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Landscape Ecological Analysis of Patterns Influencing Bat Activity in Southeast Glacial Plains of Wisconsin

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LANDSCAPE ECOLOGICAL ANALYSIS OF PATTERNS INFLUENCING BAT ACTIVITY IN SOUTHEAST GLACIAL PLAINS OF WISCONSIN

by

Angela L. Jackson

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ABSTRACT
LANDSCAPE ECOLOGICAL ANALYSIS OF PATTERNS INFLUENCING BAT HABITAT IN SOUTHEAST GLACIAL PLAINS REGION OF WISCONSIN

by

Angela L. Jackson

The University of Wisconsin-Milwaukee, 2013
Under the Supervision of Professor Glen Fredlund

Nearly half of the world’s bat species are threatened by anthropogenic land use. To contribute to the conservation of these cryptic mammals, it is imperative to understand bat habitat selection in human-dominated landscapes. Bat activity was calculated using active acoustic surveys conducted June and July for three years along river and lake transects in an agricultural matrix. Using multiple logistic regression and ANOVA regression tree analyses, I examined the relationship between bat activity of four species and habitat structure at multiple scales.

Aquatic features were determined to be the greatest predictor of bat activity with rivers supporting greater amount of bat activity than lake habitats. All analyzed species were shown to be negatively influenced by developed and agricultural land at riparian habitats, however similar patterns were not observed at lake habitats. Wooded land use was also important in describing habitats that supported higher bat activity when assessing general patterns across all surveyed sites. The observed patters are likely due to protection from wind and predators at riparian sites, and roosting habitat that forested lands provide. Sustaining a mixed-use landscape within an agricultural matrix may provide bats the diversity of habitat required to meet all life history needs.

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introduce individuals to WI bats and the importance of their conservation. It is because of Dave Redell that bat conservation is a priority in Wisconsin, and for that I am eternally grateful.

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CHAPTER 1

INTRODUCTION

Habitat loss and the landscape fragmentation are two major threats to biodiversity (Farrow and Broders, 2011). In efforts to conserve biodiversity, there is a growing emphasis on understanding pattern-process feedbacks within altered landscapes and the impacts these have on species distributions (Kent 2009, 426; Farrow & Broders, 2011). Bats provide an opportunity to assess these impacts because they are regarded as bioindicators of ecosystem health and function, particularly in the context of habitat quality related to anthropogenic influences (Jones et al., 2009; Farrow & Broders, 2011). Currently, almost half of all bat species are threatened by anthropogenic land use intensification (Akasaka et al., 2012). Agricultural intensification, water quality degradation, and urbanization are just a few of the influences affecting bat populations worldwide. Because of their sensitivity to habitat alteration, research of these cryptic mammals in altered landscapes is especially important.

Agricultural land presently composes nearly 40% of the earth's surface and is likely to continue to rise (Akasaka et al., 2012). The increased patchiness of forested landscapes and isolated wetland habitats is a result of intensification of agricultural lands. Because nearly half of the world's bat species are threatened by anthropogenic land use, it is imperative to understand foraging habitat selection in an agricultural context. Despite their ecological importance and conservation concern, most aspects of bat natural history, such as foraging habitat use in human-dominated landscapes, remain poorly understood.

Although bats are of the most abundant groups of mammals, many populations are on the decline. Presently, Wisconsin bats are threatened due to the impending spread of an invasive fungal disease, white nose syndrome (WNS), known to kill over 75% of colonies (see chapter 2, this work; Frick et al., 2010). As pressure from WNS and habitat alteration are expected to increase, it is of increasing importance to understand the patterns of habitat selection and to conserve Wisconsin bat populations. Current research is lacking in addressing habitat preferences at a variety of lake and riparian habitats within agricultural landscapes, particularly in the Midwest region of USA. This research aims to address habitat selection of 4 Wisconsin bat species by assessing landscape composition, connectivity and configuration.

Landscape ecology, a holistic framework that considers ecological processes across multiple spatial and temporal scales within a landscape, provides the necessary tools to understand the relationship of agricultural landscape composition and foraging bat populations (Forman & Godron, 1986). Additionally, landscape ecology permits the identification of relationships of individual species with landscape elements at ecologically significant that are context-specific and relevant to the species of interest (Kent, 2009). Currently, there is a need for more landscape-level research to meet conservation goals. Addressing bat populations from a landscape perspective will further contribute to the understanding of their habitat requirements and benefit the effort to more effectively conserve local populations.

The landscape mosaic model used in this analysis provides the context to assess bat foraging habitats in an ecologically significant landscape composed of complex and heterogeneous patches. Under this model, neighboring patches are identified by their ability to impede or facilitate movement of a species across the landscape and connectivity is addressed as a function of the neighboring habitat types (Estrada-Villegas et al., 2010; Threlfall, Law, & Banks, 2012). Other models consider the landscape as a binary matrix by considering characteristics of just the focal patch type. As argued by McGarigal et al. (2012), this is an oversimplification of real world patterns of landscape perception and selection by organisms. The consideration of all neighboring habitat types is a more realistic approach to perception of landscape elements by the species of interest.

Despite the growing body of research on bat ecology, there is still a paucity of studies addressing the influence of landscape structure on bat activity in an agricultural region (but see: Lundy & Montgomery, 2010; Boughey et al., 2011; Wolcott & Vulinec, 2012; Frey-Ehrenbold et al., 2013). The development of acoustic recording technology has provided a cost-effective method to surveying relative bat activity in diverse range of habitats. Active (manual) acoustic surveys were conducted for three summer seasons to determine relative bat activity at aquatic habitats in an agricultural landscape of Wisconsin. It was assumed that these surveys provided acoustic recordings of foraging bats in the landscape due to the high reliance of insectivorous bats on aquatic sites for prey (Lacki, Amelon, & Baker, 2007). I have developed a set of species-specific hypotheses based on morphological characteristics and a review of existing bat ecology literature (see chapter 2) to determine habitat-specific relationships of bats in the SEGP. Chapters 3 and 4 of this thesis will describe the methodology and analyses to test these hypotheses.

Research Goals & Objectives

My goal was to assess the effect of landscape-level variables on bat activity in water (lake and river) habitats. This study aimed to quantify the relationship of relative bat activity (defined as the total echolocation calls of a specific species recorded at an individual survey divided by the total survey length in minutes) between survey sites in a predominately agricultural landscape, the SEGP of Wisconsin. For this study, I first identified a set of landscape metrics that best described habitat suitability through the use of digital spatial data, acoustic survey data, and spatial analysis. Second, I investigated the effects of landscape characteristics on species richness at varying scales, and amongst and between river and lake survey segments. Finally, I aimed to identify the habitat requirements and conservation needs of Wisconsin's bats across the SEGP to aid in achieving the overarching goals of the Wisconsin Department of Natural Resources (WDNR) to conserve bats within the state.

Questions I aimed to address were (1) what is the relationship between landscape composition, configuration and connectivity and relative bat activity?; (2) do patterns of selection for each species differ between and amongst lake and river habitats?; (3) what role does scale play in patterns observed in habitat use?; and finally (4) which habitats support the greatest species richness and relative activity of bats in the Southeast Glacial Plains of Wisconsin?

This study will contribute to the knowledge of bat ecology and assist in future bat conservation practices in the state of Wisconsin. In addition, information on habitat selection of bat species can potentially assist in the possible need for reintroduction of bats due to the impending spread of white-nose syndrome. My overall objectives were to determine if there are significant dissimilarities in habitat selection between species, to assess how alterations in landscape characteristics affect presence of bats and species richness, and, finally to inform policy development for future ecological management.

Study Area

The SEGP region expands across approximately 20,008 square kilometers and 19 counties (Figure 1). This non-coastal region encompasses nearly 14 percent of the land area and 38 percent of residents of Wisconsin. The mean annual temperature of the SEGP is 7.72 ° Celsius (45.9 ° F), but a latitudinal variation in temperature is observed in this region. Maximum August temperatures in SEGP average 27.33 ° C (81.2 ° F) and minimum average January temperatures are -14.61 ° C (5.7 ° F). Precipitation and snowfall also exhibit latitudinal variation with an average of 85.34 centimeters and 100.1 centimeters per year respectively (WDNR, 2013a draft). Elevation in this region ranges from 209 to 404 meters above sea level (WDNR, 2013a draft).

Anthropogenic land use intensification in SEGP drastically changed the native land cover and hydrology, with urban development composing approximately 5% of the total area. The current vegetation cover is dominated by agricultural cropland which makes up nearly 60% of this landscape, followed by grassland and forest, composing approximately 11% and 10% of the region respectively. This is a drastic change from historic proportions of vegetation cover where forested areas covered nearly 50% of the region (WDNR, 2013a draft). Primary types of agriculture include cash-cropping of grains and vegetables. Historically, prairie, savanna, oak forest and patches of maple-basswood forest covered much of the landscape. Today, little of the original prairie or savanna habitat remains, and fragmentation of native habitats is severe. Current forested vegetation is composed primarily of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), basswood (*Tilia Americana*) and white ash (*Fraxinus nigra*).

Wetlands are also extensive in this region composing approximately 12% of the landscape, with most having experienced direct human modifications such as removal of natural vegetation, ditching, diking, and indirect impacts from cropland runoff and infestation of invasive species (Pohlman et al., 2006). Nine significant river systems (Wolf, Sheboygan, Milwukee, Rock, Sugar, Mukwanago, Bark, Illinois Fox and Green Bay Fox) are present in the SEGP, most of which are influenced by intensive agriculture and urban-industrial development (WDNR, 2013a draft).

Analyzing bat activity in this study region provides control for environmental variability by using predefined ecoregions developed by the WDNR. The US Forest Service developed a classification system, the National Hierarchical Framework of Ecological Units, which systematically divides the landscape into ecological regions to facilitate consistent resource and ecological management across various scales (Cleland et al., 1997). The WDNR adopted this system to organize Wisconsin into sixteen ecological landscapes, each varying in physical and biological characteristics such as vegetation, soils, climate, water bodies, and geologic features (WDNR, 2005, p. 2-5). The intense fragmentation and modification of the SEGP provides an opportunity to assess bat habitat use in the context of human-dominated landscapes in this unique region of the state.

Chapter 2

GEOGRAPHIC RANGE, FORAING HABITAT AND BEHAVIOR, & LANDSCAPE FACTORS INFLUENCING HABITAT SELECTION

Worldwide there are more than 1,000 species of bats (Order Chiroptera; Kunz & Racey, 1998; Broders et al., 2004). Seven species (*Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus borealis, Lasiurus cinereus, Myotis lucifugus, M. septentrionalis, Perimyotis subflavus*) occur in Wisconsin but many aspects of their natural history, such as foraging habitat, are poorly understood. This is due to their mobility, nocturnal nature, ability to produce sounds above human hearing, and inconspicuous roosting locations. Despite the need for research to mitigate negative impacts of human influence on bat populations, studies regarding bat behavior are minimal and bats remain among the most misunderstood of all species (Pierson, 1998; BCI, 2011).

Habitat loss due to urbanization is the greatest cause of species endangerment in the United States (Czech et al., 2000). The economic and cultural factors of urban sprawl contribute to the changing composition and configuration of landscape patches. Currently, agricultural and urban/suburban conversion is responsible for the majority of lost roosting and foraging habitat crucial to the survival of bat species (Pierson, 1998). Bats have been documented returning to roosting and foraging sites on an annual basis and are directly impacted by land cover conversion due to the potential loss of habitat (Pierson, 1998). In addition, habitat structure preference is species specific and is known to influence community composition (Hein et al., 2009; Estrada-Villegas et al., 2010;

Fukui et al., 2011). As a result, land cover change at a local landscape level can negatively impact foraging availability and ultimately bat populations.

Yates and Muzika (2006) proclaim a lack of landscape-level analysis in bat ecology, particularly in the Midwest, USA. With this research, I aim to address this gap by identifying landscape features that provide suitable foraging habitat for Wisconsin bats. Habitat use studied in this analysis is assumed to be foraging habitat, as bats are known to travel from roosting locations to nearby aquatic sites to opportunistically feed on higher insect densities (Fukui et al., 2006). In addition, identifying foraging habitat at the landscape scale may also provide insight to other habitat needs, such roost preferences. The growing need for spatial analysis of landscapes for practical resource management application provides an avenue for geographers to contribute to conservation and landscape ecology literature.

Status & Geographic Range of Wisconsin Bats

All seven species of bats native to Wisconsin are widely distributed throughout North America and are currently listed as a “species of least concern” on the International Union for Conservation of Nature Red List of Threatened Species (Arroyo-Cabrales et al., 2008a, 2008b). Wisconsin is home to four cave species (*Eptesicus fuscus, Myotis lucifugus, M. septentrionalis, Perimyotis subflavus*) and 3 migratory, or tree, species (*Lasionycteris noctivagans, Lasiurus borealis, L. cinereus*), all of which are found in Wisconsin in summer months, with cave species also occupying various hibernacula within the state throughout winter months.

Of the indigenous bat species, the migratory hoary bat (*Lasiurus cinereus*) is the most widely dispersed of all North American bats, extending to the northern range of Canadian forests, south into parts of South American into Brazil, Argentina and Chile (Shump & Shump, 1982b). The hoary bat is also found in Hawaii, making it one of two native mammals found on the islands (although the US Fish & Wildlife Service lists the Hawaiian hoary bat as a distinct species: *Lasiurus cinereus semotus*). Despite the pervasive range of the hoary bat, the WDNR suggests this species is more commonly found in northern parts of the state (WDNR, 2013b). Currently, research regarding hoary distribution within the state is lacking.

Eastern red bats (*Lasiurus borealis*) are located in eastern United States, primarily east of the Continental Divide, with portions of their range extending into the northern tip of Mexico and southern portions of Canada (Shump and Shump, 1982a). Eastern red bats (*Lasiurus borealis*) are found throughout Wisconsin from April to October, but migrate south like most migratory bats to overwinter. Silver-haired bats (*Lasionycteris noctivagans*) also experience seasonal range due to its migratory nature. Silver-haired bats can be found in parts of southern Canada and into Alaska, and throughout most of the contiguous United States (Arroyo-Cabrales et al., 2008b). Tree species migrate along southern latitudinal gradients to aid in thermoregulation but also use torpor to limit energy expenditure over shorter time periods (Cryan & Veelleux, 2007). It is uncommon for a tree species to leave the continent during migration, however the lasiurines and silver-haired bats in this region have been documented to travel up to 2,000 kilometers to wintering sites (Carter & Menzel, 2007; Cryan & Veilleux, 2007; McGuire et al., 2012).

The four Wisconsin cave bats (*Eptesicus fuscus, Myotis lucifugus, M. septentrionalis, Perimyotis subflavus*) are reliant on access to hibernacula, particularly caves and abandoned mines, which is a limiting factor to their distribution (Furlonger, Dewar & Fenton, 1987; Kunz and Reichard, 2010). Wintering sites are selected based on cool temperatures to limit metabolic processes and conserve fat storages (Cryan & Veilleux, 2007). Largest populations of little brown bats (*M. lucifugus*) occur in Northeast United States and in the Midwest. Kunz and Reichard (2010) suggest the larger concentration of little brown bats in these regions can be attributed to the higher density of caves and mines available for hibernacula.

Wisconsin's largest bat hibernaculum, Neda Mine, is located within the SEGP in Dodge County, and is considered one of the largest remaining hibernacula in North America (Redell, 2005). In 1995, it was estimated that a hibernating little brown bat colony of nearly 300,000 individuals inhabited the mine (Tuttle, 1996). More conservative estimates from 2001 determined approximately 120,000 individuals from multispecies colonies (*Eptesicus fuscus, Myotis lucifugus, M. septentrionalis,* and *Perimyotis subflavus*) hibernated in the Neda Mine (Redell, 2005). Based on these estimates, I predicted greater little brown bat activity at all survey sites relative to other Wisconsin bats due to large hibernating populations within the study region.

The little brown bat (*Myotis lucifugus*) inhabits a wide range in North America which includes Alaska-Canada boreal forest in the northern range and continues through the majority of the contiguous United States and into central Mexico (Kunz and Reichard, 2010; NatureServe, 2013). Big brown bats (*Eptesicus fuscus*) can be found throughout North and South America, from the northern most Canadian provinces and as far south as northern Brazil (Kurta & Baker, 1990). Of the cave bats, northern long-earned bats (*Myotis septentrionalis*) and eastern pipistrelles (*Perimyotis subflavus*) are more restricted in distribution with both species commonly encountered in the eastern United States and Canada (Fujita & Kunz, 1984; Caceres & Barclay, 2000; Arroyo-Cabrales et al., 2008c). Eastern pipistrelles are also native to parts of South America including Mexico, Belize, Guatemala and Honduras (Arroyo-Cabrales et al., 2008c). Northern long-eared bats are distributed as far south as Florida, United States.

White-nose Syndrome in North America

Hibernating bat colonies are currently facing widespread extirpation and potential regional extinctions due to the emerging threat of white-nose syndrome (WNS), a fungal disease named for the visible white growth on muzzles and exposed skin of infected bats (Lorch et al., 2011). WNS was first documented in 2006 in Albany, New York and has killed up to 99% of infected populations (Frick et al., 2010). As of 2011, it is estimated that more than 5.5 million bats have died as a result of WNS (Hayes, 2012). White-nose syndrome is associated with the spread of an invasive fungus, *Pseudogymnoascus destructans* (formerly known as *Geomyces destructans*) and is suspected to cause early arousal from hibernation and inevitable starvation due to premature loss of winter fat reserves (Frick et al., 2010). Species vulnerability makes habitat selection a much-needed research priority to aid in conservation of these critical animals.

White-nose syndrome has affected populations in portions of the Northeast United States and is spreading as far south as South Carolina, and west to Oklahoma as of winter 2012 (Cohn, 2008; Frick et al., 2010; Cohn, 2012). White-nose syndrome has also been documented in five Canadian provinces since its discovery in 2006 (Cohn, 2012). Kunz and Reichard (2010), in their status review of the little brown bat, suggest a federal listing of *Myotis lucifugus* as endangered under the Endangered Species Act as local and regional extinctions become a reality. Some scientists predict regional extinctions of Northeastern US's most common bat in as little as a decade (Cohn, 2012). In response to documented cases of the fungus within a small geographic distance to Wisconsin's borders, all 4 cave bats are currently listed as a threatened species within the state and are protected under the Wisconsin Endangered and Threatened Species Law (State Statute 29.604 & Administrative Rule NR27).

Government agencies, including the US Fish & Wildlife Service and state's Department of Natural Resources, have taken precautions to help slow the spread of WNS by closing caves and educating the general public to clean and disinfect gear upon entering caves. In addition to these precautions, increasing knowledge of bat behavioral ecology is of critical importance to allow for potential reintroduction efforts as local populations of Wisconsin are faced with the threat of WNS.

Foraging Behavior & Diet

When addressing species exploitation of their surrounding environments, it is imperative to consider physiological and morphological constraints and their influences on foraging ecology. Ecomorphology theory suggests that an individual's morphology influences aspects of their natural history and behavioral performance (Brigham et al., 1997; Swartz et al., 2003). Bat foraging ecology is constrained by wing morphology which, in turn, influences maneuverability and habitat selection (Aldridge & Rautenbach, 1987). Additionally, foraging site selection is interdependent with echolocation call structures of individual species (Aldridge & Rautenbach, 1987; Neuweiler, 1989; Schnitzler & Kalko, 2001). Understanding species-specific wing morphology and echolocation call variation and the influence these have on habitat selection can provide insight into where, and why, bats forage in the SEGP, Wisconsin.

Suborder Microchiroptera, which includes all seven species of bats in Wisconsin, utilize echolocation, an adaptation that allows bats to emit ultrasonic signals to aid in orientation relative to surrounding environment, and the detection, localization and classification of surrounding objects in space (Schnitzler & Kalko, 1998; Broders, Findlay, & Zheng, 2004). All Wisconsin bats are insectivorous and rely on echolocation to search and locate prey. Echolocation and foraging behavior are species-specific and vary according to foraging mode (e.g., aerial vs. gleaning), diet, and habitat structure (Schnitzler & Kalko, 1998; Broders et al., 2004). Echolocation signals also vary intraspecifically in structure, length, and frequency based on the specific behavioral task performed (e.g. searching for prey vs. capturing prey; Schnitzler & Kalso, 1998). Some suggest plasticity of call structure among individuals allows for greater efficiency in orientation and target perception in various habitats (Broders et al., 2004).

It is hypothesized, that echolocation call design (shape, frequency, duration) has evolved to favor specific habitat types and has the potential to influence the availability of prey (Barclay, 1985; Brigham et al., 1997). That is, smaller prey is less likely to be pursued by vespertilionids bats due to weaker echoes produced compared to larger prey and difficulty to detect using echolocation at longer distances (Schnitzler & Kalko, 1998). Interspecific variations in echolocation foraging tactics is expected to influence sensitivity to spatial configuration of ecological features (Ciechanowski et al., 2007). Although this hypothesis is not directly tested in this research, considerations of species-specific echolocation characteristics can provide insight to expected habitat selection of bats in this region. In general, narrow-band echolocation calls of low frequency and long duration, as emitted by *Lasiurus borealis* and *L. cinereus,* are optimized for catching prey at a distance in open spaces (Barclay, 1985; Schnitzler & Kalko, 2001). In comparison, species emitting signals with mixed components, as exhibited by *Eptesicus fuscus, Myotis lucifugus* and *M. septentrionalis*, allow for detection of prey and identification of background clutter along forest edges and gaps (Schnitzler & Kalko, 2001). Some species, such as the big brown bat, alter echolocation characteristics to best suit spatial arrangement of habitat encountered (Schnitzler & Kalko, 2001).

Morphological characteristics and echolocation call structure must be considered simultaneously in assessing habitat selection. Broders and others (2004) compared echolocation call parameters (e.g. minimum call frequency) from a capture-release study and observed varying distance perception between two *Myotis* species. This difference in distance perception of echolocation calls presents spatial limitations (Schnitzler & Kalko, 2001) reflected in the habitat selection of foraging *M. lucifugus* and *M. septentrionalis.* Broders et al. (2004) suggested the shorter distance perception and morphological adaptations of *M. septentrionalis*, such as lower wing loading (weight of bat divided by wing area) compared to *M. lucifugus*, provides this species with adaptations to navigate and forage in cluttered habitats. In contrast, Ratcliffe and Dawson (2003), suggests dissimilarities in function of echolocation calls of two morphologically similar, sympatric species remains to be understood. More research is needed on the evolution of echolocation abilities in relation to habitat and prey availability.

Likewise, resource partitioning of bats is influenced by wing morphology (Yates & Muzika, 2006). The small body size, low aspect ratio and moderate wing loadings of *Myotis lucifugus* allow this species to take advantage of relatively cluttered habitat such as forested areas due to slow and maneuverable flight patterns (Avila-Flores & Fenton, 2005; Brooks & Ford, 2005; Yates & Muzika, 2006). In contrast, the hoary bat is the only bat in this study region with both high aspect ratio (length of wingspan squared divided by surface area of wing) and high wing loading which limits this species to clear-cut habitats and forest gaps (Lacki et al., 2007). Eastern red bats also possess high wing loadings and are less maneuverable than other species in Wisconsin. Despite morphological classifications of Wisconsin bat species, more knowledge regarding foraging behavior is needed. This is evident in the observed flexibility of big brown bats in habitat use and foraging strategies despite the ideal morphological characteristics of an aerial hawking bat (Fenton & Bogdanowicz, 2002).

Currently, all seven species in this study are classified as aerial insectivores, catching prey on the wing or tail membranes (Barclay, 1985; Barclay, 1986; de la Cueva Salcedo et al., 1995). Little brown bats are opportunistic, aerial hawking foragers that forage in a variety of habitats (Clare et al., 2011) for a multitude of prey types (Anthony & Kunz, 1977; Broders et al., 2004), although they are known to forage heavily on aquatic emergent insects (Frick, Reynolds, & Kunz, 2010). Despite their labeling as aerial hawkers, Ratcliffe and Dawson (2003) have observed *Myotis lucifugus* gleaning prey from surfaces which suggests a reassessment of foraging strategies for this species as more is learned about these cryptic animals. The sympatric *M. septentrionalis* also capture prey by gleaning terrestrial insects from vegetation. This species' high maneuverability allows navigation through high cluttered habitat such as dense forested areas (Ratcliffe & Dawson, 2003; Broders et al., 2004). It is unclear whether the alternating between gleaning and aerial hawking is due to prey availability or evolutionary behavioral traits (Fenton & Bogdanowicz, 2002).

Wisconsin bats rely on multiple orders of insects for their diets. Silver-haired bats (*Lasionycteris noctivagans*) are the most taxonomically diverse foragers with evidence of consumption of 11 insect orders in North America (Lacki et al., 2007). However, dietary specialization of some species in this region is also observed. For example, big brown bats have been identified as a highly selective species (Lacki et al., 2007), selecting small Coleoptera as their most common prey type (Kurta & Baker, 1990; Agosta & Morton, 2003). Despite this, Brigham and Fenton (1991) found greater than 50% of sampled big brown bats' diets consisted of Tricopterans emerging from riverine habitats, indicating flexibility in this species dietary selection. Variability in diet has also been observed based on bat reproductive status (Belwood & Fenton, 1976; Anthony & Kunz, 1977) and seasonal influences (Agosta & Morton, 2003; Clare et al., 2011). These dissimilarities of prey selection between and within studies suggest intraspecific variation in dietary specialization based on spatial and temporal heterogeneity in prey availability (Brigham, 1990; Lacki et al., 2007; Clare et al., 2011). For this reason, identifying and conserving habitats that maintain the greatest diversity of insect prey may best meet the dietary needs of bat species in the Southeast Glacial Plains.

Diurnal Roosting Habitat

The selection of foraging sites is dependent on the proximity and accessibility to suitable roosting locations (O'Keefe et al., 2009). Bats in this study region use a variety of diurnal roosts including manmade structures (Brigham, 1991) such as attics and bridges, caves (Fenton & Barclay, 1980), rock crevices (Ormsbee, Kiser, & Perlmeter, 2007), tree foliage (Shump & Shump, 1982a; Perry, Thill & Carter, 2007), tree cavities (Barclay & Kurta, 2007; Perry, Thill, & Leslie, Jr., 2008), hollows (Vonhof & Gwilliam, 2007), and clumps of lichen (Farrow & Broders, 2011). Cavity- and foliage-roosting bats are vulnerable to land use disturbances due to the direct loss of forested roosting habitat (Henderson, Farrow, & Broders, 2008; Farrow & Broders, 2011). Northern long-eared bats (*Myotis septentrionalis*) are forest-roosting species and rely primarily on roosting cavities under bark or snags in hardwood tree species (Johnson et al., 2009). Eastern pipistrelles (*Perimyotis subflavus*) roost in the foliage of mature hardwood stands in close proximity to riparian habitats (O'Keefe et al., 2009) but have also been observed roosting under bridges (Ormsbee et al., 2007). Land use fragmentation, specifically from urbanization and deforestation, can alter day-roost availability to these species and other cavity- and foliage-roosting bats by reducing the number of old growth trees and increasing the distances between roosting and foraging sites (Lacki et al., 2007; Johnson, Gates, & Ford, 2008; Farrow & Broders, 2011).

Bats should select roosts that maximize fitness by reducing energetic costs of flight, thermoregulation, predation avoidance and rearing young (Barclay & Kurta, 2007). The interspersion of roosting and foraging habitats within a landscape can reduce energetic costs and better meet the needs of bats (Lacki et al., 2007). Landscape-level elements have been determined to largely influence the resource selection of roosting sites for multiple species (Limpert et al., 2007; Henderson, Farrow, & Broders, 2008; Farrow & Broders, 2011). Specifically, studies have found greater affinity for roosting locations adjacent to aquatic habitats by forest-roosting bats (Perry, Thill, & Leslie, Jr., 2008; O'Keefe et al., 2009). However, few species in this region, such as the big brown and little brown bats, exhibit flexible roost site selection by inhabiting manmade structures (Fenton & Barclay, 1980; Burnett & August, 1981; Kurta & Baker, 1990). These species may be less sensitive to removal of mature forest stands for agricultural and residential purposes.

Identifying foraging habitat selection of species at aquatic habitats in the SEGP may provide insight to suitable roosting locations in the surrounding landscape. This information can aid wildlife managers in the conservation of landscapes that meet all life-history needs of bats in this region. The theory and concepts of landscape ecology, a holistic framework that evaluates dynamics between human and nonhuman elements across multiple scales, is a practical approach in relating landscape structure to relative bat activity.

Landscape Ecology Application: Utility in Bat Conservation Research

Landscape ecology is recognized across multiple disciplines as a valuable framework to understand the distribution of energy and materials, and alteration of structure and function among heterogeneous ecosystems (Risser, 1987). This framework also provides a useful set of tools to analyze the dynamic relationship between human influences and ecological processes in a landscape. Despite the practical applications, a gap in the literature exists regarding the influence of landscape composition, configuration and connectivity on bat activity in Wisconsin, particularly in agricultural landscapes. By assessing the relationship of bat ecology to habitat structure in a human dominated landscape, a more holistic approach to bat conservation can be developed to benefit all actors.

Landscape & scale in bat ecology research

North American studies of bat habitat selection have largely been scale-dependent with significance of landscape features alternating at different scales of analysis (for example: Avila-Flores & Fenton, 2005; Vonhof & Gwilliam, 2007; Lookingbill et al., 2010). For this reason, scale of analysis should be determined based on species of interest and their response to landscape structure (McGarigal, Cushman, & Ene, 2012). The association of bat activity with landscape elements at varying spatial scales is influenced by morphological, behavioral and ecological differences and should be assessed on a species-by-species basis (Barclay and Kurta, 2007; Gannon et al., 2003). Until recently, the varying scales of ecological processes for bat species has rarely been addressed (but see: Ford et al., 2006; Watrous et al., 2006; Lookingbill et al., 2010; Lundy & Montgomery, 2010; Hale et al., 2012).

Assessing habitat selection using a landscape ecology approach provides the opportunity to address ecological processes at varying scales. Landscape is an important concept to geographic research and provides a key foundation to assess ecological patterns and processes. Landscapes as a unit of analysis are more flexible and take a less reductionist approach than other units of analysis (e.g., ecosystems, watersheds, political boundaries). In the context of a watershed, the unit of analysis is restricted to a particular spatial scale bounded by streams and related tributaries. This may present limitations if ecological processes, such as habitat fragmentation, interact across multiple watersheds, as they often do. Landscapes are not confined by watershed boundaries and often intersect multiple basins. In addition, landscapes provide the ability to assess phenomena at relevant, context-specific scales. Attributing habitat characteristics outside the context of an ecological relevant landscape is at risk of proposing conservation practices of vital habitat preferences that are at an inappropriate scale relevant to the patterns and processes being analyzed.

In a study relating habitat features to bat presence, Ford et al. (2005) implemented a park boundary as the scale of analysis for seven species in the study region. Although this approach is commonly used because of logistic constraints, the national park boundary analyzed in the study could be mistakenly identified as adequate habitat to support life cycles of bat species due to the presence of specific habitat types, such as riparian corridors and old growth forest. However, assessing the size of the national park at relevant scales to species being analyzed, the structural patterns relating the old growth forest and riparian habitat, and the foraging distance travelled, would more appropriately signify acceptable foraging habitat. In other words, multiple structures of landscapes and scales outside of the park boundary can influence the processes and interactions that contribute to ecosystem composition within the park (McGarigal et al., 2012). Most importantly, analysis of specific spatial scales (e.g., 1 km^2 landscape) allows the opportunity to assess habitat selection at a scale relative to the species of interest, and to compare studies in diverse geographies to aid conservation efforts.

Analyzing bat habitat distribution at multiple scales may also help determine true patterns of habitat selection, as opposed to generalization resulting from inadequate scale of analysis (Watrous et al., 2006). The hierarchical selection of resources begins "…with the geographic range of a species, and extending to individual home ranges within the geographic range, use of general features within the home range, and selection of particular elements within the general features." (Limpert et al., 2007, p. 478) To adequately evaluate habitat selection of ecologically important behavior such as foraging, multiple buffer scales of landscape composition, configuration, and connectivity will be analyzed for individual bat species and overall activity to determine selection of general landscape features. This method, as used by Lookingbill et al. (2010), provides the distance resulting in the highest correlation for each species. From this, a foraging threshold distance for each bat species can be determined. Understanding the processes occurring at smaller scales, such as the use of patches of forest stands based on echolocation characteristics, and the differences occurring at large scale processes, such as roost selection and proximity to foraging habitat, will allow natural resources managers to recognize linkages to landscape variables supporting health of these species.

Landscape matrix & influence on habitat selection

Land-use change and the restructuring of the landscape mosaic are two major contributors to the decline in bat populations. Bats require a mixed landscape for their roosting and foraging needs (Yates & Muzika, 2006; Lookingbill et al, 2010). The reshaping of landscape mosaics, and alteration of the landscape matrix, negatively impacts the availability of resources by limiting or removing vital habitat and impeding movement throughout the landscape (Lacki et al., 2007; Estrada-Villegas et al., 2010).

The matrix within a landscape, as presented in landscape ecology, is the element that dominantly influences the landscape dynamics. Characterizing, quantitatively (e.g., total area) and qualitatively (e.g. unique descriptors), the type of matrix in a landscape and how it is perceived by bat species is essential to interpreting the relationship of foraging habitat selection in the specific environment.

For example, in the context of the Southeast Glacial Plains of Wisconsin, the dominant land type and the element exhibiting the overriding influence on landscape dynamics is agriculture. Conventional farming practices of row crops is the dominant use currently in the region, however the vegetation has experienced drastic changes before becoming dominantly agricultural. Prior to European settlement, the greatest influence to Wisconsin vegetation was the use of fire. Manmade fires are speculated to have influenced the development of many prairies, meadows and pine forests (Curtis, 1959). As described previously, today little of these vegetation communities remain.

Historically, the Southeast Glacial Plains region has had among the most productive farms in the state of Wisconsin (WDNR, 2013a draft). Today agriculture still remains an important aspect to the SEGP economy with net cash farm income in 2002 totaling to $430 million. Since EuroAmerican settlement, cereals composed nearly 60% of this region’s agricultural crops. Upon the establishment of the dairy industry in the state, the agriculture in this region shifted to hay and forage crops by the 1940s. Despite the gradual decrease of total farmland since the 1970s, overall farm size has seen a gradual increase signifying a consolidating trend throughout the region. This consolidation can result in the removal of important linear habitats to bats such as hedgerows and treelines and an overall homogenization of the landscape (Boughey et al., 2011). In addition to farm consolidation, this region has one of the highest agriculture land diversion rates in the state with majority of farmland being converted to suburban developments (WDNR, 2013a, draft). Such conversion is known to cause an increase in landscape fragmentation (Hale et al., 2012) and may influence the movement of bats throughout a landscape. Understanding the economic and cultural patterns that influence the landscape matrix such as these occurring in the SEGP can provide useful insight to ecological patterns observed.

Dixon (2011) investigated echolocation activity of multiple bat species in an urban/agricultural/"natural" mosaic. As predicted, the preference of landscape characteristics (e.g., impervious surface, open area, distance to water) varied by bat species. A limitation to this study is the lack of matrix identification, which hampers the results of this study to contribute to greater bat conservation efforts. More specifically, little comparison can be made between Minneapolis (in this case) and other landscapes if the dominant landscape element is not explicitly identified and described. Despite this fallback, Dixon (2011) addressed the perception of bats in urban landscapes by human actors and the implications this may have on conserving bats in a human-dominated landscape. The integration of social and cultural factors in their research that are molding this urban landscape highlights the necessity to unify human and nonhuman needs and meets a fundamental goal of landscape ecology.

The qualitative description of economic and cultural influences in a landscape analysis allows the comparison of distant landscapes experiencing similar anthropogenic influences. Further evaluation of such patterns may lead to insight regarding human impacts on populations. Human alteration of a landscape, particularly in the agricultural matrix of the SEGP, is unlikely to be reversed. A more appropriate approach to identifying conservation needs is to assess the relationship of ecological function integrated with social patterns. The framework of landscape ecology and the goals of this framework are nested in the relationships of human and nonhuman processes. The matrix as a tool for analysis provides the opportunity to assess the link between bat species and a dominating land type within anthropogenic landscapes.

Landscape pattern & the influence on bat populations

Despite the utility of classifying the landscape matrix, solely identifying the matrix within a landscape may not sufficiently tell the story of impacts on bat populations. The composition, configuration and connectivity of all landscape elements are also important landscape characteristics when assessing suitable foraging habitat for animals with varying home and foraging ranges. In spite of the importance of quantifying spatial patterns to understand pattern-process relationships (Gustafson & Parker, 1992), the configuration and connectivity of suitable foraging habitats has seldom been addressed in bat ecology literature.

The seven bat species documented in Wisconsin are known to travel multiple kilometers in search of appropriate foraging habitat (Pierson, 1998; Ford et al., 2005). In addition, multiple Wisconsin species (*Eptesicus fuscus, Myotis lucifugus, Perimyotis subflavus*) roost in anthropogenic structures such as buildings and bridges (Ford et al., 2005). Thus, landscape alteration by loss of suitable land cover may have greater negative impacts on foraging behaviors reliant on forest and waterways than impacts observed on roosting behavior. Land use composition, configuration and connectivity, quantified using landscape metrics, and their relationship to bat presence and foraging preference has shown to be highly complex and context dependent (Haines-Young, 2009; Hale et al., 2012). Within the field of landscape ecology, a number of concepts and quantifiable metrics have been identified to characterize landscape pattern and are useful tools in identifying pattern-processes feedback loops such as bat foraging behavior and anthropogenic land use change.

Composition is the simplest component of landscape pattern to quantify. Landscape composition simply refers to the abundance and variety of patch types within a landscape. For the purpose of this analysis, a patch refers to a connected area of a specific land cover type that differs from surrounding landscape elements. Across the surveyed aquatic landscapes, proportional abundance of each land cover type, and the richness of varying patch types will be determined for each landscape. Quantifying composition will help determine minimum habitat availability (e.g. forested or wetland land cover) required for bat activity in the SEGP. Despite the utility of landscape composition, bat foraging preference cannot be analyzed on composition metrics alone (Hale et al., 2012). Unlike landscape configuration and connectivity, landscape composition is not a spatially-explicit component to landscape pattern.

Landscape configuration provides the opportunity to assess the landscape elements in a spatial-explicit context. The configuration of a landscape refers to the spatial arrangement, orientation and shape complexity of patches (McGarginal et al, 2012). A number of metrics have been employed to assess landscape configuration including edge density, similarity index, proportion of core area, and radius of gyration, all of which will be employed in this analysis. A metric calculating total edge of forested patches will test the set of hypotheses aimed to address the forested edge effect on bat activity proposed in the "Hypotheses of Species-Habitat Associations with Landscape Characteristics" section of this chapter. Additionally, radius of gyration, or average distance traveled in a patch type before encountering a boundary, will be analyzed to assess sensitivity of bat species to overall edge effect and patch isolation. The degree of contrast of landscape elements is dependent on the species being analyzed. For forest-obligate species such as *Myotis septentrionalis* a forested patch bordering an urban patch will have a higher level of contrast than for generalist species such as *Eptesicus fuscus*. In this case, the urban patch may function as a barrier to *Myotis septentrionalis*. Of landscape configuration metrics available, a number of metrics, including patch isolation and largest patch index, are linked to connectivity of the landscape.

Landscape connectivity is the most difficult component of landscape pattern to quantify. It is likely for this reason that little attention has been devoted to landscape connectivity in bat ecology research. For the remainder of this chapter, I will focus on existing literature aimed at addressing the influence of landscape connectivity on bat habitat selection. Connectivity as a broad concept refers to the joining of species communities, habitats, and processes in the disjointed landscape mosaic (Noss, 1991). Landscape connectivity is commonly assessed in the context of linear features in the landscape, but also refers to any linkage of land that allows movement of individuals.

The greatest influence on connectivity is seen in anthropogenic alterations and homogenization of the structure of a landscape (Noss, 1991). In the SEGP of Wisconsin, for example, the predominant land cover type is agriculture, composing nearly sixty percent of the landscape. An important step in understanding pattern-process relationships of bat foraging in this agriculturally dominated landscape is to quantify the structure of a landscape by describing the size, shape, number, spatial arrangement and functional connection of elements, or forest, wetland, developed and agricultural patches (Forman and Godron, 1986). Despite the worth of landscape metrics within landscape ecology, little focus is aimed at understanding the sensitivity of bat populations to connectivity (but see Lookingbill et al., 2010, Hale et al., 2012; Frey-Ehrenbold et al., 2013).

The movement between habitat patches and the use of corridors is often a function of the value of intervening patches. A landscape corridor is of little use if adjacent landscape elements are resisted by bat species. For this reason, a spatial approach to quantify the ability of a species to move within a landscape is necessary. Characterizing connectivity, in addition to composition and configuration of a landscape, avoids the reduction of the landscape within patches to a neutral matrix (McGarigal et al., 2012). A limitation of simply addressing landscape composition without the quantification of landscape connectivity can be seen in Hein et al.'s (2009) study of bat use of habitat corridors.

Hein et al. (2009) conducted a study aimed describing the use of linear forested corridors by multiple bat species in a Southeastern United States landscape based on surrounding habitat type, edge, presence of roads, and distance to water. They observed bat presence along forested corridors to be positively associated with corridor edge, and counter to expectations, presence of roads adjacent to forested corridors also positively affected corridor use for all species in the study. The main disadvantage of applying their results to conservation efforts is the lack of attention in addressing how adjacent patches may intervene with functional connectedness of the landscape. Rather, binary habitat descriptions (1 = corridor interior, 0 = otherwise) and Euclidean distance measures from corridors to known favored landscape elements (e.g. water sources) were modeled to describe corridors and assess connectivity. This binary classification of landscape elements does not account for potential influence of adjacent habitat on the perception of corridors by bats. Hein's approach runs the risk of over-simplifying the interactions of individuals with the spatial patterns and their ability to facilitate movement within the landscape. In actuality, the compositional pattern (which is *not* spatially explicit and refers to number and abundance of patches) is the landscape component being quantified in their research.

Ignoring the connectivity of a landscape can result in incorrectly describing the process of bat foraging in a landscape as a function of the pattern of spatial arrangement, or landscape configuration. The ability of an individual to move from one suitable habitat patch to another will have greatest influence on the survival of the population and its ability to avoid predation, reduce energy costs and locate adequate prey. In landscape ecology, a functional connection depends on the process being analyzed. In the case of bat activity, the movement and use of connections in a landscape depends on the functional traits of the bat species such as size, wing morphology and echolocation characteristics (Fukui et al., 2011). Taylor et al. (1993) argued the distance of a resource patch from another is not the only factor in determining an individual's ability to move throughout a landscape. They asserted that another important, and often ignored, factor is the ability of individuals to reach the resource patches based on biophysical and behavioral characteristics (Taylor et al., 1993). For example, the connectivity of patches may be hindered by large open areas that are typically avoided by silver-haired bats (*Lasionycteris noctivagans*).

Despite Taylor et al.'s (1993) claim, connectivity of habitat patches and the influence on bat activity is still primarily being assessed as a function of distance of patches (Lookingbill et al., 2010). Recent work by Lookingbill et al. (2010) assessed the influence of wetland networks in national parks on bat activity by developing a distance metric for wetland network. Similar to the study conducted by Hein et al. (2009), a Euclidean distance metric was used to describe the relationship of connected wetlands. As Lookingbill et al. (2010) discussed, a factor not addressed in this analysis was the heterogeneity of the patches surrounding "connected" wetlands. Integrating the landscape matrix into landscape connectivity assessments provides the opportunity to determine the influence of a more heterogeneous landscape mosaic by characterizing the surrounding land types and their ability to facilitate movement between resource patches. Landscape ecology provides the framework to adequately address these questions of landscape connectivity and resource availability.

Given the volant nature of bats, functional connectivity in my analysis will be assessed at a maximum dispersal threshold distance. This distance varies as foraging distance traveled by bats is species- and context-specific (Lacki et al., 2007). Despite the physical ability to traverse large areas, bats may avoid crossing specific landscape elements due to unsuitable characteristics (Frey-Ehrenbold et al., 2013). A connectance index at the land cover class level will be determined based on significant land cover types from the composition analysis per species. Connectivity will be determined at the threshold distance 100 meters for each survey location similar to methods used by Frey-

Ehrenbold et al., 2013. To mitigate the landscape boundary effect, connectivity will also be addressed at 100 m distance in the background landscape. The connectivity index will aid in determining the ability of bats to move throughout the landscape.

Behavioral and morphological characteristics of bats in this region and landscape ecology concepts were integrated to provide a useable set of hypotheses to assess habitat selection in the SEGP. In the following section, species-specific hypotheses are described using the landscape metrics defined above. The methodology and results of assessing the influence of landscape patterns on bat foraging activity can be found in subsequent chapters.

Hypotheses of Species-Habitat Associations with Landscape Characteristics

Optimal foraging theory, a theory that asserts the evolution of behaviors that increase fitness by maximizing the efficacy at which individuals forage, explains the great diversity of behavior and diet of bat species and the ability to adjust behavior based on available resources (Lacki et al., 2007). As articulated in prior sections, foraging habitat selection is influenced by landscape characteristics such as spatial clutter, proximity to roosting location and prey abundance, which are influenced by characteristics of individual species such as wing morphology and echolocation calls (Pierson, 1998; Avila-Flores & Fenton, 2005). Hypotheses integrating landscape ecology concepts were developed based on species-specific morphological and physiological characteristics from existing literature and ecological theory (Table 1, 2). The hypotheses were designed to predict bat habitat selection in the SEGP.

A landscape-level analysis of bat foraging habitat allows for the quantification of correlation between activity for individual species and land cover types. Threlfall, Law, and Banks (2012) observed species-specific variation in tolerance to anthropogenic modification at the landscape scale. Within the urban gradient of Sydney, Australia, the authors classified groups of bats based on similar morphological traits that were expected to exhibit variation in species-habitat relationships. The most tolerant group of bats to urbanization and landscape modification had relatively high wing loading and aspect ratio and low frequency echolocation calls (Threlfall et al., 2012). Bats exhibiting similar morphological characteristics as these are often categorized by low maneuverability in the literature (Lacki et al., 2007). I expect similar groupings of tolerant and sensitive species to anthropogenic intensification based on morphological traits and land cover in the agricultural landscape of SEGP.

Activity of large-bodied species in this study should correlate to habitat structure (Brooks, 2009). In a study conducted by Francl (2008), similar activity levels were observed between eastern red, hoary, and big brown bats at seasonal pools in the northern Great Lakes region. These large-bodied species were more active at larger pools which were often characterized by low canopy cover compared to relatively small and medium sized pools in the study region. This supports the hypothesis that morphology and habitat structure influence recorded activity of these large-body species.

Hoary bats (*Lasiurus cinereus*), for example, have relatively low maneuverability and should utilize more open habitats (Barclay, 1985). I expect hoary bats to be more prevalent at lake aquatic habitats versus riparian in the study region due to less clutter encountered at these locations. Similarly, agriculture fields should provide more navigable habitat for this species. Eastern red bats (*Lasiurus borealis*) are moderately sized lasurines with similar morphological characteristics to the hoary bat. The high wing loading and moderate aspect ratio of this species provides the ability to forage in forest gaps and riparian forests (Lacki et al., 2007).

Additionally, hoary and eastern red bats have shown the ability to benefit from manmade structures in foraging habitat selection (Shump & Shump, 1982a). Hickey (1990) observed individuals of hoary and eastern red bats concentrating around streetlights at a park in Canada. I expect minimal influence of proportion of developed land on bat activity based on the tolerant nature of hoary and eastern red bats to anthropogenic structures. Finally, larger areas of forested patches should negatively influence hoary bat activity due to the low maneuverability of this species. Similar to hoary bats, I expect activity of eastern red bats to be negatively influenced by large areas of cluttered habitat, such as forested and woody wetland patches. A landscape with greatest diversity of patch types to meet the foraging and foliage-roosting needs should contribute to greater activity of hoary and eastern red bats in the SEGP.

A presence-absence study conducted by Ford and others (2006) determined big brown bat (*Eptesicus fuscus*) presence to be negatively associated with canopy cover. In this study, big brown bats preferred open habitat structure to closed or forested habitats. Brooks (2009) found similar results using active and passive acoustic surveys in Northeastern, USA. These results are consistent with morphological expectations of big brown bats, which specialize in foraging in open habitats (Kalko & Schnitzler, 1998). However, Duff and Morrell (2007) found the prediction of big brown bat absence to be challenging due to the habitat generalist and widespread nature of this species. I expect relative activity of this species to be higher than other large-bodied species due to flexibility in roosting selection and ability to alter echolocation signals to suit foraging habitat. Landscapes with greatest diversity of habitat types should provide resources for all life-history needs and should increase big brown bat activity.

Ober and Hayes (2008) observed an increase in likelihood of big brown, hoary, and silver-haired bats as percent of canopy cover decreased and open area above riparian habitats increased. Unlike the larger hoary and big brown bats, silver-haired bats are slow in flight and are considered highly maneuverable (Barclay, 1985). Despite minimal research conducted, the morphology of this species is designed for foraging in small clearings of forested areas. However, this species relies primarily on coniferous or mixed coniferous/deciduous forests to forage (Kunz, 1982). I expect overall activity of this species to be minimal because of minute amount of coniferous forest stands in the SEGP. I hypothesize activity of the silver-haired bat to be greatest in areas with greatest forested and wetland cover, and minimal urban land cover.

Bats rely on forest edges when foraging for navigational features and shelter from predators (Verboom & Spoelstra, 1999). Edge habitats are expected to support higher levels of insect prey (Brigham et al., 1997). I expect an overall increase in bat activity as forest edge in the landscape increases. Forest interiors are also regarded as highly productive insect habitats. In general, I expect bat activity to be lowest in landscapes with minimal forest cover. Although forested landscapes provide clutter for larger bats, forest interiors and forest edges are important for roosting and other life cycle requirements. Varying bat activity has been observed between riparian habitats based on stream order. Rivers with fast-flowing water are known to interfere with foraging activity by producing noises that disrupt echolocation calls (Grindal et al., 1999). For this reason, I expect bat activity to increase as stream order increases.

Despite the general relation to edge habitat, Broders and others (2006) found activity levels of *M. lucifugus* to be lowest at clear-cut forest edges. This may be due to avoidance of open areas for protection from predators. Multiple studies suggest that *M. lucifugus* show a great affinity for water sites due to their opportunistic selection of prey (Broders et al., 2004; Broders et al., 2006). I suspect the differences of activity levels between lake and riparian survey sites to be minimal because both support higher levels of prey the overall high attraction to water (Broders et al., 2006; Fukui et al., 2006;). Although minimal research has been conducted on bats in this region, I predicted the overall activity of little brown bat to be highest of all species because of flexible roosting selection, generalist foraging patterns documented in other areas (Clare et al., 2011) and the reliance on aquatic emergent insects for prey (Brooks & Ford, 2005; Dixon, 2012; Frick, Reynolds, & Kunz, 2010).

M. septentrionalis is a forest-interior specialist (Broders et al., 2006). The small body size of *M. septentrionalis* provides this species the ability to utilize forest canopy gaps that are unavailable to larger species (Owen et al., 2003). I expect the overall activity of this species to be relatively low because of preferences for foraging in forest interiors. Yates and Muzika (2006) observed a decrease in occupancy by this species as patch shape increased in complexity. An increase in patch shape complexity can be regarded as an increase in habitat fragmentation. Wickramasinghe et al., (2003) determined species that were adversely influenced by habitat fragmentation experienced similar negative influences from agricultural intensification. Of the landscapes where this species is recorded, I expect a negative correlation between relative activity and patch shape complexity. Similarly, I expect relative activity of this species to decrease as agricultural land use increases. Because *M. septentrionalis* is commonly seen foraging at forested and wetland landscapes (Lookingbill et al, 2010), I hypothesize a positive correlation between largest forested patches and forested wetland patches.

Species such as eastern pipistrelle (*Perimyotis subflavus*) have been shown to be negatively influenced by greater areas of non-forested land cover in Nova Scotia, Canada (Farrow and Broders, 2011). Patchy distribution of this species at the regional scale is related to the loss of forested land cover due to anthropogenic change and the negative influence this has at the landscape level (Farrow and Broders, 2011). However, in acoustic surveys conducted by Brooks (2009) in central Massachusetts, USA, eastern pipistrelles were solely recorded in open habitats. As evidenced here, species-habitat relationships are context specific; individual bat species present in Wisconsin may be influenced differently by landscape composition at varying scales. In addition, bats may select suboptimal habitats if preferred habitat is unavailable.

Eastern pipistrelles have commonly been found roosting in manmade structures in addition to the foliage of deciduous forests or clusters of dead pine needles (Perry & Thill, 2007). Additionally, forest-edge, riparian forests, and waterways, specifically rivers, are important foraging habitats to this species (Fujita & Kunz, 1984; Broders et al., 2003). I hypothesize an increase in eastern pipistrelle activity with an increase in forest edge, wetland, and forested land cover. Despite limited knowledge on eastern pipistrelle behavior in this region, I expect the greatest diversity of habitat patches to support the greatest activity of this species based on its ability to utilize a range of roosting and foraging habitat.

Avila-Flores and Fenton (2005) suggest avoidance of urbanized areas by smaller vespertilionids due to vulnerabilities of low flying (below 12 m) flight habits. I expect landscapes with largest urban patches to support the least amount of relative bat activity. Despite the ability to coexist in human-dominated landscapes, I expect bats in this region to prefer habitats with a mix of vegetation and urban development. Additionally, increased anthropogenic pressure and modification of waterways in the SEGP requires an assessment of how changes across these landscapes affect bat distribution and richness.

Identifying habitat selection over numerous scales is imperative to successful management of bat populations in Wisconsin. By assessing the influences of landscape composition, as well as the spatial configuration and connectivity of landscape elements, it is possible to determine the major landscape factors that influence habitat choice of insectivorous bats. Understanding echolocation structure of bat species and linking species-specific characteristics to landscape structure can provide insight to patterns observed in foraging ecology. The hypotheses developed for this analysis were based on existing published research conducted in other regions. Due to the limited research conducted in the SEGP, a large part of this analysis is exploratory in hopes to expose and highlight relationships that may arise out of examining this unique landscape.

CHAPTER 3

ACOUSTIC SURVEY METHODOLOGY

Acoustic bat surveys were conducted in the SEGP as part of the state-wide Wisconsin Bat Monitoring Program implemented by the WDNR. The Wisconsin Bat Monitoring Program, developed by Wisconsin's first bat ecologist Dave Redell, created a means to estimate bat activity across the state and guide the response to white-nose syndrome. This program employs the Wisconsin citizen-based monitoring network to aid in the collection of acoustic bat data on land (walking), water, and driving transects. All surveyed transects and acoustic methodologies used for this analysis were developed by Dave Redell and colleagues at the WDNR, and were employed in efforts to contribute to the greater goal of statewide bat conservation.

Acoustic surveys are beneficial to surveying large areas of land and are critical to the field of bat conservation because they contribute expansive information regarding taxa that are otherwise challenging to track (Hughes et al., 2010). Acoustic methodology has contributed to the understanding of bat ecology by providing a means to measure relative bat activity, habitat use and composition of bat communities (Brooks, 2009). Acoustic monitoring has expansive applicability in surveying Microchiropteran bats in contrast to conventional capture methods, such as mist-net surveys, due to the capacity to store large amounts of data (Armitag & Ober, 2010), the flexibility in survey site selection, and ability to sample large spatial and temporal extents (Rodhouse et al., 2011). Additionally, the ability to record echolocation calls of species that routinely fly outside of the small area sampled by mist-nets allows for a more complete sample (O'Farrell & Gannon, 1999).

For this study, active acoustic surveys along water routes were conducted in the months of June and July 2010-2012 to detect summer residents and deter false collection of bat migration from wintering sites (Ford et al., 2005; Adam et al., 1994). Assessing survey sites over three years accounts for temporal variability in recording probability, as bat activity varies between nights and seasons. Lake and river transects were selected randomly throughout the SEGP landscape by WDNR biologists using a GIS and the WDNR hydrology geodatabase. Surveyed lakes were limited to lakes 0.4 square kilometers (100 acres) or larger in size and streams were limited to 4th order and above. Site visits of the random survey transects were conducted to assess suitability and access. Inaccessible transects were removed from the site selection. This resulted in thirty-six accessible, 8-kilometer river and lake survey transects throughout the SEGP.

Environmental conditions and logistical constraints, such as low water levels, prevented the completion of select surveys. Additionally, surveys that were below the 1 hour minimum, due to faulty equipment or inclement weather, were removed from the analysis. Each transect was surveyed once per survey season unless otherwise noted resulting in 107 acoustic surveys total for this study: Lake Mendota was surveyed twice in 2012 resulting in 4 total survey transects of this lake, Milwaukee River transect was not surveyed in 2012 due to lower water levels resulting in 2 surveys for this transect, Partridge Lake 2011 survey was removed from analysis, Powers Lake was surveyed twice in 2012 giving 4 total surveys, and White Lake 2011 survey was removed from the analysis giving 2 surveyed transects total for this lake.

Active water surveys were conducted using the Anabat SD2 ® (Titley Electronics, Ballina, NSW, Australia) broadband frequency-division ultrasound detecting system. Frequency-division detectors allow for the continuous recording of echolocation calls of all frequencies while simultaneously synthesizing an audible pulse based on the call waveform (Armitage & Ober, 2010). The Anabat detector was connected to a personal digital assistant (PDA) during surveys to allow storage of bat calls for future processing and to provide real-time view of recordings. This method ensured the proper functioning of equipment while in the field. The hand-held Anabat detector and PDA were connected to a GlobalSat global positioning system (GPS) receiver that automatically recorded the latitude and longitude, date and time of each bat call during each survey which was used in subsequent analysis.

Water surveys were conducted in a boat powered with a trolling motor (if possible) for a minimum of one hour while continuously moving at light walking speed (mean survey length = 108 minutes). Active acoustic surveys began at civil twilight (approximately half hour after sunset) to account for varying emerging times of species from roosts (Berthinussen & Altringham, 2012). Acoustic surveys were limited to nights with wind speed less than 48 kilometers per hour (30 miles per hour), zero precipitation, and when minimum daytime temperature exceeded 10° Celsius (50° Fahrenheit) to increase likelihood of detectability. The Anabat detector was held at a 45 degree angle above the water surface to reduce obstruction of bat calls from forest edge or faulty recordings from reflection of sound off of the water's surface. The boat was positioned approximately 8-23 meters (25-75 feet) from the shore for routes conducted along lake shorelines. The boat was positioned in the approximate middle of the river for surveys conducted along river transects. For each survey, start and end weather conditions were recorded, including temperature (in degrees Fahrenheit), percent humidity and wind speed in miles per hour.

Three seasons of acoustic survey data (2010-2012) within the Southeast Glacial Plains were assessed to determine habitat selection of bats in an agricultural landscape. Bat calls, defined as an individual sound pulse emitted by a bat, were recorded using acoustic technology and were further identified by 3 WDNR ecologists in the lab. For the purpose of this study, a bat pass is a sequence of ≥ 2 search-phase calls emitted by a bat separated by < 1 second. Bat calls were examined using Anabat ™ and Analook ™ software, and identified using reference calls and voucher calls collected from individuals captured in the study region and recorded upon release. Bat passes were analyzed based on qualitative characteristics such as call slope and frequency (minimum and maximum) for species identification. Recorded calls were categorically assigned to *a priori* groupings, including species, species group, and total bat passes. Additionally, High Frequency and Low Frequency groups, separated with a cutoff value of 35 kHz, were used if too few calls were recorded, calls were of poor quality, calls did not contain search-phase calls, or in cases of general uncertainty. All identifiable bat passes for species within this region were saved to determine total relative activity of the region.

Among 7 bat species known to occur in the SEGP, only Hoary bat and Big Brown bat were recorded with sufficient regularity with Anabat detectors to analyze spatio-temporal variation in activity at an individual species level. Minimal silver-haired bats were recorded in this region likely due to their preference for roosting in mature forests stands and northern boreal forests, both of which are rare or nonexistent in the SEGP

(Cryan & Veilleux, 2007; P. White, personal communication, September 13, 2013). Although the range of Eastern pipistrelles and Eastern red bats extends across the state of Wisconsin, both are rare occurrences in the SEGP (P. White, personal communication, September 13, 2013). Similar species, such as *Myotis lucifugus* and *Myotis septentrionalis* can be difficult to differentiate confidently on some recordings and are often identified at the genus level and assigned to species groups in the literature (Armitage & Ober, 2010; Berthinussen & Altringham, 2012). To avoid misidentification, these two *Myotis* species were combined to form a *Myotis* spp. group for the purpose of this analysis. The Hoary bat and Big Brown bat relative activity were analyzed on the individual species level. All identified bat passes at the species, species group and frequency group levels were totaled to develop an overall relative bat activity at each survey site.

A relative activity index for the *Myotis* spp. group, Big Brown Bat, Hoary bat, and total bat activity were calculated for each survey. The number of “bat passes” standardized by the length of the survey in minutes was used as a relative measure of bat activity between survey sites and years. No assumptions were made of total bat abundance measurements, rather the relative activity index provides a means to compare foraging activity between transects of varying lengths to determine desirable habitat characteristics.

LANDSCAPE & ENVIRONMENTAL VARIABLES

Landscape composition, configuration and connectivity variables were derived to describe habitat using a land cover dataset at the landscape level for each survey site. The land cover data source for this study was the National Land Cover Dataset (NLCD) 2006 (Fry et al., 2011). This dataset is a publicly available, hierarchical, 16-class raster derived from Landsat Enhanced Thematic Mapper+ 2006 satellite imagery at 30 meter resolution. The raster data layer was resampled to the Level I classification for all land cover types, except wetlands, which were resampled to Level II resulting in nine land classes: open water, developed, barren, forest, shrubland, grassland, agriculture, woody wetlands, and emergent herbaceous wetlands.

The appropriate scale of analysis in determining the relationship of bat activity with landscape elements is species-dependent based on morphology, behavior and ecological differences (Gannon et al., 2003; Avila-Flores and Fenton, 2005; Barclay and Kurta 2007; Dixon, 2012). The distance traveled to forage and size of home ranges of Wisconsin bat species is unknown due to the plasticity of bat behavior. Of the seven bat species documented in Wisconsin, foraging distance observed in other regions for individual species ranges nearly four kilometers. The documented minimum foraging distance based on radiotelemetry studies of 16 *M. lucifugus* individuals is one kilometer (Broders et al., 2006). Brigham (1991) determined the mean foraging distance for big brown bats (*Eptesicus fuscus*) in British Columbia to be 1.8 kilometers based on 163 radio-tracked individuals. The majority of individuals from this study commuted at distances ranging 1.0 – 1.5 kilometers. However, this same study determined the mean commuting distance of big brown bats in a different geographic location (Ontario, Canada) to be less than 1 km (Brigham, 1991). It is clear that known foraging distances vary based on species and geographic location. For this reason, landscapes at multiple scales were assessed in efforts to adequately correlate relative bat activity with landscape and environmental variables. Buffers at 500 m and 1 km scale were defined using ArcGIS 10.0 (ESRI, Redlands, USA) and used to extract the NLCD 2006 land cover data around each survey site.

The proportional abundance of the nine land cover types for each survey site was calculated using FRAGSTATS v. 4 computer software (McGarigal et al., 2012) to allow comparison between survey sites of different areas. Additional composition, configuration and connectivity variables (Table 3) were calculated to gain a better reflection of the landscape and address the hypotheses. All ecologically relevant landscape metrics, including largest patch index (LPI) of wetlands, patch richness density and forest edge density (ED), were calculated for each survey site based the NLCD 2006 dataset of the landscape using FRAGSTATS v.4.

STATISTICAL ANALYSIS

Initially, an independent sample group t-test was conducted in IBM SPSS Statistics for Windows (IBM Corp., 2012) to determine if patterns of selection differ for each analysis group between lake and river habitats. To test the null hypothesis of equal relative bat activity between lake and river survey transects, an independent group t-test was conducted to determine whether there was statistically significant variation in total, hoary, big brown, and *Myotis* spp. activity between transects conducted at lake habitats in the SEGP and transects conducted at river habitats for all 3 years.

A multiple linear regression (MLR) model was built to investigate the relationship between relative bat activity and landscape composition, configuration and connectivity, and the effect of other environmental variables (e.g., temperature, elevation). First, the linear relationship between *Myotis* spp., Big Brown, Hoary, and total bat activity and landscape variables were assessed using curve estimation in SPSS. All variables exhibited a linear relationship with bat activity and were determined appropriate for MLR analysis. A correlation matrix was calculated in SPSS to determine which landscape variables were significantly correlated with bat activity at the 0.05 α-level (Appendix B; Appendix C). Insignificant variables were excluded from the MLR analysis.

A MLR analysis using only significant explanatory variables was conducted in SPSS using the stepwise method which re-checks the significance of variables after entering new independent variables. Transect routes were assumed to be independent. All explanatory variables included in the MLR models were tested for assumption of multicollinearity using variance inflation factor (VIF). A VIF less than 5 was deemed acceptable for this analysis, indicating minimal inflation in the standard errors associated with coefficient weights. Significance of the model slopes were assessed using Analysis of Variance (ANOVA) f test. The $H_0 : \beta_i = 0$ was tested to determine if at least one of the MLR model coefficients does not equal zero. All ANOVA f tests were significant allowing me to reject the null hypothesis, indicating a true relationship between explanatory variables and bat activity, $H_A: \beta_i \neq 0$. Goodness-of-fit of the multiple regression models were assessed using coefficient of determination, or r^2.

Some of the resulting relationships in the MLR models, although significant, were weak and indicative of non-linear associations. Therefore, for all analysis groups, ANOVA Regression Tree analyses were conducted to expose these non-linear relationships. This was performed using the *rpart* package (Therneau et al., 2013) in the R statistical environment (R Core Team, 2013). Regression Trees are particularly useful for revealing non-linear relationships, such as threshold effects, and are often called upon in the literature to increase model fitness (Lloyd et al., 2006; Threlfall et al., 2012). Regression Tree model results display data as a dendogram, illustrating the thresholds, or binary splits, in the data structure.

Finally, a hot spot analysis, or Getis-Ord Gi*, was conducted in ArcMap 10.0 to test whether particular survey transects and surrounding areas have higher than average relative species richness. The Getis-Ord Gi* analysis was selected because of the ability to determine statistically significant clusters of high and/or relative bat activity between survey sites. The results of the Getis-Ord Gi* analysis were mapped and spatial locations of hotspots of bat activity within the study region were assessed.

CHAPTER 4

BAT ACTIVITY RESULTS

Acoustic surveys were conducted along lake and river transects for three consecutive summers in the SEGP. Recorded bat calls were used to calculate bat activity for 4 analysis groups to test species-specific hypotheses relating activity to landscape structure. Bat activity was calculated for four analysis groups/species: Total bat activity, *Myotis* spp., Hoary bat, and Big Brown bat. Recorded *Myotis* spp., Hoary and Big Brown activity were not equally proportioned throughout the SEGP. *Myotis* spp. and Big Brown bat activity composed the majority of passes analyzed in this research, supporting my hypotheses of greater activity of generalist species (Figure 2).

Bat activity was monitored 107 nights during June 1 – July 31 of 2010-2012. Bat calls were recorded for a total of 193 hours resulting in 28,148 recorded bat passes, of which 72.9% were classified into the three species groups studied in this analysis. *Lasiurus borealis* (Eastern red bat), *Lasionycteris noctivagans* (Silver-haired bat), and *Perimyotis subflavus* (Eastern pipistrelle) were also recorded but were not analyzed due to limited identifiable passes. Hoary bats accounted for only 4.6% percent of total calls identified to species group, Big Brown comprised 23.5% percent, and *Myotis* spp. 71.9% percent. There were twenty-six nights in which the Hoary bat was not recorded. The *Myotis* spp. group was recorded during 106 of the 107 surveys, and Big Brown bat calls were absent on just 3 nights (Table 4).

Comparison of Total Bat Activity between Lake & River Transects

To test my 2^{nd} hypothesis contrasting activity between lakes and rivers, I compared recorded bat activity between surveyed aquatic transects. The mean total bat activity between lake and river survey segments varied greatly in this study region (lake $\bar{x}$ = 1.42, river $\bar{x}$ = 3.77; Figure 3). An independent group t-test was selected to test whether this difference in mean activity was statistically significant between lake and river survey transects in the SEGP. This test strongly supports my hypothesis by indicating significantly higher bat activity at surveyed river habitats than lake habitats (Table 5). As expected, mean relative Hoary, Big Brown and *Myotis* spp. activity at river survey segments was also significantly higher than recorded activity at lake habitats (Figure 4).

Patterns of Landscape Composition, Configuration & Connectivity in SEGP

Landscape composition metrics are the simplest landscape metrics to calculate and refer to the number and proportion of land cover patch types in a landscape. The agricultural matrix dominant over the SEGP region as a whole is also dominant at the smaller, 1 km landscape scale (Table 6). Agricultural lands at 1 km landscapes compose nearly 27% of land area on average, with riverine habitats having the greatest proportion of agriculture at approximately 38% (Figure 5). Lake landscapes, in addition to riparian habitats, in the SEGP are also heavily modified by human uses. The landscape surrounding lakes at 1 km scale are dominated by urban lands ($\bar{x}$ = 19.54%), followed closely by agricultural land use ($\bar{x}$ = 18.39%). Forests, woody and emergent wetlands are minimal surrounding lakes in this region as most were converted to residential and recreational uses. Wetlands are proportionally more prevalent at riparian habitats than lakes within the SEGP. Emergent herbaceous wetlands and woody wetlands each comprise an average of 14.6% of the riparian landscape at a 1 km scale. Forest and wetlands cover types are represented equally (approximately 10% of landscape each) throughout the SEGP when considering total survey sites in the analysis. These nonhuman land uses composes an average of 30% of the landscapes surrounding aquatic survey sites at the 1 km scale, which may potentially indicate a large influence of anthropogenic use on bats in this region.

A LPI was calculated for forest, agriculture, developed, woody and emergent wetland land classes. LPI describes the percentage of the landscape that is composed of the largest patch of the class of interest. This index is particularly useful because it provides a simple measure of dominance in the landscape and allows comparison between landscapes of different sizes. Additionally, LPI provides a means to compare fragmentation between landscapes of similar land class proportion. For example, developed lands are equally abundant (~9%) at surveyed Lake Beulah and Partridge Lake transects. The largest developed patch at Lake Beulah composes 4% of the landscape, whereas at Partridge Lake, the largest developed patch composes 9% of the landscape (Figure 6). Thus, developed patches in the Lake Beulah landscape are more fragmented than at Lake Partridge despite equal abundance.

Fragmentation of developed lands is variable between lake and river habitats in the SEGP. Lake habitats have larger continuous patches of developed land on average than riverine habitats or survey sites as a whole (Figure 7). The largest dominant developed patch of all survey sites composes 56.6% of the landscape at 1 km scale. This occurs at Little Lake Butte des Morts in Winnebago County, a lake that is dissected east to west by four-lane U.S. Highway 10, with Menasha and Neenah cities bordering the eastern and southern banks. The lake is connected by the Fox River to the largest freshwater lake completely within Wisconsin's boundaries, Lake Winnebago, from which it receives its inflow as a part of the Fox-Wisconsin Waterway. Despite the connectivity within a network of lakes, Little Lake Butte des Morts is bordered by a continuous patch of developed lands. The dominance of development within this landscape likely contributes to the lake's highly degraded state (WDNR, 2013a, draft). The degraded use and continuity of urban uses may make this landscape unsuitable to bats.

In contrast, the survey location with minimal dominance of developed land cover at 1 km scale is a Fox River segment south of Little Lake Butte des Morts in Green Lake County. This segment of the Fox River has a developed LPI of 0.97%, meaning the largest urban patch composes less than one percent of the landscape. The Fox is the 2nd largest river in area in the SEGP, and also connects Lake Butte des Morts and Lake Winnebago, two of the largest lakes in the region. As evidenced at Little Lake Butte des Morts, the Fox River becomes progressively more developed as it flows northeast connecting these waterways (developed LPI Lake Butte des Morts = 6.3%; Lake Winnebago = 9.9%).

The majority of riverine sites within the SEGP are dominated by agricultural lands with an average LPI of approximately 18% (Figure 7). At its maximum, agriculture land dominates riverine habitat at 1 km scale by composing 71.1% of the landscape with a single patch. This intense agriculture use occurs along a Crawfish River segment surveyed in 2011 in Dodge County. As of 2002, Dodge County had the 3rd highest percentage of agricultural land in the region (WDNR, 2013a, draft). In comparison, lake habitats have a maximum agriculture LPI of 27.2%, which suggests rivers have a much greater connection to agricultural lands. Similar patterns are seen when comparing agriculture edge between surveyed lake and river habitats at 1 km scale in the study region. The mean agriculture edge density (ED) at river segments was 53.2 meters/hectare while lake habitats had a mean agriculture ED of 33.8 m/ha.

There is nominal difference in forested land dominance between lake and river habitats despite dissimilarities in agriculture and developed landscape structure. Similar forest LPI and forest edge between lakes and river may provide the opportunity to assess effects of adjacent developed and agriculture lands to these habitats, which are the dominant classes at lakes and rivers respectively. The mean forest LPI at all surveyed transects is 2.52%, signifying a much weaker dominance relative to agriculture and developed lands. A surveyed transect along Rock River had the largest dominant forested patch with an LPI of 14.16%. The Rock River is characterized as a warm water stream, owing to pond and dam construction, and is classified as impaired within the state due to point source pollution. Despite this, the Rock supports prominent invertebrate diversity and flows through significant forested lowlands relative to the rest of the region, potentially providing prime habitat to bats (WDNR, 2013a, draft). Forest ED at lake habitat is comparable to the amounts of agricultural edge in this landscape (forest ED $\bar{x}$ = 34.7 m/ha; agriculture ED $\bar{x}$ = 33.8 m/ha). A high amount of forest edge relative to the low proportion and LPI in the landscape signifies multiple small, irregular forested patches as opposed to larger, compact (maximally square) and continuous forested patches.

Landscape continuity is a numerical measurement of the traversability of a landscape to the organism of interest. In other words, landscape continuity provides an average distance (in meters) that an organism can travel within the landscape while staying in a single patch type. Landscapes with larger, less compact patches will provide a greater landscape continuity distance. Average landscape continuity for all survey sites is 755.8 meters at 1 km scale (Table 6). In the SEGP, lake landscapes are more continuous than riverine habitats, with Lake Mendota in Dane County and Lake Koshkonong in Jefferson County having the greatest traversability at 1 km buffer. Lake Mendota is primarily a residential lake, surrounding by a heavily developed matrix at 1 km scale. Despite the high continuity of the landscape, the developed matrix may not provide suitable foraging habitat for bats.

To address the issue of generalized landscape continuity, a connectance index was calculated for emergent herbaceous and woody wetlands. At 1 km scale, connectivity of wetlands is minimal, with an average of 2.7% of woody wetlands having functional joinings, and 3.4% of emergent wetlands at all surveyed sites. A similarity index was also calculated for the wetland classes and forested land cover. The similarity index takes a less binary approach at assessing the fragmentation of a landscape than the connectance index by analyzing all surrounding land types. The similarity index increases as the landscape is increasingly similar to the focal patch and less fragmented in distribution. At the 1 km scale, riverine habitats have a greater average similarity index of forested landscapes; in contrast, landscapes surrounding lakes are more similar to wetland features. Exploring landscape structure at survey sites has provided some insight as to why variability in total bat activity is evidenced between lake and river habitats.

Additional hypotheses were explored as a result of these dissimilarities in subsequent sections.

MLR Results of Landscape Characteristics on Total Bat Activity

Total relative bat activity at all surveys sites from 2010-2012 were correlated with the explanatory variables (Table 3) to determine linear relationships of foraging activity and habitat characteristics. Significant linear relationships at the α-level of 0.05 were observed for composition, configuration and connectivity explanatory variables at a 1 km scale with total relative bat activity (Appendix B). None of the Environmental Variables had significant linear relationships with total bat activity. Variables that were significantly correlated with total bat activity at a 1 km scale were entered into a MLR model to determine habitat associations. The VIF indicated that no assumptions of multicollinearity were broken for this and all subsequent MLR models. ANOVA F test showed that all MLR model slopes included in this analysis were significant.

The results of the MLR model indicated landscape composition, specifically proportion of land cover, as having the greatest influence on predicting total bat activity at all surveyed sites with an overall model fitness of $r^2 = 0.584$. At the 1 km landscape scale for 2010-2012, total relative bat activity is influenced greatest by nonhuman land classes – forest, woody and emergent wetlands – indicating an increase in bat activity as proportion of forests and wetlands increase (Table 7; Appendix H). Landscape continuity and proportion of agriculture have a weaker, although still positive, influence on total bat activity. Despite initial predictions, emergent herbaceous wetland similarity index negatively influences total bat activity at this scale with a coefficient of -0.321. This linear regression model determined that while bat activity increases as proportion of emergent wetlands in the landscape increase, an increase in neighborhood similarity to emergent wetlands negatively influences total activity.

The relationship of activity and assumed foraging habitat was also assessed at a 500 m scale by conducting a correlation analysis between explanatory variables and total bat activity (Appendix C). Similar to the correlation results at a 1 km scale, none of the Environmental Variables were significant at the 0.05 α-level for total relative bat activity. The relationship of patch richness density (number of patches/100 hectares) is significantly correlated at a 500 m scale although a relationship is not observed at a 1 km scale with total relative activity. All significantly correlated explanatory variables were entered into a MLR model to determine habitat associations of total bat activity at a 500 m landscape scale.

The coefficient of determination, indicating the percentage of variation that is explained by the linear model, showed that greater than 60% ($r^2 = 0.605$, 21.696, $p<0.001$) of variability in total bat activity was explained by the 500 m MLR results. This improvement of model fitness at the 500 m scale suggests that landscape structure better explains overall bat activity across the landscape at smaller scales. Proportion of woody wetlands had the highest significant positive regression weights under this model, indicating landscapes with higher proportion of woody wetlands at a 500 m scale are expected to support higher levels of relative total bat activity. Proportion of agricultural lands, forested lands, emergent herbaceous wetlands, and patch area variability significantly positively influenced total bat activity while controlling for other variables in this model (Table 8). Despite the strong positive association of total bat activity with proportion of woody wetlands, the model indicates activity will decrease as the largest patch index of woody wetlands increases after accounting for landscape proportion. This suggests that large, continuous areas of woody wetlands restrict bat activity while smaller, dispersed areas of wooded wetlands increase presence of bats in the landscape.

Species-Specific MLR Results with Landscape & Environmental Variables

Myotis spp., Hoary, and Big Brown relative activity recorded during acoustic surveys conducted 2010-2012 were correlated with explanatory variables at a 1 km and 500 m landscape scale. Multiple regression models predicted significant explanatory variables between the relationships of relative bat activity to landscape structure. Regression model results prompted secondary hypotheses and further analyses, including alternative model approaches, exploration and spatial analyses.

Myotis *spp. Relative Bat Activity*

The correlation analysis determined landscape composition, configuration and connectivity explanatory variables to be significantly correlated with *Myotis* spp. activity. Similar to total bat activity correlation results, none of the environmental variables were statistically correlated with *Myotis* spp. activity. The results of the step-wise MLR model explained 44% of the variability of *Myotis* spp. activity across the study region ($F = 27.020$, $p < 0.001$; Table 7), and indicated significant model effect of proportion of woody and emergent herbaceous wetlands, and developed LPI on *Myotis* spp. bat activity (Appendix I). Proportion of woody wetlands had the highest coefficient ($\beta = 0.429$. $p<0.001$) under this model, indicating an increase in *Myotis* spp. activity as proportion of woody wetlands increase. Interestingly, proportion of emergent herbaceous wetlands at a

1 km scale negatively influences *Myotis* activity in this same model, as does an increase in largest developed patch size (LPI). The remaining explanatory variables were not strong predictors and were not included in the final regression model to explain the effect of landscape-level habitat structure on relative *Myotis* spp. bat activity at 1 km scale.

The MLR model of *Myotis* activity at a 500 m scale provided varying results with lower model fitness ($r^2 = 0.350$, $F = 28.048$, $p<0.001$) than the 1 km model (Table 8). These results are in opposition with effect of scale observed for MLR results of total bat activity in the landscape. Proportion of woody wetlands and agricultural land positively influence *Myotis* activity at this scale, with proportion of woody wetlands having a stronger effect.

Hoary Relative Activity

A correlation analysis determined eleven explanatory variables to have a statistically significant linear relationship with Hoary activity at both 1 km and 500 m scales (Appendix B, C). The linear regression model for relative hoary activity at 1 km scale determined the proportion of woody wetlands to have the strongest positive influence ($\beta = 0.438$, $p<0.001$; Table 7). This result is similar to Total and *Myotis* spp. 1-km linear regression results in which woody wetland proportion was the most influential explanatory variable in these MLR models. Distance to major roadway and proportion of emergent herbaceous wetlands also positively influence hoary bat activity, indicating an avoidance of landscapes dissected by highways. The 1 km linear regression model explains 44.2% of the variability in relative hoary bat activity ($F=27.202$, $p<0.001$).

Model fitness of linear regression results at the 500 m scale are comparable to the 1 km results, with an r^2 of 0.424 (F= 25.657, p<0.001). However, woody wetlands LPI (β = 0.372, P = 0.021) was determined to be the greatest influence of hoary bat activity at the 500 m scale as opposed to proportion of woody wetlands (Table 8), indicating a greater effect of fragmented patches in the landscape. Under this same model, agriculture edge density and landscape continuity negatively influence hoary bat activity, which is in contrast with the positive association of Total, *Myotis*, and Big Brown with agriculture proportion.

Big Brown Bat Relative Activity

The MLR model assessing the relationship between relative Big Brown activity and habitat characteristics at 1 km scale explained minimal variability ($r^2 = 0.299$, F= 14.676, p<0.001); the model fitness of the regression model at 500 m explained 37% of the Big Brown activity variability (F= 14.960, p<0.001) within the SEGP. The Big Brown 1 km model results differed from the other three analysis groups in that woody wetland proportion did not contribute to the model. The emergent wetland similarity index had a significant negative weight, indicating a decrease in Big Brown activity as the neighboring patches of emergent wetlands increase in similarity. Under this same model, the proportion of emergent wetlands and forest core positively influences Big Brown activity. However, the model did not produce an acceptable goodness-of-fit to justify management practices based on the results.

At a 500 m scale, four explanatory variables were included in the model to best explain variability of Big Brown activity within the landscape. Forest core area, proportion of woody wetlands, agriculture, and emergent wetland LPI all positively influence Big Brown relative activity. These results are similar to Total and *Myotis* results in that the increase of proportion of woody wetlands and agriculture in the landscape at a 500 m scale also positively influences Big Browns at the same scale. Despite the increase in r^2 at 500 meter buffer, the model fit is still below an acceptable range, indicating the need to explore alternative modeling approaches.

Species Richness at Surveyed Lakes & Rivers in SEGP

Species richness varied greatly throughout the study region. The lowest recorded species count at a study site in any given year was two species which occurred during 14 of the 107 surveys. Of these 14 sites, only 3 were at riverine habitats and the remaining were lakes surveys within the SEGP. Additionally, the two recorded species at 13 of these sites were *Myotis* spp. and Big Brown bats, which indicates a more generalist nature of these species compared to Hoary, Silver-haired, Eastern Red, and Eastern Pipistrelle bats in the region. During the surveys conducted from 2010-2012, only one survey recorded all seven bats known to Wisconsin. This survey transect was along the Rock River in Rock County, Wisconsin in 2012 with a total relative bat activity of 4.52 bat passes per minute.

The species richness of a given survey only tells part of the story. The varying lengths in minutes of the acoustic surveys conducted require the standardization of number of species by survey time in order to compare between surveys. Species richness per hour was calculated based on the total hours each survey was conducted. When assessing species richness per hour, the Rock River survey conducted in 2012 has the 2nd highest number of species recorded per hour of all three survey seasons. This suggests that the seven species recorded at Rock River 2012 is a true pattern of high species richness and not a result of survey length.

Similar to total species richness, the survey sites with less than one species recorded per hour all occurred at lake habitats. Upon further investigation using an independent sample group t-test, riverine habitats (2.69 ± 0.87 species per hour) had significantly higher species richness per hour in 2010-2012 than lake habitats (1.97 ± 0.74 species per hour) during the same time period in the SEGP (Figure 8). The significant variability between surveyed aquatic sites indicates the need to further explore the landscape structure and environmental conditions contributing to these patterns of relative activity between lake and river habitats in the SEGP.

Locations of relative species richness outliers in the data are likely attributed to temporal variability and not true patterns of high species richness. July of 2011 saw greater species richness at Lac La Belle, Como, Partridge, and Big Cedar lakes. The higher species richness was likely due to warmer than average temperatures during July compared to historical averages. The mean species richness of these lakes for all years falls within the normal range. This supports the need to assess patterns over multiple seasons due to the between season variability.

Spatial Analysis of Species Richness in SEGP

A hot spot analysis was conducted (Getis-Ord Gi*) in ArcMap 10.1 to test whether particular survey transects and surrounding areas have higher than average relative species richness. The Getis-Ord Gi* analysis identified spatial patterns of relatively high species richness within the study region, with the northern reach and the southern-most portion of SEGP having significantly higher relative species richness compared to the average of the entire region (Figure 13). This hotspot analysis identified a both Wolf River survey transects in Waupaca County and Sugar and Rock River survey transects in Rock County as supporting relative species richness between 1 and 2 standard deviations above the mean. Survey sites with significantly lower relative species richness are more dispersed in the region. The Getis-Ord Gi* analysis indicated 4 survey locations to have an average relative species richness less than 2 standard deviations of the mean, all of which occur at lake habitats in the region. These results are consistent with my analyses of bat activity between lake and river habitats.

MLR Analyses Results of Bat Activity between Lake & River Survey Sites

Following the primary analyses, disparities were evidenced in between lake and river landscape composition, configuration and connectivity in the SEGP. Analyses suggest that the relationship between relative bat activity and habitat characteristics may differ between the two aquatic habitats. Additional correlations and multiple regression models were conducted to assess relative bat activity at lake and riverine habitats independently in efforts to further understand habitat-bat activity connections.

MLR Results of Relationship between Bat Activity and Lake Habitat

Similar to the multiple regression models analyzing river and lake survey sites simultaneously, models assessing differences between the surveyed aquatic sites provides equivalent results for both total bat activity and *Myotis* spp. analysis groups. Proportion of woody wetlands and mean elevation were determined to significantly influence total and *Myotis* relative activity at surveyed lake habitats at 1 km scale (Table 9a). Mean elevation of the landscape surrounding lake waterways is the greatest influence of bat activity in these models (total: $\beta = 0.535$, $p<0.001$; *Myotis* spp.: $\beta = 0.545$, $p<0.001$). Woody wetland proportion also positively influences total and *Myotis* activity at lake habitats with regression coefficients of 0.255 and 0.243, respectively. Model results assessing all survey sites indicated similar results of the relationship of woody wetland proportion to bat activity at both scales of analysis.

Multiple scale analyses were also conducted when contrasting habitat selection between lake and river habitats. Comparatively, multiple regression model results differed minimally at the varying scales (1 km vs. 500 m) for total activity at surveyed lake sites. Total relative bat activity at lake habitats is also influenced by proportion of woody wetlands and mean elevation at 500 m scale (Table 10a). Despite the similar significant regression coefficients between 500 m and 1 km models, greater variability of total bat activity at lake habitats can be explained at 500 m scale with a model fitness of $r^2 = 0.495$.

Results for *Myotis* spp. 500 m regression models provided an increase of model fitness at lake habitats compared to the 1 km model (Table 10a), with $r^2 = 0.491$. Under this model, *Myotis* spp. are positively influenced by the core area of woody wetlands, or proportion of wooded wetlands minus edge, at the 500 m scale, as opposed to total proportion woody wetlands in the landscape. Similar to the 1 km scale model, mean elevation is also the greatest indicator of *Myotis* spp. relative activity at 500 m scale.

Relative activity of *Myotis* spp. is expected to increase as the average elevation surrounding surveyed lakes increases in the SEGP.

Lake model results for both Hoary and Big Brown relative activity did not explain a great amount of variability at either 1 km or 500 m scales (Table 9a, 10a). None of the explanatory variables were included in the MLR models to significantly explain Big Brown activity variability at lake habitats. Additional model approaches may be necessary to better understand Big Brown activity at lakes in the SEGP. Models explaining the relationship of Hoary bat activity and habitat structure at 1 km and 500 m scales indicated a significant positive influence of maximum wind speed on relative Hoary activity surveyed at lake habitat sites. Based on these model results, hoary activity is expected to increase as the maximum recorded wind speed during an acoustic survey increases. However, it is important to note the low R-squared values for Hoary bat models, indicating the need to further investigate the habitat-bat activity relationship.

MLR Results of Relationship between Bat Activity and River Landscape Structure

Relative bat activity was also assessed for each analysis group using survey results conducted at river habitats. Greater hoary relative bat activity can be explained using MLR models at riverine habitats as opposed to lake habitats. Under this model, agriculture edge density is the single significant influential variable on Hoary activity at 1 km scale ($\beta = -0.675$, $p<0.001$; Table 9b). Woody wetland LPI was determined to have the greatest influence of Hoary activity at the 500 m scale, while agriculture edge exhorts slightly weaker influence on activity at this scale (Table 10b). The greatest amount of variability of relative Hoary activity at rivers within the SEGP can be explained at 1 km scale ($r^2 = 0.455$, F = 37.598, $p<0.001$), with Hoary bat activity increasing as agricultural edge decreases.

Model results explaining the relationship of Big Brown activity to habitat characteristics provided improved results when assessing riverine habitats. At the 500 m scale, Big Brown bat activity is expected to increase as proportion of developed lands decreases and core forest area increases (Table 10b). Under this model, percent of core forested lands has the greatest effect on relative Big Brown bat activity at river habitats with a model coefficient of 0.516 ($p<0.001$). The regression model predicting Big Brown activity at riverine sites 1 km scale accounts for 36.9% variability. The forest similarity index positively influences bat activity while developed LPI exhorts a negative effect at this scale. Under both models, derivatives of forested and developed lands are the greatest influential variables on Big Brown activity at riverine survey sites.

In contrast to MLR model results for total and *Myotis* spp. at lake habitats, bat activity for these analysis groups at riverine habitats proved to be more difficult to model based on R-squared values. At 1 km scale, total bat activity is negatively influenced by proportion of developed land use in the landscape and positively associated with forest similarity index (Table 9b). In this model, total bat activity is expected to decrease as rivers become more developed and less similar to forest habitat in structure and function. As the landscape size decreases, developed lands is the only explanatory variable that significantly explains total bat activity (table 10b), however greater activity variability is explained at the 1 km scale for total relative activity at riverine habitats.

The MLR model analyzing the relationship of *Myotis* spp. relative activity at riverine habitats in 1 km landscapes best explained bat activity variability with an R-squared value of 0.352 (Table 9b). Developed LPI and forest similarity index significantly influence *Myotis* spp. activity under this model, with β = -0.406, p=0.002 and β = 0.353, p =0.007 respectively. Proportion of developed lands and landscape continuity were determined to significantly influence *Myotis* spp. activity at the 500 m scale (Table 10b). Under both 500 m and 1 km *Myotis* spp. models, developed lands negatively influence activity at riparian habitats.

Regression Tree Analyses

As discussed in Chapter 3, linear models, although significant, predicted weak relationships between habitat characteristics and relative bat activity. These findings suggest that nonlinear model approaches may be more appropriate to explain habitat-bat activity associations. Regression tree analyses were employed to determine potential threshold effects of landscape structure, and to achieve improved model fitness of the relationship between bat activity and habitat. A primary benefit of regression trees, specifically in ecological modeling, is there is no implicit assumption of linear relationships between explanatory and dependent variables. Results are displayed in a hierarchical manner, indicating binary splits of influential variables which highlight threshold effects within the data. Because the model results are in hierarchical form, explanatory variables at the top of the dendogram signify most influential variables in model. The binary splits are interpreted in a "true or false" manner. If condition is true, proceed to left branch of the node, otherwise proceed right. Values at the base of each node (vertical lines) represent mean bat activity for each threshold effect.

Regression Tree Analyses of Relative Bat Activity at All Surveyed Transects

ANOVA Regression Tree analysis for Total relative activity at all sites determined developed LPI to be the greatest influential variable at 1 km scale (Figure 9). A developed LPI ≤ 5.1% is expected to contribute to a mean 3.795 bat passes per minute. In contrast, a developed LPI greater than 5% contributes to the decrease of total bat activity under this model. Elevation is the 2nd greatest influential variable contributing to higher total bat activity at 1 km scale. Landscapes where largest patch of developed land makes up less than 5% and average elevation less than 235 meters support the highest level of total bat activity at all sites (5.763 bat passes/minute).

The regression tree results are dissimilar from MLR results for total activity at all sites. Developed LPI was not considered a significant influencing factor of total activity in the MLR models, instead proportion of developed lands was determined to have a negative influence. Additionally, woody wetlands, the explanatory variable with greatest effect in MLR, were not included in the regression tree model. The R-squared of the regression tree model improved relative to MLR by explaining 66.23% of total bat activity variability at 1 km scale in the SEGP. This indicates potential threshold relationship of developed lands and elevation, as opposed to linear relationship assumed in MLR between bat activity and landscape structure.

Regression Tree results for *Myotis* spp. are similar to the total activity regression tree model (Figure 10). This is likely due to the large proportion of *Myoti*s spp. composing total activity in the study region. Under this model, *Myotis* spp. activity is highest in landscapes with a developed LPI ≤ 5.1% and elevation lower than 235.8

meters. Model performance also increased for *Myotis* spp. using the regression tree model with $r^2 = 0.625$, as opposed to $r^2 = 0.440$ with MLR model.

The regression tree goodness-of-fit also increased when modeling Hoary bat activity, explaining 50.8% of variability of Hoary bat activity. Regression tree model results indicated the proportion of woody wetland as having the largest influence on hoary bat activity at 1 km scale (Figure 11). Landscapes that contain greater than 35.32% of woody wetland cover are expected to support greatest activity of hoary bats in SEGP. These results agree with the MLR model, which also determined woody wetland proportion to be most influential variable on hoary bat activity. Landscape continuity was identified as the 2nd greatest predictor at all surveyed sites. Despite predictions, Hoary bats were determined to be negatively influenced by increasing distance of traversability, reflected in both MLR and regression tree models. It is likely that underlying processes not accounted for in this analysis are contributing to this pattern. Radio tracking may be necessary to further understand movement of Hoary bats within these landscapes.

Multiple linear regression results for Big Brown activity at all survey sites at 1 km scale provided an $r^2 = 0.299$, which signifies a low goodness-of-fit for predicting the relationship of activity to habitat structure. The ANOVA Regression Tree model approach successfully increased the amount of variability in Big Brown activity explained by the explanatory variables chosen for analysis, $r^2 = 0.475$. Under this model, Big Brown activity is expected to be highest at sites with smaller patch sizes, greater than 50 meters of agriculture edge per hectare, and dominant forested patches composing more than 2 % of the landscape (Figure 12). Proportion of emergent herbaceous wetlands is also expected to support greater relative Big Brown bat activity in landscapes with greater than 15% emergent wetland cover. This model suggests that Big Brown activity will be lowest in sites with the least amount of agriculture edge at 1 km scale.

Regression Tree Results assessing Relative Activity at Lake Habitats

To determine if threshold effects are evident at lake habitats, regression tree models were built for all analysis groups at both 500 m and 1 km scales. The model results improved marginally for total bat activity at lake habitats with an r^2 of 0.503. MLR models better explained bat activity for *Myotis* spp. and Hoary bat activity at both scales, which suggests threshold effects have little impact on these bats at lake habitats. Big brown activity could not be modeled by MLR or regression tree approach. Of the 60 lake transects assessed, mean elevation was determined to be the most influential factor predicting total bat activity at 500 m scale (Figure 14). Elevation is also the decision factor in describing sites with the lowest total bat activity. Lakes below 228 m in elevation support the least amount of activity.

Regression Tree Results assessing Relative Activity at River Habitats

Anthropogenic land use had a large influence on activity of total, *Myotis* spp., and Hoary bats as developed was the first split for total and *Myotis* and agriculture ED was the first for Hoary bats at river habitats (Figure 15, 16, 17). Total and *Myotis* spp. activity was highest at sites where proportion of developed lands composed less than 20% of the riparian landscape at 500 m scale. The second greatest influential factor of activity for total and *Myotis* was mean elevation. Riparian sites occurring at elevations lower than 237 m had a positive influence on total and *Myotis* spp. activity. Goodness-of-fit for both of these models increased from MLR results, which suggests a nonlinear relationship and supports the need to assess ecological processes using different modeling approaches.

Hoary bat activity at riparian sites is negatively impacted by agriculture edge and is expected to be lowest in sites with greater than 42 meters of agricultural edge per hectare, high proportion of woody wetlands, and agriculture LPI greater than 6% (Figure 17). Hoary Bat differs than other bats analyzed in that it is the only analysis group influenced by agriculture land cover using regression tree models. The regression tree model had an $r^2 = 0.760$ which is a large improvement from the MLR goodness-of-fit ($r^2=0.455$). Hoary bat was the only analysis group that regression tree models performed better at 1 km scale at riparian sites, which supports the need to use multiple scale analysis when assessing habitat selection of multiple species.

The regression tree results increased in model fitness compared to MLR results for Big Brown activity at riparian sites. The largest influence of Big Brown activity at river sites is proportion of forested lands followed by proportion of developed lands (Figure 18). A riparian landscape composed of more than 18% forest supports the greatest amount of Big Brown activity at 500 m scale. Proportion of developed lands and developed LPI are the 2nd and 3rd most influential variables included in this model, respectively. Big Brown bat activity is shown to be lowest at sites with less than 18% forest and greater than 13% developed lands.

Goodness-of-fit (R-squared) increased for all four analysis groups using ANOVA Regression Tree analysis approach to model relative activity across all sites and riparian sites, though lake regression tree models only improved for total activity. These results suggest a threshold effect across the SEGP and at riparian sites of landscape structure on relative bat activity. It appears that habitats at rivers become unsuitable for bats once the landscape is modified past a certain point. Similar relationships are not observed at lake habitats in this region. Conservation and restoration of aquatic sites should analyze species activity between specific habitat types using multiple model approaches in order to best identify patterns in the landscape.

CHAPTER 5

DISCUSSION

The primary objective of this study was to address the relationship of bat activity and species richness to habitat structure in an agricultural landscape. Analysis of an agricultural landscape can contribute to understanding the impacts of habitat modification and aide in the management of resources as anthropogenic use continues to intensify. Landscape ecology theory and spatial analysis approaches were used in this study to test relationships between relative bat activity and landscape characteristics. The goal of this research was to identify structural features of a heterogeneous, human-dominated landscape to which bat activity was hypothesized to be correlated. It was assumed that observed relationships between activity and landscape structure indicated suitable foraging habitat in the landscapes. However, the findings suggest that the most important factors influencing bat activity in landscapes are more complex than foraging processes. The remainder of this chapter will contrast the observed relationships of bat activity between lake and river transects for all analysis groups, and will conclude with general patterns of bat activity within the region.

Contrast of Bat Activity Between Lake & Riparian Habitats

Difference in bat activity between lakes and rivers emerged as the single strongest predictive variable. Riparian sites supported significantly higher species richness and activity in the SEGP. This difference is due both on how bats take advantage of these features as well as landscape composition, configuration, and connectivity. While both lake and river landscapes are intricately linked to greater influences of the agricultural matrix, lakes in the SEGP are characteristically more developed and fragmented, indicating greater subdivision and less connectivity than riparian habitats. Agriculture, which makes up nearly 40% of riparian landscapes, exhorts a greater influence on rivers in the SEGP. High quality wetland and forested habitat is more commonly found in riparian sites than lake habitats, and composed an additional 40% of all landscapes analyzed. Bat activity, and the response to these dissimilarities in landscape patterns between lake and river habitats, is species- and scale-specific. I discuss the influences of habitat structure, the difference between lakes and rivers for each analysis group, and the patterns observed in the landscape as a whole.

Observed Relationships of Myotis spp. Activity between Lake & River Habitats

I predicted *Myotis* spp. activity to decrease as human-dominated elements, such as developed and agricultural lands, increased. In the context of riparian habitats, it is apparent that *Myotis* spp. are found less often in landscapes that are dominated by urban development, while preferring landscapes that are more similar in function and structure to forested lands (Figure 16; Table 9a). An example is the Rock River 10 segment (Figure 19), which supports the lowest *Myotis* spp. activity of all surveyed rivers in the region. At the 1 km scale, the Rock River landscape was composed of 40% of developed land cover, while the dominant developed patch also composed nearly 40%. The equivalency in proportion to LPI, describing the town of Beloit, WI, is indicative as one large, continuous developed patch. Gleaning foraging behavior is expected to deter bats from loud background noise in efforts to reduce echolocation interception and increase foraging success (Schaub et al., 2008). *Myotis* bats are known to glean to capture prey, a method that relies on rustling noises of vegetation to detect insects. Therefore, gleaning bats such as *Myotis* spp., may be negatively influenced by potential ambient noise from residential and commercial land uses in Beloit surrounding Rock River. Additionally, large expanses of developed lands may be difficult to traverse for the relatively small, gleaning *Myotis* spp. (Swift & Racey, 2002; Avila-Flores & Fenton, 2005).

These results conflict with patterns observed by Gehrt and Chelsvig (2004) in the nearby metropolitan area of Chicago, Illinois. In their study, *Myotis* species were more frequently recorded in urban lands than surrounding rural land. These patterns lead the authors to hypothesize a negative influence of surrounding agriculture and open areas on *Myotis* species. The differences in findings between this analysis and the Chicago study may be a result of microhabitat characteristics. The urban heat island effect is known to contribute to warm urban centers and may potentially reduce costs of thermoregulation in Chicago, IL (Coleman & Barclay, 2011). Additionally, Little Brown bats take advantage of manmade structures for roosting needs. It is possible that *Myotis* spp. in urban centers, such as Chicago, travel from roosting structures in developed areas to nearby rural or aquatic sites for food and water sources and other ecological needs. Additionally, higher abundance of bats in an urban landscape, as in Gerht and Chelsvig (2004), does not necessarily correlate to healthier populations and caution should be used when drawing conclusions based on abundance (Coleman & Barclay, 2011). Gerht and Chelsvig (2004) analyzed habitat selection at a single 2 km scale. It is possible that patterns of selection may differ at smaller scales, such as those used in this analysis.

The difference of influence from proportion of developed lands versus LPI of developed lands provides interesting insight as to how residential, commercial and industrial lots influence *Myotis* bat activity. The data indicate the total area of developed land in a landscape has less of an effect than the large connected expanses of developed lands when foraging or commuting through riparian habitats. I hypothesize that *Myotis* bats are able to tolerate landscapes if developed lands are intersected by a diversity of habitat types, such as forested or wetland habitats, instead of one dominant developed patch.

Indirect relationships between *Myotis* activity and riparian sites were suggested by the strong correlation with mean elevation as an explanatory variable in the regression tree model. This nonlinear response of *Myotis* activity is expected to be highest at sites lower 237 m elevation, if the prior condition (developed<20%) is met (Figure 16). Although this environmental variable was determined to significantly influence activity at riparian sites, low elevation is representative of streams in the upper watershed that drain south in the SEGP, such as Wolf and Fox rivers. This relationship is likely correlated with the higher quality habitat that is characteristic of these riparian sites in the upper SEGP. Further analysis of activity at riparian sites is necessary to test this hypothesis.

Forest similarity, an index quantifying the similarity of the structure and function of the landscape mosaic to forest habitat, was determined to influence increased *Myotis* activity at riparian sites in linear models (Table 9). *Myotis septentrionalis* are forest obligates that are able to navigate cluttered vegetated landscapes and roost in tree cavities and under bark (Barclay & Kurta, 2007), and likely prefer habitats that most closely mimic forested lands. Evidence of forest selection by *Myotis lucifugus* has also been observed, in which bats more often selected roost locations in forested watersheds that have confined, adjacent river channels (Hagen & Sabo, 2011). A high forest similarity index likely identifies riparian landscapes that reflect these preferred forested watersheds.

The similarity to forest as an activity indicator, as opposed to simply forest proportion, suggests a loyalty to habitat structure and the benefits provided, instead of specific vegetation types.

Analysis of riparian habitats in the SEGP may benefit from classification along an urban-rural gradient. This may provide greater insight into how landscapes transitioning from agriculture to residential development influence bat activity in riparian habitats. In this analysis, the MLR and regression tree models did not determine *Myotis* spp. to be negatively impacted by agriculture at riparian sites at either 500 m or 1 km scales. Although not directly tested here, the lack of expected agricultural influence at riparian sites may be due to the intermediate landscape composition along the rural-urban gradient that is seen throughout the SEGP where the transition to urban development is gradual. This gradual transition, as opposed to a stark difference, may provide the variety of habitat required to meet all life history needs (Coleman & Barclay, 2011). Further analysis is needed to test this hypothesis in the SEGP.

Floodplain forests have been identified as important roosting habitats for *Myotis* species found in southeastern United States (Fleming et al., 2013). I hypothesized a higher activity of *Myotis* spp. in woody wetland habitats due to the forest-obligate species, such as *Myotis septentrionalis*. *Myotis* spp. activity is positively related to woody wetlands and average elevation at lake habitats in the SEGP. It is likely that bats rely on the shelter provided by wooded wetlands while foraging or commuting adjacent to open lakes in this region. It is important to consider the intermediate wetland habitats between lakes and development, and the benefits they provide, when assessing restoration and conservation needs in a modified landscape.

The unexpected relationship resulting from the MLR model is the effect of mean elevation of surveyed lakes. The Kettle Moraine State Forest, characterized as having kettles, or shallow sediment-filled bodies of water formed by glaciation, is located within the SEGP. This State Forest is considered the highest quality upland habitat in the region, and is composed of ash swamps, ephemeral ponds, extensive upland forests, and lakes. The kettle lakes, characteristic of this region, can provide drinking sources and higher prey density within a dense network of protected State Forest. The highest elevated lakes in the SEGP occur within, or in close proximity to, the Kettle Moraine State Forest, which is regarded as an important breeding site for forest interior specialists such as *Myotis septentrionalis* (WDNR, 2013a, draft).

Regression tree models did not improve model results for Myotis at lake habitats, indicating a more linear relationship of habitat structure around lake habitats than any overriding threshold effects. This results contrasts with the riparian results, which determined threshold effects to better explain bat activity at river habitats. The regression tree model assessing all surveyed sites predicted *Myotis* spp. activity to increase as agricultural edge composes more than 54 m/ha, in a landscape with less than 5% developed LPI and elevation less than 235 m. MLR results at all sites indicated influences of woody and emergent wetlands, and developed LPI. The varying results between MLR and regression tree models at all sites indicate a more complex relationship of *Mytois* spp. to landscape elements in SEGP than simply “linear relationships” or “threshold effects.” Habitat selection varies depending on ecological needs and reproduction states, and it is likely that intricate mix of ecological characteristics contribute to *Myotis* spp. activity in aquatic habitats. Ecological modeling can provide just a glimpse at pattern-process relationships these dynamic open systems.

Observed Relationships of Hoary Activity between Lake & River Habitats

The landscape patterns that were quantified in the agricultural matrix of the SEGP are shown to influence Hoary activity at riparian sites. Edge of agricultural lands is the greatest influential factor of relative Hoary activity at riverine habitats. Landscapes with less than 42 meters of edge per hectare are expected to support the greatest activity based on regression tree results. Commercial farming methods are known to reduce species richness and evenness of insects due to chemical applications and homogenization of the landscape. This results in an unhealthy food web structure (Crowder et al., 2010) upon which the Hoary bat depends for prey. The selective diet, relative to other species in this analysis, may limit the habitats in which Hoary bats can forage for insects, specifically in agricultural landscapes. This hypothesis in the agricultural context of the SEGP, albeit logical, is dependent on the assumption that Hoary bats were foraging when recorded during survey transects in the SEGP. It is necessary to consider that Hoary bats may have also been using riparian sites as connectivity corridors within the landscape when interpreting these results. This relationship provides an original identification of Hoary bat activity to agricultural lands, but additional research in this region is necessary to further understand the negative impacts of croplands.

No significant relationships were observed between landscape characteristics and Hoary bat activity at lake habitats using regression tree analysis, but the MLR determined weak relationships between lake habitat and bat activity. A weak r^2 indicated a low goodness-of-fit of MLR results and therefore are not explored in this study. Stronger relationships likely could not be identified because minimal Hoary bats were recorded at lake habitats assessed in this analysis of the SEGP. Average hoary activity observed at surveyed lake transects was 0.05 calls/min, which is equal to 3 calls per hour. The maximum Hoary activity of 2010-2012 surveys was 0.36 calls/hour, compared a mean of 0.73 and maximum of 5.44 calls/min for *Myotis* spp.

It is unclear if the relatively low recorded Hoary bat activity at all lake and river sites is a result of landscape factors, a consequence of temporal scale, or bias in the time of acoustic surveys. Greatest success at recording Hoary bats in other regions was noted to be 3-4 hours after sunset (Shump, Jr. & Shump, 1982b), while surveys used for this analysis were typically completed approximately 2 hours after sunset. The interspecific variability in night emerging behavior may explain the relatively low activity observed at lake habitats in the SEGP.

The MLR model for all survey sites suggests Hoary bat activity will increase as the distance of survey site from the nearest highway increased. The negative influence of major roads conflicts with my hypotheses and observed relationships in other regions, in which motorways are expected to have less effect on bats that forage in open spaces (Kerth & Melber, 2009). Despite this, Hoary bat is the only species negatively influenced. The lack of effect of highways on *Myotis* spp. in this region was unexpected due to the flight behaviors of these small, low-flying species.

Of all sites surveyed in SEGP, landscapes with the greatest proportion of woody wetlands were determined to be the greatest contributing factor to Hoary bat activity in both regression tree and MLR results; however the model fitness for Hoary bat activity at all sites significantly increased using the regression tree approach. Hoary bats appear to be more sensitive to landscapes lacking woody wetlands by avoiding landscapes at a "tipping point." The threshold effect indicates a higher dependence of Hoary bats on benefits of forested floodplains surrounding lake and river habitats, in contrast to the linear correlations observed for Total, *Myotis* and Big Brown in this analysis. These patterns observed in the SEGP may be due to the limited connectivity and availability of mature forested patches seen in the more developed areas of this region due to the increase in conversion of lands to residential and commercial lots.

Observed Relationships of Big Brown bat activity between Lake & River Habitats

Ecomophology theory suggests larger bats, such as Big Browns, should use less cluttered landscapes (Francl, 2008) such as open water and fields however opposite results were observed in the SEGP. Riparian models predicting Big Brown bat activity determined a positive influence of proportion of forest and forest core areas. The MLR and regression tree results both indicated the relationship of Big Brown to forest core area to be stronger at 500 meter scale. This scale-specific interaction with forested lands may identify underlying ecological needs, such as shelter surrounding more open foraging sites, proximity to maternity colony roosts, or nocturnal roosts needed for resting while foraging (Agosta, 2002; Hagen & Sabo, 2011). Additionally, the core area metric has been regarded as a metric that predicts overall habitat quality because it is a compound measure of patch shape, area and edge (McGarigal et al., 2012). Therefore, a larger amount of core forested area should indicate high quality habitats. This unexpected relationship of high quality forested landscapes to Big Brown bat activity highlights the need to integrate the context of surrounding landscape matrix when assessing habitat selection.

Big Brown bat activity was found to be positively correlated with proportion of agricultural land across all survey sites. These results differ from patterns observed in the United Kingdom, in which foraging bats avoided arable lands despite high proportion of agriculture in the landscape (Razgour, Hanmer, & Jones, 2011). An additional study in the UK observed higher bat activity at organic farms versus conventional farms, suggesting greater habitat quality in sites using less intensive farming methods (Wickramasinghe et al., 2003). Linear features, such as hedgerows and treelines, are expected to increase bat activity in European agricultural landscapes (Walsh & Harris, 1996; Boughey et al., 2011), but little is known about North American bat foraging behavior in agricultural landscapes.

Large numbers of waterways in the SEGP are bordered by linear vegetation (Anecdotal), and could possibly provide navigational features contributing to observed relationships. However, the NLCD 2006 dataset used in this analysis is at too course of a scale to identify these features and test this hypothesis. A further assessment of farm characteristics and hedgerows in the context of the SEGP is necessary to understand the processes of habitat selection and relationships of agricultural features. Nevertheless, this study provides an original investigation of North American bats in an agricultural landscape.

Regression tree results predicts Big Brown bats to be most active in sites with less variability in patch size, higher agricultural edge density, and a dominant forested patch composing greater than 2% of landscape at all surveyed sites in SEGP. Similarly, forest core, wetland composition and agriculture were significant explanatory factors determined by MLR model. Significance of edge habitat, as observed at agriculture edge, has been detected previously in the literature, where more Big Brown activity occurred at edges between gaps and forests (Menzel et al., 2002). The significance of both woody wetland and emergent wetland structure at all survey sites in the SEGP is not surprising. Francl (2008) determined seasonal wetland pools to be important sites for foraging and water resources and observed larger bats consistently selecting larger wetland sites. The MLR and regression tree models results for all survey sites were most explanatory at the 500 meter scale. Landscape features observed in this study may highlight important resources for Big Brown bats within the home range of this species.

Overall Patterns of Bat Activity in the SEGP

The correlation and multiple linear regression analyses produced results that mostly agreed with hypothesized relationships of landscape structure. For all 4 analysis groups, landscape composition, specifically land cover proportion, exhibited the greatest influence on relative bat activity in this region. However, a species- and scale-specific assessment of landscape influence paints a unique picture of the relationship between individual species and their habitat. As I dove deeper, it became clear habitat structure and bat activity differed between lake and river transects in the SEGP, and therefore necessitated additional exploration to decipher this added layer of complexity to bat habitat selection.

Dissimilarities in access to prey between lake and river habitats may be one contributing factor to the significant difference in relative bat activity and species richness at these habitats. The linear features characteristic of riparian corridors in the SEGP may provide navigational features and predator avoidance (Verboom & Spoelstra, 1999), and have been found to support significantly higher insect biomass than open habitat (Holloway & Barclay, 2000; Broders et al., 2006). Wolf River survey segments in the northern portion of the study region, and select river segments in the south, were identified as hotspots of relative species richness. The Wolf River flows through remote habitat and contains a greater concentrated network of mature forest stands than the central, heavily developed portion of the landscape. These forested habitats have been identified as significantly influencing bat activity in this analysis and in the literature. However, it is important to note that the greater activity over riparian habitats may also be attributed to commuting individuals throughout the landscape, and not solely the assumed foraging preferences.

Human land use, developed and agriculture, exhorts a negative impact on bat activity for all analysis groups, but the effect of human-dominated landscapes appear to be context-specific. The most influential habitat characteristics impacting total activity at riparian sites is size of the dominant developed patch and overall proportion of developed lands. These effects are consistent with *Myotis* and Big Brown MLR and regression tree models predicting bat activity at riparian sites. Similar relationships of *Myotis* spp. to developed habitat predicted in this analysis have not been observed in nearby urban areas. For example, Dixon's (2012) study between percent impervious land cover or other open habitats (agriculture, rural landscape) and bat activity in Minneapolis, Minnesota observed contrasting results for generalist species, such as *Mytois* and Big Brown bats. Dixon did not detect a significant negative influence of urban lands on *Myotis* spp.

activity, but Big Brown activity was determined to be negatively correlated with impervious surfaces. I was not surprised by the negative influence of urban lands on *Myotis* spp. activity in the SEGP, despite Dixon's (2012) results, due to the low flying characteristics of these smaller bats, and the forest-obligate nature of Northern Long-Eared (*M. septentrionalis*) bats. On the contrary, the negative association of anthropogenic land use with Big Brown and Hoary bats in the SEGP was not expected due to the tolerant nature of these species observed in other regions (Williams & Brittingham, 1997).

Proportion of woody wetlands and forested habitats were also important predictors of total relative bat activity MLR results at all sites and lake habitats. The NLCD 2006 dataset used in this analysis describes woody wetlands as having forest or shrubland composing more than 20% of the vegetative cover. Floodplain forests, a type of wooded wetland in this region dominated by a mix of swamp white oak (*Quercus bicolor*), red maple (*Acer rubrum*), and ash (*Fraxinus* spp.) that commonly occur along rivers, are often used as migration corridors because they provide some of the only contiguous stands of forest in this heavily modified landscape (Eggers & Reed, 1997). Maintaining forested vegetation, such as woody wetlands, surrounding lake habitats may provide bats with protection from elements when opportunistically foraging for prey in exposed, open spaces.

The models that best indicated woody wetlands and forest influences on bat activity at all sites differed among species. The 500 meter MLR models produced the best fitting results, and included woody wetlands and forested habitat as key indicators, for total and Big Brown activity. However, the 1 kilometer models better performed for

Myotis spp. and Hoary bats. This indicates that bats navigate landscape structure, and therefore suitable habitat, at varying scales. This finding agrees with the ecologic differences between species of this region, and has been observed previously in the literature (See: Ober & Hayes, 2008; Lookingbill et al., 2010; Lundy & Montgomery; 2010; Dixon, 2012).

Emergent herbaceous wetland proportion influenced bat activity both positively and negatively at the individual species level. Total, Big Brown and Hoary bat activity are expected to increase, as emergent wetlands in the landscape increase. Conversely, *Myotis* spp. are negatively impacted by proportion of emergent wetlands. This pattern of habitat selection may be a result of niche partitioning within this densely modified landscape. Emergent herbaceous wetlands, such as marshes, sedge meadows, fens and open bogs, are considered structurally open habitats. As discussed in Chapter 2, larger bats such as Big Brown and Hoary bats are likely to use more open habitats due to larger wing loading and aspect ratios, and lower maneuverability. In the SEGP, emergent wetland habitats may be a preferred foraging habitat for larger species due to the minimal clutter encountered. As a result, small *Myotis* bats may take advantage of more structurally complex foraging habitat such as woody wetlands. Similar patterns were observed by Leighton, Lee and Francl (2009) when assessing bat habitat associations at palustrine habitats in the Northern Great Lakes region. In their study, Big Brown and Hoary preferred open water habitats and were negatively impacted by closed canopy.

The apparent positive influence of some cluttered habitats, such as wooded lands, on larger bats in the SEGP suggests plasticity in habitat selection. The plasticity of larger bat species in the use of closed habitat suggests the need to further investigate their tolerance to cluttered environments. For example, the relationship of Big Brown and Hoary bats to closed habitats may be less of a linear relationship and exhibit more of a threshold effect once the habitat becomes too cluttered. Additionally, bat habitat selection is not only influenced by habitat structure, but also varies based on gender, reproductive status, distance to roosting habitat and season (Papadatou et al., 2009). However, these post-hoc hypotheses regarding niche partitioning and habitat selection plasticity are an extension of the explorative nature of bat activity research in this region. As our understanding of these cryptic species improves, relationships to wetland habitats and habitat clutter may be better understood.

As evidenced in the initial MLR results, the influence of habitat structure on bat activity is unique to the species and varies based on scale of analysis. Within the SEGP, total relative bat activity at all sites is correlated with a multitude of landscape metrics, including landscape similarity, proportion, and continuity for a variety of cover types. These results provide valuable insights to the successful management and conservation of bats. Specifically, multiple cover types including wetlands, forest, and agriculture, support the greatest activity while landscapes with greater homogeneity are expected to negatively influence bats in this region. Analogous results have been found in other regions, in which the greatest diversity of cover provides the greatest benefit (Bernard, 2001; Leighton, Lee, & Francl, 2009). Restoring wetlands and forested patches to increase the diversity of habitat structure surrounding aquatic sites is likely to benefit the greatest number of species.

CHAPTER 6

SUMMARY & CONCLUSIONS

Human-modification of landscapes is altering the way in which species interact with their environment and is having a negative effect on native species diversity (Rogers et al., 2008). The landscapes of SEGP are no exception. Currently, there is a region-wide decrease of highly specialized species and overall habitat quality as generalist species flourish in response to anthropogenic land use intensification (WDNR, 2013a, draft). Understanding landscape-level influences of human-controlled habitats may allow resource managers to steward habitats in a way that humans and nonhumans can better coexist.

Bats provide a prime opportunity to assess the implications of increasing monotonous features in an anthropogenic landscape for multiple reasons: (1) insectivorous bats are bioindicators due to their role as secondary consumers and sensitivity to landscape modifications (Frey-Ehrenbold et al., 2013); (2) mammals, and bats specifically, are poorly understood relative to avian taxa in regards to habitat modifications (Coleman & Barclay, 2011); and (3) species with broad geographic ranges, such as bats, tend to be overlooked in the assessment of North American conservation priorities despite the potential of isolated populations in expansive anthropogenic landscapes (Pierson 1998). Statistical analyses were employed to determine potential impacts of anthropogenic modifications on relative bat activity in the Southeast Glacial

Plains region of Wisconsin, a region in which the overriding influence on landscape dynamics is cultivated croplands.

This thesis has examined the influence of landscape structure on relative bat activity of four species in an agricultural landscape of Wisconsin. Patterns of bat activity at aquatic habitats in the SEGP were expected to be closely correlated to landscape metrics, such as proportion of urban, agricultural, and forested lands, landscape connectivity and similarity. Statistical analyses of landscape metrics showed more subtle correlations between habitat structure and relative bat activity than hypothesized. The significant, although weak, relationships determined in these analyses are suggestive of complex species-habitat interactions that could not be fully explained through this research. A study exploring multiple survey methodologies (e.g., mist nest, radio transmitters) may lead to refined conclusions about bat interactions with landscapes. However, this research highlights key relationships that can further bat conservation in Wisconsin.

The majority of hydrologic features in the SEGP have experienced modifications and negative impacts from human development. Invasive species, such as common carp (*Cyprinus carpio*), dammed outlets, lakeshore development, recreation pressure from metropolitan areas, and agricultural runoff have contributed to the impaired state of the lakes and rivers in the region (WDNR, 2013a, draft). Despite the similar anthropogenic effects at the larger, regional scale within the agricultural matrix of SEGP, the landscape patterns at the landscape-level between lake and river habitats are dissimilar and appear to influence bat activity in different ways. In contrast to my expectations, relative bat activity and species richness were significantly higher at riparian survey sites compared to lake habitats from 2010-2012. A possible explanation is the benefits provided by linear characteristics of riparian habitats, such as connectivity corridors and higher insect availability (Hagen & Sabo, 2011). Additionally, lake habitats are more dominated by urban development as agricultural lands are converted to residential developments.

Effects of human-dominated landscapes are manifested at riparian habitats in the SEGP, where total, *Myotis* spp., Hoary and Big Brown were determined to be significantly negatively impacted by developed and agricultural lands in all models at all scales. Similar influences of anthropogenic land use at lake habitats were not observed. Large, dominant patches of developed lands, commonly seen in towns dissected by rivers, are the greatest deterrent of bat activity. High quality riparian corridors are scattered throughout the SEGP, and it is likely that bats are discriminating against the higher developed riparian sites and selecting the highly vegetated rivers for resources. The observed anthropogenic-sensitivity by all species at riparian sites highlights the importance of maintaining vegetated buffers surrounding rivers to foster connectivity within the landscape.

Within the SEGP, total relative bat activity at all sites is impacted by a multitude of landscape metrics, including emergent wetland landscape similarity, continuity, and proportion of forest, wooded wetlands, and agricultural lands. The conservation of riparian corridors, and forested and wetland patches surrounding aquatic habitats within an agricultural landscape can sustain a mixed landscape mosaic on which bats depend for roosting and foraging sites. Forested patches can increase prey abundance within an agricultural landscape and provide protection from wind and predators while traversing the landscape. As developed areas within this landscape, and regions throughout the country, continue to intensify, the significance of maintaining intact forested and aquatic habitats cannot be underestimated. The results at all survey sites suggest that the most efficient conservation of suitable bat habitat, or the "bigger bang for the buck," would be in heterogeneous landscapes containing wetlands and forest that provide habitat for multiple species' needs.

The natural world is dynamic and chaotic, and uncertainty is inherent in all models attempting to predict ecological processes. As with most ecological research, this thesis is not without caveats. It is important to note that bat activity has been known to respond differently to types of forest, which may be of significance when assessing habitat selection and conservation needs in more heterogeneous regions. Broders et al. (2006) showed a positive relationship between *M. lucifugus* and coniferous forest locations, and a negative association with deciduous forest patches at a 1 kilometer scale. Similarly, Perry and Thill (2008) determined Big Brown bats to strictly select snags of one species of pine in Arkansas. Despite the minimal conifers in the SEGP, these studies signify the importance of specificity when making conservation management decisions. In landscapes with varying woodland communities, it may be necessary to address specific forested types to avoid misidentifying suitable habitat based on general forest classifications. This study did not distinguish between types of forests in the landscape because of the relative homogeneity of forest communities in the SEGP.

While acoustic data may provide insight into activity of bats in specific landscapes, the methodology presents some limitations to interpretation. Currently, our knowledge is limited on how conspecifics alter their echolocation calls and the influences this has on foraging and social interactions (Schnitzler & Kalko, 1998), and thus, not disregard of extreme caution used in species identification, there is inherent error in echolocation call processing. In addition, acoustic methods do not allow sex or reproductive status of species to be distinguished. Broders et al. (2004) and Broders et al. (2006) found foraging and roost habitat selection to differ between males and maternity colonies of Little Brown and Northern long-eared bats within the same landscape. Based on this, caution should be used when inferring relationships that are not sex-specific.

Moreover, care should be used in applying *Myotis* spp. results from this analysis to conservation of Northern Long-Eared bats. In spite of known occurrences of Northern Long-Eared bats in the SEGP, anecdotal observations suggest that majority of *Myotis* species recorded within the SEGP were Little Brown bats. Because of this, the *Myotis* spp. group, resulting from similarities and difficulty in distinguishing between echolocation calls of these species, may indicate a potential bias in acoustic recordings and findings. Even with the unequal proportions of *Myotis* spp. recorded, Northern Long-eared bats were recorded in the SEGP and patterns found in this analysis may provide valuable insight into critical habitat for the rapidly declining populations of this species due to WNS (UWFWS, 2013).

As is the case with numerous studies, it is likely that majority of the total bat activity analyzing was comprised of *Myotis* spp. group and Big Brown bats due to the close spatial proximity to a major Midwest hibernaculum, Neda Mine (Redell, 2005; Johnson, Gates, & Ford, 2008), and the generalist foraging nature of big brown (Furlonger et al., 1987) and little brown bats (Anthony & Kunz, 1977). However, total bat activity also included detections of Silver-haired, Eastern Pipistrelle, Eastern Red and Hoary bats in the region. Finally, activity indexes are an assessment of echolocation activity and it is important to not interpret relative activity as a count of individuals. Notwithstanding these conditions, this study furthers current understanding of spatial relationship of bat activity and habitat selection and provides a first look into bat-habitat interactions in the SEGP, which can aid in management efforts and conservation of bats in this region.

The assumption for this thesis was that recorded bat activity at aquatic sites indicated foraging preferences due to high density of prey. However, this assumption cannot be confirmed. Bats use search-phase calls for detecting objects in space - both food and obstacles. It is likely that recorded calls used in this analysis were bats commuting and foraging in the landscape. This is suggested by the increased activity over riparian sites which may be used as connectivity corridors in the landscape. Despite this, these results are indicative of habitat needs surrounding lakes and rivers within an anthropogenic matrix.

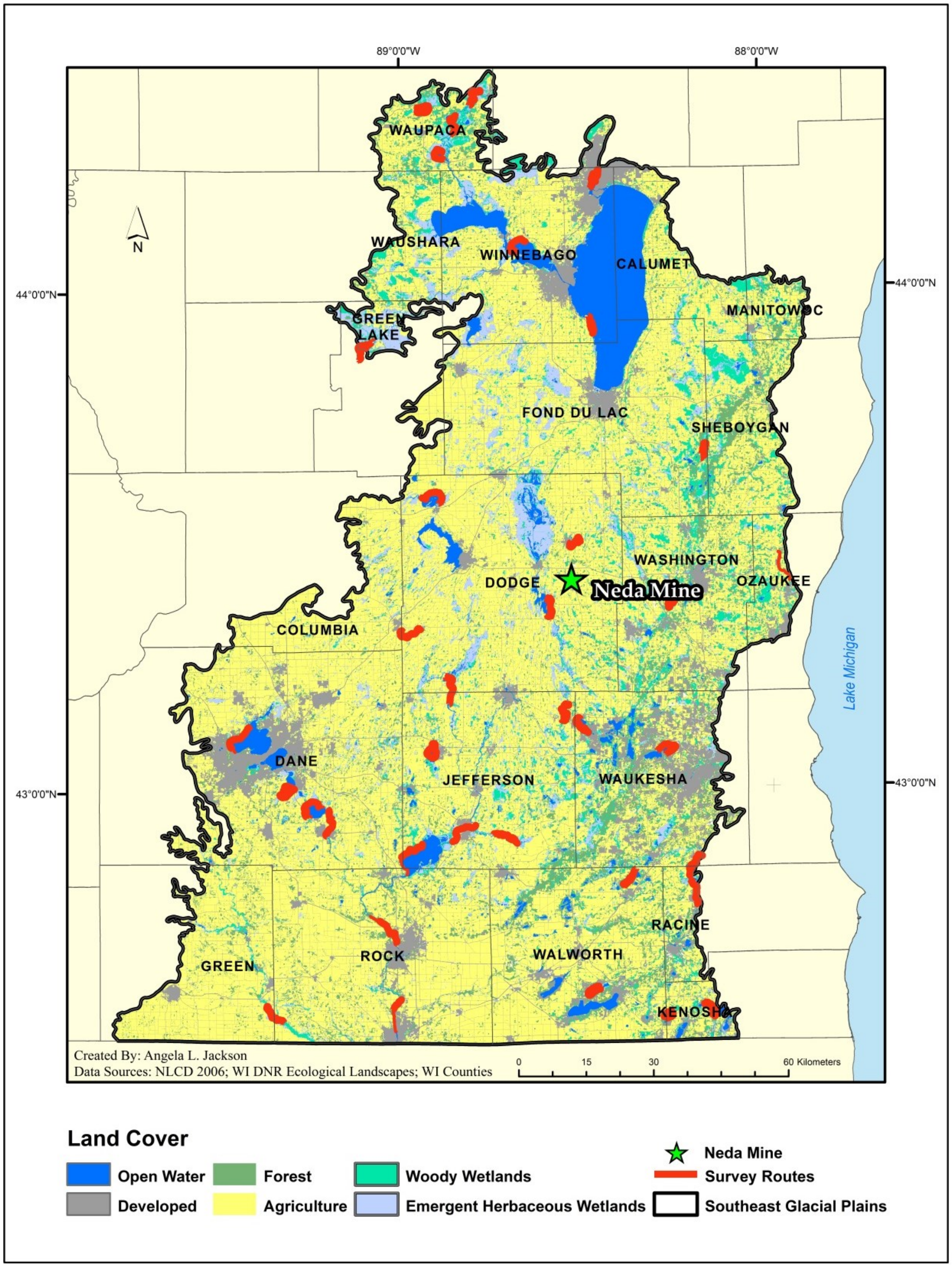
A decline in bat populations in the United States is just part of the story. North America has also been experiencing a widespread trend in decreasing avian aerial insectivore populations since the 1990s (Nebel et al., 2010). Decline in insect populations due to agricultural practices and overall habitat alteration are two causes that have been hypothesized to cause these declines. A clear association was observed in this data between insect supporting habitats, such as aquatic features, and bat activity. This research presents valuable knowledge of interactions between landscapes and insectivorous species in a highly modified landscape, which may not only support bat population health, but the health of additional compromised populations relying on insect for prey in human-dominated landscapes. Restoration and conservation of these landscapes can potentially rebound declining populations due to suspected unavailability of food.

Currently, it is debated whether agricultural land use has an influence on decreasing arthropod density. In the face of this debate, Benton et al. (2002) observed a decline in insect abundance and bird populations over 27 years as agriculture use heightened in Scotland. Based on these findings, one could assume similar negative impacts would be seen on other aerial insectivorous species such as bats in these landscapes. However, this analysis has shown a positive influence of agriculture proportion on total, *Myotis* spp., and Big Brown bat activity in a dense agricultural matrix. A possible hypothesis may be the opportunistic foraging of bats due to the declined competition from farmland birds. Future studies in this region may benefit from comparing effects of croplands on birds and bats simultaneously. Nevertheless, this analysis provides an original look into the relationship of agriculture and bats in the region.

Factors that were shown to influence bat activity between species and within species include patch size, presence of edge, dominant landscape elements and landscape connectivity (Yates and Muzika, 2006). The data show that bats require a mix of habitats to meet ecological requirements, such as foraging sites and roosting locations (Lookingbill et al., 2010), and are expected to use linear features to forage and move throughout a landscape (Lundy and Montgomery, 2010). For this reason, wildlife management decisions should not be made based on one bat species or landscape characteristic alone, but should elucidate species-habitat relationships by considering diurnal and nocturnal roosting, and foraging requirements at multiple scales. Although the relationships found in this analysis are slightly weak and are indicative of more complex processes, the results provide some conclusions to how bats interact within and between habitat types. It is important for landscape managers to go beyond landscape composition when addressing suitable habitat for species of interest. This study strongly suggests that bats would benefit from conservation of riparian corridors and the improvement of forested lands.

FIGURES

Figure 1: Location of Southeast Glacial Plains in Wisconsin and 1 km buffers surrounding 38 lake and river acoustic survey sites.



Created By: Angela L. Jackson
Data Sources: NLCD 2006; WI DNR Ecological Landscapes; WI Counties

Figure 2: Proportion of Relative Activity for *Myotis* spp., Hoary and Big Brown bat in SEGP (2010).

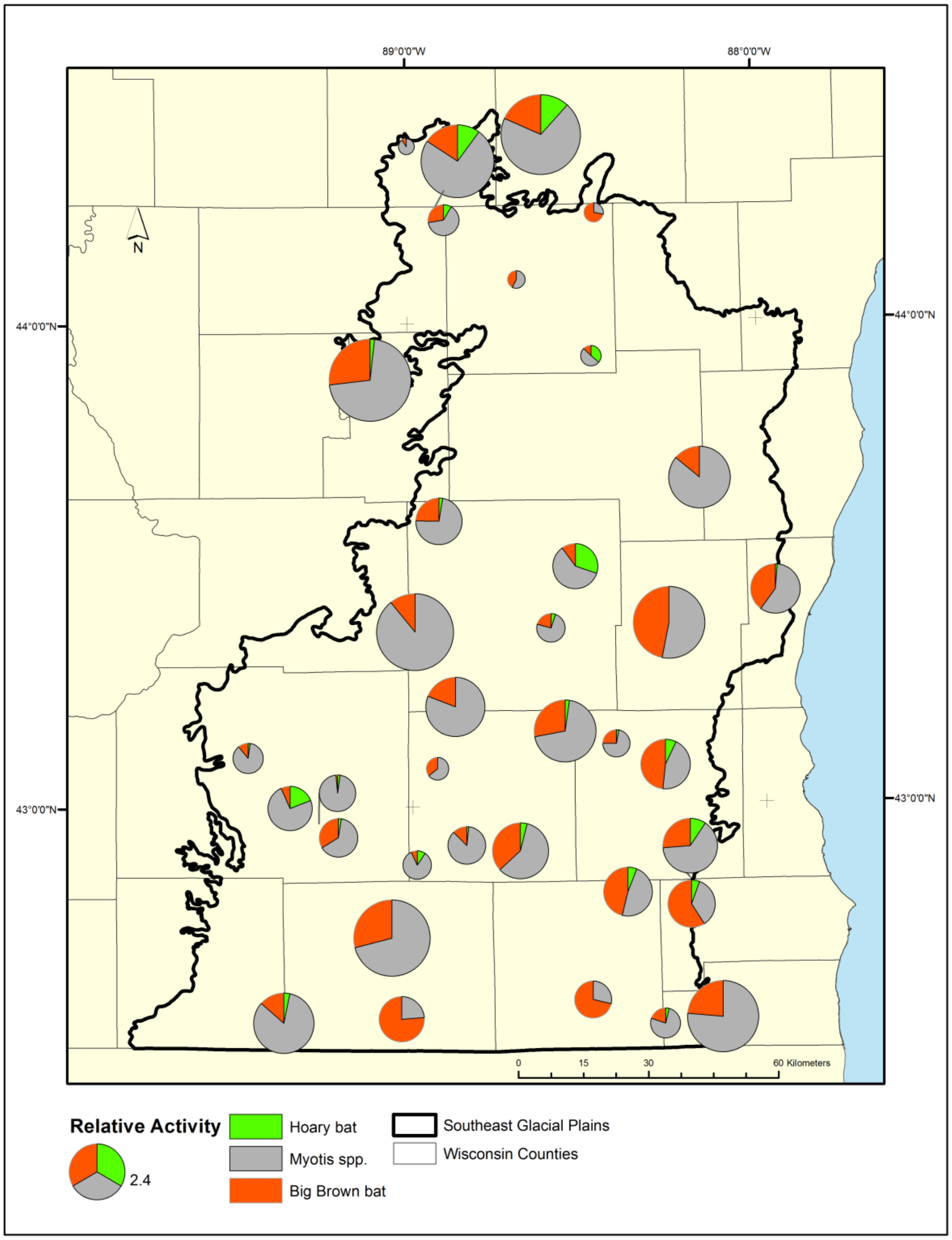


Figure 3: Total Relative Bat Activity (passes/minute) summarized using boxplots by year for Lake and River habitats in SEGP, WI.

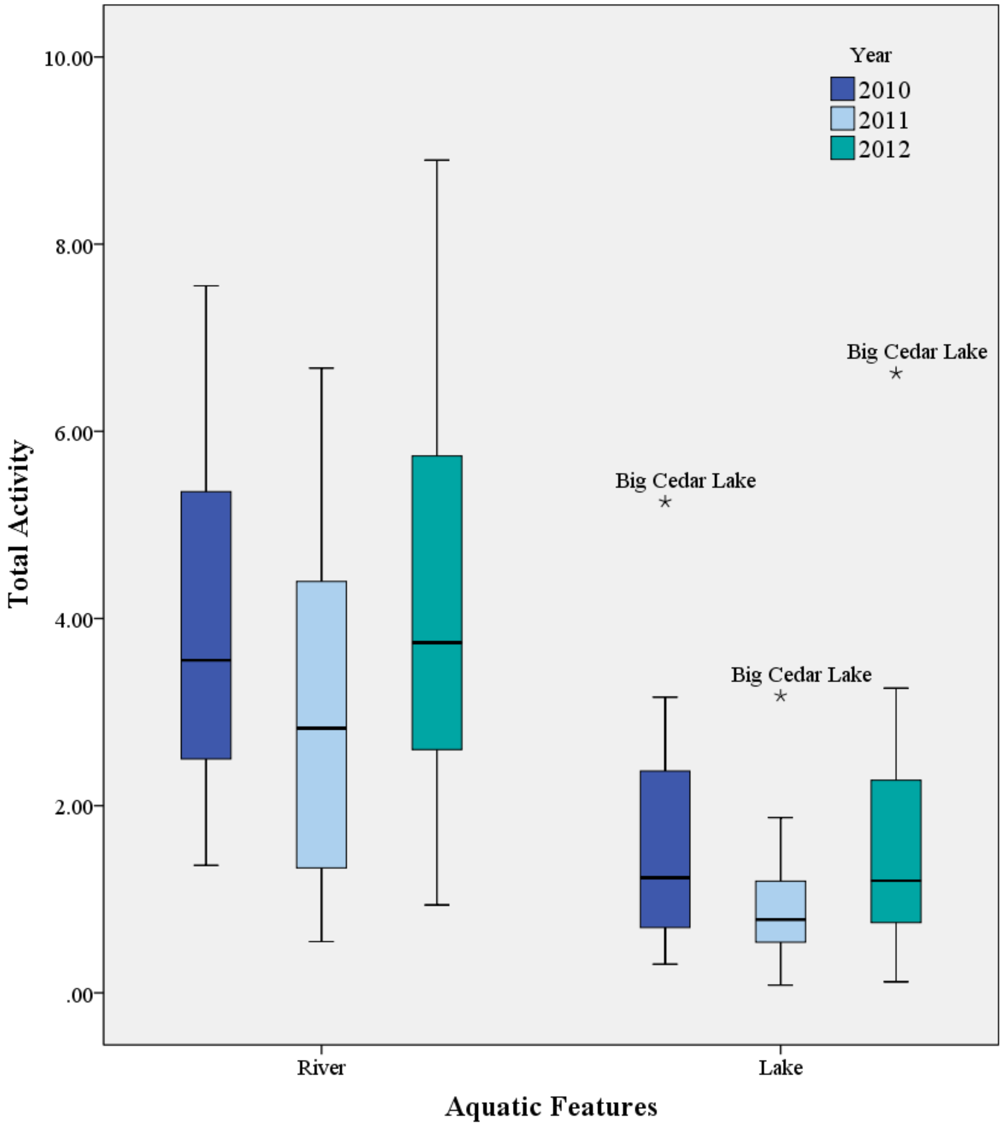


Figure 4: a) Mean Relative Activity (bat passes/total survey minutes) of *Myotis*, Big Brown and Hoary bat between Lake and River habitats in SEGP, and b) standardized relative activity.

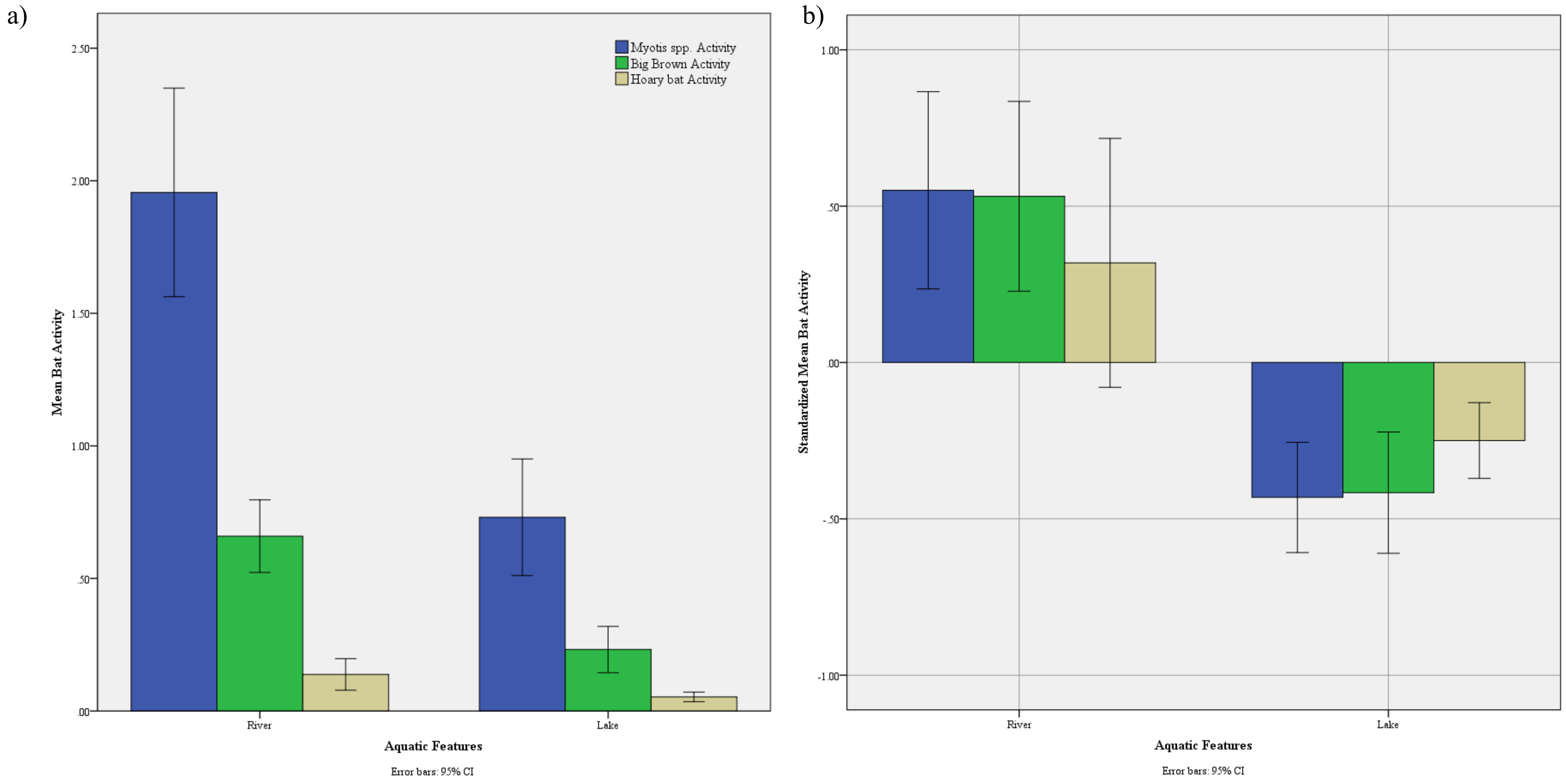


Figure 5: Comparison of average land cover proportion between lake and river habitats at 1 km scale.

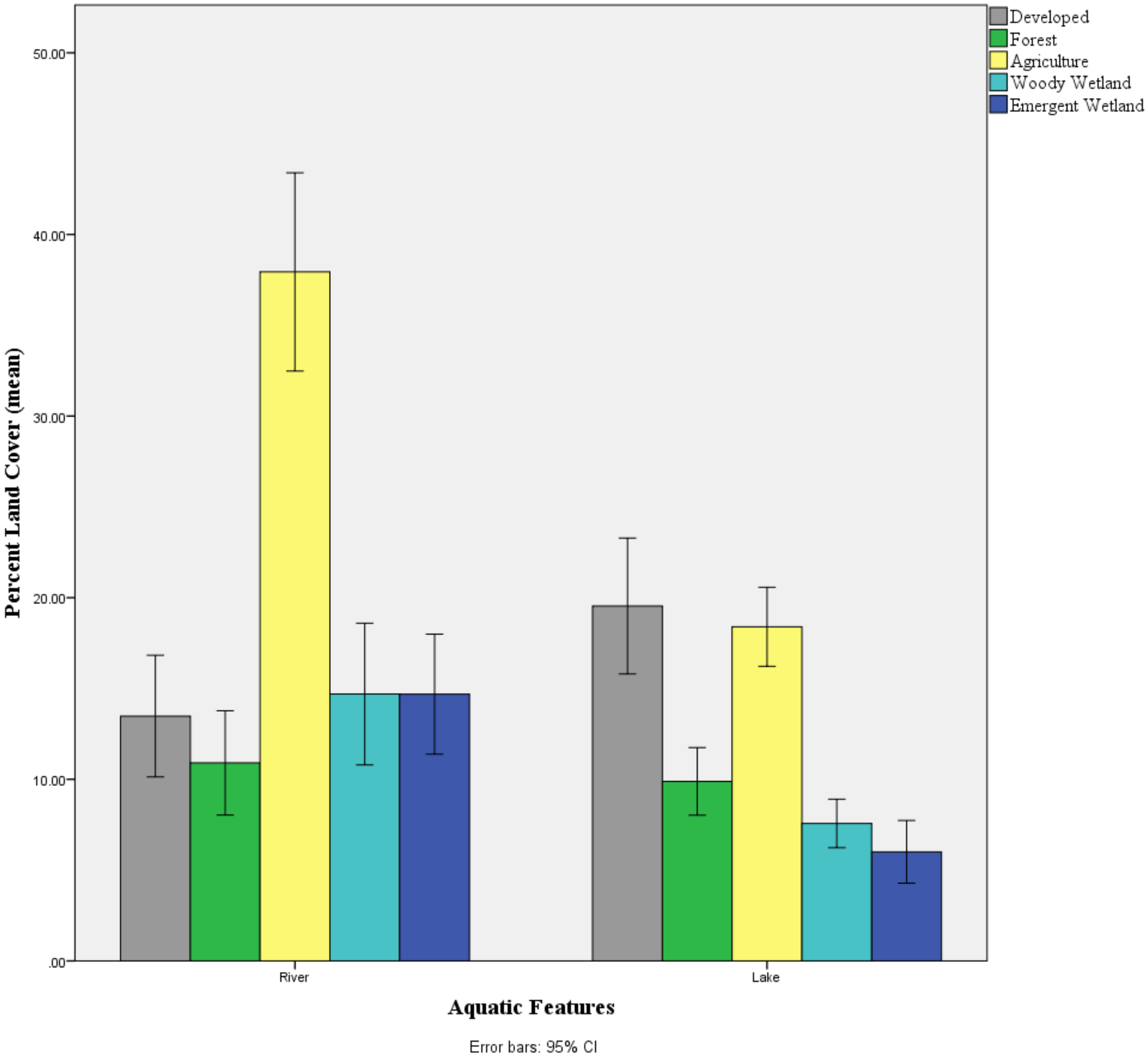


Figure 6: Land cover surrounding Lake Beulah and Partridge Lake at 1 km scale. The lakes have equivalent developed proportion but Partridge Lake has higher Developed LPI, indicating less fragmented developed patches.

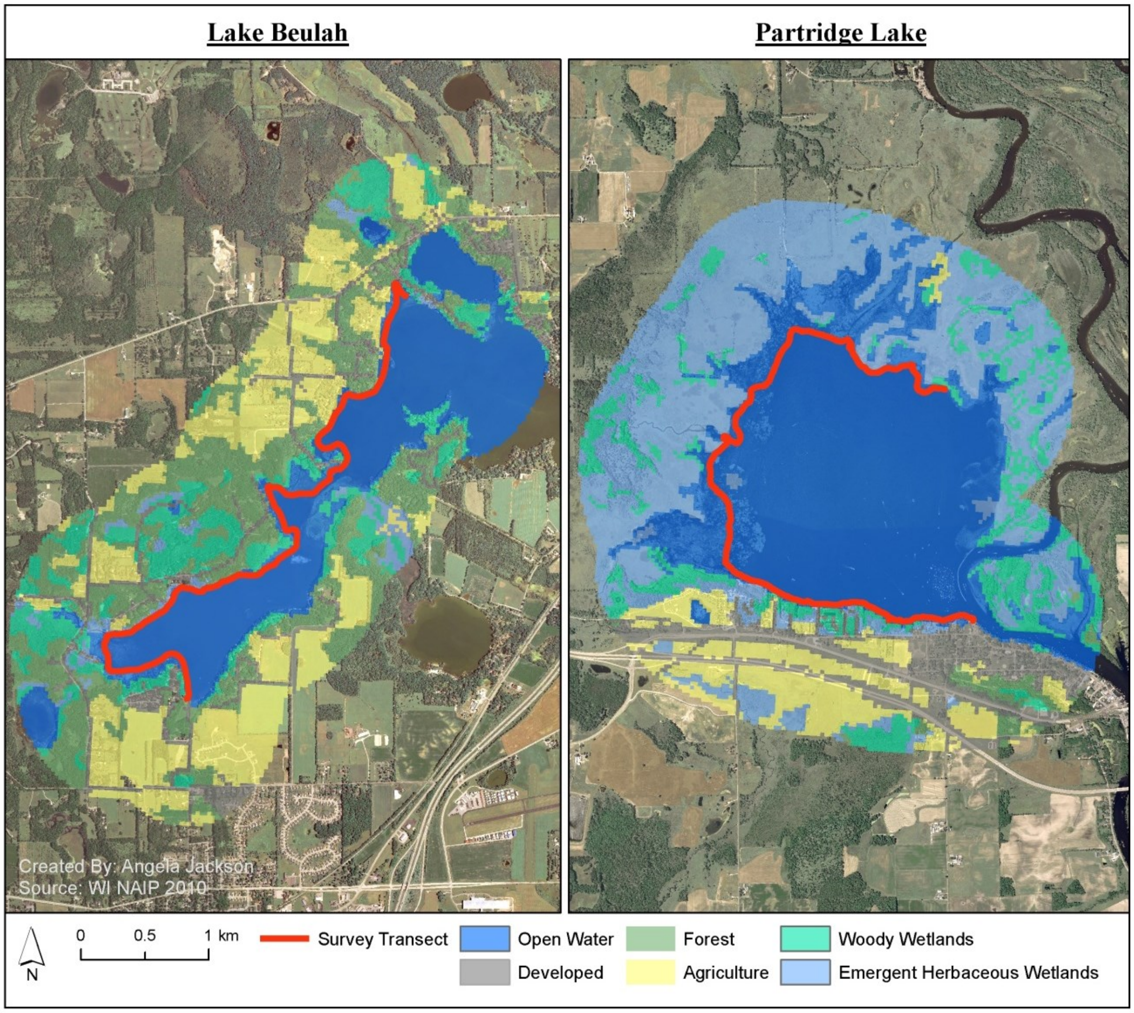


Figure 7: Comparison of mean LPI between lake and river habitats for each land class.

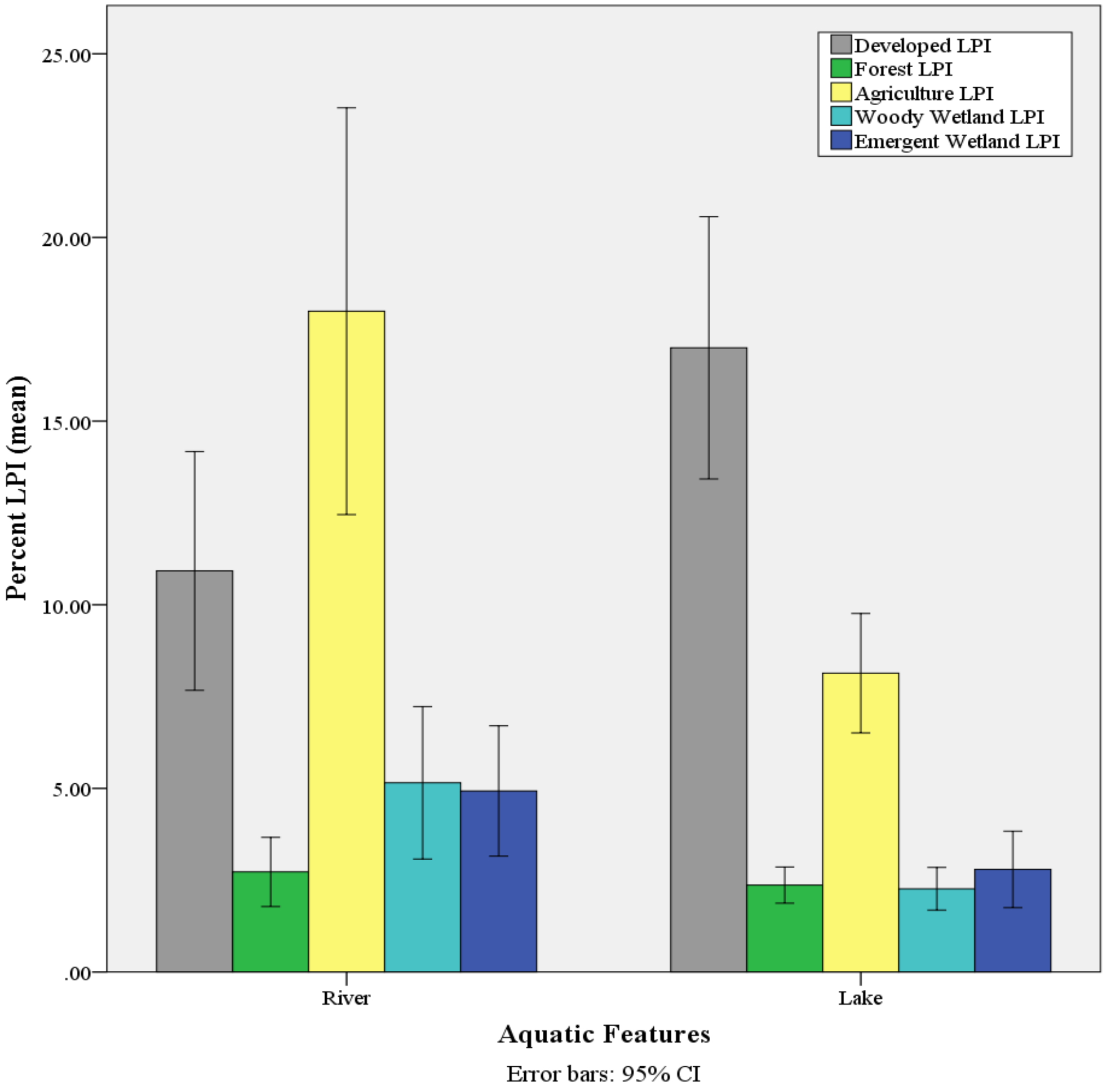


Figure 8: Relative Species Richness (species/hour) at surveyed lake and river habitats in the SEGP, 2010-2012.

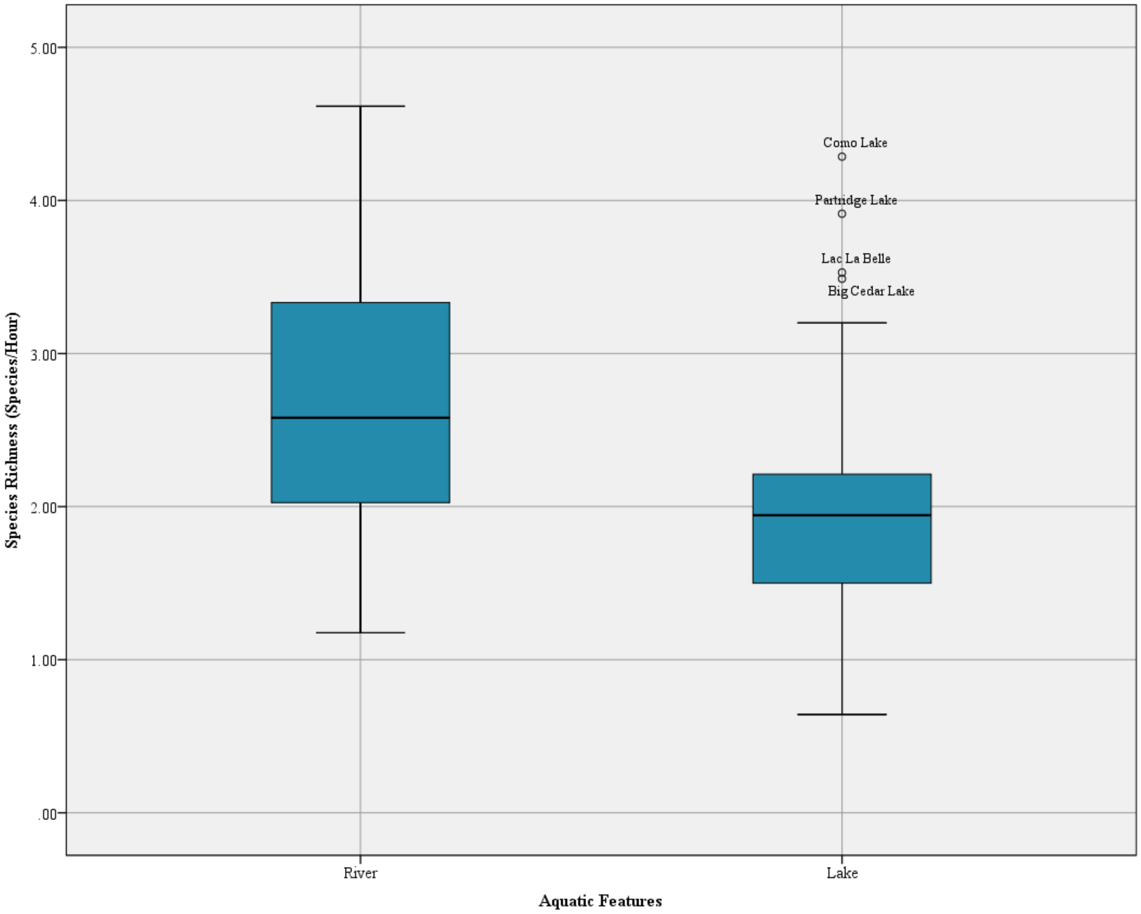
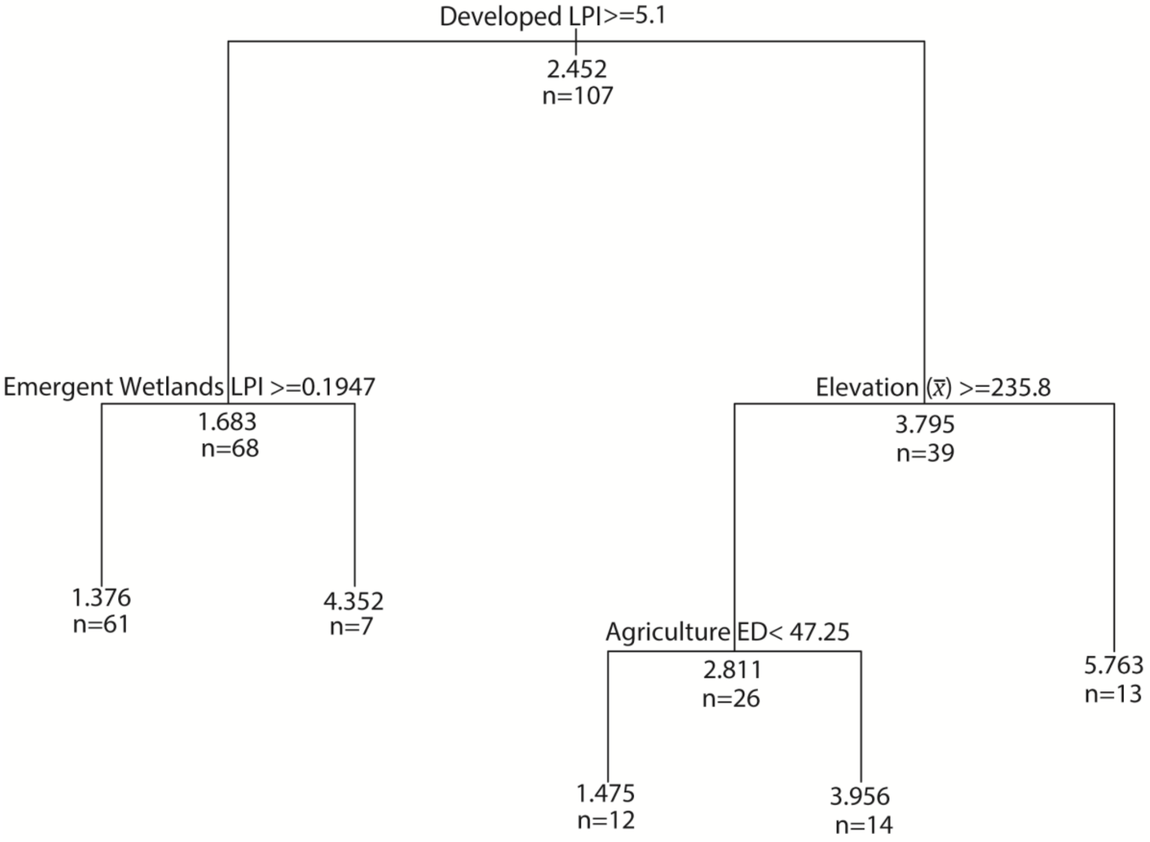


Figure 9: ANOVA Regression Tree Analysis Results for Total Relative Bat Activity at 1 km scale for all Survey Sites in SEGP, 2010-2012. Values at base of nodes represent mean bat activity.



`Figure 10: ANOVA Regression Tree results for *Myotis* spp. activity at all survey sites in the SEGP at 1 km scale. Values at base of nodes represent mean bat activity.

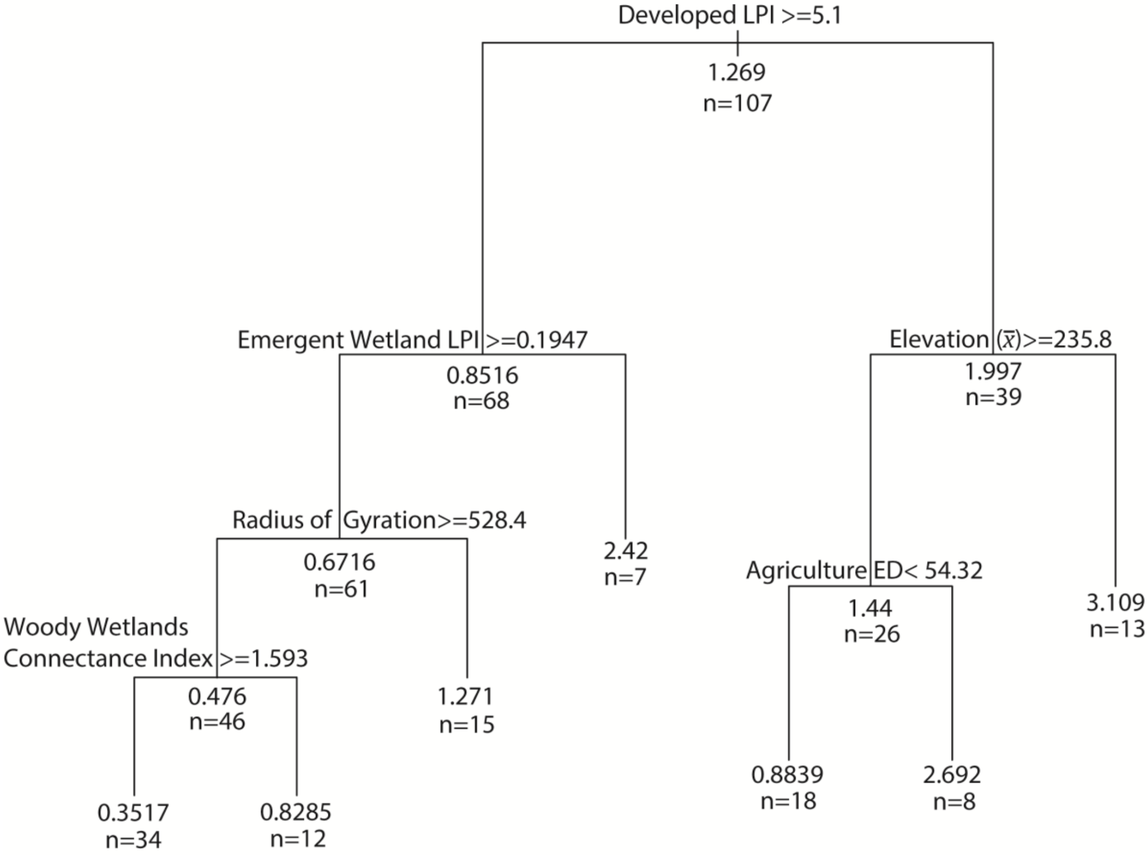


Figure 11: ANOVA Regression Tree Results for Hoary Relative Bat Activity for all sites at 1 km scale in SEGP. Values at base of nodes represent mean bat activity.

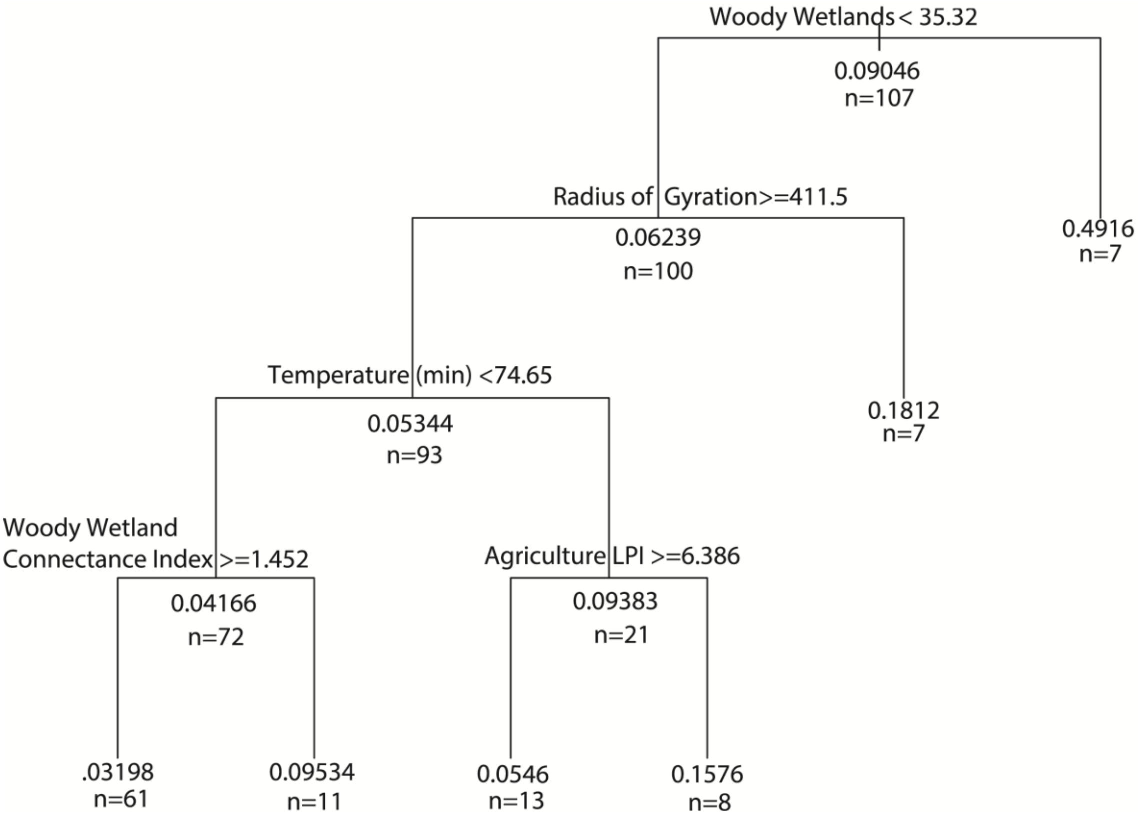


Figure 12: ANOVA Regression Tree Model Results for relative Big Brown bat activity at 500 m for all survey sites, SEGP. Values at base of nodes represent mean bat activity.

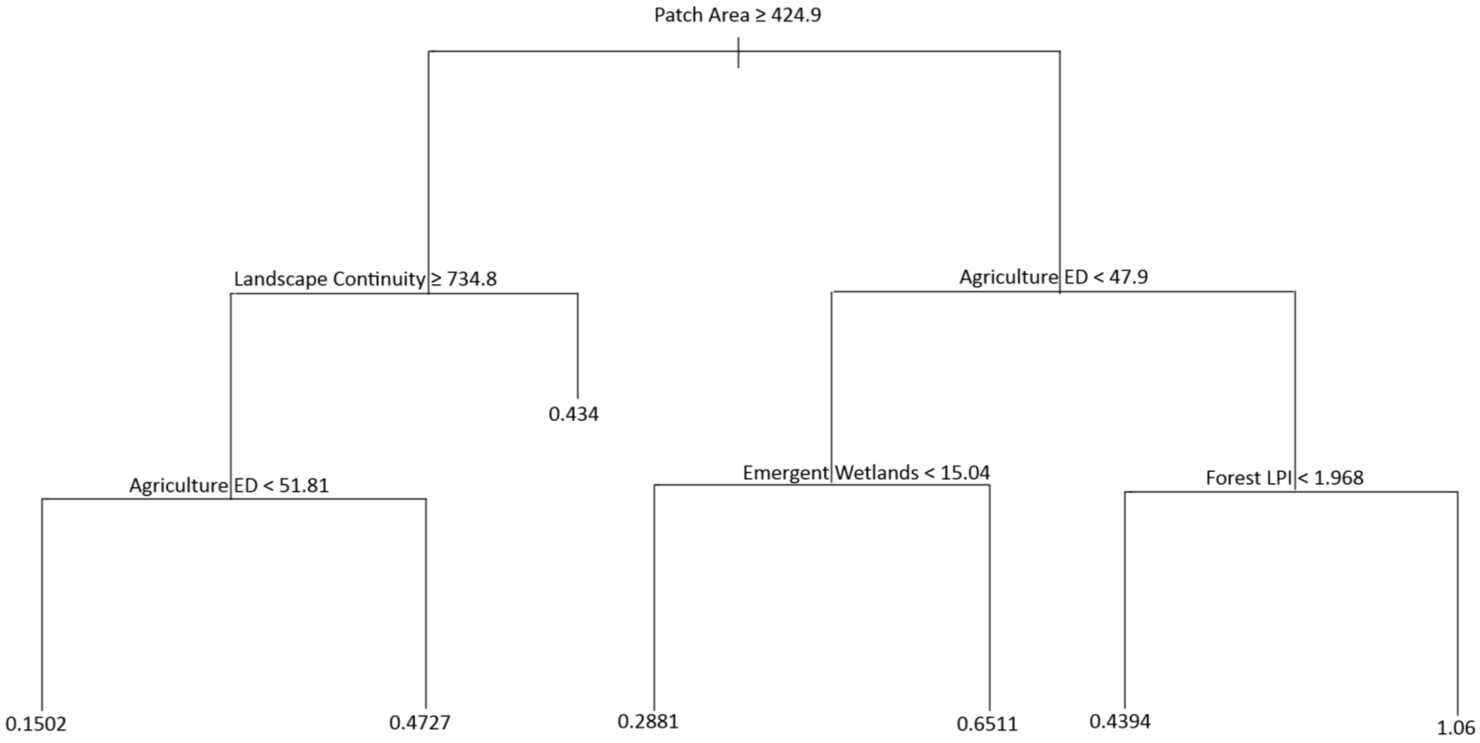
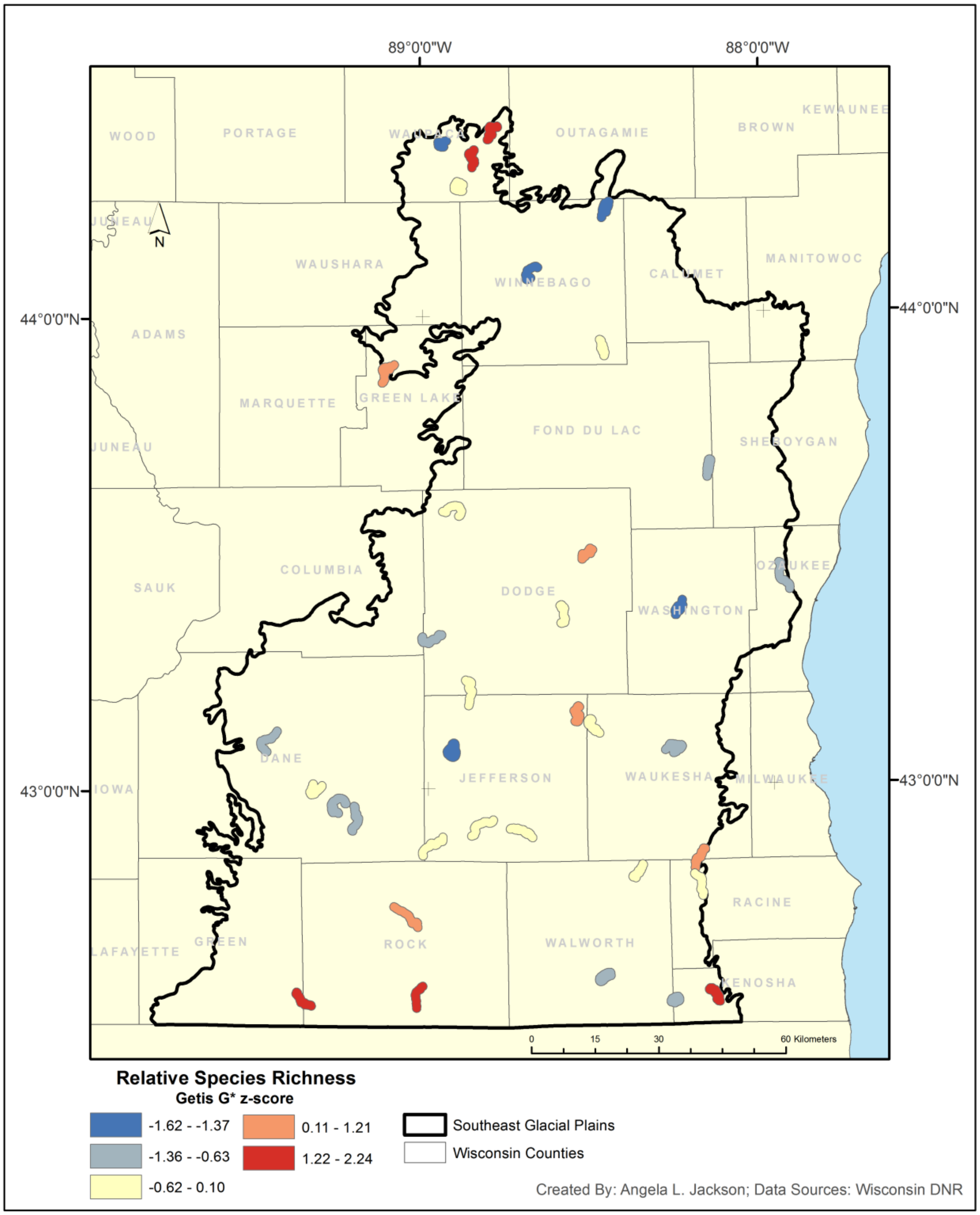


Figure 13: Getis-Ord Gi* Analysis of Relative Species Richness in SEGP.



Created By: Angela L. Jackson; Data Sources: Wisconsin DNR

Figure 14: ANOVA Regression Tree Model Results for relative Total bat activity at Lake survey sites, 500 m in SEGP. Values at base of nodes represent mean bat activity.

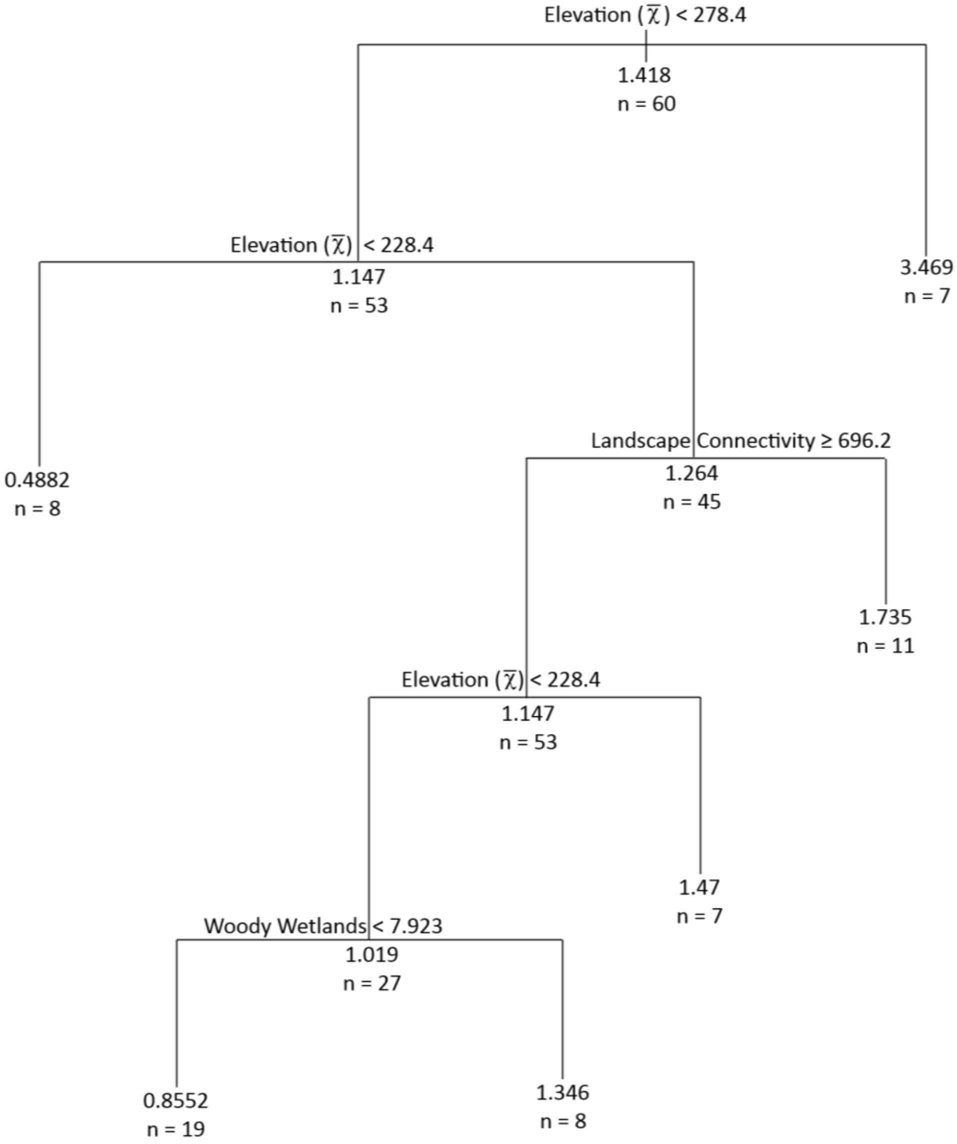


Figure 15: ANOVA Regression Tree Model Results for relative Total bat activity at River survey sites, 500 m in SEGP. Values at base of nodes represent mean bat activity.

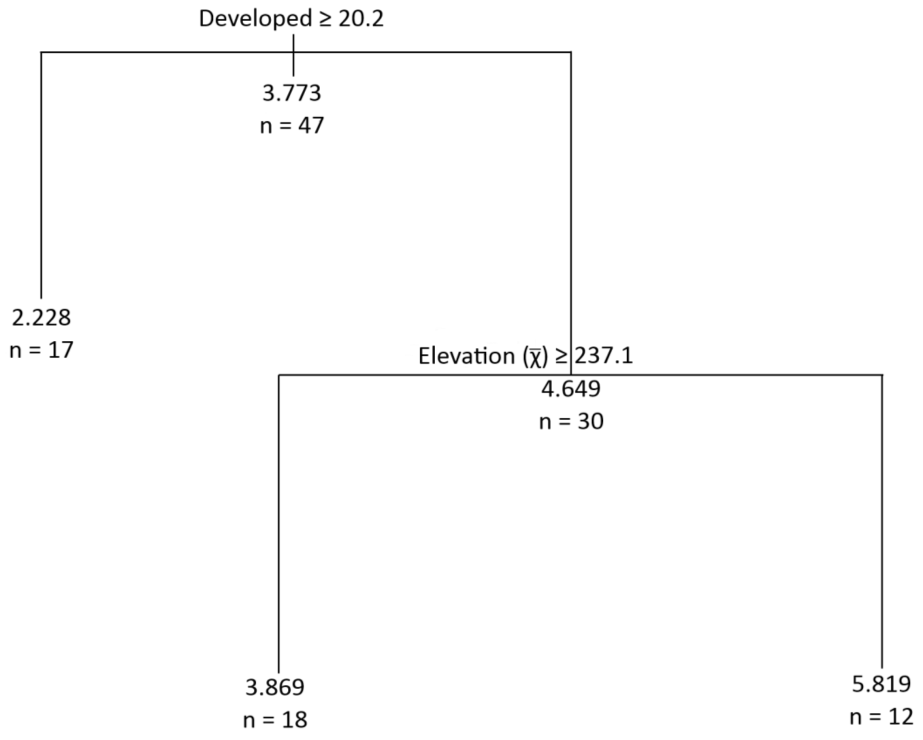


Figure 16: ANOVA Regression Tree Model Results for relative *Myotis* bat activity at River survey sites, 500 m in SEGP. Values at base of nodes represent mean bat activity.

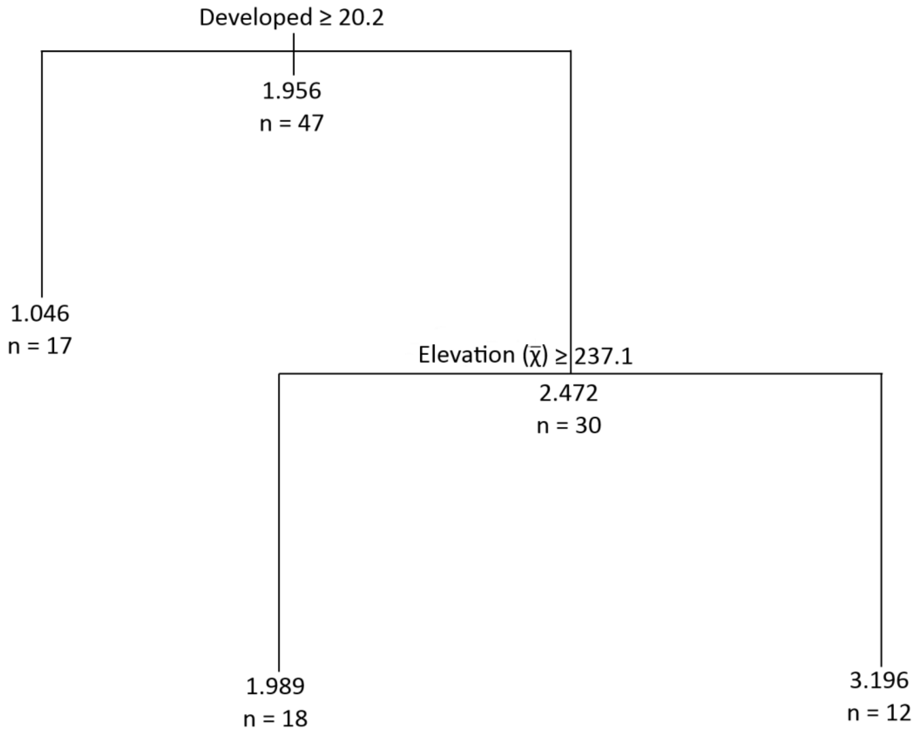


Figure 17: ANOVA Regression Tree Model Results for relative Hoary bat activity at River survey sites, 1 km in SEGP. Values at base of nodes represent mean bat activity.

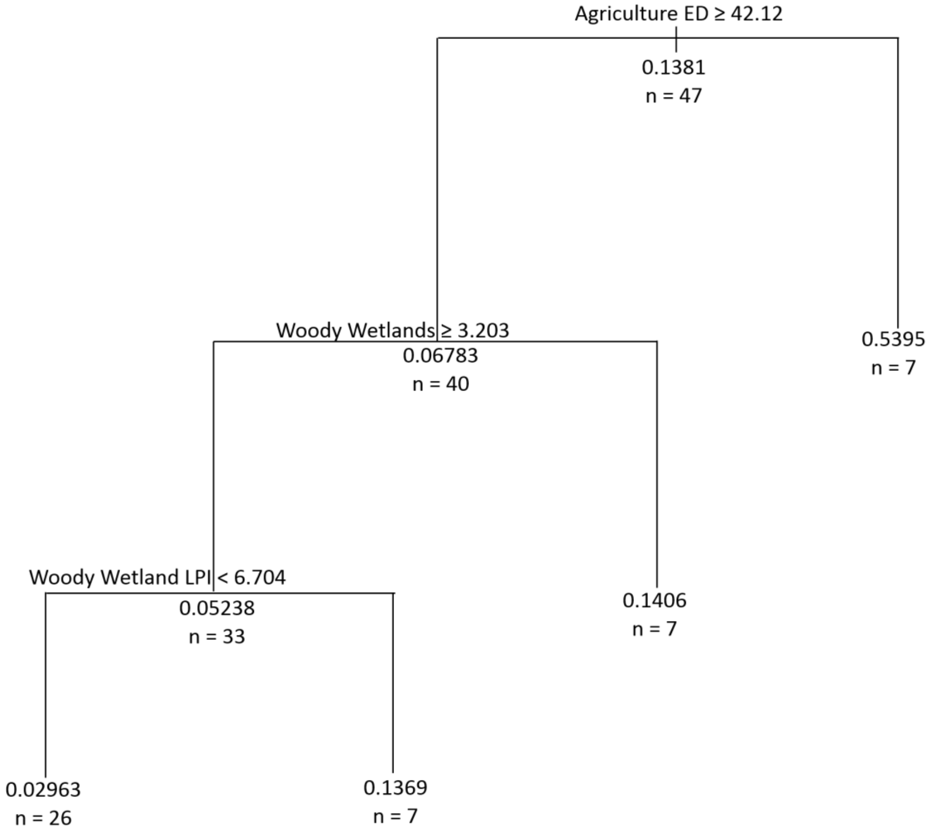


Figure 18: ANOVA Regression Tree Model Results for relative Big Brown bat activity at River survey sites, 500 m in SEGP. Values at base of nodes represent mean bat activity.

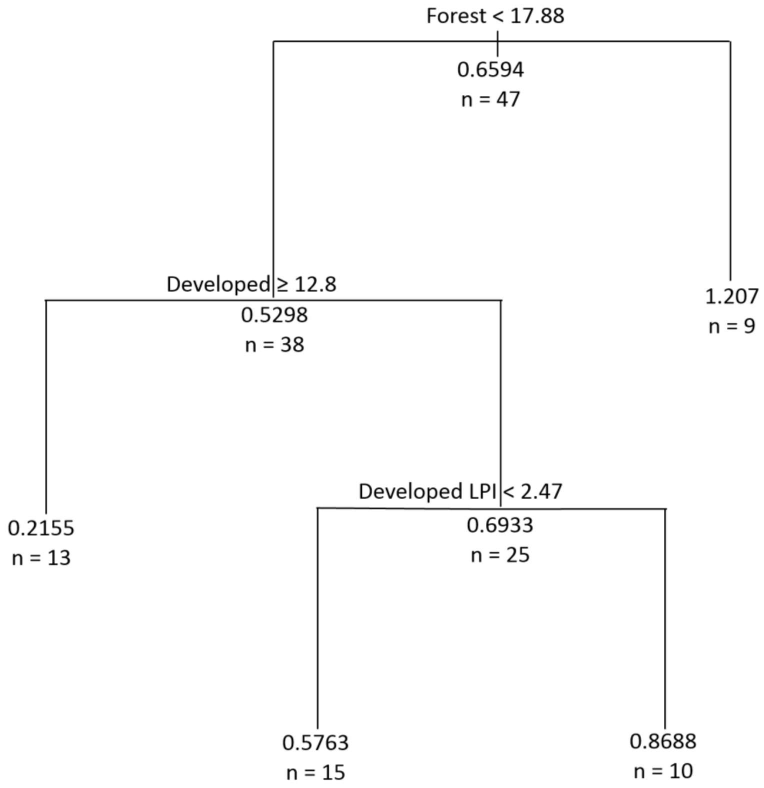
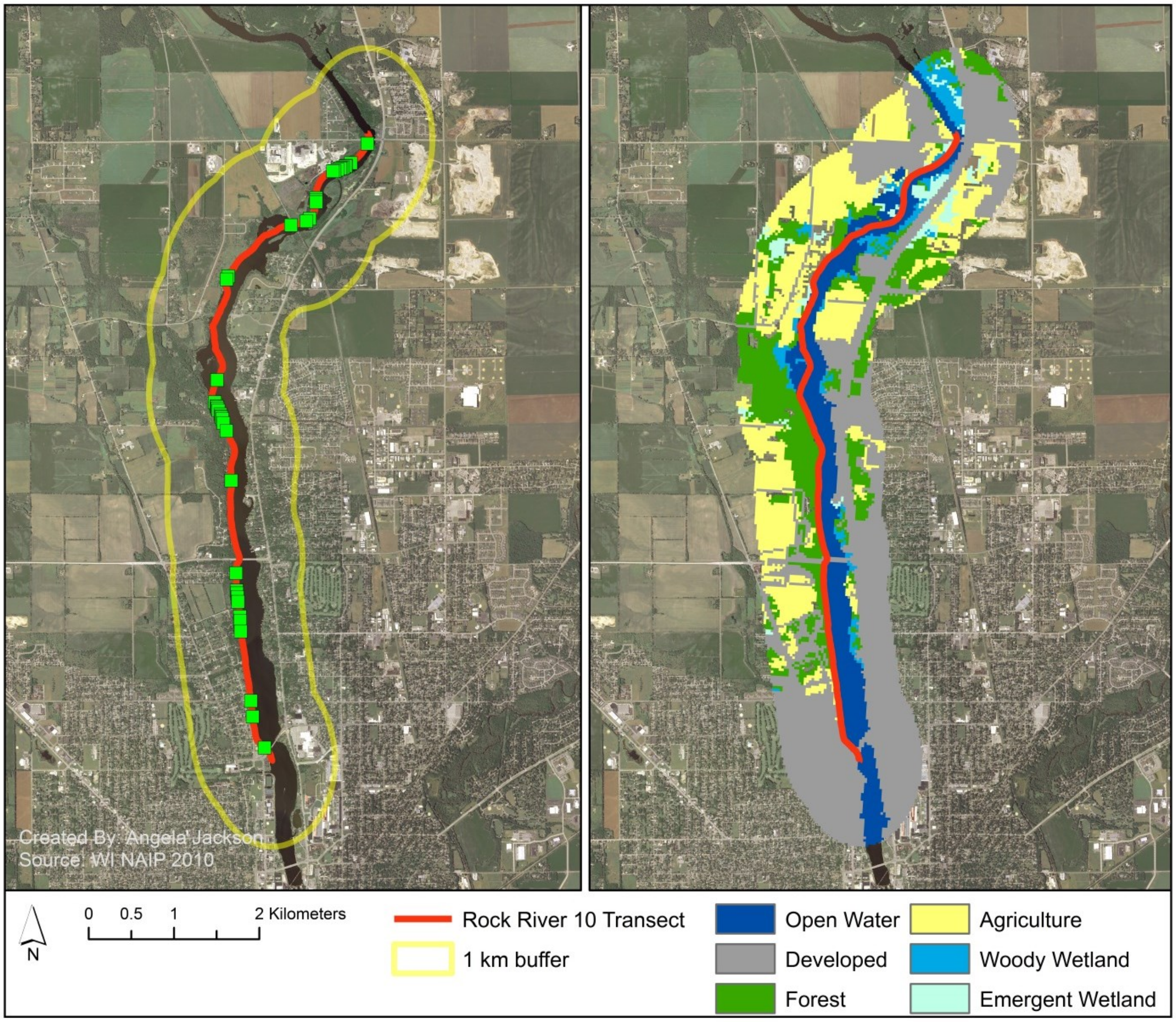


Figure 19: 2011 Rock River 10 survey transect in Beloit, Rock County, WI, with recorded *Myotis* spp. calls and NLCD 2006 land cover at 1 km landscape buffers.



Created By: Angela Jackson
Source: WI NAIP 2010

TABLES

Table 1: Species-specific hypotheses developed based on bat ecology literature. References for hypotheses in body of the text and "References" section, this volume.

Analysis Group	Hypothesis
Total Bat Activity	Overall preference of mixed habitat (vegetation and developed cover)
	Positive correlation to forest proportion and edge due to high insect productivity
Myotis spp. Activity	High overall activity due to flexible roosting, generalist foraging, preference of emergent aquatic insects of *M. lucifugus*
	Minimal difference in activity between lake and river transects due to high attraction to water and prevalence of preferred aquatic insects at both sites
	Positively correlated to all forest metrics because of *M. septentrionalis* preference
Big Brown Activity	High overall activity due to large hibernating populations and generalist nature
	Increase in activity as forest cover decreases
Hoary Activity	Utilize open habitats (agriculture) due to low maneuverability flight characteristics
	Higher activity at lakes vs. rivers because less clutter at lakes
	Increase in activity as forest cover decreases
	Minimal influence of developed lands due to tolerant nature of bat

Table 2: Hypotheses developed based on bat ecology literature and landscape ecology theory organized by landscape metric used in the analysis. References for hypotheses in body of the text and "References" section, this volume.

Landscape Characteristic	**Hypothesis**
Developed Proportion	Negatively correlated to *Myotis* spp. based low flying behavior of bats
Agriculture proportion	Decrease of *Myotis* spp. due to forest-interior specialist of *M. septentrionalis*
Forest proportion	Increase in bat activity as edge increases due to high insect productivity
	Negative influence on Hoary bat activity (low maneuverability)
Forest Core	Positive correlation with *Myotis* spp. because reliance on forest interiors
Forest Edge	Increase in bat activity as edge increases due to high insect productivity
Forest LPI	Increase in *Myotis* spp. activity as forest LPI increases
Woody Wetland LPI	Increase in *Myotis* spp. activity as woody wetland LPI increases
Forest Similarity Index	Negative correlation to big brown activity due to big brown preference of diversity of habitats
	Decrease of hoary bat activity with increase due to hoary preference of diversity of habitats
Connectance Index	Positively correlated to all analysis groups because necessity of connected landscapes
Stream Order	Higher activity at higher stream order, fast-flowing waters (low stream order) disrupt echolocation calls
Distance to Roadways	Activity increase as distance increase. Highways predicted to hinder landscape connectivity.

Table 3: Explanatory variables used to explore relationships of relative bat activity and SEGP landscapes. Insignificant variables at the 0.05 α-level were not included in MLR or regression tree analysis.

Variable	Description
Composition	
Land Cover Proportion	Relative abundance of developed, forest, agriculture, woody and emergent herbaceous wetland classes (%)
Patch Richness Density	Number of patches per 100 hectares at landscape-level (patches/ha)
Largest Patch Index	Percent of landscape comprised by largest patch of developed, forest, agriculture, wetland classes (%)
Patch Area	Relative variability about the mean of patch size in landscape
Configuration	
Edge Density	Length of edge in meters per hectare of forest and agriculture classes (m/ha)
Landscape continuity	Average distance traveled in patch type before encountering boundary (meters)
Proportion of Core Area	Relative abundance of core area of forest and wetland classes when edge is eliminated (%)
Similarity Index	Index considers size and proximity of patches within neighborhood (100 m) of focal patch and determines similarity at forest and wetland class level based on similarity weights
Connectivity	
Connectance Index	Proportion of joinings (at 100 m distance) within woody and emergent herbaceous wetlands (%)
Distance to Major Roadways	Distance in meters to Wisconsin State, U.S., and Interstate highways from survey routes
Environmental	
Elevation	Mean elevation of landscape in meters
Temperature	Mean, minimum, and maximum survey temperature (Celsius)
Wind Speed	Mean, minimum, and maximum survey wind speed in meters per second
Lake Area	Area (km^2) of lakes in study region
Stream Order	Relative size of streams (medium streams to rivers)

Table 4: The relative bat activity (number of passes during survey divided by survey length in minutes) and percent occurrence of all survey sites for four species analysis groups.

Species Group	**Relative Activity** Mean (SD)	**% of sites (n=107)**
Total	2.45 (2.00)	100
Hoary	0.091 (0.149)	24
Big Brown	0.420 (0.451)	97
***Myotis* spp.**	1.27 (1.25)	99

Table 5: Independent Sample t-test* of difference of mean relative activity between lake and river habitats in SEGP, 2010-2012.

	t	**Degrees of Freedom**	**Sig. (2-tailed)**	**Mean Difference**	**Standard Error**
Total Activity	6.99	70.381	<0.001	2.36	0.337
Myotis spp. Activity	5.46	73.926	<0.001	1.23	0.224
Big Brown Activity	5.29	81.088	<0.001	0.428	0.081
Hoary bat Activity	2.75	54.641	0.008	0.085	0.031

*Equal variances not assumed based on Levene’s test for Equality of Variances.

Table 6: Descriptive Statistics of Explanatory Variables at Lake, River, and All sites at 1 km scale.

	Lake (n=60)			River (n=47)			All (n=107)		
Variable	**Mean**	**Std. Dev**	**Min-Max**	**Mean**	**Std. Dev**	**Min-Max**	**Mean**	**Std. Dev.**	**Min-Max**
Developed (%)	19.54	14.47	4.06-62.43	13.48	11.41	2.53-39.94	16.88	13.5	2.53-62.43
Forest (%)	9.89	7.21	0.63-28.02	10.9	9.78	1.1-38.76	10.33	8.41	0.63-38.76
Agriculture (%)	18.39	8.42	0.82-33.32	37.94	18.59	2.9-80.33	26.98	16.87	0.82-80.33
Woody Wetland	7.57	5.16	1.55-21.23	14.69	13.3	1.28-44.85	10.7	10.21	1.28-44.85
Emergent Herbaceous Wetland (%)	6.01	6.69	0.42-31.56	14.69	11.25	0.26-35.58	9.82	9.93	0.26-35.58
Patch Richness Density (Patches/ha)	0.62	0.15	0.31-0.96	0.583	0.142	0.4-1.26	0.6	0.15	0.31-1.26
LPI Developed (%)	16.99	13.82	1.48-56.57	10.92	11.07	0.97-37.61	14.33	12.99	0.97-56.57
LPI Forest (%)	2.37	1.91	0.16-7.98	2.73	3.21	0.15-14.16	2.52	2.56	0.15-14.16
LPI Agriculture (%)	8.14	6.29	0.2-27.21	17.99	18.86	0.37-71.11	12.47	14.16	0.2-71.11
LPI Woody Wetland (%)	2.27	2.25	0.25-10.79	5.15	7.074	0.15-30.6	3.53	5.16	0.15-30.6
LPI Emergent Herb. Wetland (%)	2.79	4.03	0.17-23.57	4.93	6.04	0.08-21.23	3.73	5.1	0.08-23.57
Forest Edge Density (ED)	34.74	21.8	3.57-82.1	36.41	23.51	6.38-86.89	35.47	22.47	3.57-86.89
Agriculture ED	33.76	11.54	3.72-50.31	53.24	16.12	12.87-74.37	42.32	16.77	3.72-74.37
Forest Core Area	1.6	1.6	0-7.32	2.43	3.05	0-11.86	1.96	2.37	0-11.86
Woody Wetland Core Area	7.57	5.16	1.55-21.23	14.69	13.3	1.28-44.85	10.7	10.21	1.28-44.85
Emergent Wetland Core Area	6.01	6.69	0.42-31.56	14.69	11.25	0.26-35.58	9.82	9.93	0.26-35.58
Landscape Continuity	849.18	259.04	418.42-1464.85	636.5	243.25	376.68-1241.81	755.78	272.52	376.68-1464.85
Patch Area	475.33	86.78	292.59-703.45	410.77	142.44	229.84-809.71	446.98	118.46	229.84-809.71
Woody Wetlands Similarity Index	1839.76	1322.74	290.2-7453.19	746.53	646.44	22.61-2159.74	1359.55	1205.14	22.61-7453.19
Emergent Wetland Similarity Index	2762.52	1917.37	92.17-7977	811.74	844.61	20.9-3284.75	1905.63	1817.14	20.9-7977
Forest Similarity Index	48.87	58.39	0.3-250.85	120.15	205.94	0.35-1180.93	80.18	146.86	0.3-1180.93
Temperature mean (degrees C)	21.26	2.6	14.4-30.0	21.35	2.5	15.69-31.0	21.28	2.8	14.4-31.0

Temperature min. (degrees C)	20.32	3.72	13.9-29.4	20.5	2.45	15.3-30.0	20.4	2.7	13.9-30.0
Temperature max. (degrees C)	21.18	2.76	14.5-31.1	22.1	2.65	16.1-32.0	21.14	2.77	14.5-32.0
Elevation mean (m)	257.98	24.69	224.08-327.24	242.84	15.14	227.22-287.92	251.33	22.27	224.08-327.24
Wind mean	2.28	3.46	0-25.5	2.067	1.94	0-7	2.18	2.88	0-25.5
Wind min.	1.29	1.48	0-5.1	1.65	1.89	0-6.9	1.45	1.67	0-6.9
Wind max.	3.26	6.46	0-50	2.49	2.09	0-8.2	2.92	5.03	0-50
Distance to Major Roadway (m)	571.56	636.49	0-5820.84	816.99	1481.22	0-5820.84	679.36	1092.05	0-5820.84
Woody Wetlands Connectance Index	2.75	1.96	0-10.61	2.71	1.27	1.1-6.06	2.73	1.68	0-10.61
Emergent Herbaceous Wetland Connectance Index	4.24	3.3	0-16.67	2.24	1.48	0-6.88	3.36	2.83	0-16.67

Table 7: Results of MLR model examining the relationship between relative bat activity and habitat characteristics for all survey sites at a 1 km landscape scale.

Variable	β	SE	p	r^2	F (p)
Total Activity				0.584	23.354 (<0.001)
Woody Wetland	0.516	0.015	< 0.001		
Agriculture	0.204	0.011	0.034		
Emergent Herbaceous Wetland	0.476	0.019	< 0.001		
Emergent Wetland Similarity	-0.321	0.145	0.002		
Landscape Continuity	0.277	0.001	0.004		
Forest	0.408	0.020	< 0.001		
***Myotis* spp. Activity**				0.440	27.020 (<0.001)
Woody Wetland	0.429	0.010	< 0.001		
Emergent Herbaceous Wetland	-0.419	0.067	< 0.001		
Developed LPI	-0.289	0.008	< 0.001		
Hoary Activity				0.442	27.202 (<0.001)
Woody Wetland	0.438	0.001	<0.001		
Distance to Major Roadway	0.244	<0.001	0.003		
Emergent Herbaceous Wetland	0.162	0.001	0.049		
Big Brown Activity				0.299	14.676 (<0.001)
Forest Core Area	0.371	0.017	<0.001		
Emergent Herbaceous Wetland	0.337	0.004	<0.001		
Emergent Wetland Similarity	-0.385	0.000	0.001		

Table 8: Results of MLR model examining the relationship between relative bat activity and habitat characteristics for all survey sites at a 500 m landscape scale.

Variable	β	SE	p	r^2	F (p)
Total Activity				0.605	21.696 (<0.001)
Woody Wetland	1.026	0.036	< 0.001		
Agriculture	0.216	0.009	0.003		
Forest	0.474	0.016	< 0.001		
Emergent Herbaceous Wetland	0.357	0.013	< 0.001		
Patch Area Variability	0.346	0.002	< 0.001		
Emergent Wetland Similarity	-0.172	0.000	0.021		
Woody Wetland LPI	-0.474	0.057	0.027		
***Myotis* spp. Activity**				0.350	28.048 (<0.001)
Woody Wetland	0.485	0.008	< 0.001		
Agriculture	0.361	0.006	< 0.001		
Hoary Activity				0.425	25.657 (<0.001)
Woody Wetland LPI	0.372	0.003	0.021		
Agriculture Edge Density	-0.340	0.002	0.004		
Landscape Continuity	-0.156	<0.001	0.050		
Big Brown Activity				0.370	14.960 (0.001)
Forest Core Area	0.451	0.013	<0.001		
Woody Wetland	0.334	0.003	<0.001		
Agriculture	0.204	0.002	0.015		
Emergent Wetland LPI	0.197	0.005	0.012		

Table 9: Results of MLR models examining the relationship between relative bat activity and (a) surveyed lake habitat characteristics for all analysis groups at a 1 km landscape scale, and (b) surveyed river habitat characteristics at a 1 km scale for all analysis groups.

a) Lake 1 km						**b) River 1 km**					
Variable	**β**	**SE**	**p**	**r^2**	**F (p)**	**Variable**	**β**	**SE**	**p**	**r^2**	**F (p)**
Total Activity				0.481	26.424 (<0.001)	**Total Activity**				0.361	12.429 (<0.001)
Elevation Mean	0.535	0.005	< 0.001			Developed	-0.480	0.022	< 0.001		
Woody Wetland	0.255	0.025	0.023			Forest Similarity Index	0.272	0.001	0.033		
Myotis spp.				0.484	26.698 (<0.001)	***Myotis* spp.**				0.352	11.942 (<0.001)
Elevation Mean	0.545	0.004	< 0.001			Developed LPI	-0.406	0.015	0.002		
Woody Wetland	0.243	0.018	0.029			Forest Similarity Index	0.353	0.001	0.007		
Hoary				0.274	10.746 (<0.001)	**Hoary**				0.455	37.598 (<0.001)
Wind Speed (Max)	0.441	0.001	<0.001			Agriculture ED	-0.675	0.001	<0.001		
Emergent Wetland	0.326	0.001	0.006								
Big Brown						**Big Brown**				0.369	12.851 (<0.001)
None						Forest Similarity Index	0.515	0.019	<0.001		
						Developed LPI	-0.461	0.005	0.001		

Table 10: MLR model results examining relative bat activity and (a) surveyed lake habitat characteristics at 500 m scale and (b) surveyed river habitat characteristics for all analysis groups at a 500 m landscape scale.

a) Lake 500 m						b) River 500 m					
Variable	**β**	**SE**	**p**	**r^2**	**F (p)**	**Variable**	**β**	**SE**	**p**	**r^2**	**F (p)**
Total Activity				0.495	27.962 (<0.001)	**Total Activity**				0.273	16.927 (<0.001)
Elevation Mean	0.544	0.005	< 0.001			Developed	-0.523	0.024	< 0.001		
Woody Wetland	0.265	0.030	0.014								
***Myotis* spp.**				0.491	27.508 (<0.001)	***Myotis* spp.**				0.327	10.670 (0.001)
Elevation Mean	0.549	0.003	< 0.001			Developed	-0.412	0.016	0.002		
Woody Wet Core	0.256	0.021	0.019			Landscape Continuity	0.345	0.001	0.008		
Hoary				0.223	8.194 (0.001)	**Hoary**				0.425	16.289 (<0.001)
Wind Speed (Max)	0.371	0.001	0.003			Woody Wet LPI	0.372	0.003	0.021		
Survey Temp. (Minimum)	0.238	0.001	0.050			Agriculture ED	-0.340	0.002	0.034		
Big Brown						**Big Brown**				0.392	14.174 (<0.001)
None						Forest Core Area	0.516	0.014	<0.001		
						Developed	-0.447	0.005	0.001		

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APPENDICES

Appendix A: A listing of all sites surveyed in 2010, 2011, and 2012 and their distance, given in kilometers, and length, given in minutes.

2010			**2011**			**2012**		
Route	**Distance (km)**	**Length (min)**	**Route**	**Distance (km)**	**Length (min)**	**Route**	**Distance (km)**	**Length (min)**
Bark River 1	8.70	141.00	Bark River	8.59	102.00	Bark River	8.32	102.00
Big Cedar Lake	7.91	173.00	Big Cedar Lake	7.99	86.00	Big Cedar Lake	7.80	135.00
Como Lake	7.20	116.00	Como Lake	7.02	70.00	Como Lake	7.69	106.00
Crawfish River 2	9.14	142.00	Crawfish River 2	8.19	103.00	Crawfish River 2	9.68	196.00
Crawfish River 5	8.49	117.00	Crawfish River 5	7.73	84.00	Crawfish River 5	8.05	87.00
East Branch Rock River	7.14	102.00	East Branch Rock River	7.50	139.00	East Branch Rock River	5.75	80.00
Fox River 1	8.04	108.00	Fox River 1	7.91	80.00	Fox River 1	7.33	74.00
Fox Lake	7.88	115.00	Fox Lake	7.88	83.00	Fox Lake	8.39	130.00
Illinois/Fox River 4	8.25	93.00	Illinois/Fox River 4	8.41	95.00	Illinois/Fox River 4	8.91	101.00
Illinois/Fox River 7	8.06	83.00	Illinois/Fox River 7	8.37	95.00	Illinois/Fox River 7	8.37	88.00
Lake Koshkonong	8.91	120.00	Lake Koshkonong	12.08	165.00	Lake Koshkonong	7.19	125.00
Lac La Belle	8.06	120.00	Lac La Belle	7.29	85.00	Lac La Belle	7.64	129.00
Lake Beulah	7.00	113.00	Lake Beulah	6.52	85.00	Lake Beulah	7.36	112.00
Lake Buttes Des Morts	7.90	110.00	Lake Butte des Morts	7.76	75.00	Lake Butte Des Morts	7.59	130.00
Lake Kegonsa	9.54	127.00	Lake Kegonsa	9.07	103.00	Lake Kegonsa	7.70	84.00
Lake Mendota	8.34	143.00	Lake Mendota	7.58	97.00	Lake Mendota	7.27	187.00
-	-	-	-	-	-	Lake Mendota	7.29	102.00
Lake Waubesa	7.29	118.00	Lake Waubesa	7.89	88.00	Lake Waubesa	10.17	154.00
Lake Winnebago	7.61	122.00	Lake Winnebago	5.21	60.00	Lake Winnebago	6.78	131.00
Little Lake Butte des Morts	9.29	135.00	Little Lake Butte des Morts	8.62	108.00	Little Lake Butte des Morts	8.40	158.00
Long Lake (Fon Du Lac Co)	7.87	125.00	Long Lake (Fon Du Lac Co)	7.46	109.00	Long Lake (Fon Du Lac Co)	6.03	125.00

Milwaukee River 3	8.36	163.00	Milwaukee River 3	8.61	133.00	Milwaukee River 3	Not Surveyed	Not Surveyed
Partridge Lake	7.39	115.00	Partridge Lake	Not Surveyed	Not Surveyed	Partridge Lake	6.09	92.00
Pewaukee Lake	8.22	131.00	Pewaukee Lake	7.39	71.00	Pewaukee Lake	8.22	171.00
Powers Lake	7.69	118.00	Powers Lake	6.91	84.00	Powers Lake	7.34	104.00
-	-	-	-	-	-	Powers Lake	6.95	81.00
Rock Lake	8.00	137.00	Rock Lake	7.91	87.00	Rock Lake	8.14	111.00
Rock River 03	8.27	92.00	Rock River 03	5.60	72.00	Rock River 03	9.07	105.00
Rock River 10	6.28	62.00	Rock River 10	8.61	122.00	Rock River 10	3.12	98.00
Rock River 06	8.21	103.00	Rock River 06	8.22	96.00	Rock River 06	8.20	109.00
Rock River 08	8.70	80.00	Rock River 08	9.04	90.00	Rock River 08	7.50	93.00
Sinissippi Lake	7.12	125.00	Sinissippi Lake	7.84	75.00	Sinissippi Lake	7.76	150.00
Sugar River 3	9.44	100.00	Sugar River 3	9.07	101.00	Sugar River 3	9.02	78.00
Unnamed Lake	7.12	117.00	Unnamed Lake	7.52	98.00	Unnamed Lake	6.59	76.00
White Lake	4.57	111.00	White Lake	Not Surveyed	Not Surveyed	White Lake	8.26	120.00
Wolf River 1 (Waupaca Co)	8.26	85.00	Wolf River 1 (Waupaca Co)	7.65	84.00	Wolf River 1 (Waupaca Co)	8.00	95.00
Wolf River 2	8.20	86.00	Wolf River 2	8.22	70.00	Wolf River 2	8.21	115.00
Yahara River 1	7.95	105.00	Yahara River 1	8.80	102.00	Yahara River 1	7.22	72.00

Appendix B

Correlation Matrix between Bat Activity and Landscape Metrics at all survey transects, 1 km.

Species	**Total**		***Myotis* spp.**		**Hoary**		**Big Brown**	
Variable	**Pearson Correlation**	**Sig.**	**Pearson Correlation**	**Sig.**	**Pearson Correlation**	**Sig.**	**Pearson Correlation**	**Sig.**
Developed	-.371**	.000	-.372**	.000	-.251**	.009	-.170	.079
Forest	.205*	.035	.143	.141	.049	.619	.306**	.001
Agriculture	.342**	.000	.335**	.000	-.179	.065	.280**	.003
Woody Wetland	.484**	.000	.468**	.000	.602**	.000	.221*	.022
Emergent Wetland	.366**	.000	.288**	.003	.404**	.000	.193*	.046
Patch Richness Dens.	-.151	.121	-.145	.137	-.076	.439	-.073	.454
LPI Developed	-.382**	.000	-.379**	.000	-.246*	.011	-.189	.051
Forest LPI	.228*	.018	.166	.088	.144	.140	.303**	.001
Agriculture LPI	.212*	.028	.255**	.008	-.106	.278	.068	.489
Woody Wet LPI	.323**	.001	.346**	.000	.504**	.000	.108	.266
Emergent Wet LPI	.197*	.042	.129	.184	.166	.087	.132	.175
Forest ED	.200*	.038	.149	.126	.022	.826	.289**	.003

Forest Core Area	**.238***	**.013**	**.159**	**.101**	**.061**	**.533**	**.363****	**.000**
Woody Wetland Core Area	.484**	.000	.468**	.000	.602**	.000	.221*	.022
Emergent Wetland Core Area	.366**	.000	.288**	.003	.404**	.000	.193*	.046
Landscape Continuity	-.354**	.000	-.281**	.003	-.257**	.008	-.320**	.001
Patch Area	-.237*	.014	-.135	.166	-.171	.078	-.322**	.001
Woody Wet. Simi. Index	-.251**	.009	-.217*	.025	.087	.374	-.270**	.005
Emergent Wet Simi. Index	-.337**	.000	-.284**	.003	.019	.848	-.349**	.000
Temp. Mean	.036	.710	-.036	.715	.147	.130	.055	.573
Temp. Min,	.040	.679	-.034	.727	.142	.146	.060	.537
Temp. Max.	.028	.778	-.043	.661	.148	.129	.049	.620
Elevation Mean	-.028	.774	.040	.684	-.216*	.025	-.085	.386
Wind Mean	.007	.941	.004	.963	.038	.698	-.012	.901
Wind Max	.051	.599	.053	.585	-.086	.380	.035	.720
Wind Max	-.009	.929	-.013	.898	.072	.462	-.026	.794
Dist. To Highway	.209*	.031	.158	.104	.462**	.000	.086	.380

**Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed).

Correlation Matrix between Bat Activity and Landscape Metrics at all survey transects, 500 m.

Species	**Total**		***Myotis* spp.**		**Hoary**		**Big Brown**	
Variables	**Pearson Correlation**	**Sig.**	**Pearson Correlation**	**Sig.**	**Pearson Correlation**	**Sig.**	**Pearson Correlation**	**Sig.**
Developed	-.403**	.000	-.391**	.000	-.277**	.004	-.216*	.026
Forest	.223*	.021	.159	.103	-.025	.802	.354**	.000
Agriculture	.336**	.000	.339**	.000	-.143	.143	.242*	.012
Woody Wetland	.499**	.000	.469**	.000	.555**	.000	.278**	.004
Emergent Wetland	.371**	.000	.276**	.004	.335**	.000	.229*	.018
Patch Richness Density	-.193*	.047	-.176	.069	-.071	.470	-.121	.216
Developed LPI	-.383**	.000	-.367**	.000	-.252**	.009	-.238*	.014
Forest LPI	.133	.171	.075	.444	-.022	.825	.275**	.004
Agriculture LPI	.255**	.008	.318**	.001	-.082	.401	.073	.453
Woody Wet LPI	.422**	.000	.392**	.000	.595**	.000	.213*	.027
Emergent Wet LPI	.274**	.004	.169	.082	.128	.187	.216*	.025
Forest ED	.212*	.029	.156	.108	-.070	.472	.331**	.001
Agriculture ED	.254**	.008	.218*	.024	-.193*	.046	.264**	.006
Forest Core Area	.256**	.008	.178	.066	-.007	.941	.410**	.000
Woody Wet Core Area	.499**	.000	.469**	.000	.555**	.000	.278**	.004
Emergent Wet Core Area	.371**	.000	.276**	.004	.335**	.000	.229*	.018
Landscape Cont.	-.341**	.000	-.227*	.019	-.236*	.014	-.370**	.000
Patch Area	-.199*	.040	-.061	.531	-.150	.122	-.349**	.000

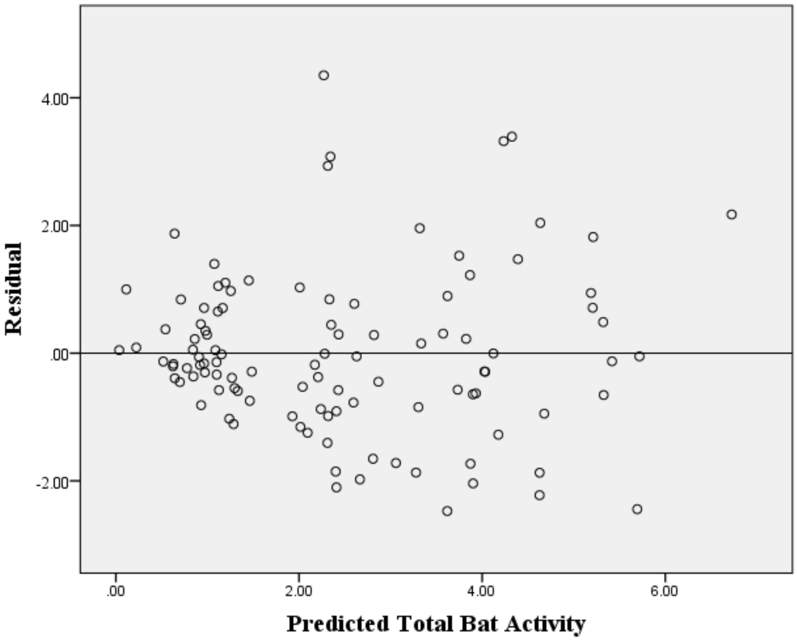
Woody Wet Simi Index	**-.234***	**.015**	**-.182**	**.060**	**.016**	**.868**	**-.179**	**.065**
Emergent Wet Simi Index	-.299**	.002	-.228*	.018	-.026	.793	-.246*	.011
Forest Simi Index	.146	.133	.159	.102	-.039	.688	.222*	.021
Temp. Mean.	.036	.710	-.036	.715	.147	.130	.055	.573
Temp. Min.	.040	.679	-.034	.727	.142	.146	.060	.537
Temp. Max.	.028	.778	-.043	.661	.148	.129	.049	.620
Elev. Mean	-.025	.796	.035	.721	-.209*	.031	-.058	.550
Wind Mean	.007	.941	.004	.963	.038	.698	-.012	.901
Wind Min.	.051	.599	.053	.585	-.086	.380	.035	.720
Wind Max.	-.009	.929	-.013	.898	.072	.462	-.026	.794
Distance to Hwy	.209*	.031	.158	.104	.462**	.000	.086	.380

**Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed).

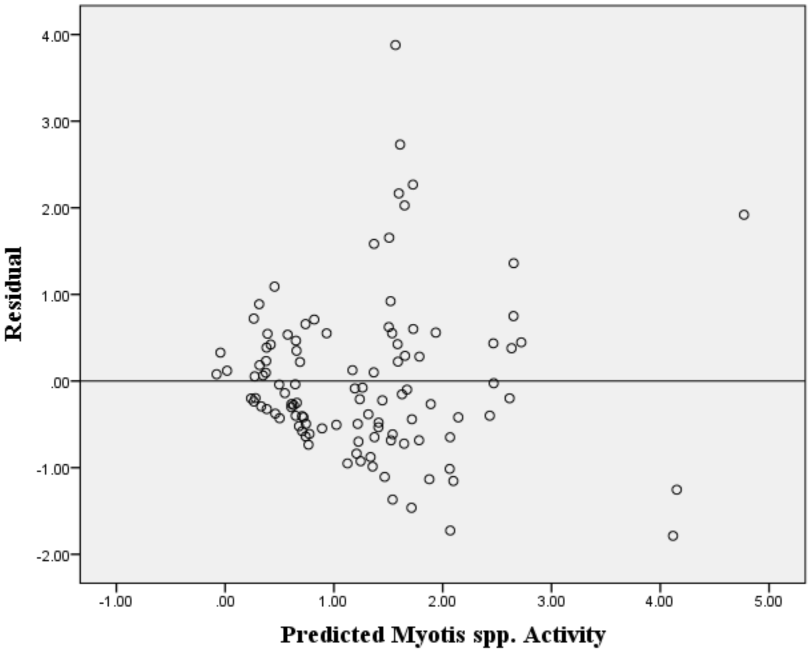
Appendix C

Residual plots for 1 km MLR models at all SEGP survey sites, a) Total Bat Activity b) *Myotis* spp. Activity c) Hoary Activity, d) Big Brown Activity.

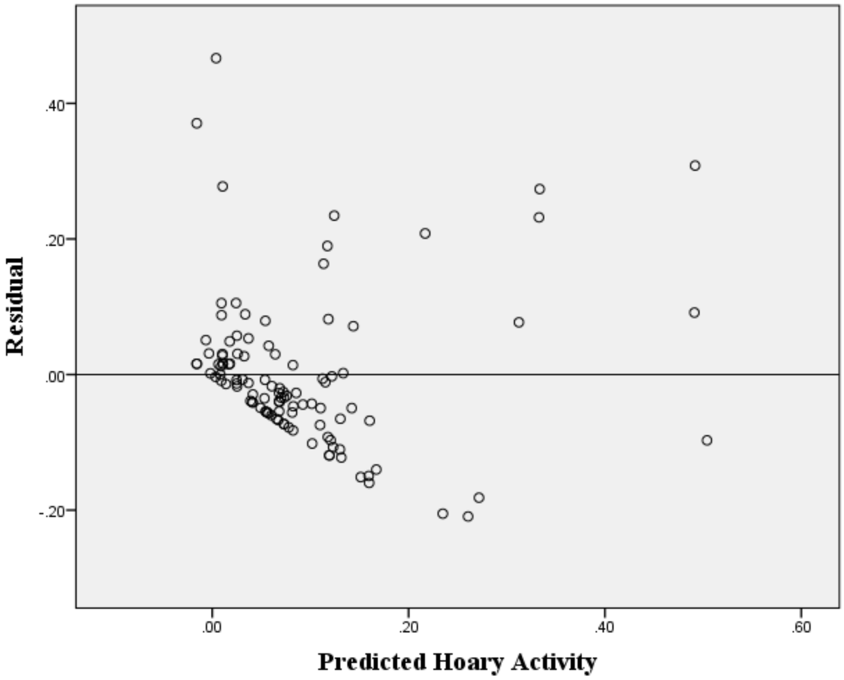
a)



b)

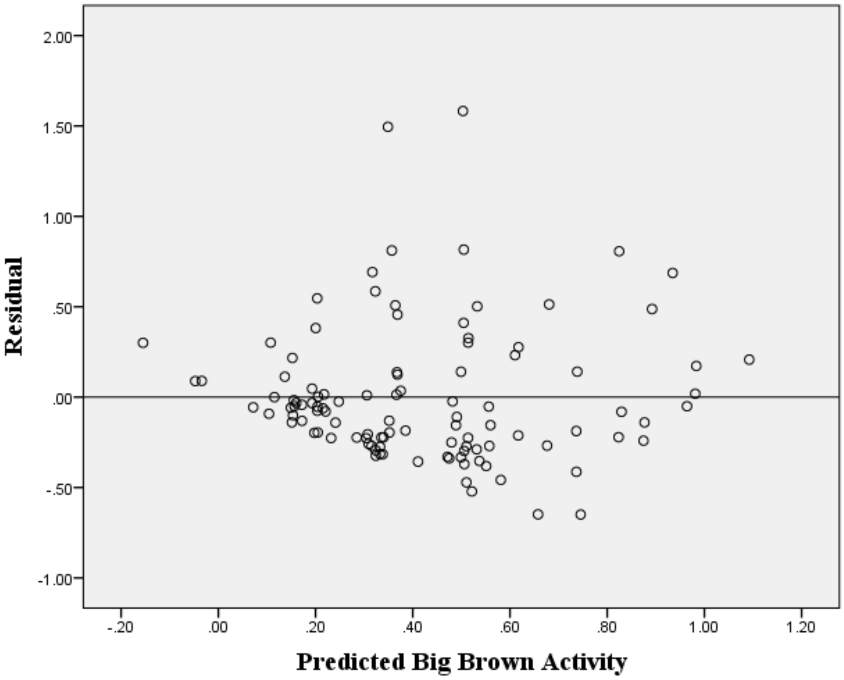


c)



Residual
.40
.20
.00
-.20
.00
.20
.40
.60
Predicted Hoary Activity

d)

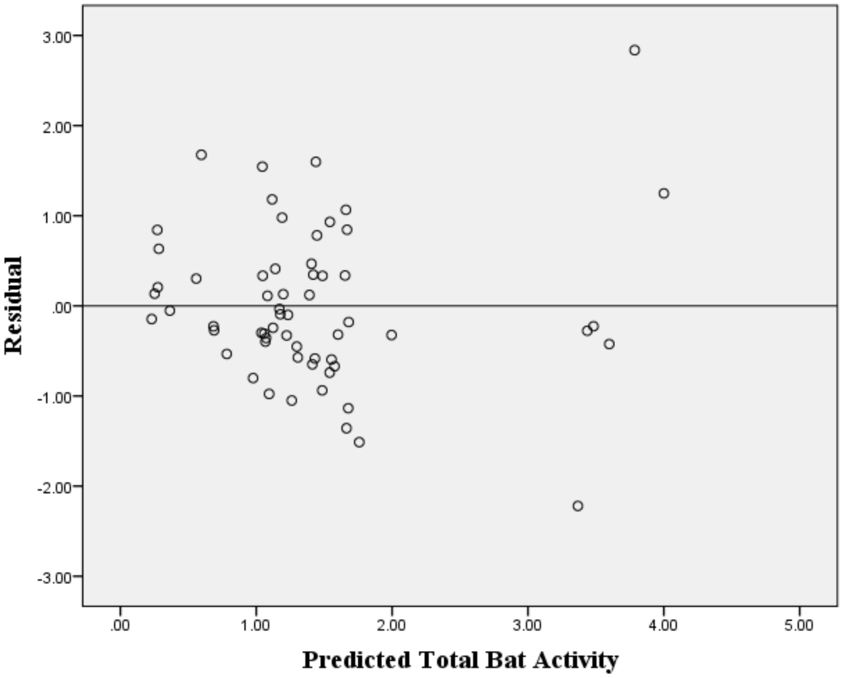


Residual
2.00
1.50
1.00
.50
.00
-.50
-1.00
-.20
.00
.20
.40
.60
.80
1.00
1.20
Predicted Big Brown Activity

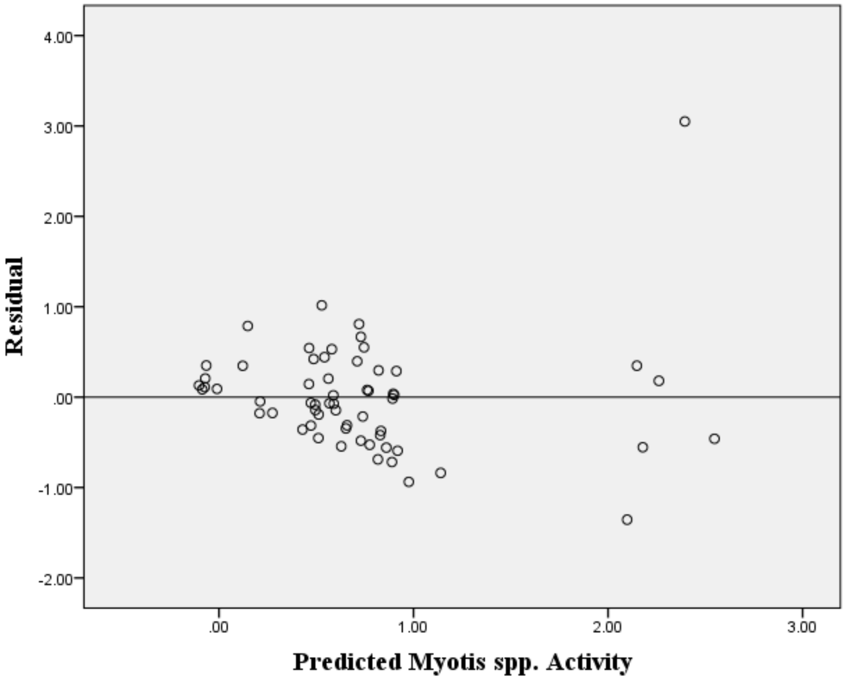
Appendix D

Residual Plots at Lake Habitats in the SEGP for a) Total bat activity at 500 m scale, b) *Myotis* spp. activity at 500 m scale, and c) Hoary bat activity at 1 km scale.

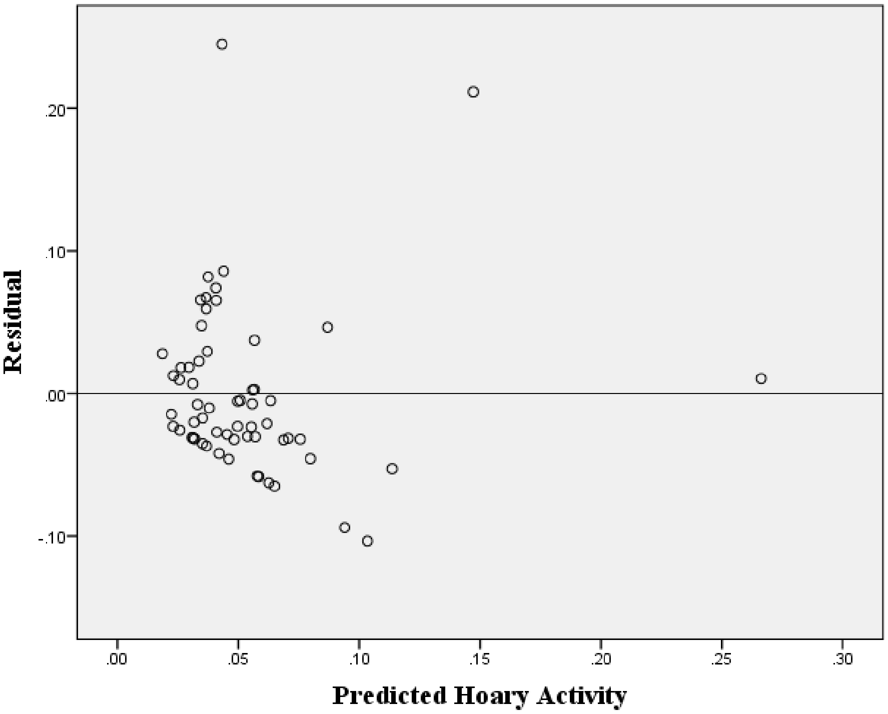
a)



b)



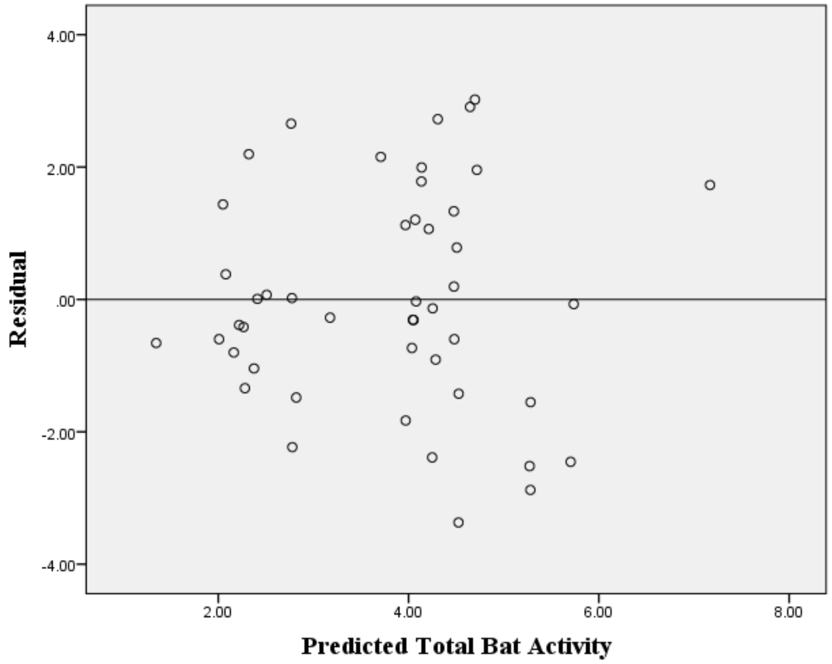
c)


Residual
.20
.10
.00
-.10
.00
.05
.10
.15
.20
.25
.30
Predicted Hoary Activity

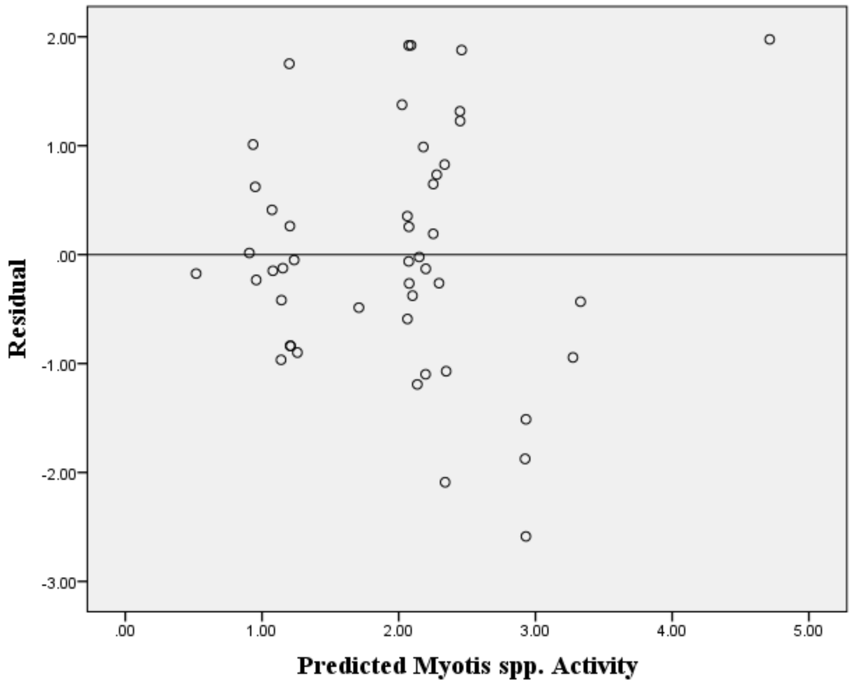
Appendix E

Residual Plots at Riparian Habitats in the SEGP for a) Total bat activity at 1 km scale, b) *Myotis* spp. activity at 1 km scale, c) Hoary bat activity at 1 km scale, and d) Big Brown bat activity at 1 km scale.

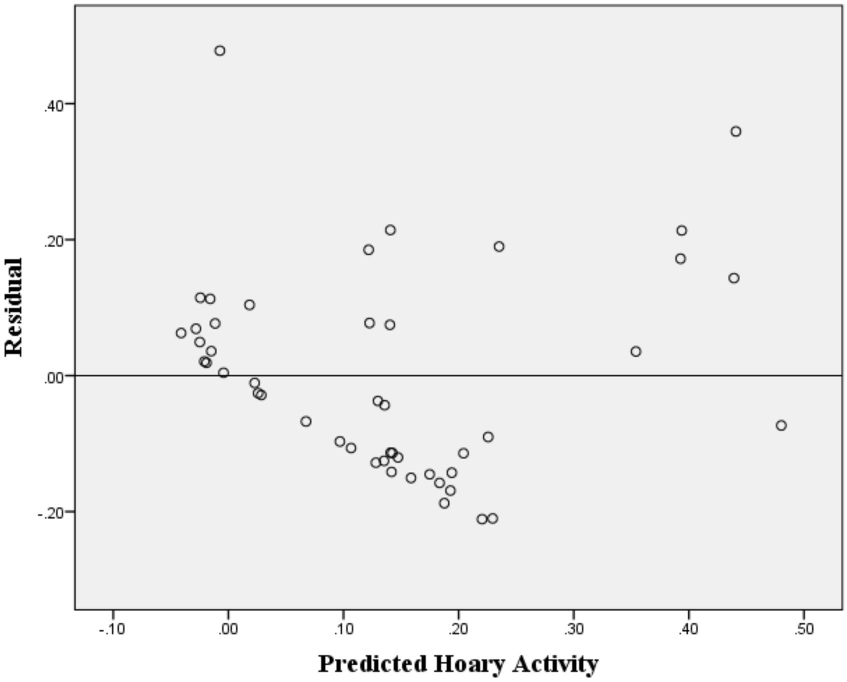
a)



b)



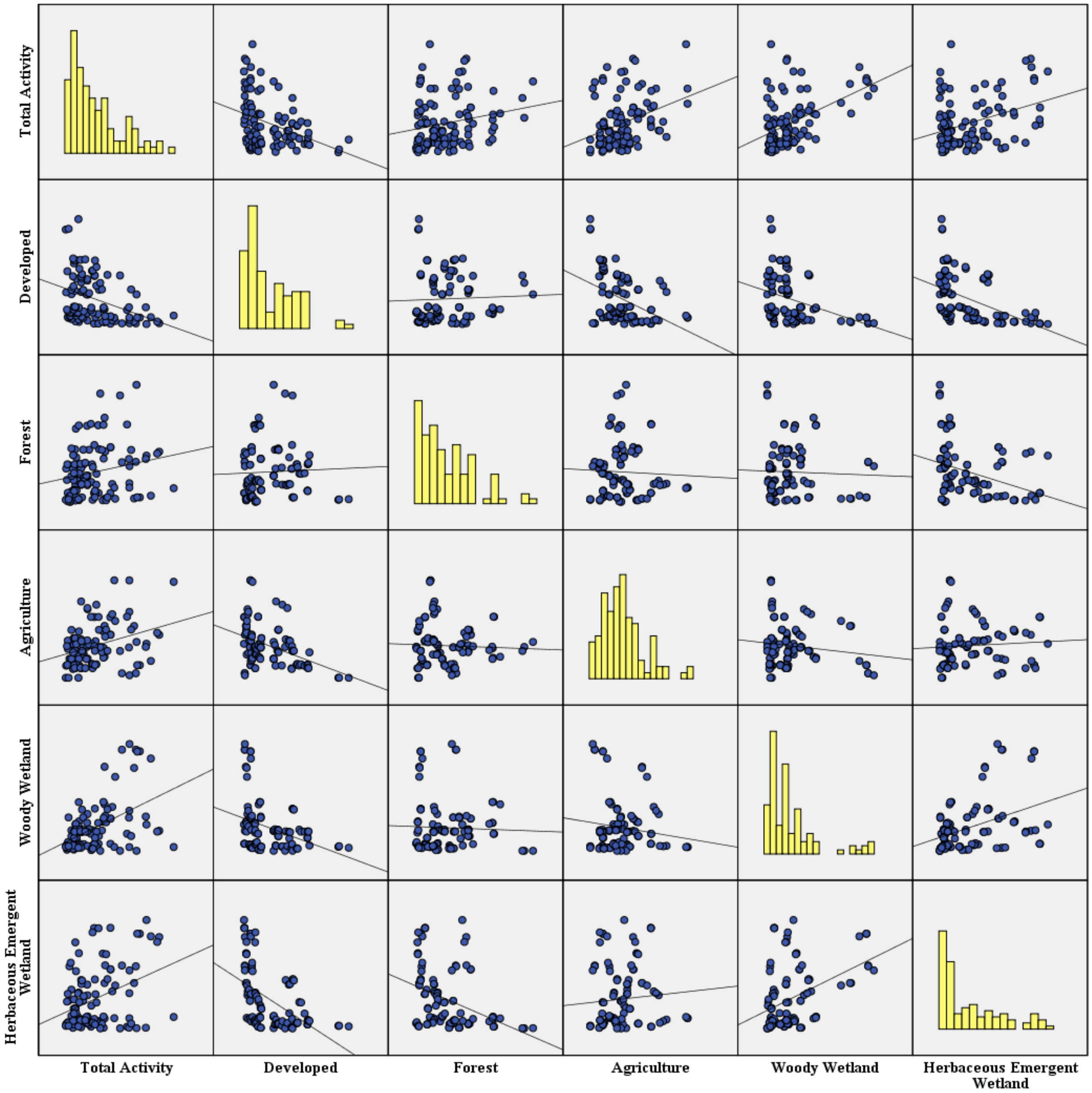
c)


Residual
.40
.20
.00
-.20
-.10
.00
.10
.20
.30
.40
.50
Predicted Hoary Activity

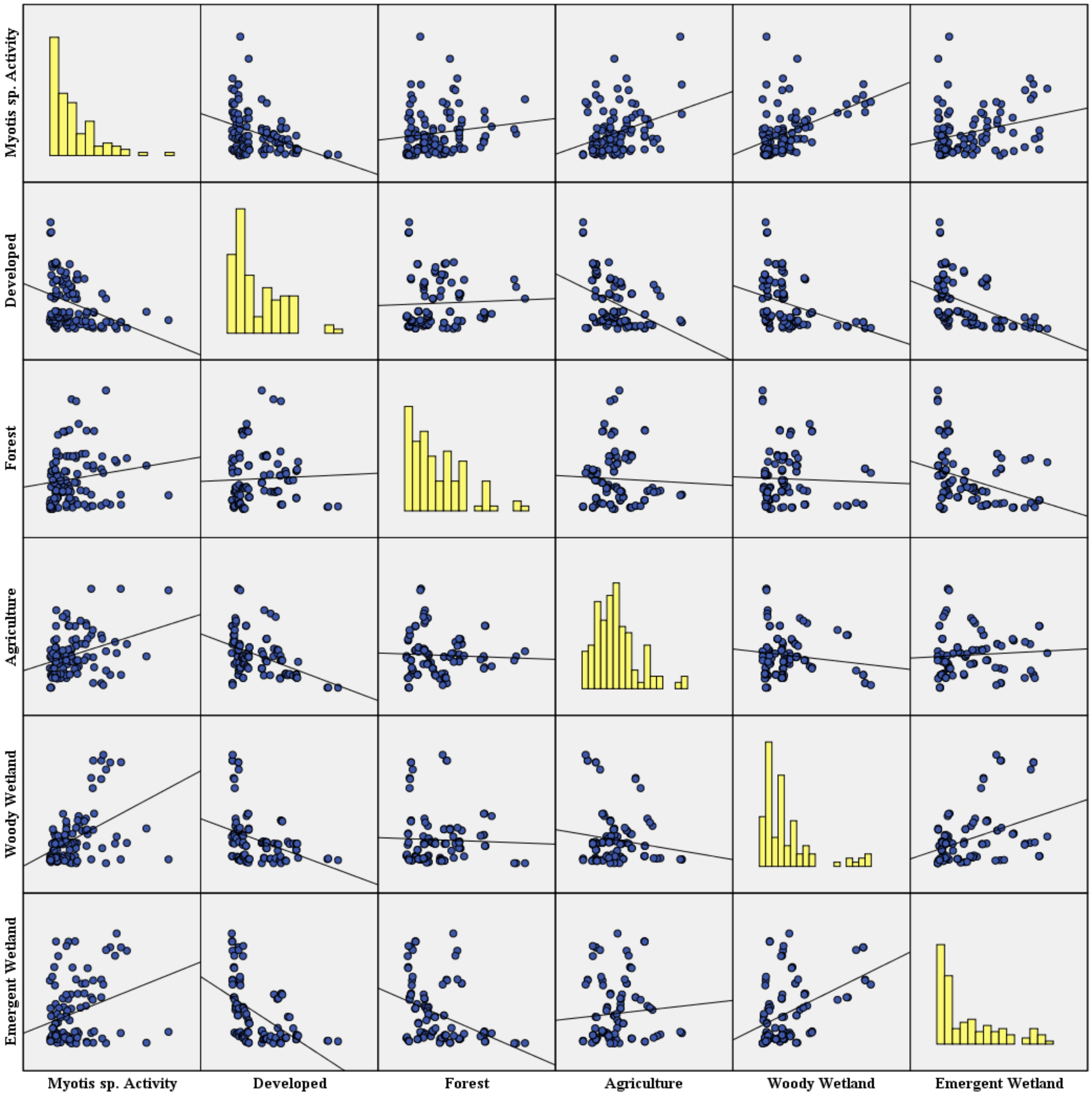
Appendix F

Scatter plot matrix of Bat Activity and Land Cover Proportion at all sites in the SEGP sites for a) Total bat activity at 1 km, b) *Myotis* spp. at 1 km, c) Hoary bat at 1 km, d) Big Brown at 500 m. Histogram included for each variable.

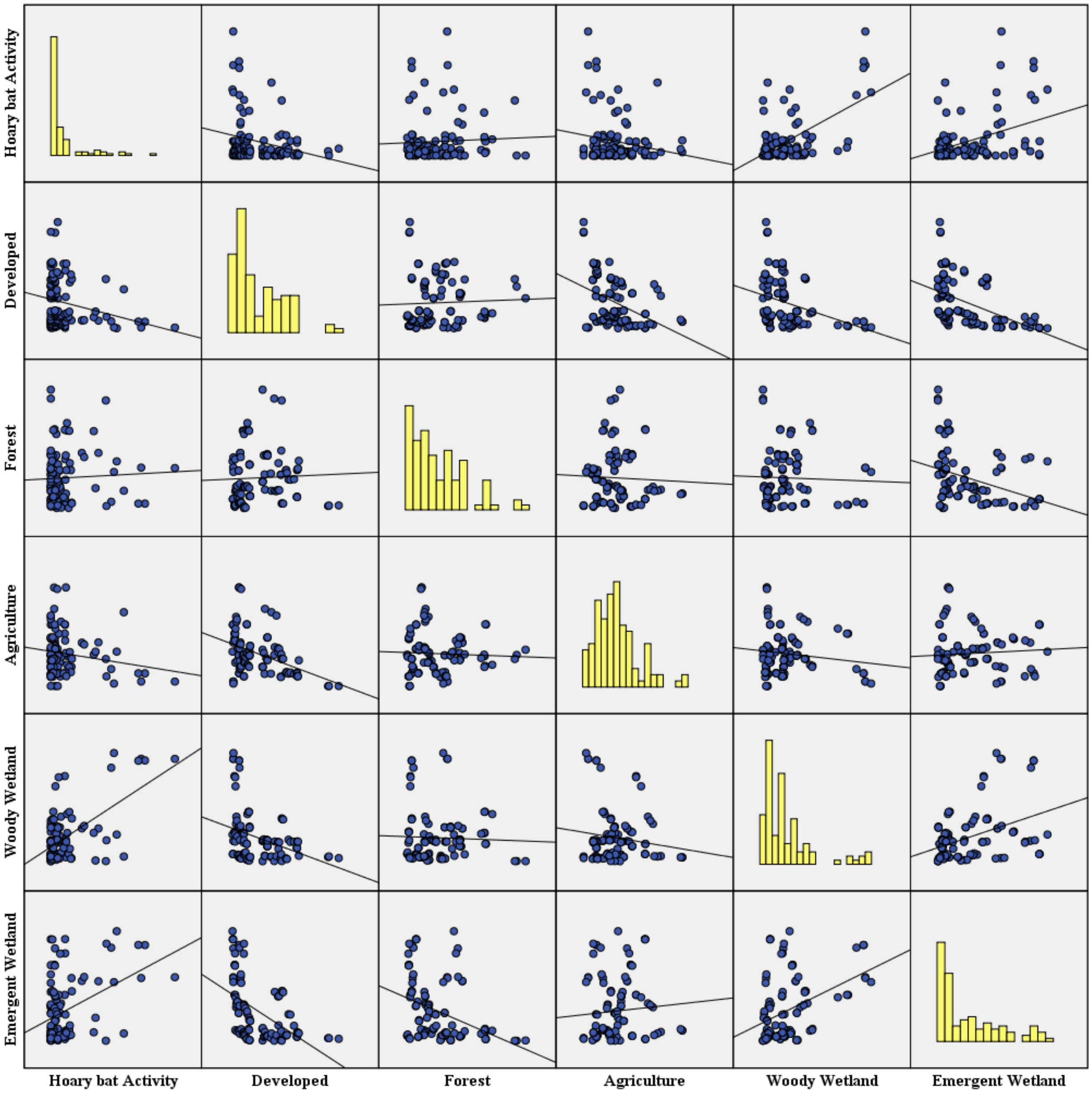
a)



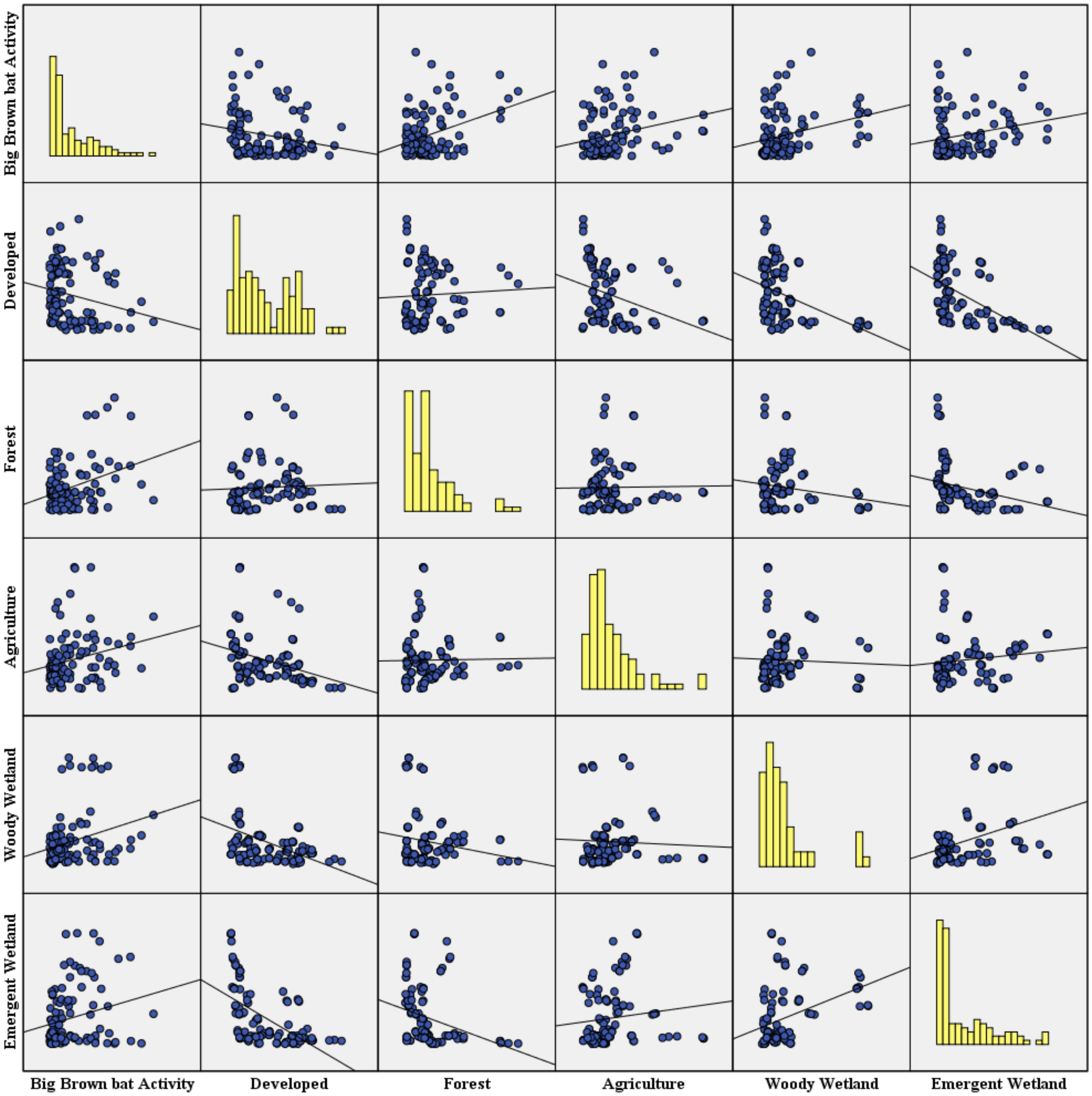
b)


Myotis sp. Activity
Developed
Forest
Agriculture
Woody Wetland
Emergent Wetland
Myotis sp. Activity
Developed
Forest
Agriculture
Woody Wetland
Emergent Wetland

c)

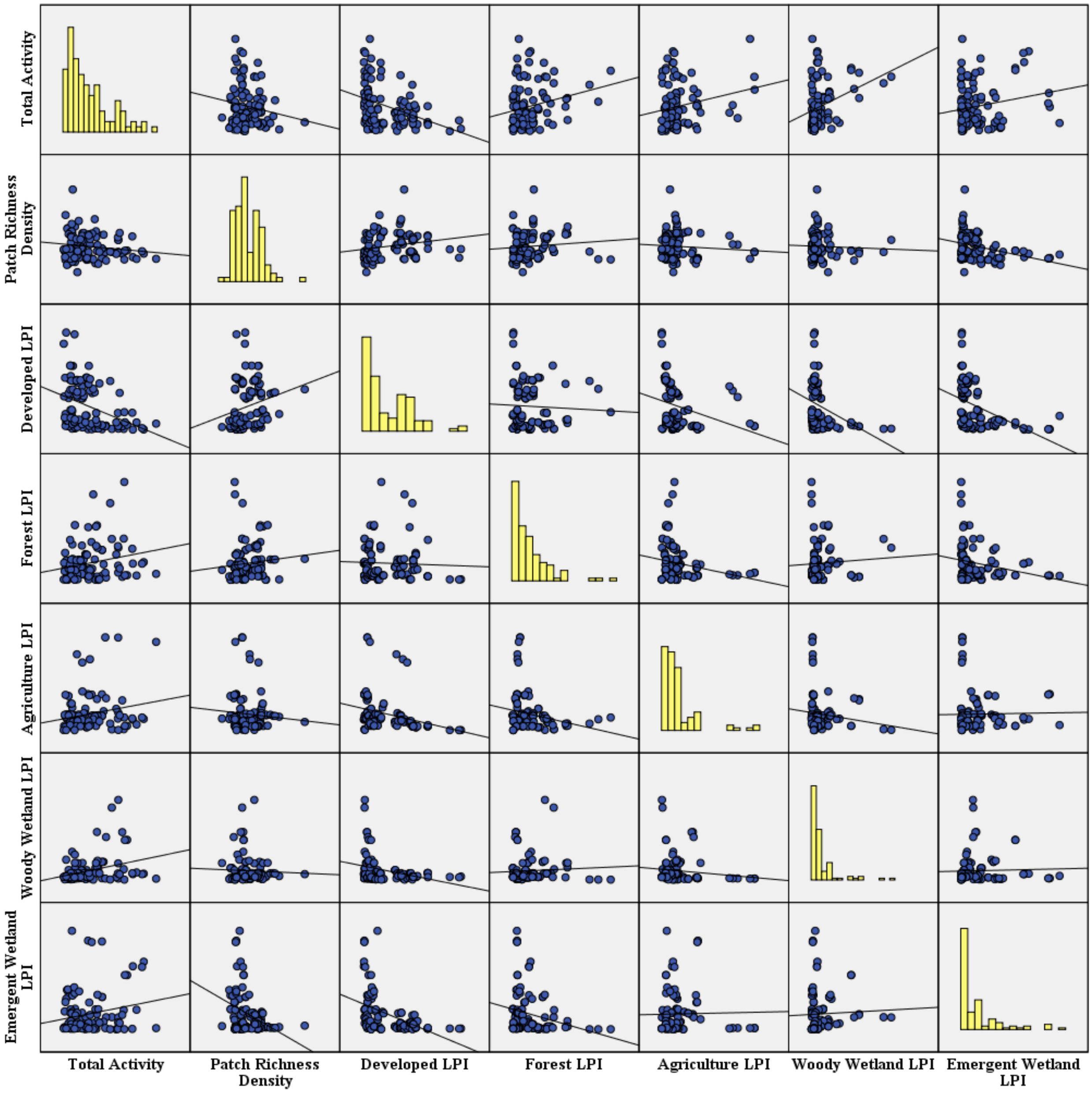

Hoary bat Activity
Developed
Forest
Agriculture
Woody Wetland
Emergent Wetland
Hoary bat Activity
Developed
Forest
Agriculture
Woody Wetland
Emergent Wetland

d)

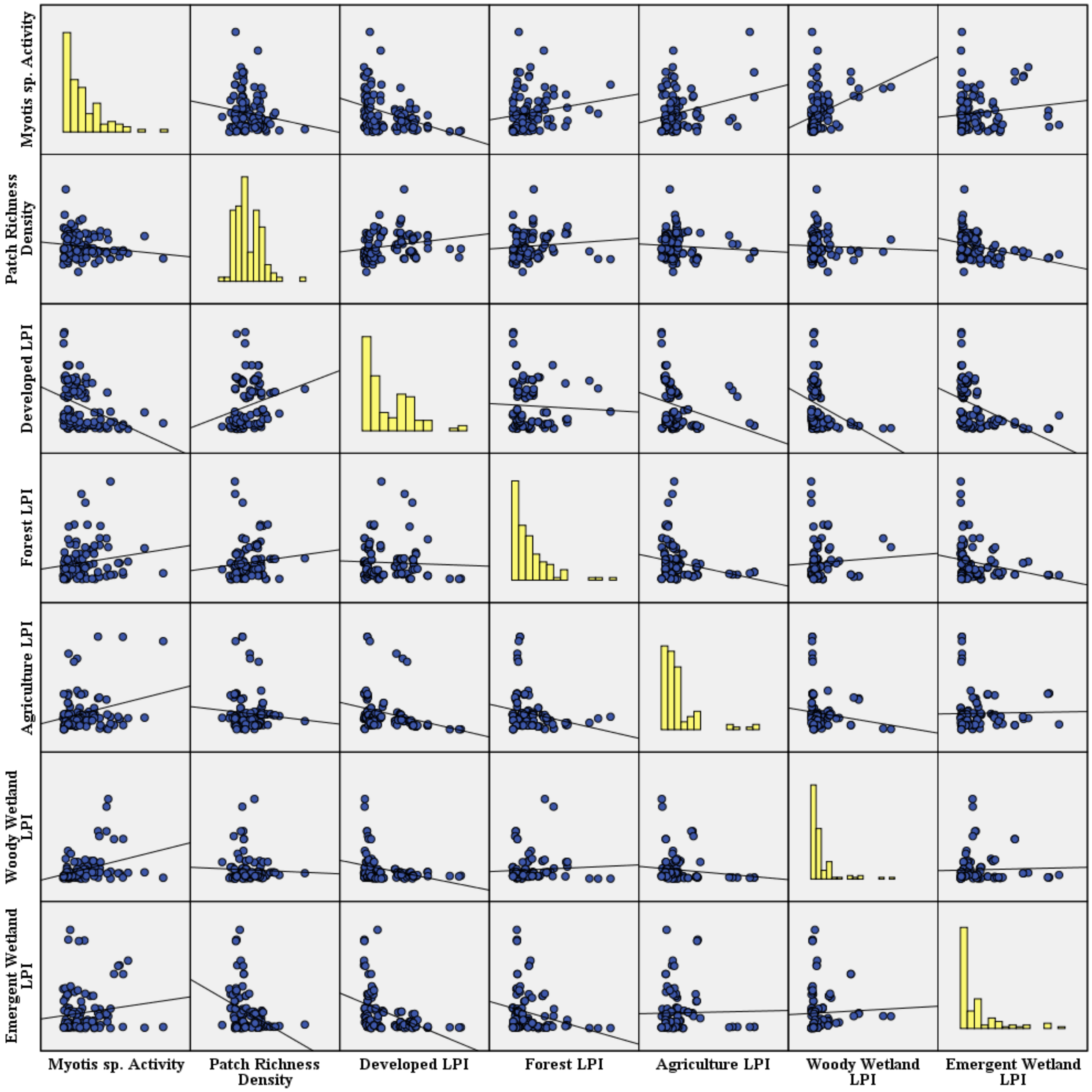

Big Brown bat Activity
Developed
Forest
Agriculture
Woody Wetland
Emergent Wetland
Big Brown bat Activity
Developed
Forest
Agriculture
Woody Wetland
Emergent Wetland

Scatter plot matrix of Bat Activity and Patch Richness Density & LPI at all sites in the SEGP sites for a) Total bat activity at 1 km, b) *Myotis* spp. at 1 km, c) Hoary bat at 1 km, d) Big Brown at 500 m. Histogram included for each variable.

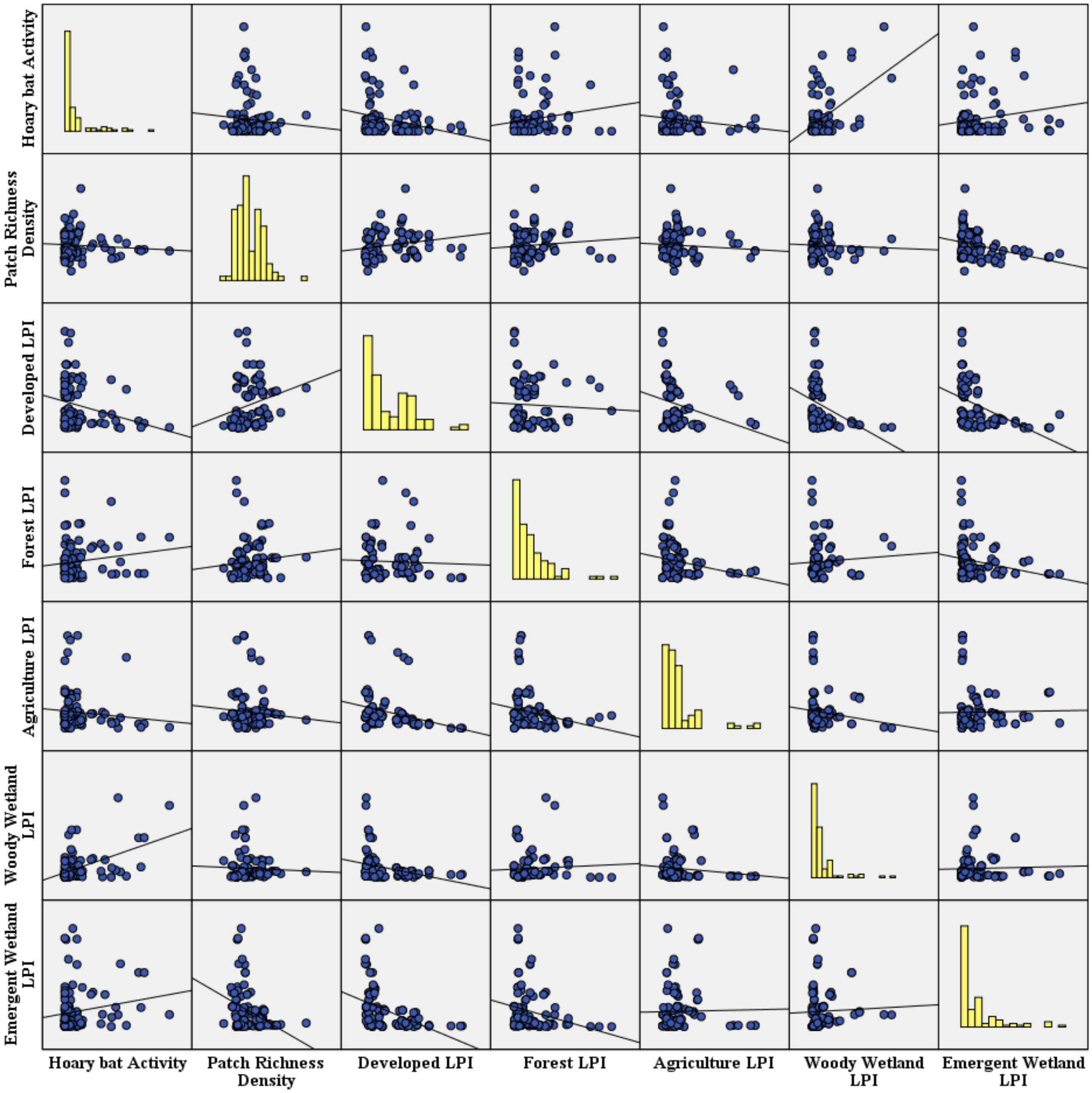
a)



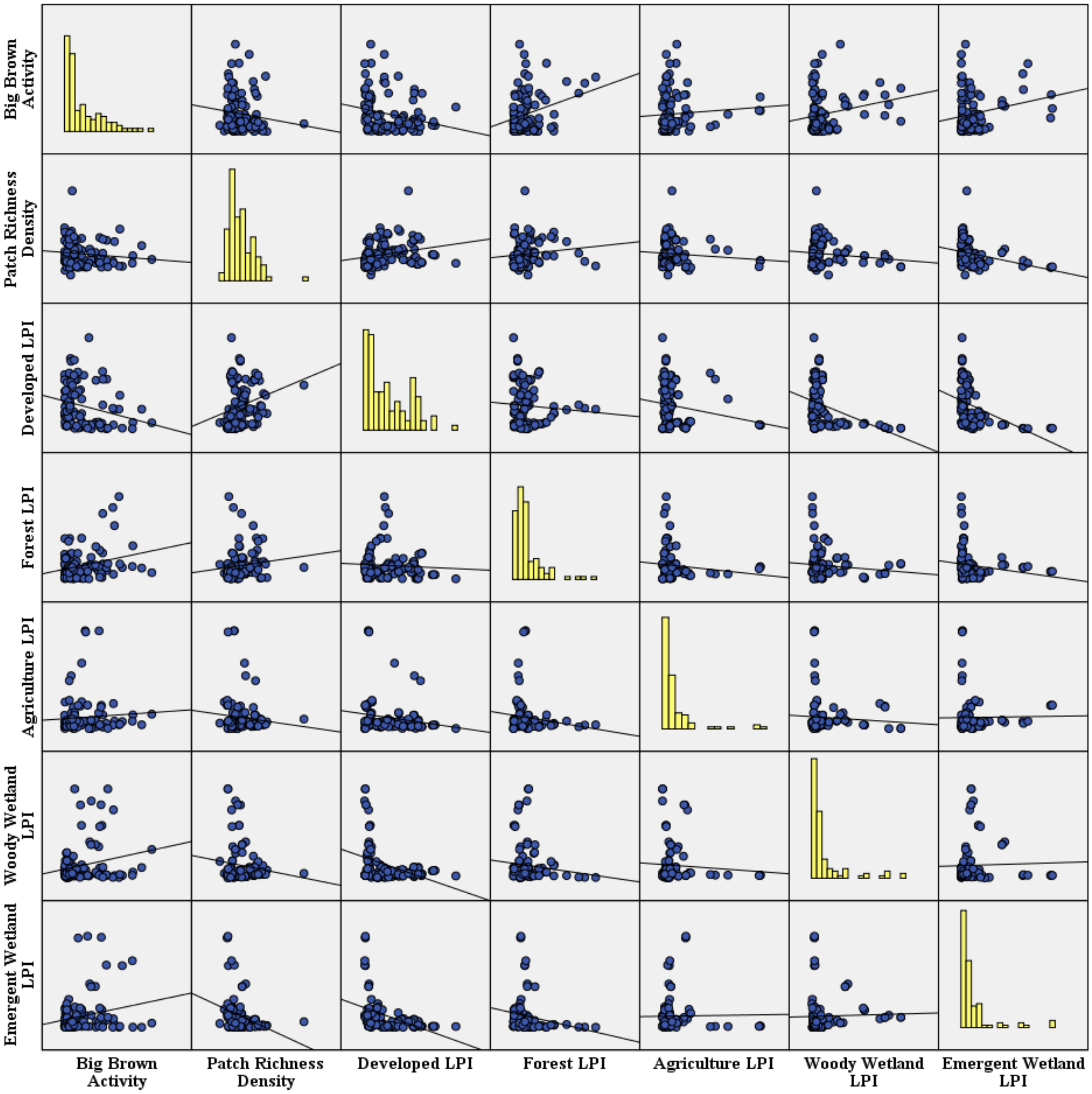
b)


Myotis sp. Activity
Patch Richness Density
Developed LPI
Forest LPI
Agriculture LPI
Woody Wetland LPI
Emergent Wetland LPI
Myotis sp. Activity
Patch Richness Density
Developed LPI
Forest LPI
Agriculture LPI
Woody Wetland LPI
Emergent Wetland LPI

c)


Hoary bat Activity
Patch Richness Density
Developed LPI
Forest LPI
Agriculture LPI
Woody Wetland LPI
Emergent Wetland LPI
Hoary bat Activity
Patch Richness Density
Developed LPI
Forest LPI
Agriculture LPI
Woody Wetland LPI
Emergent Wetland LPI

d)


Big Brown Activity
Patch Richness Density
Developed LPI
Forest LPI
Agriculture LPI
Woody Wetland LPI
Emergent Wetland LPI
Big Brown Activity
Patch Richness Density
Developed LPI
Forest LPI
Agriculture LPI
Woody Wetland LPI
Emergent Wetland LPI