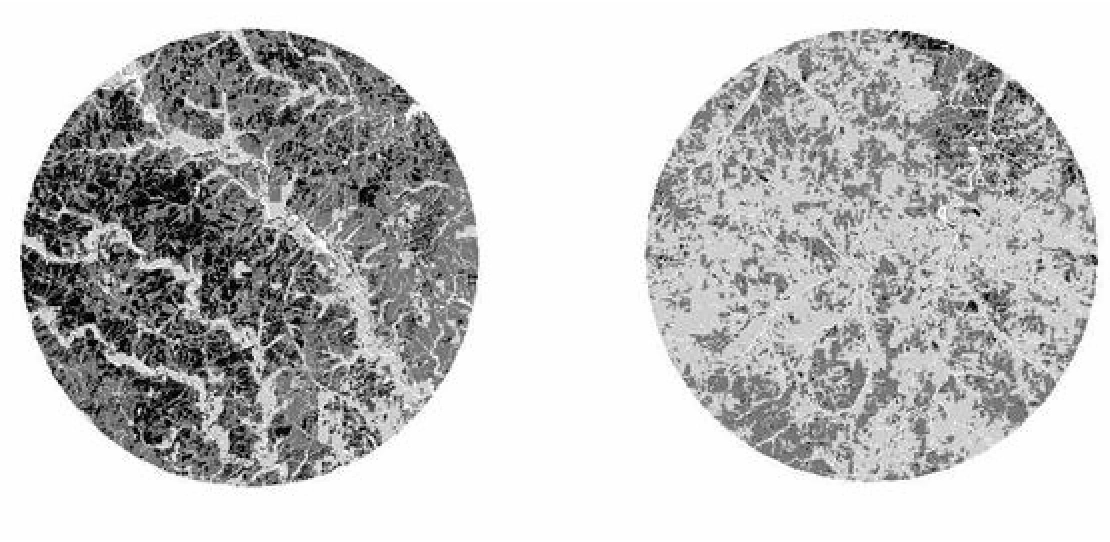


Figure 28. Examples of landscape patterns affecting predicted site occupancy of *M. septentrionalis* at 16 km landscape scale. Occupancy in (a) is 0.9 as a result of moderate levels of non-forest (15–25%) with interspersion below 50 and moderate levels of pine forest with interspersion above 60. Occupancy in (b) is 0.5 as a result of higher levels of non-forest (>45%) and interspersion of non-forest above 60. (White=water, light gray=non-forest, dark gray=deciduous forest, black=pine or mixed pine forest).

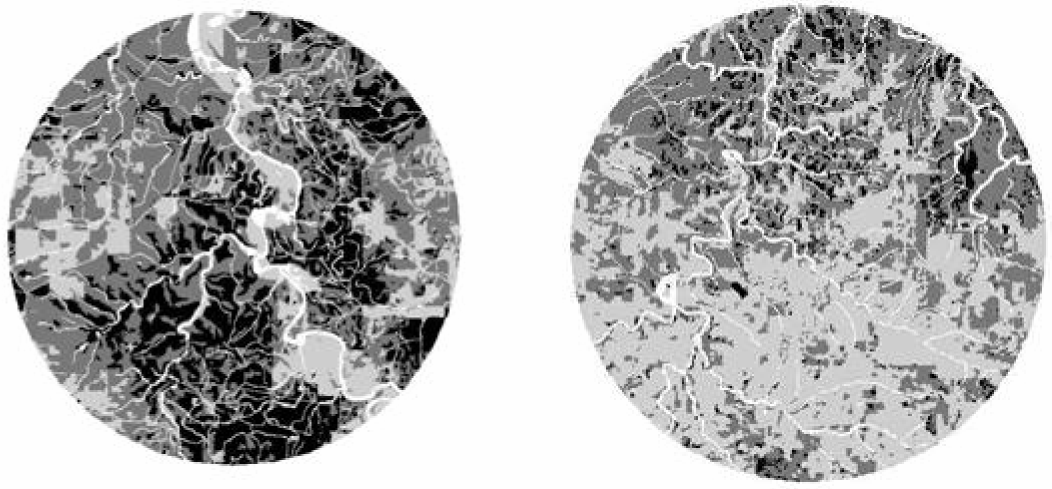


Figure 29. Examples of landscape patterns affecting predicted site occupancy of *M. lucifugus* at 8 km landscape scale. Occupancy in (a) is 0.5 as a result of moderate levels of pine (20–30%) with interspersion below 55 and low levels of non-forest with interspersion below 60. Occupancy in (b) is 0.1 as a result of higher levels of non-forest (>30%) and interspersion of non-forest above 60 and lower levels of pine (<20%) with interspersion above 60. (White=water, light gray=non-forest, dark gray=deciduous forest, black=pine or mixed pine forest).

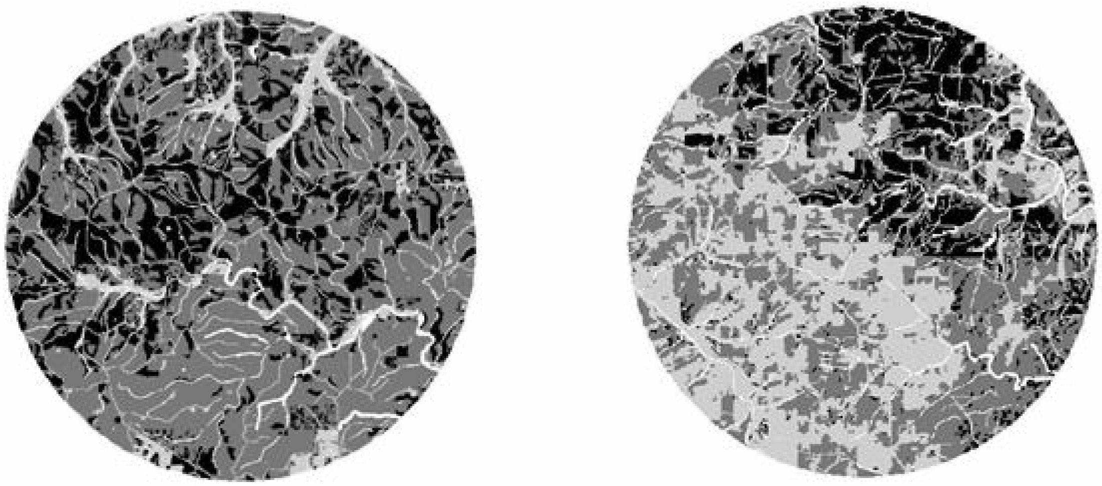


Figure 30. Examples of landscape patterns affecting predicted site occupancy of *L. cinereus* at 8 km landscape scale. Occupancy in (a) is 0.7 as a result of moderate levels of non-forest (25–35%) with interspersion above 70 and interspersion of oak-pine above 60. Occupancy in (b) is 0.4 as a result of higher levels of non-forest (>45%) and low levels of oak-pine with less interspersion of both. White=water, light gray=non-forest, dark gray=deciduous forest, black=pine or mixed pine forest).

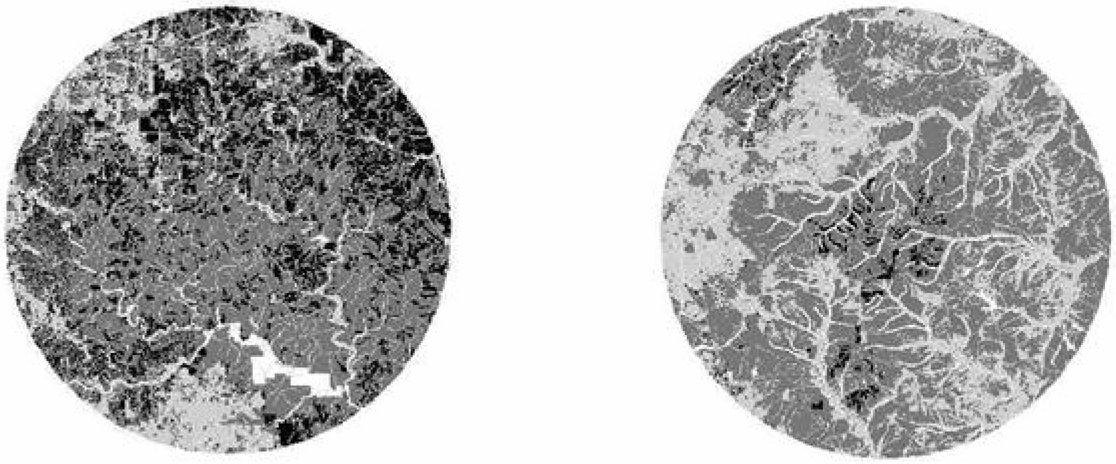


Figure 31. Examples of landscape patterns affecting predicted site occupancy of *N. humeralis* at 8 km landscape scale. Occupancy in (a) is 0.7 as a result of moderate levels of pine (25–35%) with interspersion above 60 and low levels of non-forest with interspersion below 70. Occupancy in (b) is 0.1 as a result of higher levels of non-forest (>25%) and interspersion of non-forest below 55 and lower levels of pine (<15%) with interspersion below 50. (White=water, light gray=non-forest, dark gray=deciduous forest, black=pine or mixed pine forest).

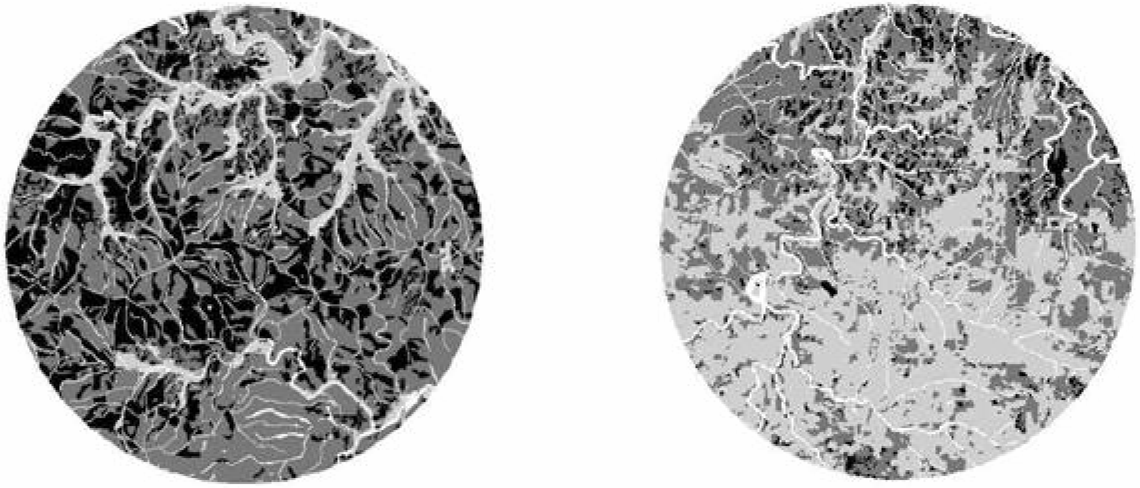
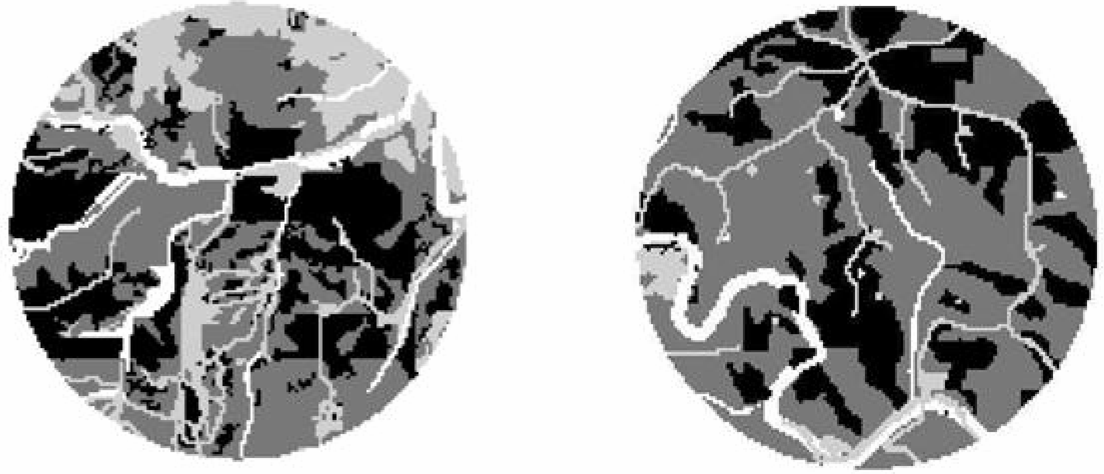


Figure 32. Examples of landscape patterns affecting predicted site occupancy of *E. fuscus* at 2 km landscape scale. Occupancy in (a) is 0.9 as a result of moderate levels of non-forest (25–35%) with interspersion above 60 and interspersion of oak-pine below 70. Occupancy in (b) is 0.2 as a result of lower levels of non-forest (<15%) and moderate levels of oak-pine with less interspersion of both types. (White=water, light gray=non-forest, dark gray=deciduous forest, black=pine or mixed pine forest).



CHAPTER 2

RESOURCE SELECTION BY FORAGING EASTERN RED BAT, (*Lasiurus borealis*) IN THE OZARK REGION OF MISSOURI.

ABSTRACT

Bats represent nearly 20% of mammal species worldwide and play key roles in temperate forest ecosystems. Effective conservation of bat populations requires understanding the associations between bats and their use of resources. By quantifying resource use over time and space, resource selection models provide insight into how a species meets its life history needs. We evaluated use of resource utilization functions (RUFs) to assess habitat, landform and landscape factors affecting foraging resource use by female red bats, *L. borealis*, during the maternity season. We found, on average, foraging use was highest for low canopy cover deciduous forest patches on ridges and upland drainages in areas close to non-forest edge and with relatively high road density. Resource selection for this demographic group is highly variable among individuals, geographic location, stage of lactation and temperature regime. The strong positive relationship between edge factors in a forested landscape suggests that gaps within mature forests as well as the presence of non-forest patches will provide good foraging habitat for *L. borealis*. The variability in individual responses to resource attributes suggests that management strategies that provide a range of composition and structural diversity will favor foraging use by *L. borealis*.

Introduction:

Bats represent nearly 20% of mammal species worldwide (Simmons 2005), and demonstrate higher diversity of behavior, diet, and morphology than any other mammalian order. In temperate latitudes, insectivorous bats play key functional roles as predators of insects in terrestrial ecosystems. Declining bat populations are a conservation concern for land-management agencies throughout North America (N. A.) (Kunz and Racey 1998). As with other wildlife, bat conservation has focused primarily on rare and endangered taxa (Pierson 1998). However, because of their role in ecosystem health, Pierson (1998: 318) suggested widespread or abundant species may be the most ecologically and economically important. Relatively abundant species provide opportunities to highlight conservation emphasis areas that can be applied to rarer species (Agosta 2004).

Effective management for bat populations is dependent on our understanding associations between bat populations and their habitats. Habitat refers to resources and conditions present in an area that produce occupancy, survival and reproduction, by a given organism. Habitat implies more than vegetation or vegetative structure, it is the sum of the specific resources that are needed by organisms (Thomas 1979). Habitat (resource) use is typically understood as the extent to which different resources are used (Garshelis 2000). It is assumed that high quality resources will be used more than low quality ones, that availability is not uniform, and that use may change with availability (Manly et al. 2002).

For many bat species, resource relationships are poorly understood. In contrast to most small mammals, bats are highly mobile, allowing them to access a wide range of habitats. Historically, the importance of foraging resource selection to conservation of forest bats has been viewed as secondary to importance of roost selection (Kunz 1982). Loss or modification of roosting and foraging habitat, or their juxtaposition, may affect critical life history parameters, such as birth rate or adult survivorship. Recent advances in radio-tracking and bat-detector technology have allowed for significant progress in our understanding of bat–resource relationships (Barclay and Brigham 1996, Fenton 2003), but there continues to be a lack of quantified information to address foraging habitat use by forest bats (Lacki et al. 2006). Factors potentially influencing the distribution of foraging bats include the distribution of prey (Barclay 1985), energetic costs associated with foraging in the habitat (related to wing morphology) (Aldridge and Rautenbach 1987, Brigham et al. 1997), ability to detect and locate prey in the habitat (related to echolocation call structure) (Simmons and Stein 1980) (Neuweiler 1989) Fenton and Griffin 1997), risk of predation in the foraging area, proximity of the foraging area to drinking water, and level of human disturbance in the foraging area.

Lasiurus borealis typically begin foraging at dusk; and may forage throughout the night (Kunz 1973). Prey species are diverse and include Coleopterans, hemipterans, lepidopterans, homopterans, and hymenopterans (Carter 1998, Whitaker 1972). Habitat types reported for this species include upland and bottomland hardwoods, pine, and non-forest (Hickey 1987, Carter

1998 , Hutchinson and Lacki 2000, Mager and Nelson 2001). *Lasiurus borealis* activity may be less affected by stand age than other species.

Resource selection is a multilevel, hierarchical process (Johnson 1980, Senft 1987) referring to the behavioral process whereby a species searches for features within an environment that are directly or indirectly associated with supplying factors needed to survive, reproduce, and persist. If an individual or species demonstrates disproportional use of any factor, then selection is inferred for those criteria (Block and Brennan 1993). “Selected” resources are used more often than random and “avoided” resources are used less often than random.

By quantifying resource use over time and space, resource selection models provide insight into how a species meets its life history needs. Typically, resource use studies compare used to available resources (Manly et al., 2002). Used resources are commonly defined by the resource attributes at telemetry relocation points (Erickson et al. 2001). Several interacting factors including pre-adaptation to certain environmental cues, exposure to predation or disease, location of resting sites or prey species may play important roles in resource selection. Available resources are quantified within a spatially and temporally defined area that the researcher considers “available” to the animal. Manly et al. (2002:1) defined the availability of a resource as “the quantity accessible to the animal (or population of animals) during that same period of time.” Resource availability infers accessible and obtainable physical and biological components and may contrast the abundance of resources, which refers only to their quantity in the environment, irrespective of the organism's ability to procure them (Buskirk and Millspaugh 2004). Measuring resource availability is important in understanding resource selection, but in practice it is not always possible to assess from an animal's point of view (Litvaitis and Kane 1994). Quantification of availability usually consists of *a priori* or *a posteriori* measure of the abundance of resources in a defined area.

In contrast to most resource selection analysis methods, the utilization distribution (UD) approach uses a probability density function (Silverman 1986) that quantifies an individual's or group's relative use of space (Kernohan et al. 2001). It depicts the probability of an animal occurring at each location within its home range as a function of relocation points (White and Garrott 1990:146). The UD has been used to relate relative space use to resource attributes in a spatially explicit way (Marzluff et al. 2004). Use of the UD to analyze resource use by foraging bats quantifies this relationship by providing a continuous measure of use throughout the area of interest. Advantages of using the UD include quantifying use with a continuous metric, reducing the impact of location error, reducing concerns about independence of points (Swihart and Slade 1997) and considering the entire distribution of animal movements instead of focusing solely on individual sampling points.

This study is one component of a cooperative project between the USDA, Northern Research Station (NRS) and the Mark Twain National Forest (MTNF), focused on conservation of forest bats. Our objectives were (a) to evaluate the use of resource utilization functions (RUFs) to test the hypothesis that habitat, landform and landscape factors affect foraging resource use and (b) to document individual variability in space use by female *L. borealis* during the spring and summer maternity period.

METHODS:

Study Area

We studied *L. borealis* in two landscapes within the Salem Plateau physiographic region, Ozark Highlands aquatic sub-region of Missouri (Sowa 2005) (Figure 1). A pine-savanna restoration project (Pineknot) encompassing 4100 hectares represented our un-fragmented landscape; the landscape within 10 kilometers of this southern unit was 7.5 percent non-forest and 92.1 percent forest (Table 1). Historic land cover within the uplands primarily consisted of shortleaf pine (*Pinus echinata* Mill.) and mixed shortleaf pine with black oak (*Quercus velutina* Lamark), scarlet oak (*Q. coccinea* Muench.), and white oak (*Q. alba* Linnaeus) with an open understory of grasses and shrubs. Occasional prairie and savanna openings were also common in areas along river bluffs. Two oak-savanna restoration projects representing 1500 hectares represented our fragmented landscape; the landscape within 10 kilometers of this northern unit was 40.6 percent non-forest and 59.1 percent forest (Table 1). Historic land cover within the uplands consisted of open woodlands and savannas comprised of post oak (*Quercus stellata* Wang.), black oak, and white oak, with an understory of shrubs and grasses such as big and little bluestem (*Andropogon gerardii* Vitman., *Schizachyrium scoparium* Michx.) (Missouri Department of Conservation 2006). Within each landscape, potential bat trapping sites associated with water features were field checked and feasible trapping sites identified. Trapping locations were selected randomly from the set of feasible trapping sites.

Capture and Handling of Bats

Bats were captured in ground level (3 – 10 m high) mist nets (70/2 denier, 38 mm) at the randomly selected watering sites or at travel corridor locations in the study areas. All capture and handling procedures were approved by the University of Missouri's Institutional Animal Care and Use protocol. Information on species (identification criteria following (Hamilton and Whitaker 1979)), mass (measured to nearest 0.1 g with digital electronic scale (Ohaus®, PS Series)), forearm length (measured to nearest 0.5 mm with calipers (Forestry Suppliers Inc., Jackson, Mississippi)), sex, and reproductive condition were collected. Reproductive condition of females was assessed by palpation and visual examination as pregnant (fetus present), lactating (milk expressed from mammary gland) or post-lactating (hair absent around nipple, no evidence of active milk production). We classified bats as adults or juveniles by shining a light through the wing membrane and observing degree of fusion of the finger joints (Anthony, 1988). Lactating *L. borealis* were instrumented with a 0.6 g ± 0.02 SD (Blackburn, Nacogdoches, Texas) or a 0.52 g ± 0.02 SD (model LB-2, Holohil Systems, Inc. Ontario, Canada) radio transmitter attached between the scapulae using non-toxic surgical glue (Smith and Nephew United, Inc.). Individual bat weights were used to determine model of radio to use; entire transmitter package mass represented 4.4% ± 0.5% (mean + SE) of bats body weight (two bats exceeded the 5% rule by 0.2 and 0.3%). After allowing the transmitter to bond to the skin (< 45 mins), bats were released at the point of capture by allowing them to fly from an open hand and direction of flight was determined. Bats were monitored for initial movements the night of release to determine approximate direction of flight from the release site; however, locations from the tagging night were not used in analyses.

We continued capture and tagging activities while tracking bats until 10 – 15 individuals had been tagged, we resumed capture and tagging activities when the number of bats with transmitters fell below five. A minimum of five bats with active transmitters were maintained throughout the maternity period (June 1 through August 15th).

Radiotelemetry

We radio-tracked bats in summers of 2001--2003 using Advanced Telemetry Systems (ATS) receivers (Model R2000/2100) with either 5 element antennas mounted on vehicles (Telonics RA-4A VHF) or 14 element antennas (Telonics RA-4C VHF) mounted 9 meters above the ground on a receiver tower (Amelon et al. 2003, Woeck 2003). Geographic coordinates of all tower locations were determined using a Trimble™ Global Positioning System (GPS) (1-3 meter accuracy). Coordinates of mobile positions were determined with Garmin™12XL GPS units (5-7 meter accuracy) (http://users.erols.com/dlwilson/gpsacc). Bearings to the nearest $\pm$ 0.5° were measured with an electronic compass (KVH

Industries, Inc; C100™ Compass Engine) calibrated to eliminate interference from mounting materials and attached to a digital readout at the base of the fixed tower or inside the vehicle.

We radio-tracked bats each night for the life of the transmitter (approximately 10 – 21 days) or until the transmitter was groomed from the bat. Two observers at towers and 2 – 4 in vehicles obtained simultaneous azimuth bearings for triangulation. The temporal sampling scheme was based on the number of bats with active radios and their relative locations. Constant intervals between bat readings were used each night and ranged from 5 – 15 minutes (Walsh and Mayle 1991). Bats were scheduled for simultaneous bearings each night at pre-specified times; and times were rotated each night so locations represented the range of times bats foraged. We attempted to determine each bat's location at least once per hour during the night. Azimuths were determined as the center of the bisected angle between the nulls (Fuller et al. 2005). As bats flew, the fluctuating polarization of the transmitting antenna caused the signal to fluctuate. Foraging bats tend to work an area in a predictable interval and pattern that can be monitored between readings (Entwistle et al. 1996, Wai-Ping and Fenton 1989, Winkelmann et al. 2000); we used the interval between bats to isolate the range of signal fluctuation for the next bat in sequence. This allowed observers to work with a narrow range as the time of each scheduled reading approached. During rapid movements by the bats or when a single bat was being tracked; readings were sometimes taken more frequently. We used watches set automatically to the atomic clock (http://usno.navy.mil; Master Clock

#2) to obtain simultaneous bearings. Due to the relatively short range of the transmitters, all observers taking bearings on a particular bat had to be relatively close; tower distance 50 – 1500 m or vehicle distance approximately 20 – 700 m. With each reading, information on relative signal strength and movement information (whether moving quickly towards or away from a location or foraging in a routine pattern) was recorded by each observer, when a bat was particularly close to one of the observers we used a "close approach" to validate triangulated locations (Smith and Racey 2005). We communicated by FM radios or cellular telephones to confirm readings and to determine if observers needed to relocate.

We determined standard deviation of directional bearings and bearing error for each observer based on 6 receiver locations with stationary transmitters placed in multiple locations throughout the study area and with transmitters attached to a fiberglass pole mounted to a vehicle and driven at 5 mph within the study area. Locations of these transmitters were logged by time with a Trimble™ GPS (White and Garrott, 1990). The SD of the bearings averaged ± 4.1° and ranged from 1.7° – 7.7° for individual observers. Bearing error (absolute difference of observed bearing from true bearing) averaged ± 5.2° and ranged from 1º – 13º for individual observers. Bat locations were estimated from bearings with the computer program GTM (Sartwell 2003) using the Lenth maximum likelihood estimator (MLE) and estimated bearing SD for each observer (White and Garrott 1990). GTM is a Windows-based system that imports and incorporates geographic coordinate information, telemetry bearings, internally generated location estimates, and animal sightings as graphic data overlays on a base map(s). Locations with error polygons greater than 15 ha were not used. Error polygons of relocations used in the analysis had a mean size of 4.1 ± 0.11 ha.

Estimating the Utilization Distribution

Bat locations determined by triangulation or visual observations were entered onto a georeferenced base map using Arc-Info GRID® and Arc-View 3.2 (ESRI: Environmental Systems Research Group, Inc., Redlands, California). Thirty to 50 locations are sufficient for kernel methods to accurately define a home range (Seaman et al. 1999). We estimated a UD for female *L. borealis* with ≥ 30 foraging locations. We estimated UD's using fixed-kernel estimation using the KDE folder (Beardah and Baxter 1995) in MATLAB (MathWorks, INC; Version 5.3 (R11)). We used the plug-in method (Gitzen et al. 2006) and smoothed the x and y coordinates independently. We used 99% kernel isopleths to delineate foraging areas (White and Garrot 1990). We excluded the outer 1% of the utilization distribution (by volume) to reduce potential bias from lowest use areas of the UD (Millspaugh et al. 2006). Foraging areas only include roost locations if the bat was actively foraging near the roost location at a scheduled reading. Data on roost locations is analyzed in a separate analysis.

Relating Resource Utilization To Patch And Landscape Characteristics

We hypothesized that habitat type, landform, landscape composition and landscape diversity would influence foraging behavior. We predicted that female bats would forage in locations: (a) based on relative amounts of important habitats and landforms available in the landscape (Best and Hudson 1996, Arnett and Hayes 2000, Fenton and Bogdanowicz 2002); (b) with minimum distances between roosting, foraging and watering areas (Rydell 1989, Adams 2000, Luszcz 2001); and (c) that provide the best interspersion and diversity of roosting, foraging, commuting and watering opportunities across the landscape (Wethington et al. 1996, Feldhammer et al. 2001, Bonney et al. 2002, Henry et al. 2002). Based on these hypotheses, we developed a generalized foraging model:

Foraging Use = [LANDFORM] + [LANDCOVER] + [EDGE] + [DIVERSITY]

Landform was represented by 4 category levels with slopes as the reference category, landcover was represented by 5 category levels with deciduous forest as the reference category; edge and landscape variables were continuous variables resulting in the model:

$$\begin{aligned} RUF_{(\text{foraging})} = {} & \beta_{(\text{intercept})} + [\beta_{(\text{ridge})} + \beta_{(\text{lowlands})} + \beta_{(\text{upland drainage})}] + [\beta_{(\text{non-forest})} + \beta_{(\text{water})} + \\ & \beta_{(\text{mixed forest})} + \beta_{(\text{urban})}] + [\beta_{(\text{dist forest edge})} + \beta_{(\text{road density})}] + [\beta_{(\text{percent water})} \\ & + \beta_{(\text{diversity index})} + \beta_{(\text{percent forest canopy})}] \end{aligned}$$

We estimated resource use ($RUF_{(\text{foraging})}$) at each grid cell in the UD as the average height of the kernel density estimate. We related the resource attributes (independent resource variables) to the height of the UD (z-value; dependent resource variable) using multiple linear regression. We examined the covariates in the model for multicolinearity by calculating tolerance values (range 0.74 – 0.91) (PROC REG (SAS 2001)). The kernel analysis induces correlation among adjacent cells in the UD; this spatial correlation requires an adjustment so the variance estimates for individual model coefficients are not underestimated (Marzluff et al. 2004). Spatial autocorrelation is relevant when inference is for an individual animal. Spatial autocorrelation only effects the variance estimates and not the parameter coefficients (McCullagh and Nelder 1983) (i.e. estimates of coefficients are unbiased and variance goes to 0 as sample size goes to infinity). In our analysis, individual bats are the experimental unit, so spatial autocorrelation in the locations of any particular animal can be ignored because they do not affect the parameter coefficients. Because the individual points are no longer the experimental units, any autocorrelation in the points is irrelevant (Aebischer et al. 1993, Erickson et al. 2001). We fit the above multiple regression with PROC MIXED in SAS® version 9.1 (Copyright© 2002-2003 by SAS Institute Inc., Cary, NC, USA). We compared our global landscape model and the null model using an objective model selection criterion (Akaike's Information Criteria, AIC) (Burnham and Anderson 2002) and a likelihood ratio test.

We fit a RUF for each individual bat (Type III design of Manly et al., 2002); and then calculated an average RUF for the population or other groups by a simple average of the unstandardized coefficients across animals with variance computed using

$$Var\left(\hat{\bar{\beta}}_{j^*}\right) = \frac{1}{n^2}\sum_{i=1}^{n} SE^2 \ \hat{\beta}_{ij^*}$$

In this analysis, coefficients for each resource for each bat become the independent, replicated measures of resource use (Marzluff et al. 2004, Millspaugh 2006). We tested H_0 that the population $\bar{\beta}=0$ for each coefficient in the population RUF with a t-test and report p-value or 95% confidence intervals (CI). Sample size was the number of bats; therefore, we used coefficients for resource variables from models without the spatial autocorrelation function. Coefficient values significantly greater than 0 indicated use of a resource greater than expected; and coefficients significantly less than 0 indicated use of a resource less than expected.

We evaluated relative use of each resource by the study population of *L. borealis* by assuming that each bat's use of the area was independent (*L. borealis* are believed to be solitary). To evaluate the population over the maternity period we evaluated all bats as one group. To evaluate geographic differences we evaluated bats by north or south units. Since we were not sure whether stage of lactation or a relationship to climatic conditions would influence resource use over the season, to evaluate seasonal differences, we developed 2 sets of groups, one based on stage of lactation, the other on temperature regime. We hypothesized foraging patterns would reflect a balance between energetic needs of the female bat (stage of lactation) with locations constrained by the volancy stage of her pups. For stage of lactation groups, we estimated that the period from parturition to approximately 26 days represented the stage when the pups were non-volant and rapidly growing. From approximately day 27 to 52 represented the period when pups were mostly non-volant but beginning to fly short distances (based on observation of pups with mothers and dates when juveniles were first captured). From approximately day 52 to the end of the monitoring period, pups were volant or weaned. Based on these dates, we divided the maternity season into 3 periods and assigned each bat to the group coinciding with the dates it was tracked. For the temperature regime groups, we calculated mean temperature for each 10 day period from June 1 – August 15 (May 21 – August 25) and compared histograms of temperature to divide each season into 3 distinct temperature groups. Mean temperatures of tracking periods were: Group 1 <19°C, Group 2 >19°C and <26°C and Group 3 >26°C.

Patch and Landscape Covariates

Landcover, landform, distance to edge and canopy density were measured at each grid point in each bat's UD by intersecting individual bat UD's with georeferenced landscape data using ArcInfo® GRID functions. Landscape data were derived from 30-m x 30-m resolution Landsat Thematic Mapper satellite imagery classified into 16 vegetative land cover classes http://www.cerc.usgs.gov/morap/ (MORAP 2005). Landcover classes were condensed from 16 classes using ArcInfo® (ESRI, 1995) to reflect 6 land cover types: (1) deciduous forest and woodland representing oak (*Quercus spp.*), hickory (*Carya spp.*) and mixed hardwood types (2) pine and oak-pine forest and woodland representing shortleaf pine (*Pinus echinata* Miller) and oak-pine (*Quercus spp.-P. echinata*) types (3) bottomland hardwoods representing sycamore (*Platanus occidentalis* Linnaeus), cottonwood (*Populus deltoides* Bartram*)*, elm (*Ulmus americana* Linnaeus*, U. rubra* Muhlenberg*)*, ash (*Fraxinus pennsylvanica* Marshall) and mixed hardwood types (4) non-forest representing grassland and shrub types including cool or warm season grassland with forbs and shrubs (5) urban representing areas of human development and (6) water including swamp, marsh, wet herbaceous and open water habitats.

Landforms were derived from a digital elevation model (DEM) using a Topographic Position Index (TPI) (Jenness 2006). TPI is calculated as the elevation of a particular cell minus the mean elevation of cells in a moving window neighborhood divided by the standard deviation of the mean cell elevation. Slope and aspect layers were created from the digital elevation model. The slope layer along with 2 moving windows of different sizes representing a large and small scale were used to evaluate a cell's elevation compared to the large scale variation and small scale variation in elevation to define 5 landform classes: bottomlands, upland drainage, S&W slopes (>5%), N&E slopes, ridges (< 5%) (Tirpak et al. 2007).

Distance to edge (DISTFOREDGE) was calculated as the distance (m) to the nearest edge between non-forest and forest cover types. Percent tree cover was derived from 500-m data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument on board the National Aeronautics and Space Administration's (NASA's) Terra spacecraft. The data is the finest-scale global forest information measured by a multiresolution calibration method. Percent tree canopy cover is estimated from a regression tree algorithm (Hansen et al. 2002). The output of the algorithm is the percent canopy cover per 500-m MODIS pixel and represents the amount of skylight obstructed by tree canopies equal to or greater than 5 m in height (Hansen et al. 2003) (MODIS product in tile format for canopy cover is available online at the EROS data center http://edcimswww.cr.usgs.gov/pub). We combined the water class from the landcover classification with the county level perennial stream coverage (MSDIS, 2004) to identify water sources. Similarly, a county-wide roads and trails layer (MSDIS 2004) was used to calculate road density (meters per hectare). Landscape diversity was calculated as a Shannon-Weaver diversity index based on the amount of each landcover.

We estimated the individual covariate effects on foraging use by geographic location. For each covariate evaluated, we estimated foraging use over the range of values for that covariate in the geographic unit while holding all other covariates at their mean value. We plotted predicted foraging use for the range of observed values in our data for the explanatory variables with significant effects in either geographic unit.

We used the parameter coefficients from each geographic landscape model to predict landscape level use across study area landscapes by calculating use estimates for each 30 x 30 m pixel with ArcInfo® and projected the results using our DEM as a reference with ArcScene® (ESRI, 2005).

Results:

We radio-tracked 64 lactating *L. borealis* for 3 – 21 days. Recaptured individuals showed no signs of injury and had maintained weight at or slightly above initial capture; we therefore concluded that transmitter mass did not negatively affect flight performance of the tagged individuals. We estimated UD's for n=53 bats with $\geq$ 30 locations ($\overline{X}$=79, range 31 – 163) (Table 2). Numbers by early, mid and late lactation groups were 18, 15, and 20, respectively. Numbers based on mean temperature of the tracking period were 18, 20, and 15 for low, medium and high temperature, respectively. Although the numbers in these groups are similar, individual bats in each group vary (Table 2).

Individual home range size (99%) ranged from 202 – 3727 hectares (ha) ($\overline{X}$=1357; SE=122); smoothing (h) values used to compute the UD ranged from 30 – 591 (Table 2). Most bats had an area of high use near their roosts and multiple areas of lower use (Figures 2 and 3). By groups, mean number of days tracked ranged from 11 – 19 (SE=0.78 – 1.67) and mean home range size ranged from 1040 – 1587 ha (SE 122 – 333) (Table 3). Size of foraging areas were not correlated with number of locations or days tracked (r^2=0.086, *p*=0.50; r^2=0.076, *p*=0.55, respectively).

Individual bats varied considerably in their use of specific resources; the global RUF model was significantly better than the null RUF model for 36 of the individuals (70%) (Table 4). Population level RUFs evaluated by groups are presented in Tables 5 – 11. Considering all bats, the average RUF indicates highest use of ridges and upland drainages associated with forested patches. Used areas are close to edges and have relatively high road density.

Effects of land cover on foraging habitat use by geographic location, stage of lactation and mean temperature indicated that use of deciduous forest, mixed forest, non-forest and water were similar for all groups (Tables 5 – 8). Urban landcover was used less than deciduous forest by each group; however, group T2's use was not significantly different than deciduous forest (Table 8). Foraging use associated with landform indicates differences among groups. Bats in the southern unit used all landforms at similar levels; while those in the north used ridges and upland drainages more than side slopes (Table 6). Based on stage of lactation, bats during early lactation used other landforms significantly more than side slopes; while those in mid-lactation used all landforms at approximately equal rates (Table 7). Based on temperature regimes during tracking period, bats tracked during the lowest temperatures selected upland drainages more than side slopes; bats tracked during the highest temperatures used both ridges and upland drainages more than side slopes (Table 8).

Patterns of foraging use associated with measures of edge were fairly strong across the entire population and northern unit (Tables 5 and 6). Among temperature and lactation groups, foraging use was positively associated with road density for high temperature regime and mid-lactation groups (Tables 7 and 8); negatively associated with distance to edge in mid and late lactation and low and mid temperature regimes; and positively associated with the high temperature group.

Effects of landscape diversity factors indicated foraging use in the southern unit was positively associated with canopy cover. In the northern unit, percent water was negatively associated with foraging use (Table 6).

We examined factors with significant effects and high percentages of individual bat parameter estimates associated with the direction of significant effects (i.e.73% and 83% of individuals had a positive association with ridges and road density, respectively) by groups within units (Tables 9 – 11). Within the north unit, effect of upland drainages suggested higher effects for groups later in the season (late lactation, medium and high temperature regimes). Effect of road density suggested earlier stages of lactation and/or higher temperatures were associated with importance of this factor.

Predicted effect of landscape factors on foraging use across our study area using parameter coefficients from each unit indicated differences between the northern and southern groups of *L. borealis* (Figure 4). Predicted $\mathrm{RUF}_{(\mathrm{foraging})}$ across the landscape supports the importance of forested lowlands and ridges to foraging use by *L. borealis* (Figures 5 and 6).

Discussion

We developed RUFs to investigate factors affecting foraging habitat use by female *L. borealis* during the maternity period. Our results suggest that resource selection for this demographic group is highly variable among individuals, geographic location, stage of lactation and temperature regime. However, on average foraging use was highest for low canopy cover deciduous forest patches on ridges and upland drainages in areas close to non-forest edge and with relatively high road density. We focused on resource use by groups of bats defined by biologically relevant spatial and temporal differences.

Lasiurus borealis typically began foraging at dusk, often when there was still enough light to observe their behavior. Individuals were highly habitual in their use of foraging areas, usually returning to them night after night. Based on acoustic detections in the area (See Chapter 1), *L. borealis* were most active before midnight although some activity continued further into the night. Kunz (1973) similarly reported some individuals foraging throughout the night. Home ranges were among the largest found for temperate insectivorous bats. Previously reported home ranges for *L. borealis* are 10-20 ha in the Galapagos Islands (McCracken et al. 1997), $\bar{X}$=334 ha in upland hardwoods in Kentucky (Hutchinson and Lacki 2000), $\bar{X}$=453 ha in South Carolina (Carter 1998) and $\bar{X}$=82 ha for adult females in Mississippi (Elmore et al. 2004). Only 9 of 53 individual home ranges in our study were smaller than 500 ha; the mean (1357 ha) was nearly three times that of other studies reported. Several factors may influence home-range size including foraging mode, availability, distribution of food in space and time and commuting distance. Similarly sized bats commute over distances of 1– 50 km from their roosts to foraging areas (Fenton 1990, Sahley et al. 1993, Fenton 1997). Some small species fly remarkably long distances (Amelon et al. 2000, O'Donnell 2002), which in turn results in very large home ranges. *Lasiurus borealis* are adapted for fast, open air flight (Jung et al. 1999) and migrate over long distances (Cryan 2003); their ability to forage over large areas is consistent with their morphology and behavior. Exploitation of larger areas has been reported for several species of bats (Wai-Ping and Fenton 1989, Entwistle et al. 1996), indicating detailed knowledge of locations within a home range with high prey availability. Food intake may be maximized by preferentially feeding in such sites (Entwistle et al. 1996). We observed highly predictable foraging behavior and space use in the majority of our individual bats. Although overall home ranges were large, most individuals concentrated use in relatively small core areas (Figure 1) and there was fairly high spatial overlap between foraging and core areas of individual bats within each geographic unit.

The larger home ranges measured in our study are partially due to our use of the 99% kernel to describe continuous use. Most kernel analysis programs have a 95% maximum kernel. Another explanation relates to the nature of the equipment used. Transmitter signals can be detected at greater distances with higher gain receiving antennas. Greater reception range and more precise directionality can be obtained by using larger antennas and elevating receiving antennas (Anderka 1987). Use of an elevated tower system greatly enhanced reception distance of bat transmitters (Amelon et al. 2003). Additionally, we had a relatively large crew that could locate in separate locations across the area being traversed by the bats; allowing us to determine locations further away from the central area (Figure 1).

Foraging resource use by L. borealis

Lasiurus borealis have long narrow wings adapted for rapid, poorly maneuverable flight. These traits are generally associated with foraging activities along edge habitats of agricultural fields, streams, and other linear landscapes or in forest with open canopies or above the forest canopy (Hickey 1987, Hickey and Fenton 1990, Salcedo et al. 1995). *L. borealis* have been found to prefer open stands (Sealander and Heidt 1990, Carter 1998 , Jung et al. 1999, Elmore et al. 2004) and areas with water (Furlonger et al. 1987, Hutchinson and Lacki 2000) and are associated with many, well interspersed patches of non-forest and pine (See Chapter 1).

Landform - Our results for the population and northern landscape group of eastern red bats, indicated foraging activity was positively associated with ridges and upland drainages compared to side slopes (Tables 5 and 6). Associations for stage of lactation and temperature groups were more variable. Bats during early lactation were positively associated with bottomlands; bats during mid-lactation showed no apparent association with landform; and females in late lactation were positively associated with ridges and upland drainages (Table 6). By temperature regime, landforms were equivalent in the lowest temperature period; while ridges and upland drainages were positively associated with both higher temperature groups (Table 7).

Predicted use by landform indicated very similar patterns among both north and south groups of bats (Figure 5); in both groups, slopes were used less for foraging than any of the other landforms.

Landcover - The population as a whole and each group (geographic location, stage of lactation or temperature)were negatively associated with urban landcover compared to deciduous forest (Table 5). We expected urban landcover to have a positive influence on at least the northern group of bats. One of 9 south unit and 15 of 43 north unit bats were visually observed foraging at lights (either at rural residences or in rural towns) at least once during their tracking period. Several individuals foraged along a fairly regular "circuit" starting at one side of a small town and moving rather systematically between lights at various businesses or residences. McCracken et al. (1997) and Hickey (1996) similarly reported *L. borealis* concentrating foraging activity around street lights.

A close examination of the generalized landcover maps we used indicated that urban land cover was only designated for sites with no vegetative cover. Many individual residences and housing areas outside the rural towns, where bats were frequently seen, had relatively high vegetative cover and were; therefore, included in other vegetative categories. This is a relatively common limitation of large scale vegetative maps (Wiens 1989). Because *L. borealis* have commonly been noted foraging at street lights, future analysis of these data may be better served to incorporate either a distance to urban factor or an additional urban GIS coverage to capture locations where streetlights are common.

The only other landcover factor with a significant association with foraging activity was water which had a positive effect for the north unit (Table 6). We expected to see this result at the full population level as well. *Lasiurus borealis* roost in foliage of deciduous trees during summer where they can be exposed to high summer temperatures; which could contribute to a fairly high evaporative water loss. Additionally, lactating females should have an increased need for water. Many of our tagged bats would initially commute to water and then move to foraging sites. Hutchinson and Lacki (1999) determined *L. borealis* in mixed mesophytic forests of Kentucky foraged over water more than expected. They also showed foraging areas were associated with stream corridors. While only one group in our study indicated a positive association, 37 of 52 individuals had a positive parameter coefficient for this factor (Table 5). On average, percentage of water in our landscapes was low (< 1%). The southern unit had very low percent surface water; most streams were losing streams (discharging water into subsurface outlets) and very few manmade ponds were present. While for this factor, we did supplement the generalized landcover maps with additional known locations of water, the overall very low amounts of surface water, especially in the southern landscape may explain the lack of significant association at the population level.

Lack of significant association (other than those noted above), indicates that non-forest, mixed forest and deciduous forest are similarly associated with foraging use by *L. borealis*. At the population level, numbers positively affected by non-forest and mixed forest were 22 and 27 of the 52 individuals respectively (Table 5).

Patterns of predicted foraging use by landcover were very similar even though significant associations were only supported for the northern group (Figure 5). This most likely relates to the much smaller sample size in the southern group. The southern group had slightly lower overall association with non-forest, which can be explained by the much lower percentage of non-forest in the southern landscape.

Edge - The population, northern unit, and mid-lactation group were positively associated with road density and negatively associated with distance to edge (Tables 5, 6 and 7). The highest temperature group indicated a positive association with both (Table 8). The late lactation and low temperature groups indicated only a negative association with distance to edge; the southern landscape and early lactation group indicated no significant association (Tables 7 and 8).

The differences observed in association between foraging activity and geographic units could reflect individual variability in use of heterogeneous landscapes. The southern unit is characterized as a contiguous forest landscape with a few large openings of pasture mostly located in alluvial areas. Owing to steep topography and low human population density, roads are mostly unpaved access roads. The landscape in the northern unit is characteristically less steep topographically with high frequency of forest clearings (mostly pastures), well distributed across gentler sloping areas. Human population density, although low, is higher than in the southern unit. With increased density of human populations, more paved roads and many unpaved access roads were present in the landscape. These landscape differences also produce additional edge habitat. Although we found no differences in use between forest and non-forest at the population level, there was considerable variation in magnitude and direction of associations with landscape features by individual bats. Forty-two percent of individuals were positively associated with non-forest and 71% were negatively associated with distance to edge habitat. These factors together support the importance of edge habitat to eastern red bats. Similar to other studies, our results indicate, *L. borealis* are adaptable to a variety of habitats but show strong associations with either openings within forests (Hickey et al. 1996, Jung et al. 1999)or to open canopy forest (Hart et al. 1993, Elmore et al. 2004) suggesting the distribution of non-forest or canopy gaps may be an important resource characteristic.

Roads provide additional edge habitat and provide linear corridors for both commuting and foraging within a forested landscape. Our results indicate a positive association with road density for 43 of the 52 individuals, further supporting the importance of edge habitat to this species.

Predicted foraging resource utilization in the northern (fragmented) and southern (unfragmented) landscapes showed several differences in foraging use between these groups. The relationship of resource use to distance to edge and was similar between these groups while relationships to other edge factors differed (Figure 4). Association with percent water in the landscape was negative for the south group and positive for the north group of bats. As noted previously, this is most likely due to the very low landscape percentage of water in the southern unit. Similarly, a positive association with canopy cover was indicated for the north group while no clear association was indicated for the south group. This result is also related to differences in the landscapes between these groups. The southern unit is primarily contiguous forest with very similar structure, whereas the north unit has much higher interspersion of openings in the canopy. This suggests that where the landscape is forested in the northern unit, *L. borealis* is associated with areas of fairly high canopy coverage. This supports the prediction that *L. borealis* forage above the canopy when foraging is associated with forested areas.

Predicted foraging resource use was strongly positive related to road density for the southern group and negatively related to road density for the northern group of bats (Figure 4). In heavily forested landscape of the south unit, roads are the primary edge habitat available over much of the area and therefore, provide foraging areas for this species. The negative association in the northern landscape reflects the much higher percentage of edge habitat. Edge habitat is not concentrated along road locations in this more highly fragmented landscape providing a greater number of foraging opportunities for *L. borealis*.

Ecological Implications

Temperate region bats are subject to selective pressures for both roosting and foraging habitats during the summer and migratory periods (Kunz 1982, Kunz and Lumsden 2003). Radio-tagging of small bats, to investigate questions about where they forage and their patterns of habitat use, is a relatively new approach. Most studies have evaluated ten or less individuals by demographic group (Miller et al. 2003). Despite their relatively small size, eastern red bats foraged over large areas. Our findings support the hypothesis that home-range size and foraging use reflect abundance and dispersion of food resources. Most studies that have used radiotelemetry to assess habitat use by bats while foraging have compared size of area used, associations with habitats in the landscape near roosting sites and the length of distance traveled in flight (Audet 1990, Clem 1993, Adam et al. 1994, Robinson and Stebbings 1997). Lactation is an energetically costly reproductive state (Racey 1982, Kurta et al. 1989, Kunz et al. 1995), and energy demands on reproductive females are likely high compared with those of non-reproductive bats (O'Donnell 2002). Owing to our large sample size of radiotracked bats, we were able to explore differences in space use during different stages of the maternity period. We found home range size to be consistent between geographic locations, stage of lactation and temperature regime (Table 3).

Data on forest bats have traditionally been analyzed using classification-based methods that place animal locations into distinct habitat categories for analysis (Conner et al. 2003, Miller et al. 2003). Frequency of animal locations among habitats is then either rank-order by habitat availability or compare among habitats scaled against the proportional availability of habitats in the landscape. Habitats are classified as selected, used at random, or avoided. Implicit to this approach is that the area of inference, or area of habitat available to the animal, is known and can be quantified. Among these, the method of Neu et al., (1974) has been used most frequently in studies of N. A. bats (Clark et al. 1993, Adam et al. 1994). Euclidean distance is another approach recently used to evaluate habitat use by bats (Conner et al. 2003, Elmore et al. 2004). In this method, the individual animal is the sampling unit and distances are estimated from locations to all available habitat types; these distances are then compared to a null model to determine if habitat selection occurred and to rank habitats in order of preference (Conner et al., 2003). These methods do not account for variability in the intensity of use among resource factors where locations were recorded.

Our use of UD's included estimating resource use throughout the home range as a continuous probabilistic process (Kernohan et al. 2001, Millspaugh et al. 2006). Inferences about resource use by bats are dependant on the estimated spatial extent of the area used, regardless of analysis method used. For species such as bats, where determining used locations at greater distances is problematic owing to limitation of transmitter size, increased bias may be introduced into the results as distant areas used, as well as those available, may be underestimated. An inherent strength of the RUF approach is the use of a continuous and probabilistic response variable that can be used to predict habitat use based on relative use of resource factors measured at each grid point within the home range (Marzluff et al. 2004, Millspaugh et al. 2006). The difference between our RUF approach and other UD approaches used in bat habitat studies relates to two issues. The first is evaluation of home range size. Most studies use the UD to define the extent of use area by kernel bands (usually 95%); then used locations are compared to available locations as defined by the home range or study boundaries (Menzel et al. 2001, O'Donnell 2001, Elmore et al. 2004). Secondly, our RUF approach quantifies bat habitat use of the landscape as a continuum of use classes determined from actual use locations rather than from the individual locations themselves. Availability, therefore, becomes relative to intensity of use rather than from an arbitrary boundary.

Our results point to several important considerations when evaluating resource use by bats. Inter-individual variation in resource use is very high, even among demographically similar bats of the same species. This suggests the importance of having a large enough sample size, by demographic group within species, to capture the range of variation to make valid inference to habitat use. While eastern red bats may be highly adaptable to different foraging habitats compared to other species, small sample sizes may not capture the magnitude of population variance and could lead to erroneous inferences.

The high variation in use observed among individuals in our study may simply indicate lactating *L. borealis* are capable of behavioral plasticity to meet demands of foraging and providing nourishment for growth and development of young. An alternative possibility is that habitat selection may be occurring at a different spatial scale. For example, Johnson (1980) and Manley (2002) describe habitat selection as a hierarchical process where selection occurs first at a geographic range then specific landscapes within that range, followed by a home range and then specific areas within the home range. In the case of *L. borealis*, due to their ability to cover large areas very quickly, and their broad diet base, selection at a larger landscape or geographic scale may be more important.

Implications for Conservation and Management

The strong positive association of foraging eastern red bats with forests and edge habitat suggests that gaps within mature forests as well as the presence of linear landscape features (including agricultural areas, pasture, utility corridors, roads and forested ridge tops cleared for wind energy facilities) provide suitable foraging habitat for eastern red bats. Our results indicate the importance of considering landscape context when making land management decisions for eastern red bats. In landscapes with low structural diversity, implementation of management practices that create openings and gaps within mid- and late-successional stands would improve their suitability for eastern red bats. However, in landscapes dominated by non-forest, contiguous patches of forest provide important habitat for these bats and our results suggest there may be an upper limit to amount of non-forest in a landscape for optimal populations of eastern red bats. The variability in individual bat response to resource attributes suggests that management strategies that provide a range of composition and structural diversity through the creation of openings or canopy gaps associated with ridges and upland drainages will favor foraging use by eastern red bats. Although forest type per se does not appear to be an important factor determining foraging habitat use, it is likely an important factor in roosting ecology as eastern red bats more frequently roost in deciduous forest trees (Perry and Thill 2003). Our predicted landscape foraging use indicates the importance of forests associated with streams and rivers to this species (Figure 6). Conservation and/or restoration of riparian forest is an important management objective for eastern red bats.

Eastern red bats are widely distributed and one of the more common forest bats in the eastern U. S. As predators of agricultural and forest beetles and moths this species is an ecologically important species of eastern forests. Recent evidence indicates large numbers of eastern red bats are being killed at utility-scale wind energy facilities, especially along forested ridge tops in the eastern US (Kunz et al. in press). These fatalities raise important concerns about cumulative impacts of land management activities and proposed wind energy development on eastern red bat populations. Our results indicate the importance of suitable foraging habitat associated with ridges and upland drainages; however, creation of edge habitats in association with wind facilities along forested ridge tops may contribute to the high fatalities of eastern red bat (Kunz et al. in press). Assessment of ecological impacts associated with management activities typically require base-line population estimates and demographic information (Munns 2006). However, virtually no data exist for any foliage-roosting species (O'Shea and Bogen 2003), either on regional or continental scales that would make it possible to conduct a meaningful assessment of cumulative management impacts at this time. There is an urgent need for estimating population sizes of bat species, especially migrating, foliage-roosting species such as eastern red bat.

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Table 1: Landcover types by percent in 10 km area surrounding study units.

Landcover Type	South	North
urban	0.4	0.2
non-forest	7.5	40.6
deciduous forest	59.2	50.5
mixed forest deciduous/coniferous	24.6	6.4
coniferous forest	8.2	2.3
water	0.0	0.1
Total	100.0	100.0

Table 2. Identification number, unit and group designation, days radio tracked, number of relocations, smoothing values (h) for utilization distributions and 99% fixed kernel home range size for female, *L. borealis* in the Ozark Region of Missouri, 2001-2003. See text for descriptions of units and groups

BatID	Unit	Groups	Days	Re-locations	h-values	Home Range Size (ha)
150101	1	B1, T1	9	72	30, 108	206.59
150137	2	B1, T2	16	86	47, 241	942.44
150240	2	B2, T1	17	83	211, 176	1230.68
150256	2	B2, T2	10	51	178, 523	2290.68
150318	2	B2, T2	18	133	61, 201	699.93
150379	2	B1, T2	14	82	112, 276	1097.24
150389	1	B1, T1	10	52	243, 343	1363.62
150395	2	B3, T2	8	39	165, 437	1122.37
150431	1	.	6	11		474.53
150436	2	B3, T3	5	74	92, 121	614.30
150451	1	B1, T1	12	43	352, 109	676.62
150478	2	B3, T2	7	37	50, 272	307.29
150491	2	B1, T2	14	90	101, 150	897.75
150540	2	B2, T2	5	78	264, 176	1373.76
150580	2	B2, T3	12	65	134, 225	1507.89
150610	2	B2, T2	5	70	138, 75	523.58
150615	1	.	6	28		1303.16
150636	2	.	4	11		3251.06
150678	2	B3, T2	13	79	81, 304	1305.60
150698	2	B3, T3	9	76	235, 458	3727.63
150722	2	B2, T3	13	51	294, 188	2166.11
150750	2	B2, T2	13	58	263, 262	1325.39
150756	2	B3, T3	10	48	381, 565	3720.60
150810	2	B2, T2	13	101	265, 89	1147.50
150850	2	B2, T3	11	62	212, 326	3608.21
150868	1	.	4	18		1551.03
150889	2	B2, T3	13	88	90, 204	897.56
150900	2	B2, T3	12	42	188, 315	1763.00
150918	1	B1, T1	14	64	493, 322	3505.95
150944	1	B1, T1	20	138	161, 172	2187.41
150963	2	.	4	27	206, 136	440.30
150964	2	B2, T3	13	84	139, 433	2966.92
150979	2	B2, T1	13	46	161, 269	891.99
150984	1	B1, T1	13	31	192, 142	684.50
151070	1	.	4	20		1289.63
151096	1	B1, T1	16	149	250, 89	1190.49
151146	2	B3, T2	16	71	100, 261	587.44
151202	2	B2, T3	4	36	265, 158	914.41

Table 2. continued

BatID	Unit	Groups	Days	Re-locations	h-values	Home Range Size (ha)
151320	2	B2, T3	13	81	140, 169	1307.37
151381	2	B2, T3	13	110	123, 214	1603.50
151461	1	.	3	14		135.83
151480	2	B3, T2	7	37	297, 264	1173.17
151517	2	B3, T2	7	57	132, 122	368.85
151520	1	B1, T1	17	140	138, 171	1800.89
151598	2	B1, T1	12	61	106, 591	1314.90
151600	1	B1, T1	21	163	142, 220	2026.45
151620	1	.	4	8		1688.31
151639	2	B3, T2	17	130	193, 170	2173.06
151640	2	*	12	34	166, 203	845.39
151661	1	.	8	28		419.65
151702	1	.	4	18		217.06
151711	2	B3, T2	18	109	72, 125	546.91
151718	2	B1, T1	21	149	162, 187	1500.46
151758	2	B2, T3	11	97	180, 324	3302.84
151800	2	B2, T3	11	46	228, 174	1475.62
151822	2	B3, T2	14	37	134, 102	201.57
151860	2	B1, T1	14	63	72, 250	543.57
151900	2	B1, T1	17	97	60, 274	851.65
151919	2	B2, T1	9	58	353, 118	756.66
151921	2	B3, T2	19	81	97, 167	771.64
151922	2	B3, T2	10	73	232, 175	632.40
151957	2	B1, T1	17	118	86, 362	1057.72
151978	2	B1, T1	19	82	456, 213	2079.08

Table 3. Mean, standard error, minimum and maximum home range size (99%) by geographic location, stage of lactation and temperature regime for *L. borealis* in the Ozark Region of Missouri 2001-2003.

Group	n	Mean (ha)	se	Min (ha)	Max (ha)
All Bats	52	1357.12	122.21	201.57	3727.63
South	9	1515.84	333.17	206.59	3505.95
North	43	1323.11	131.59	201.57	3727.63
B1	18	1329.30	182.63	206.59	3505.95
B2	20	1587.68	194.29	523.58	3608.21
B3	14	1040.94	267.46	201.57	3727.63
T1	18	1260.61	181.00	307.29	3505.95
T2	15	1224.50	244.90	206.59	3727.63
T3	19	1546.27	216.65	201.57	3608.21

B1= early lactation, B2=mid lactation, B3=late lactation; T1 mean temperature during tracking < 21°C, T2 mean temperature between 21°C and 26°C, and T3 mean temperature > 26°C

Table 4. Global landscape model and null model results for foraging habitat use for 52 individual *L. borealis* in the Ozark Region of Missouri 2001-2003. Bold values significant.

	global			null					
BATID	-2mloglik	k	AIC	-2mloglik	k	AIC	delta AIC	Chi Square	p-value
150101	**-3403.03**	**13**	**-3377.03**	**-2903.27**	**2**	**-2899.27**	**477.75**	**499.75**	**0.0000**
150137	-1165.94	14	-1137.94	-1190.91	2	-1186.91	48.97	-24.97	1.0000
150240	**-1718.15**	**14**	**-1690.15**	**-1408.05**	**2**	**-1404.05**	**286.10**	**310.10**	**0.0000**
150256	**-2650.86**	**14**	**-2622.86**	**-2574.59**	**2**	**-2570.59**	**52.27**	**76.27**	**0.0000**
150318	**-1213.44**	**14**	**-1185.44**	**-1180.18**	**2**	**-1176.18**	**9.26**	**33.26**	**0.0005**
150379	**-1048.69**	**14**	**-1020.69**	**-912.543**	**2**	**-908.543**	**112.14**	**136.14**	**0.0000**
150389	**-691.926**	**14**	**-663.926**	**-527.868**	**2**	**-523.868**	**140.06**	**164.06**	**0.0000**
150395	**-462.149**	**14**	**-434.149**	**-281.282**	**2**	**-277.282**	**156.87**	**180.87**	**0.0000**
150436	-1003.03	14	-975.026	-1046.98	2	-1042.98	67.96	-43.96	1.0000
150451	**-2726.29**	**13**	**-2700.29**	**-1724.35**	**2**	**-1720.35**	**979.94**	**1001.94**	**0.0000**
150478	**-1758.02**	**14**	**-1730.02**	**-1686.86**	**2**	**-1682.86**	**47.16**	**71.16**	**0.0000**
150491	**-1738.43**	**14**	**-1710.43**	**-1593.83**	**2**	**-1589.83**	**120.60**	**144.60**	**0.0000**
150540	-719.208	14	-691.208	-787.692	2	-783.692	92.48	-68.48	1.0000
150580	-1153.91	14	-1125.91	-1188.36	2	-1184.36	58.45	-34.45	1.0000
150610	-2774.11	14	-2746.11	-2755.23	2	-2751.23	5.13	18.87	0.0634
150678	-86.7276	14	-58.7276	-152.207	2	-148.207	89.48	-65.48	1.0000
150698	**-3094.28**	**14**	**-3066.28**	**-2919.19**	**2**	**-2915.19**	**151.09**	**175.09**	**0.0000**
150722	**-1508.54**	**14**	**-1480.54**	**-1425.89**	**2**	**-1421.89**	**58.65**	**82.65**	**0.0000**
150750	**-1539.35**	**14**	**-1511.35**	**-1440.77**	**2**	**-1436.77**	**74.59**	**98.59**	**0.0000**
150756	-1807.75	14	-1779.75	-1858.59	2	-1854.59	74.84	-50.84	1.0000
150810	-1828.2	14	-1800.2	-1863.13	2	-1859.13	58.94	-34.94	1.0000
150850	**-2048.73**	**14**	**-2020.73**	**-1932.31**	**2**	**-1928.31**	**92.42**	**116.42**	**0.0000**
150889	**-1789.91**	**14**	**-1761.91**	**-1652.47**	**2**	**-1648.47**	**113.44**	**137.44**	**0.0000**
150900	**-1627.83**	**14**	**-1599.83**	**-1410.75**	**2**	**-1406.75**	**193.08**	**217.08**	**0.0000**
150918	**-2217.05**	**14**	**-2189.05**	**-2043.32**	**2**	**-2039.32**	**149.73**	**173.73**	**0.0000**
150944	-2444.28	14	-2416.28	-2476.09	2	-2472.09	55.81	-31.81	1.0000
150964	**-1762.37**	**14**	**-1734.37**	**-1658.31**	**2**	**-1654.31**	**80.06**	**104.06**	**0.0000**

Table 4. continued

Bat ID	global			null			delta AIC	Chi Square	p-value
	-2mloglik	k	AIC	-2mloglik	k	AIC			
150979	**-2732.23**	**14**	**-2704.23**	**-2463.34**	**2**	**-2459.34**	**244.89**	**268.89**	**0.0000**
150984	-1982.78	14	-1954.78	-2014.18	2	-2010.18	55.4	-31.4	1.0000
151096	**-3242.72**	**14**	**-3214.72**	**-2918.9**	**2**	**-2914.9**	**299.82**	**323.82**	**0.0000**
151146	**-2493.22**	**14**	**-2465.22**	**-2405.94**	**2**	**-2401.94**	**63.28**	**87.28**	**0.0000**
151202	**-276.85**	**14**	**-248.85**	**-236.066**	**2**	**-232.066**	**16.78**	**40.78**	**0.0000**
151320	-967.816	14	-939.816	-1002.23	2	-998.23	58.41	-34.41	1.0000
151381	**-1777.82**	**14**	**-1749.82**	**-1654.51**	**2**	**-1650.51**	**99.3**	**123.3**	**0.0000**
151480	**-1020.64**	**14**	**-992.642**	**-967.491**	**2**	**-963.491**	**29.15**	**53.15**	**0.0000**
151517	**-2110.99**	**14**	**-2082.99**	**-1534.37**	**2**	**-1530.37**	**552.62**	**576.62**	**0.0000**
151520	-2996.97	14	-2968.97	-3002.56	2	-2998.56	29.58	-5.58	1.0000
151598	**-1434.65**	**14**	**-1406.65**	**-1404.17**	**2**	**-1400.17**	**6.48**	**30.48**	**0.0013**
151600	**-2949.58**	**14**	**-2921.58**	**-2909.97**	**2**	**-2905.97**	**15.62**	**39.62**	**0.0000**
151639	**-1501.04**	**14**	**-1473.04**	**-1467.6**	**2**	**-1463.6**	**9.44**	**33.44**	**0.0004**
151711	-1804.58	14	-1776.58	-1793.65	2	-1789.65	13.06	10.94	0.4486
151718	**-4917.42**	**14**	**-4889.42**	**-4875.58**	**2**	**-4871.58**	**17.85**	**41.85**	**0.0000**
151758	**-2542.51**	**14**	**-2514.51**	**-2374.75**	**2**	**-2370.75**	**143.76**	**167.76**	**0.0000**
151800	**-759.076**	**13**	**-733.076**	**-713.956**	**2**	**-709.956**	**23.12**	**45.12**	**0.0000**
151822	**-2034.68**	**14**	**-2006.68**	**-1730.23**	**2**	**-1726.23**	**280.45**	**304.45**	**0.0000**
151860	**-2726.84**	**14**	**-2698.84**	**-2555.22**	**2**	**-2551.22**	**147.62**	**171.62**	**0.0000**
151900	-439.961	14	-411.961	-484.874	2	-480.874	68.91	-44.91	1.0000
151919	-915.508	14	-887.508	-922.467	2	-918.467	30.96	-6.96	1.0000
151921	**-2462.12**	**14**	**-2434.12**	**-2228.37**	**2**	**-2224.37**	**209.75**	**233.75**	**0.0000**
151922	**-429.234**	**14**	**-401.234**	**-183.915**	**2**	**-179.915**	**221.32**	**245.32**	**0.0000**
151957	**-1340.43**	**14**	**-1312.43**	**-1320.23**	**2**	**-1316.23**	**3.8**	**20.2**	**0.0427**
151978	**-1220.29**	**14**	**-1192.29**	**-983.849**	**2**	**-979.849**	**212.44**	**236.44**	**0.0000**

Table 5. Population estimates of mean unstandardized RUF coefficients for *L. borealis* in the Ozark Region of Missouri 2001-2003. Significant results in bold.

Resource Attribute	All bats n=52				
	$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	Number by direction of effect	
				+	-
Bottom	0.01010	0.00641	0.11637	30	22
Ridge	**0.01050**	**0.00278**	**0.00293**	**38**	**14**
Upland drainage	**0.01076**	**0.00293**	**0.00239**	**37**	**15**
Slopes	0.00000	0.00000			
Mixed forest	0.00072	0.00377	0.81977	27	25
Non-forest	-0.00839	0.00459	0.13586	22	30
Urban	**-0.05380**	**0.00748**	**0.00000**	**7**	**43**
Water	0.00783	0.00369	0.03853	37	15
Deciduous forest	0.00000	0.00000			
Distance to edge	**-0.00008**	**0.00002**	**0.00156**	**15**	**37**
Landscape diversity	-0.01552	0.00858	0.07631	20	32
Percent tree cover	0.00045	0.00026	0.09374	33	19
Percent water	-0.00058	0.00041	0.16104	13	39
Road density	**0.00018**	**0.00004**	**0.00005**	**43**	**9**

Table 6. Population estimates of mean unstandardized RUF coefficients by geographic unit for *L. borealis* in the Ozark Region of Missouri 2001-2003. Significant results in bold.

Resource Attribute	north					south				
	$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect	
				+	-				+	-
Bottomland	0.01051	0.00749	0.16774	25	18	0.01035	0.01270	0.43883	5	4
Ridge	**0.00915**	**0.00272**	**0.00166**	**30**	**13**	0.01184	0.00894	0.22197	8	1
Upland drain	**0.00972**	**0.00333**	**0.00562**	**29**	**14**	0.01453	0.00679	0.06494	8	1
Sideslope	0.00000	0.00000				0.00000	0.00000			
Mixed forest	0.00252	0.00372	0.50274	23	19	-0.01128	0.01259	0.39661	3	6
Non-forest	-0.00891	0.00492	0.07728	18	25	-0.01084	0.01309	0.43188	4	5
Urban	**-0.05476**	**0.00780**	**0.00000**	**5**	**38**	-0.04790	0.02522	0.10626	2	5
Water	**0.00839**	**0.00426**	**0.05577**	**31**	**12**	0.00517	0.00660	0.45638	6	3
Deciduous	0.00000	0.00000				0.00000	0.00000			
Distance to edge	**-0.00009**	**0.00003**	**0.00132**	**12**	**31**	-0.00003	0.00005	0.63919	3	6
Landscape diversity	-0.01287	0.00965	0.18957	18	25	-0.02819	0.01870	0.17019	2	7
Canopy cover	0.00002	0.00024	0.91818	25	18	**0.00250**	**0.00070**	**0.00753**	**8**	**1**
Percent water	**-0.00111**	**0.00039**	**0.00741**	**6**	**37**	0.00192	0.00117	0.13767	7	2
Road density	**0.00022**	**0.00003**	**0.00000**	**38**	**5**	-0.00003	0.00016	0.87601	5	4

Table 7. Population estimates of mean unstandardized RUF coefficients for *L. borealis* in the Ozark Region of Missouri 2001-2003 by stage of lactation. Early lactation=B1, mid-lactation=B2 and late lactation=B3. Significant results in bold.

	B1					B2					B3				
Resource Attribute	$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect	
				+	-				+	-				+	-
Bottomland	**0.01853**	**0.00769**	**0.02758**	**12**	**6**	0.00128	0.00867	0.88426	10	10	0.01329	0.01865	0.48870	8	6
Ridge	**0.01394**	**0.00477**	**0.00951**	**16**	**2**	0.00287	0.00405	0.48807	11	9	**0.01370**	**0.00498**	**0.01646**	**11**	**3**
Upland drain	**0.01000**	**0.00445**	**0.03822**	**14**	**4**	0.00985	0.00559	0.09398	13	7	**0.01226**	**0.00551**	**0.04442**	**10**	**4**
Deciduous	0.00000	0.00000				0.00000	0.00000				0.00000	0.00000			
Mixed forest	-0.00557	0.00701	0.43804	9	9	0.00011	0.00429	0.98033	11	8	0.00731	0.00879	0.42023	6	8
Non-forest	-0.00370	0.00776	0.63910	9	9	-0.00301	0.00453	0.51504	10	10	-0.02120	0.01162	0.08948	3	11
Urban	**-0.06143**	**0.01366**	**0.00042**	**3**	**13**	**-0.05050**	**0.00968**	**0.00005**	**2**	**18**	**-0.04978**	**0.01742**	**0.01345**	**2**	**12**
Water	0.00666	0.00504	0.20330	13	5	0.00595	0.00642	0.36579	14	6	0.01201	0.00821	0.16705	10	4
Sideslope	0.00000	0.00000				0.00000	0.00000				0.00000	0.00000			
Distance to edge	-0.00004	0.00004	0.24823	6	12	**-0.00007**	**0.00003**	**0.04376**	**5**	**15**	**-0.00013**	**0.00006**	**0.03266**	**4**	**10**
Landscape diversity	-0.00461	0.01182	0.70129	8	10	-0.01537	0.00916	0.10969	7	13	-0.02978	0.02520	0.25863	5	9
Canopy cover	**0.00133**	**0.00048**	**0.01326**	**13**	**5**	0.00052	0.00031	0.11189	15	5	-0.00076	0.00050	0.14697	5	9
Percent water	0.00015	0.00072	0.84070	7	11	**-0.00126**	**0.00022**	**0.00002**	**2**	**18**	-0.00055	0.00118	0.64767	4	10
Road density	0.00010	0.00009	0.26470	13	5	**0.00028**	**0.00005**	**0.00001**	**19**	**2**	0.00013	0.00006	0.06364	12	2

Table 8. Population estimates of mean unstandardized RUF coefficients for *L. borealis* in the Ozark Region of Missouri 2001-2003 by temperature regime of tracking period. Mean temperature < 21oC=T1, mean temperature <26^{o}C and >21^{o}C=T2, and mean temperature >26^{o}C=T3. Significant results in bold.

	T1					T2					T3				
Resource Attribute	$\bar{\beta}$	se $\bar{\beta}$	*p*($\bar{\beta}$ =0)	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	*p*($\bar{\beta}$ =0)	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	*p*($\bar{\beta}$ =0)	number by direction of effect	
				+	-				+	-				+	-
Bottomland	0.00350	0.01309	0.79224	10	8	0.00753	0.00802	0.36359	8	7	0.01797	0.01092	0.11627	12	7
Ridge	0.00504	0.00530	0.35520	13	5	**0.01802**	**0.00415**	**0.00068**	**12**	**3**	**0.00978**	**0.00451**	**0.04314**	13	6
Upland drain	0.00756	0.00584	0.21298	12	6	**0.0149**	**0.0051**	**0.01117**	**13**	**2**	**0.01054**	**0.00438**	**0.02649**	12	7
Deciduous	0.00000	0.00000				0.00000	0.00000				0.00000	0.00000			
Mixed forest	-0.00024	0.00871	0.97807	11	7	0.00412	0.00510	0.43250	7	8	-0.00105	0.00508	0.83873	8	10
Non-forest	-0.00865	0.00903	0.35138	8	10	-0.01836	0.01012	0.09111	4	11	-0.00069	0.00484	0.88857	10	9
Urban	**-0.0334**	**0.0132**	**0.02225**	**5**	**12**	**-0.0755**	**0.01854**	**0.00133**	**2**	**12**	**-0.0561**	**0.00622**	**0.00000**		19
Water	0.00908	0.00590	0.14236	13	5	0.00721	0.00609	0.25611	9	6	0.00579	0.00692	0.41303	15	4
Sideslope	0.00000	0.00000				0.00000	0.00000				0.00000	0.00000			
Distance to edge	**-0.0001**	**4.6E-05**	**0.04157**	**5**	**13**	**-9E-05**	**4.2E-05**	**0.04542**	**4**	**11**	**-0.00004**	**0.00003**	**0.00003**	6	13
Landscape diversity	-0.02368	0.01292	0.08436	7	11	-0.02082	0.02275	0.37570	5	10	-0.00982	0.01097	0.38198	8	11
Canopy cover	0.00090	0.00060	0.15128	13	5	-0.00003	0.00050	0.95141	6	9	0.00037	0.00022	0.10533	14	5
Percent water	-0.00006	0.00095	0.94732	5	13	-0.00018	0.00072	0.80362	6	9	**-0.00120**	**0.00039**	**0.00572**	2	17
Road density	0.00006	0.00006	0.34406	12	6	0.00015	0.00010	0.14305	12	3	**0.0003**	**0.00004**	**0.00000**	19	

Table 9. Population estimates of mean unstandardized RUF coefficients for landform factors for *L. borealis* in the Ozark Region of Missouri 2001-2003 by geographic unit, stage of lactation and temperature regime. Significant results in bold.

		Mean estimates of unstandardized RUF coefficients (CI)														
		bottom					ridge					upland drain				
Bat Group	N	$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect	
					+	-				+	-				+	-
South	9	0.01035	0.01270	0.43883	5	4	**0.01184**	**0.00894**	**0.22197**	**8**	**1**	0.01453	0.00679	0.06494	8	1
North	43	**0.01051**	**0.00749**	**0.16774**	**25**	**18**	0.00915	0.00272	0.00166	30	13	**0.00972**	**0.00333**	**0.00562**	**29**	**14**
SB1	9	0.01035	0.01270	0.43883	5	4	**0.01184**	**0.00894**	**0.22197**	**8**	**1**	0.01453	0.00679	0.06494	8	1
ST1	6	0.01589	0.01754	0.40636	4	2	0.00586	0.01261	0.66160	5	1	0.01248	0.00993	0.26429	5	1
ST2	3	-0.00074	0.01751	0.97024	1	2	0.02380	0.00754	0.08750	3		0.01862	0.00695	0.11573	3	
NB1	9	0.02672	0.00856	0.01419	7	2	0.01605	0.00397	0.00373	8	1	0.00547	0.00574	0.36799	**6**	**3**
NB2	20	0.00128	0.00867	0.88426	10	10	0.00287	0.00405	0.48807	11	9	**0.00985**	**0.00559**	**0.09398**	**13**	**7**
NB3	14	0.01329	0.01865	0.48870	8	6	0.01370	0.00498	0.01646	11	3	0.01226	0.00551	0.04442	10	4
NT1	12	-0.00269	0.01780	0.88244	6	6	0.00463	0.00539	0.40847	8	4	0.00509	0.00741	0.50633	7	5
NT2	12	0.00960	0.00930	0.32407	7	5	0.01658	0.00489	0.00601	9	3	0.01397	0.00623	0.04651	10	2
NT3	19	0.01943	0.01140	0.10555	12	7	0.00731	0.00398	0.08299	13	6	**0.00996**	**0.00458**	**0.04313**	**12**	**7**

Table 10. Population estimates of mean unstandardized RUF coefficients for landscape factors distance to edge and road density for *L. borealis* in the Ozark Region of Missouri 2001-2003 by geographic unit, stage of lactation and temperature regime. Significant results in bold.

Bat Group	N	Mean estimates of unstandardized RUF coefficients (CI)									
		distance to edge					road density				
		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect	
					+	-				+	-
South	9	-0.00003	0.00005	0.63919	3	6	-0.00003	0.00016	0.87601	5	4
North	43	**-0.00009**	**0.00003**	**0.00132**	**12**	**31**	**0.00022**	**0.00003**	**0.00000**	**38**	**5**
SB1	9	-0.00003	0.00005	0.63919	3	6	-0.00003	0.00016	0.87601	5	4
ST1	6	0.00002	0.00007	0.74733	3	3	-0.00002	0.00014	0.87453	4	2
ST2	3	-0.00013	0.00004	0.09546		3	-0.00003	0.00045	0.95295	1	2
NB1	9	-0.00006	0.00005	0.27548	3	6	**0.00022**	**0.00005**	**0.00283**	**8**	**1**
NB2	20	**-0.00007**	**0.00003**	**0.04376**	**5**	**15**	**0.00028**	**0.00005**	**0.00001**	**18**	**2**
NB3	14	**-0.00013**	**0.00006**	**0.03266**	**4**	**10**	0.00013	0.00006	0.06364	12	2
NT1	12	**-0.00017**	**0.00005**	**0.00852**	**2**	**10**	0.00010	0.00006	0.10758	8	4
NT2	12	-0.00008	0.00005	0.13720	4	8	**0.00019**	**0.00007**	**0.01712**	**11**	**1**
NT3	19	-0.00004	0.00003	0.20383	6	13	**0.00031**	**0.00004**	**0.00000**	**19**	**0**

Table 11. Population estimates of mean unstandardized RUF coefficients for landscape factors distance to edge and road density for *L. borealis* in the Ozark Region of Missouri 2001-2003 by geographic unit, stage of lactation and temperature regime. Significant results in bold.

		Mean estimates of unstandardized RUF coefficients (CI)															
		landscape diversity					canopy cover					percent water					
Bat Group	N	$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect		$\bar{\beta}$	se $\bar{\beta}$	$p(\bar{\beta}=0)$	number by direction of effect	
					+	-				+	-					
South	9	-0.00003	0.00016	0.87601	5	4	**0.00250**	**0.00070**	**0.00753**	**8**	**1**	0.00192	0.00117	0.13767	7	2
North	43	**0.00022**	**0.00003**	**0.00000**	**38**	**5**	0.00002	0.00024	0.91818	25	18	**-0.00111**	**0.00039**	**0.00741**	**6**	**37**
SB1	9	-0.02819	0.01870	0.17019	2	7	**0.00250**	**0.00070**	**0.00753**	**8**	**1**	0.00192	0.00117	0.13767	7	2
ST1	6	-0.03870	0.02623	0.20013	1	5	0.00235	0.00102	0.06972	5	1	0.00159	0.00175	0.40631	4	2
ST2	3	-0.00716	0.02062	0.76153	1	2	0.00279	0.00081	0.07496	3		0.00260	0.00082	0.08632	3	
NB1	9	0.01896	0.01025	0.10147	6	3	0.00016	0.00038	0.68641	5	4	-0.00163	0.00018	0.00002		**9**
NB2	20	-0.01537	0.00916	0.10969	7	13	0.00052	0.00031	0.11189	15	5	**-0.00126**	**0.00022**	**0.00002**	**2**	**18**
NB3	14	-0.02978	0.02520	0.25863	5	9	-0.00076	0.00050	0.14697	5	9	-0.00055	0.00118	0.64767	4	10
NT1	12	-0.01617	0.01467	0.29374	6	6	0.00017	0.00067	0.80252	8	4	-0.00089	0.00110	0.43557	1	11
NT2	12	-0.02423	0.02827	0.40957	4	8	-0.00074	0.00038	0.08075	3	9	-0.00088	0.00076	0.27061	3	9
NT3	19	-0.00361	0.00954	0.70928	8	11	0.00041	0.00022	0.08004	14	5	**-0.00139**	**0.00035**	**0.00095**	**2**	**17**

Figure 1. Study Areas in Missouri that were surveyed for bats, 2001-2003. Lines indicate Mark Twain National Forest Ranger Districts, North and South Units (South Unit bold) radio telemetry locations shown as cross-hatched circles.

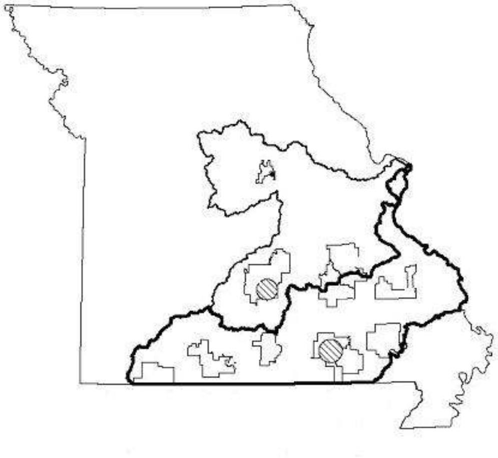


Figure 2.— Examples of utilization distribution for selected *L. borealis* during summer period (June 1 – Aug 15) to illustrate range in home range configurations, central foraging locations with dispersed patches of addition foraging locations (a) Bat 151711 (b) Bat 150944. Calculations from MATLAB. Colors indicate intensity of use: red highest use to dark blue lowest use.

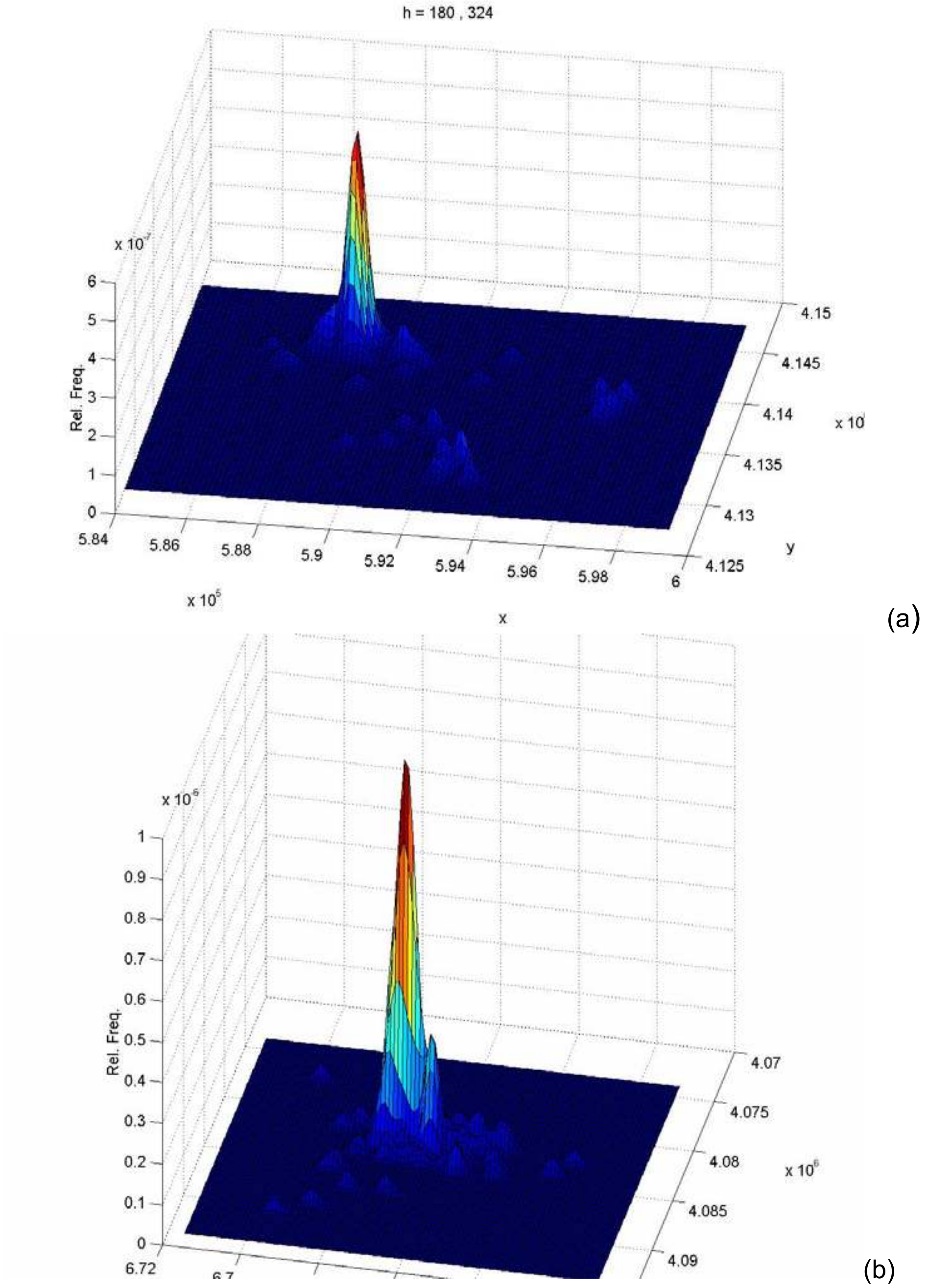
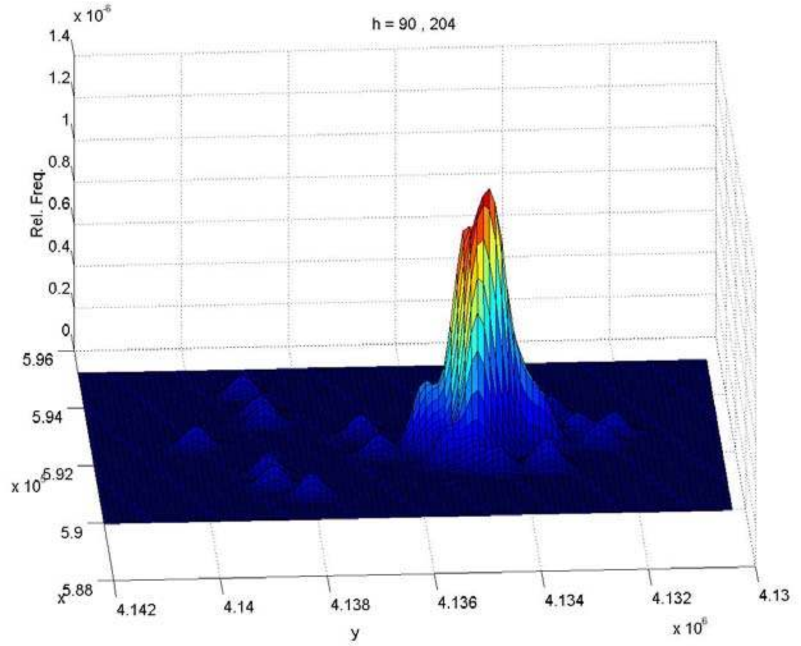
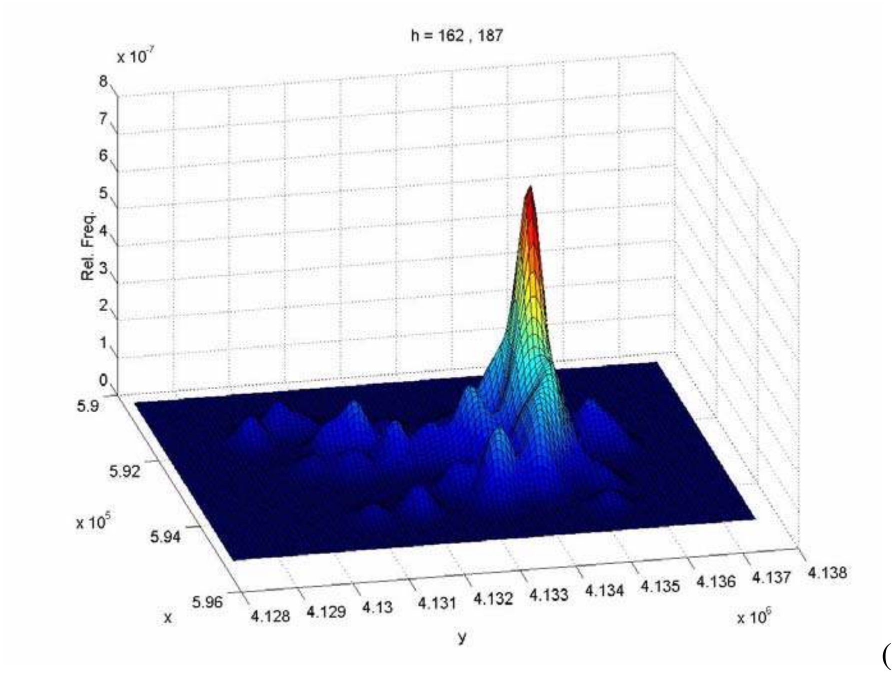


Figure 3.— Examples of utilization distribution for selected *L. borealis* during summer period (June 1 – Aug 15) to illustrate single central foraging location with dispersed patches of addition foraging locations (a) Bat 150889 and (b) Bat 151718. Calculations from MATLAB. Colors indicate intensity of use: red highest use to dark blue lowest use.



(a)



(b

Figure 4.— Predicted use, RUF$_{(foraging)}$, by landscape factors for *L. borealis* by geographic unit in the Ozark Region of Missouri 2001-2003. north =closed circles; south= closed triangles.

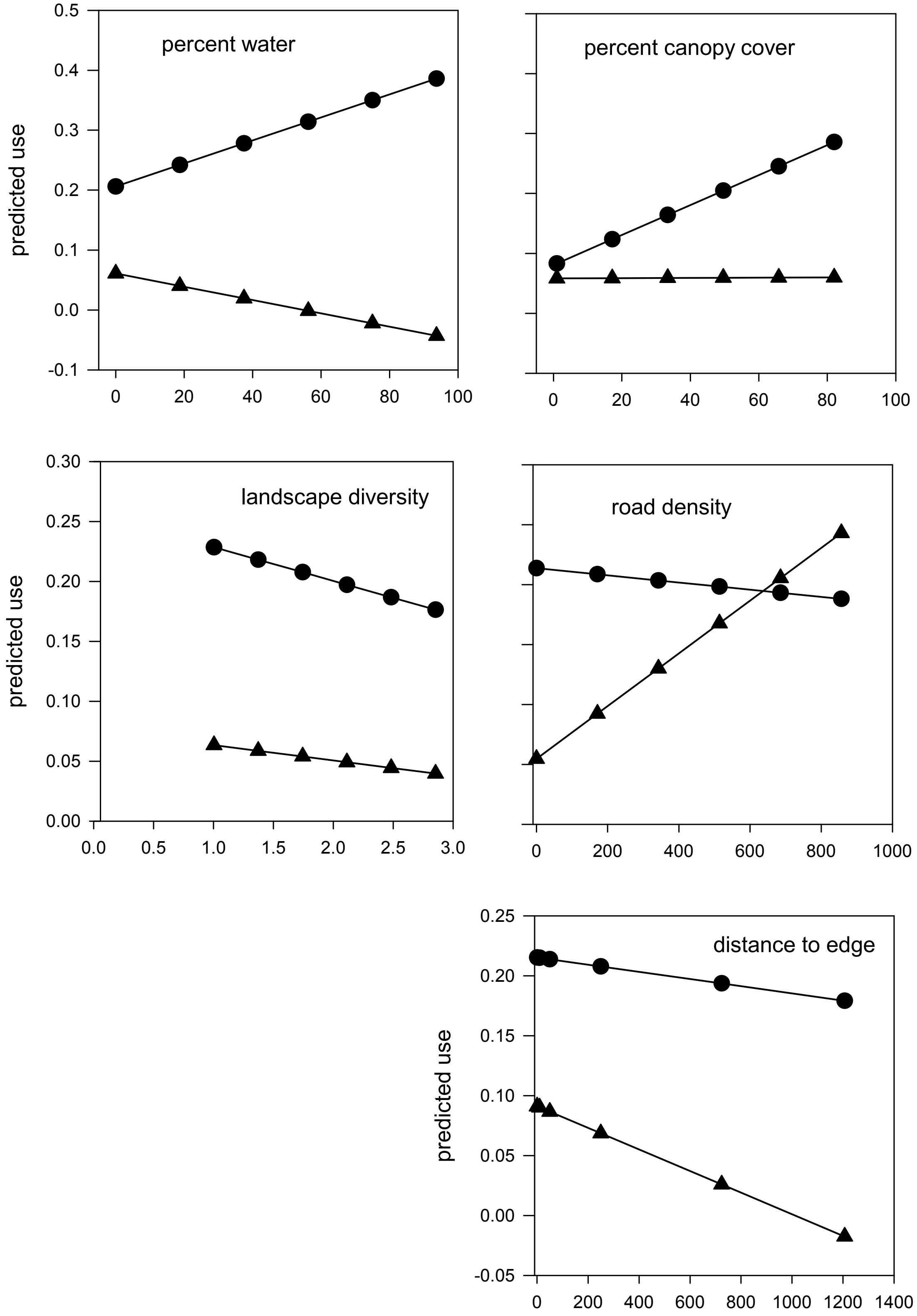


Figure 5.— Predicted foraging resource use by (a) landcover type and (b) landform for *L. borealis* by geographic unit in the Ozark Region of Missouri 2001-2003. North =gray bar, south= black bar; Mixed=mixed forest, nonf=non-forest, urban=no vegetation, decid=decidous forest; bottom=low elevation, streams, ridge=ridge, drain=upland drainage, slopes=side slopes.

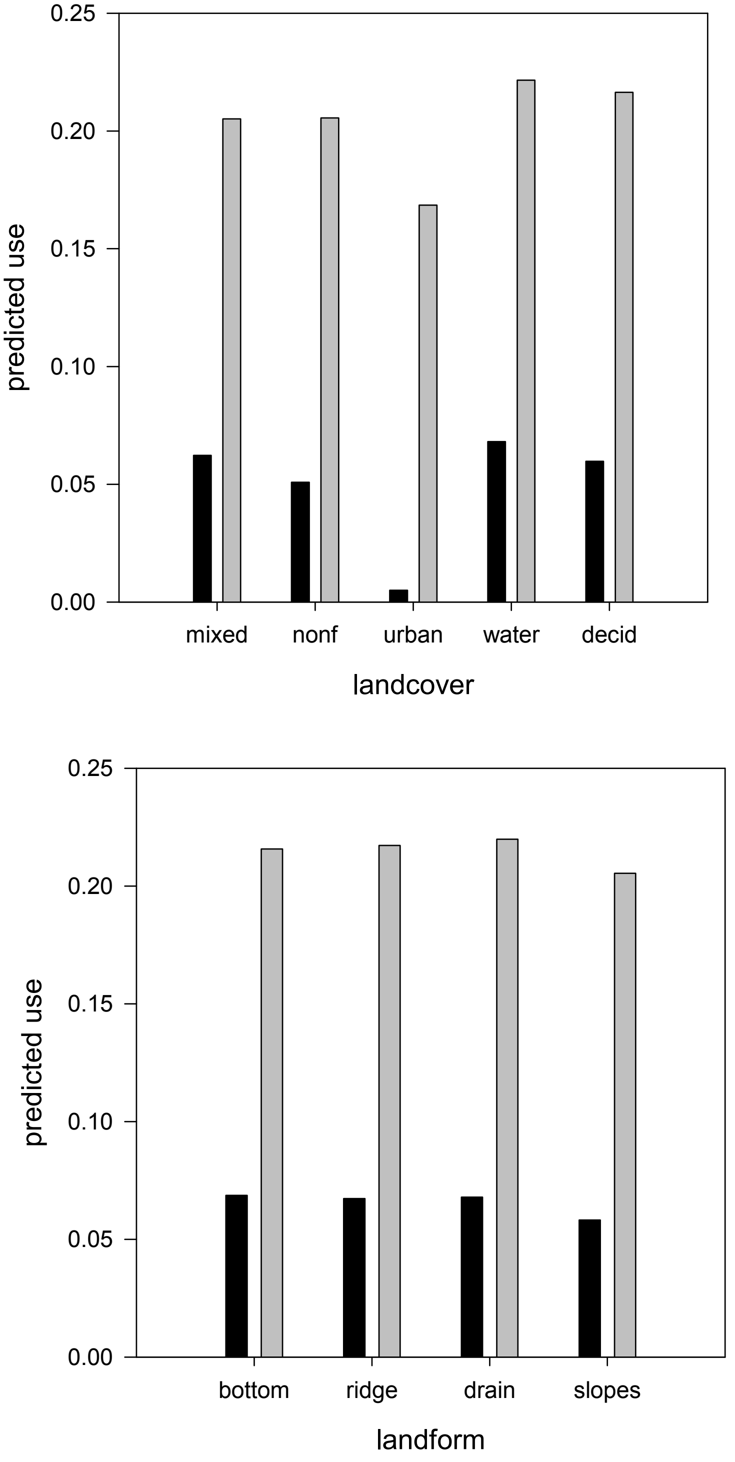
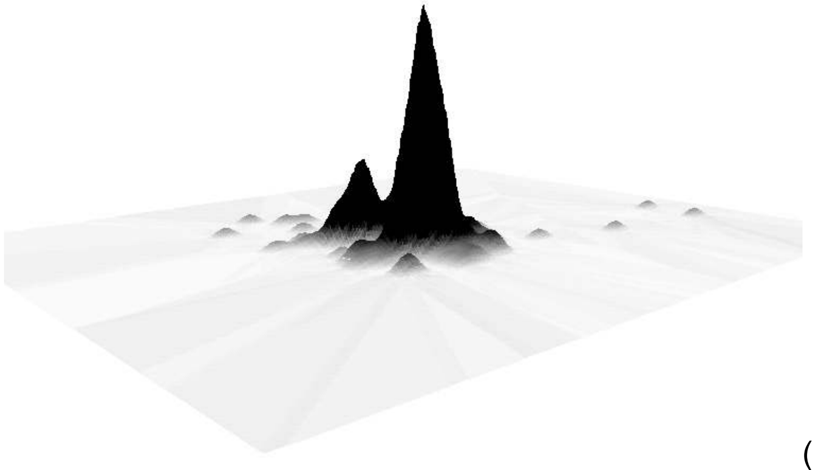
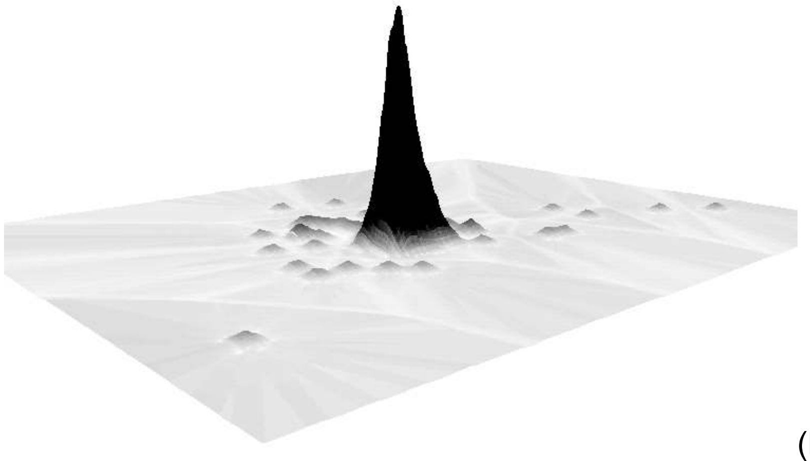


Figure 6.— Examples of utilization distributions for two *L. borealis* radiotracked in the southern study unit of Missouri Ozarks (a) bat 151600 and (b) bat 150944 projected with ArcScene (height of UD (z) calculated in MATLAB).

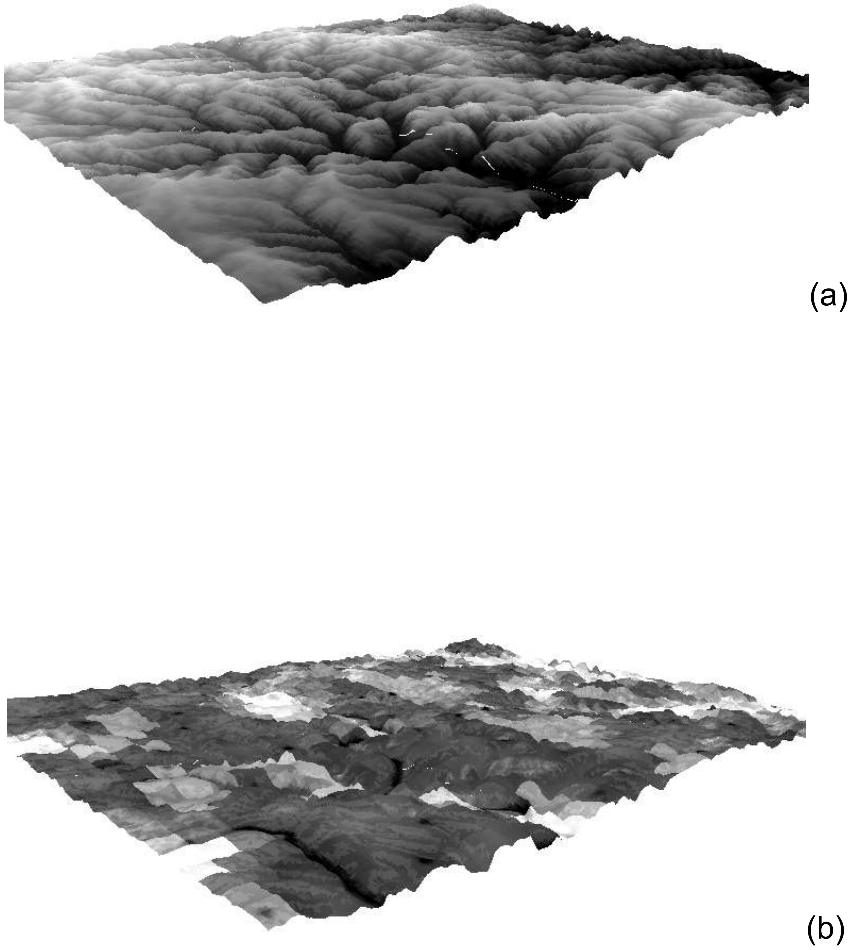


(a)



(b)

Figure 7.— Digital elevation model (a) and predicted foraging resource use by *L. borealis* for the southern study unit in Missouri Ozark Region; highest use areas are black, lowest use areas are white.



Vita

Sybill K. Amelon was born in Muscatine, Iowa and graduated from Hickman Mills High School in Hickman Mills, Missouri in 1974. She received a Bachelor of Science with double majors in Wildlife Biology and Soils from Central Missouri State University in 1978. While employed as a Soil Scientist with the U. S. Forest Service she completed her Master of Science in Forestry from the University of Missouri in 1991. She continued employment with U. S. Forest Service as a Wildlife Biologist for the Mark Twain National Forest and Region 9. Her research interests stem from concern for the conservation of wildlife in managed forests. Her research interests are wildlife ecology and application of ecological findings to develop applied solutions to problems of wildlife conservation, in particular forest bats. She completed her doctoral program in Fisheries and Wildlife Sciences at the University of Missouri. She is currently employed by the Northern Research Station of the U. S. Forest Service as a Wildlife Ecologist.