SEX-SPECIFIC FORAGING HABITS AND ROOST CHARACTERISTICS OF THE EVENING BAT (*NYCTICEIUS HUMERALIS*) IN AN INTENSIVELY MANAGED FOREST IN NORTH-CENTRAL ARKANSAS

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ABSTRACT

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The synergistic effects of white-nose syndrome (WNS) and habitat destruction have caused declines in bat populations throughout eastern North America, deeming knowledge of the spatial-temporal patterns of many bat species increasingly important to conservationists. Although many studies address the roosting ecology of imperiled forest-dwelling bats, little is known about the foraging habits of more abundant, sympatric forest-dependent species. There is even less knowledge pertaining to foraging differences between male and female bats. Therefore, during June-August 2013 and 2014, I evaluated the foraging and roosting habits of the evening bat (*Nycticeius humeralis*) in north-central Arkansas, using radio-telemetry. Foraging range size was estimated from bat foraging locations via kernel density and minimum convex polygon methods. Additionally, I measured forest stand characteristics at roost sites and random-paired sites to determine sex-specific diurnal roosting habits. Foraging ranges differed between years and sexes with females exhibiting larger foraging ranges than males. Annual precipitation and resource availability likely contributed to variability between years, and sex-specific energetic requirements or habitat availability likely influenced differences detected between males and females. Also, evening bats, primarily males, used multiple core foraging areas. Likewise, differences in roosting characteristics were detected between sexes at the plot level (but not at the roost level). Specifically, males selected roost sites at lower elevation, with more canopy cover, and a larger tree basal area than females. Results suggest that differences in male and female foraging habits and roosting requirements do exist. Therefore, sex-specific preferences should be more consistently considered in bat studies in order to produce better informed habitat management decisions.

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CHAPTER I

GENERAL INTRODUCTION

Bat Conservation

One of the goals of conservation biology is to maintain forest biodiversity, especially for highly vulnerable species. Bats, belonging to the order Chiroptera, are an immensely diverse taxon of mammals with species worldwide (Kunz & Parsons 2009), but particularly vulnerable because of (1) low resilience to disturbances and (2) a very low reproductive output relative to their body size (BCI 2013). Public misconception and lack of scientific knowledge have undermined the importance of bats in ecosystems. Yet, as keystone species, they provide critical ecosystem services such as insect control through consumption of large amounts of both native and invasive insect species, distribution of nutrients, and support of primary production through plant pollination and seed dispersal. Bats are important indicators of environmental health (Fenton 1997) and a taxon of increasing concern for land managers and conservationists.

In the last decade, interest in bat research has increased as a direct response to habitat alteration, development of wind-energy projects (Hayes 2013; Smallwood 2013), and spread of white-nose syndrome (WNS), a fungal disease fatal to many bat species (Blehert et al. 2009). Similarly, anthropogenic forces have destroyed or degraded the majority of wildlife habitat, specifically forest habitat. Diverse, heterogeneous forests have been replaced with less diverse, increasingly homogeneous forest stands, largely due to agriculture and timber harvest practices, which has led to an overall reduction in ecosystem biodiversity (Patriquin & Barclay 2003). Additionally, the development of wind energy facilities has resulted in an increasing number of annual bat fatalities (Hayes 2013; Smallwood 2013). The synergistic effects of WNS (Blehert et al. 2009), wind facility fatalities (Hayes 2013; Smallwood 2013), and habitat loss at the landscape level (Lacki et al. 2007), specifically, have led to a decline in abundance of bat populations in the northeastern United States. As WNS-susceptible species decline, non-susceptible, forest-dwelling bats become increasingly important in filling bat niches. Therefore, information of non-susceptible species (e.g., *Nycticeius humeralis* and *Lasiurus borealis*) is of equal importance to land managers and biologists. Particularly, the population status of many forest-dwelling species remains unknown because of a lack of data. Furthermore, the effects of habitat alterations on the spatial movements and requirements of many species have poorly been documented. Therefore, research effort is needed to determine the status and habitat requirements of common species throughout various habitat types (Lacki et al. 2007). This would allow inference throughout species' ranges, which is crucial to the future of bat conservation.

Forest-dwelling Bats

Of the 45 bat species known to inhabit North America, 25 depend on forest habitat for foraging and/or roosting (Lacki et al. 2007). It is hypothesized that species dependent on ephemeral roosts (e.g., snags, peeling bark, and leaf litter), are declining due to anthropogenic disturbances to forest habitats (Kunz 1984; Miles et al. 2006), primarily because of the destruction of snags and mature roost trees (Lacki et al. 2007). Prior research has largely focused on bats that use permanent roost sites and hibernacula (i.e., cave-obligate species) with an emphasis on threatened and endangered species. Yet, little is known about the relationship between changes in forest habitat and the effects on fitness, home range, and foraging behavior on many common bat species, the majority of which depend on ephemeral roosts (Miller et al. 2003; Lacki et al. 2007). Unlike cave-obligate species, many tree roosting species use multiple roosts over brief periods (i.e., 2-7 days) making them more difficult to monitor. Despite evolved morphological (e.g., wing size) and behavioral (e.g., echolocation call structure) adaptations to inhabit specific forest conditions (e.g., cluttered environments; Norberg & Rayner 1987), it is unknown whether species are capable of adapting at the current rate of human development and habitat alteration. Furthermore, the effects of woodland management regimes to bat communities cannot be accurately assessed without first determining species-specific habitat requirements (Murphy et al. 2012).

Forest Management

Bats, critical to forest health, provide free ecosystem services, such as pest control, and should be included in forest management plans for both public and private sectors. The presence or absence of bats can indicate ecosystem health (Fenton 1997, Jones et al. 2009). Despite their ecological importance, little attention is directed toward the conservation of forest bats in the private sector. Contrarily, public lands (i.e., U.S. National Forests) are strategically managed as multiple-use areas to provide timber resources and conserve wildlife habitat, especially for endangered species. Historically, natural phenomena (e.g., wind and fire) were primary factors influencing forest stand communities (Krusic et al. 1996). Today, replication of such events is achieved via timber harvest and prescribed fire.

Commonly used forest management techniques, such as logging and prescribed burning, alter forest-stand age, density, and diversity. These management practices, especially prescribed burning, are commonly used to mitigate forest stand diversity by promoting the regeneration and establishment of early and mid-successional stages (Armitage & Ober 2012). At the proper frequency and scale, forest management regimes can provide suitable habitat for a variety of forest-dwelling species. Improper forest management may negatively affect bats by decreasing prey abundance (i.e., insects) and roost availability (Patriquin & Barclay 2003) via degradation or complete loss of critical foraging habitat and water sources.

Management regimes, such as thinning, prescribed burning or the combination of both alter stand composition and structure. Likewise, the ability of bats to maneuver and exploit food resources is likely influenced by prior management practices. Additionally, forest management practices influence insect populations with highly fragmented habitats supporting the highest densities of insects in the short-term (Grez et al. 2004). While stand heterogeneity is considered most beneficial to bats, research is needed to adequately evaluate the effects of forest management regimes on individual species (Patriquin & Barclay 2003) and entire bat communities (Murphy et al. 2012).

Habitat Use

Research on home range and habitat use patterns is critical to properly develop management plans (Krusic et al. 1996; Fenton 1997). Habitat is defined as any area occupied by an animal that includes site-specific resources and conditions critical to survival and reproduction (Leopold 1933). Spencer (2012) defines home range as “that area over which an animal regularly exploits and updates information stored in a cognitive map.”

Animal movements can vary between species but also between sexes and among age classes, temporally and spatially (Aebischer et al. 1993), and can occur at various scales. Johnson (1980) defined a hierarchal scale that ranks habitat selection at four different levels. The first-order selection encompasses the total geographic range of a species. Second-order selection refers to home range. For a given species, movements of tracked individuals are commonly used to estimate a mean home range (Powell & Mitchell 2012). Third-order selection is limited to the use of habitat types within the home range. Lastly, fourth-order selection is the finest scale and focuses on characteristics such as specific prey foraged within a habitat.

Common analytical methods used to estimate an animal’s use of space include minimum convex polygon (MCP) and kernel density methods. Among kernel methods, adaptive kernel (AK) and fixed kernel (FK) methods are two of the most accurate, well-understood statistical methods.

A minimum convex polygon (MCP), also known as a convex hull, is a non-parametric technique used to estimate an animal’s use of space (Mohr 1947). The MCP method is an appropriate analytical technique for estimating space-use because it can be easily manipulated for comparison with other, similar studies. It can be described as the smallest 2-dimensional polygon encompassing all animal locations. The MCP method uses the furthest outlying locations as range boundaries to create a 2-dimensional closed polygon in which the inner angles never exceed 180 degrees (Burgman & Fox 2003). Due to this constraint, estimates are derived under the assumption that an animal is using the entirety of the encompassed area equally (Powell 2000). Therefore, MCPs can limit the researcher's ability to differentiate biologically important areas or resources within the estimated range from other areas that the animal may rarely use.

Among most accurate, non-parametric statistical approaches to estimating home range are kernel methods (Kie et al. 2010). Although the term "home range" is commonly used in conjunction with kernel methods, perhaps a better term would be "utilization distribution (UD)". After all, kernel methods are probability density functions that estimate the likelihood of an individual being in a given place at a specified time. Thus, UDs attempt to describe the intensity at which individuals use space (Seaman & Powell 1996) by plotting points (location estimates) on a pre-determined grid. At each point, a probability density function is computed to determine a bandwidth, also referred to as a smoothing factor that is superimposed on a grid to estimate an animal's use of an area (Seaman and Powell 1996). Kernels or concentric contours are plotted around the estimated grid points, forming an estimate of home range referred to as UD. Kernel methods, adaptive and fixed, have the capability of producing more accurate estimates of animal space use than the MCP method. Yet, one major limitation to kernel estimates is the inability to compare them across studies (Harris et al. 1990).

Monitoring Spatial Movements

Information on the spatial relationship between foraging areas and roost sites is vital to the future of bat conservation. Yet, studies on foraging bats have received little attention compared to roost site studies because roost site availability has been considered the primary limiting factor to bat populations (Lacki et al. 2007). However, there is a need to obtain knowledge on the effects of forest management on bat foraging areas as they may alter predator-prey dynamics (i.e., reduction of insect abundance). In general, there is a paucity of information on bat foraging behavior, largely due to technological, logistical, and financial limitations (Miller et al. 2003). Nocturnal and highly mobile bats are difficult subjects to study (Lacki et al. 2007). However, recent advancements in technology (e.g., acoustic monitoring devices and software; reduced radio transmitter size and cost; chemiluminescent tags) may shed new light on small mammal movements and foraging behavior (Lacki et al. 2007). Tracking individuals is a necessary step to determine species-specific habitat use among bat species for which knowledge is limited, and to gain a better understanding of the role bats play in ecosystems.

Since the late 1980s, very high frequency (VHF), satellite, and global positioning system (GPS) technologies have improved substantially making remote monitoring highly mobile species more practical. Currently, VHF transmitters are the only devices small enough to be attached to microchiropterans. Radio telemetry has been used to record the spatial movements for several North American species including: Indiana bats (*Myotis sodalis*; Womack et al. 2013; Kniowski & Gehrt 2014), eastern red bats (*Lasiurus borealis*; Carter et al. 1998; 2004; Elmore et al. 2005; Amelon et al. 2014), Seminole bats (*Lasiurus seminolus*; Carter et al. 1998; 2004), evening bats (*Nycticeius *humeralis*; Clem 1993; Carter et al. 1998; 2004; Duchamp et al. 2004; Morris et al. 2011), big brown bats (*Eptesicus fuscus*; Brigham 1991; Duchamp et al. 2004),Ozark big-eared bats (*Corynorhinus townsendii ingens*; Wilhide et al. 1998), and Rafinesque's big-eared bats (*Corynorhinus rafinesquii*; Menzel et al. 2001).

Research on the spatial movements of bats has increased substantially in the last 20 years; yet, small sample sizes have remained a constraint for inferences. For example, pooling data between sexes has often been necessary to increase sample size (e.g., Morris et al. 2011), but this practice may mask important underlying patterns of differences between sexes. Furthermore, many species (e.g., *N. humeralis* and *L. borealis*) have large geographic ranges which span a variety of habitats and climates. Therefore, comprehensive research with adequate sample sizes is needed to properly evaluate species' habitat use throughout their geographic range.

Sex-Specific Habitat Requirements

Sexual segregation, common in mammalian species, suggests differentiating habitat needs among sexes (Encarnção 2012). The majority of research on sexual segregation in mammals is limited to wild ungulates (Main & Coblentz 1996; Kie & Bowyer 1999; Alves et al. 2012), and has not been adequately addressed in bats. Kie and Bowyer (1999) define sexual segregation as "the exclusive use of different areas by males and females at specified spatial and temporal scales." The underlying factors influencing sexual segregation are complex and poorly understood. Factors possibly influencing sexual segregation are: population density, intra-specific competition, variation in male and female energy requirements and body size, social structure, sex ratio, and risk of predation (Kie & Bowyer 1999).

Sexual segregation is common among polygynous species, especially those with a marked sexual dimorphism in body size (Kie & Bowyer 1999; Alves et al. 2012). Several hypotheses have been proposed to explain sexual segregation in ungulates: reproductive-strategy hypothesis (RSH), forage-selection hypothesis (FSH), social factor hypothesis (SFH), social affinity hypothesis (SAH), and activity budget hypothesis (ABH) (Alves et al. 2012). Similarly, many bat species exhibit polygynous mating strategies, but male and female body size does not vary to the extent of other mammals such as ungulates. Most studies addressing sexual segregation in bats (Bradbury & Vehrencamp 1977; Cryan & Wolf 2003; Altringham & Senior 2005; Safi et al. 2007; Safi 2008; Amichai et al. 2012; Encarnção 2012) focused on latitudinal or altitudinal segregation for either temperate or subtropical species, but none of the aforementioned hypotheses has clearly been tested. However, two, more integrative, hypotheses for sexual segregation in bats have been developed: (1) Sexual segregation is a behavioral response to minimize male and female competition for food resources, mates, and roosting sites; (2) sexual segregation results from biological differences between sexes (e.g., thermoregulatory requirements, sociality, and body size; Levin et al. 2013). A recent study on sexual segregation in a subtropical bat species (*Rhinopoma microphyllum*) suggests that sexes use different foraging and roosting areas because females require more insulated roosts than males (Levin et al. 2013).

Many ephemeral-roost dependent bat species remain sexually segregated throughout the summer. Females will commonly form maternity roosts while males remain solitary, which indicates that some extent of spatial and temporal segregation is occurring. Likewise, the distribution of roost sites throughout the landscape likely influences foraging location, and it is possible that sexual segregation in foraging habits also exists. It is unknown whether males remain spatially segregated from females solely during roosting, during roosting and foraging, or temporally during foraging as well.

Problem Statement

Due to the spread of white-nose syndrome, and more importantly the loss of forest habitat diversity (i.e., decreased forest stand heterogeneity), the statuses of forest-dwelling species are of increasing concern. Determining the spatial habitat requirements of common bat species would allow biologists to better manage for a guild of bat species (Morris et al. 2011). My goal was to evaluate the foraging habits and roosting requirements of the evening bat, *N. humeralis*, which has never been studied in the western periphery of its geographic range. Moreover, even though sexual segregation is suspected, to my knowledge, it has not been thoroughly addressed in previous evening bat foraging studies (but see Morris et al. 2011). Studying evening bats in areas where they are abundant would provide larger sample sizes than previously used in other portions of their range. This would allow for more precise ideas of foraging habits applicable to areas where they are likely in decline (Boyles & Robbins 2006). Evening bat foraging behavior needs to be evaluated to determine if management regimes provide good foraging habitat for both males and females in the Ozark National Forest Sylamore Ranger District in north-central Arkansas. Thus, I investigated sex-specific habitat requirements of evening bats, a common species in Arkansas, in an area where they are abundant enough to males and females in sufficient numbers.

Objectives

The objectives of my study were to evaluate sex-specific foraging habits (e.g., home range) and roost requirements of evening bats in a landscape intensively managed for timber resources, using VHF radio-telemetry equipment. The spatial movements of evening bats have been investigated in previous studies (Clem 1993, Carter 1998, Duchamp et al. 2004, and Morris et al. 2011); however, inadequate sample sizes have not allowed evaluation of sex-specific differences in foraging habits. Furthermore, evening bat spatial movements have never been monitored in a largely forest-dominated landscape nor the western periphery of the species range.

The proposed research intended to address the following questions:

1. Are home range estimates for *N. humeralis* consistent with studies conducted in the central and eastern portions of its geographic range?
2. Do males and females use different forage sites? If so, what/where are they, how do they differ, how distant are they from each other? Otherwise, do males and females use the same sites at different times?
3. Do males and/or females exhibit foraging-site fidelity?
4. Do males and females select diurnal roosts with different characteristics? If so, what are these characteristics, and how do they differ from each other?

Study Area

The study area is located at the USDA Forest Service's Ozark National Forest Sylamore Ranger District, approximately 10 km northwest of Mountain View, Arkansas (35.8683° N, 92.1175° W; Figure 1.1). The Sylamore Ranger District is contained within the counties of Stone, Searcy, Marion, Baxter, and Izard in the Ozark Highlands Ecoregion of north-central Arkansas. The low-elevation district, approximately 53,000 hectares, is dominated by oak and hickory tree species, and characterized by steep mountainous slopes consisting of limestone and sandstone ridges. The main drainages of the district are North Sylamore Creek, South Sylamore Creek, and the White River. During the summer, the warmest month is July, and average temperature is approximately 27°C. Average monthly rainfall over the period June, July, and August is 9 cm.

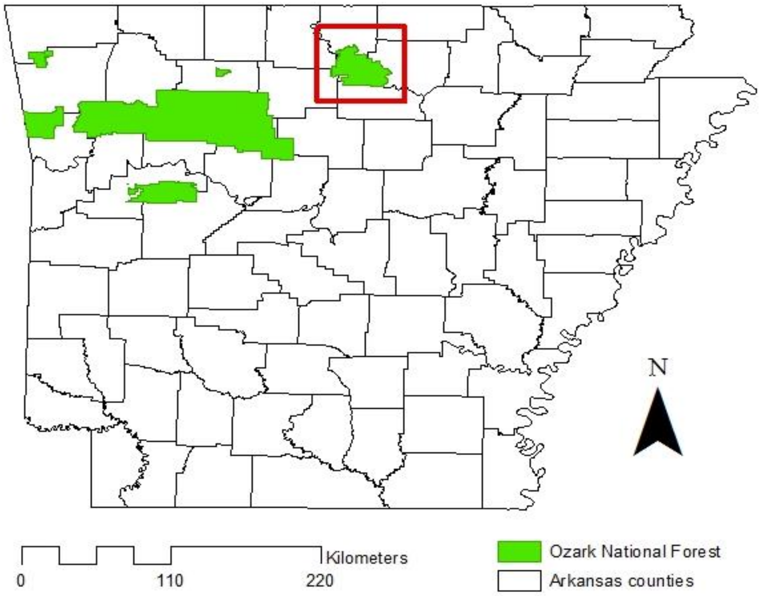

Figure 1.1. Location of study site in north-central Arkansas. The area outlined in red highlights the Sylamore Ranger District located in the Ozark National Forest.

Study Species

Nycticeius humeralis, commonly called the evening bat, is a relatively small bat (5-14 grams; Reid 2006; Perry & Thill 2008). The lifespan of the evening bat is unknown; however, females older than 5 years have been recorded (Wilkinson 1992). Knowledge on the reproductive cycle of the evening bat is limited, but like most bats, mating primarily occurs in late fall. After copulation, females enter hibernation and delay fertilization until the following spring. Sexual segregation is common after copulation, with males remaining solitary and females congregating into nursing colonies (Watkins 1972). On average, evening bats give birth to 2 pups between May and June. Pups are capable of flight after approximately 20 days, but will remain with the colony for an additional 2 to 3 weeks (Jones 1967; Watkins 1972).

Nycticeius humeralis occur from Michigan to northern Mexico and from the east coast to portions of Kansas and Oklahoma (Watkins 1972; Reid 2006; Figure 1.2). Although common in the southern and western portions of the range, evening bats are considered endangered in Indiana (Whitaker & Clem 1992) and are thought to be declining in areas with extensive human development, such as the eastern United States (Boyles & Robbins 2006). Although individuals in the far northern populations migrate south for overwintering (Watkins 1972; Watkins & Shump 1981), evening bats more commonly remain in the same area throughout the year (Boyles & Robbins 2006).

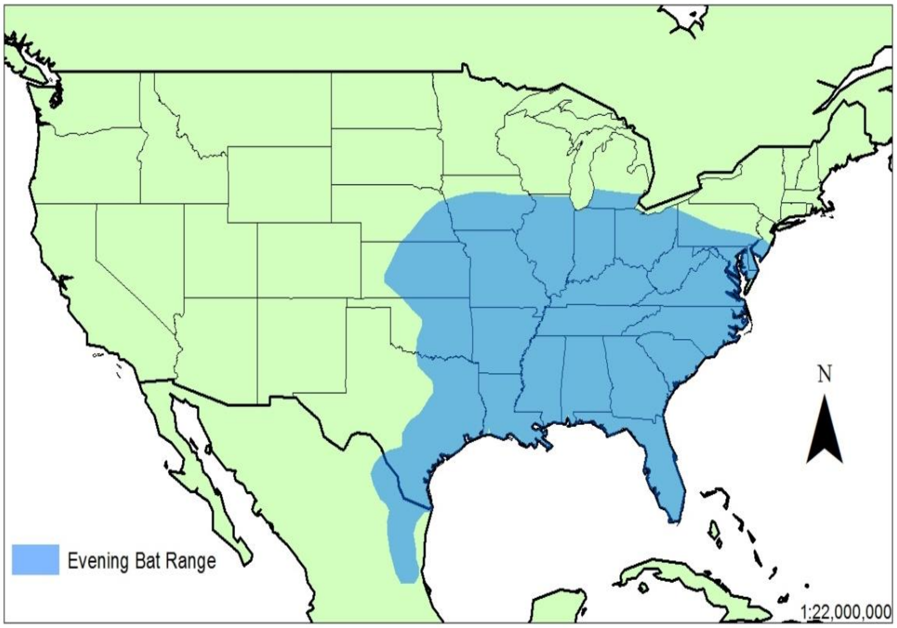

Figure 1.2. Historical range map for the evening bat (USGS National Gap Analysis Program, Species Data Portal).

The roosting requirements of *N. humeralis* are better documented than foraging behavior. During summer, evening bats commonly roost underneath exfoliating bark of mature trees (Menzel et al. 2001), within snags (Menzel et al. 2001; Boyles & Robbins 2006), and vacant man-made structures (Watkins 1969). Evening bats frequently switch roosts during summer, the majority of which are located in close proximity to previous roosts (Menzel et al. 2001; Boyles and Robbins 2006; Timpone et al. 2006). Seasonal variation in roost type has been observed between winter and summer (Boyles & Robbins 2006); however, knowledge of winter roosting habits is limited. Sexual segregation is common during summer with males remaining solitary and females roosting either alone or more commonly in maternity colonies (Menzel et al. 2001; Miles et al. 2006; Hein et al. 2009). Maternity colonies typically contain between 4 and 130 bats (Boyles & Robbins 2006; Hein et al. 2009); however, a maternity colony with 490 individuals has been observed in Southwest Georgia (Miles et al. 2006). Although males and females select different summer roosts, studies on roost site-selection have often pooled data for males and females (Menzel et al. 2000; Miller et al. 2003; Miles et al. 2006) or evaluated only juveniles and adult females (Menzel et al. 2001; Timpone et al. 2006). Studies of female roosting habits have primarily focused on evening bat use of man-made structures (Watkins 1969; Watkins & Shump 1981; Wilkinson 1992). Perry & Thill (2008) studied roosting behavior in males and warned that females may not benefit from the same roosting habitat as males. For example, male and female big brown bats (*Eptesicus fuscus*) exhibited differences in torpor patterns and roost-site selection which likely reflect differences in thermoregulatory requirements associated with reproduction (Hamilton & Barclay 1994). Because both males and females rely on ephemeral roosts, it is hypothesized that promoting a heterogeneous forest landscape, dominated by mature trees will likely provide both sexes with better quality roosting habitat than homogenous forest stands (Miles et al. 2006).

Evening bats are insectivores that commonly feed in the few hours around dusk and dawn (Reid 2006). The first of often multiple foraging trips begins soon after sunset (Wilkinson 1992) with individuals foraging above the canopy and descending to lower areas with the progression of nightfall (Carter 1998). Foraging locations include forest stands, agricultural areas, and along waterways by aerial hawking small, flying insects (Lacki et al 2007). Aerial hawking is the capture and consumption of prey during flight. Primary food sources include small beetles, moths, and leafhoppers (Whitaker & Clem 1992). Like most bat species, knowledge on foraging behavior and habitat use is limited.

Thesis Outline

This thesis contains four chapters. Following this general introduction (Chapter I), Chapters II and III report foraging and roosting data obtained during the summers 2013 and 2014. In Chapter II, I estimate evening bat home range size using minimum convex polygon and fixed kernel methods. More specifically, I examine the spatial movements of both male and female evening bats to determine if sexes exhibit different foraging habits. In Chapter III, I determine sex-specific roosting requirements and roost-site selection in relation to forest stand characteristics. In the final chapter (Chapter IV), I provide general conclusions from Chapters II and III, propose directions for future research, and discuss the implications of my research in relation to forest management practices and current bat conservation initiatives.

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CHAPTER II

SEX-SPECIFIC FORAGING HABITS OF THE EVENING BAT (*NYCTICEIUS HUMERALIS*) IN THE OZARK REGION OF NORTH-CENTRAL ARKANSAS

ABSTRACT

Although many studies address the roosting ecology of forest-dwelling bats, little is known about the foraging habits for abundant, forest-dependent species. There is even less knowledge pertaining to behavioral differences between male and female bats. During summers 2013 and 2014, I monitored the sex-specific foraging habits of the evening bat (14 males & 10 females) in the Ozark National Forest, Sylamore Ranger District of north-central Arkansas. I used fixed kernel (FK) with least squares cross validation and minimum convex polygon (MCP) methods to estimate the space-use patterns of male and female evening bats during their nightly foraging bouts. Evening bats, primarily males, used multiple core foraging areas. Females exhibited larger FK foraging ranges (852 ± 198 ha) than males (332 ± 85 ha), likely reflecting differences in energetic requirements or habitat availability (i.e., female roosts). MCP estimates were not different between sexes but varied among years. Similarly, FK foraging range estimates were significantly larger in 2014 (739 ± 163 ha) than 2013 (323 ± 106 ha) possibly due to differences in annual precipitation and resource availability. Results suggest that differences in foraging habits between males and females do exist. Further research is needed to produce better informed habitat management decisions.

INTRODUCTION

Bats play key roles in maintaining ecosystem health (Fenton 1997, Jones et al. 2009) and are a taxon of increasing concern due to habitat alterations (i.e., degradation and loss) of forest ecosystems. Despite the ecological importance of forest-dwelling bats, species susceptible to white-nose syndrome (WNS) have been the primary focus of research efforts, particularly species federally listed as threatened or endangered. As species susceptible to WNS decline, forest-dwelling species considered non-susceptible to WNS become increasingly important to land managers because the loss of WNS susceptible species will likely influence other forest bats by altering niche roles. Knowing the spatial relationship between foraging areas and diurnal roosts of forest-dwelling bats is therefore imperative to the establishment of successful conservation initiatives.

Advancements in wildlife tracking technology, specifically the reduced size and mass of radio-transmitters, have allowed monitoring the spatio-temporal patterns of relatively small species (i.e., bats, songbirds, and insects). Although VHF transmitters have been successfully used for decades to monitor a variety of wildlife species, their use to study highly-mobile, nocturnal species such as bats is somewhat limited. More specifically, ephemeral roost-dependent species (i.e., tree-roosting species) are particularly difficult to monitor because of their ability to exploit numerous roosts throughout the landscape. Because of differences in energy strategies associated with reproduction and timing of reproductive processes between males and females during the summer (e.g., intersexual variation in torpor patterns), roost-site characteristics are sex-specific (Hamilton & Barclay 1994; Encarnção 2012). Similarly, foraging habits might be sex-specific. In recent decades, research addressing the foraging habits of forest bats has increased considerably; yet, small sample sizes have remained a limitation for inferences.

Among the bat species of Eastern North America, the evening bat (*Nycticeius humeralis*) is not susceptible to WNS and probably the only bat species (out of 16 in Arkansas) lacking documented fatalities at wind-turbine facilities, likely because they are low flyers. Though the species is not directly affected by these threats, the evening bat has faced historic population declines in the eastern United States (Boyles & Robbins 2006). As WNS and development of wind turbine facilities continue to decimate forest bat populations, non-susceptible species (i.e., evening bat) should be the focus of conservation initiatives as they may be among the few species present in the future. The majority of research directed toward this species has focused on identifying roosting requirements. Its spatial movements have been evaluated in a few studies (Clem 1993; Carter 1998; Duchamp et al. 2004; Morris et al. 2011), but small sample sizes have prohibited the evaluation of sex-specific foraging habits. In general, there is a paucity of knowledge on the spatiotemporal patterns of the evening bat, specifically at the species level and in landscapes managed for timber resources (Miller et al. 2003).

The evening bat is a small insectivorous species endemic to eastern North America. Evening bats obtain food in flight by aerial hawking small, flying insects (Lacki et al 2007). Primary food sources include small beetles, moths, and leafhoppers (Whitaker & Clem 1992). It exhibits biphasic foraging patterns, meaning foraging activity occurs for a few hours around dusk and dawn (Reid 2006). The first or primary foraging bout, of often multiple foraging trips, begins soon after sunset (Wilkinson 1992) with individuals foraging above the canopy and descending to sub-canopy areas with the progression of nightfall (Carter 1998). Time spent foraging is influenced by multiple factors (e.g., temperature, sex, reproductive status) but primary foraging bouts generally do not exceed 2.5 hours (Clem 1993). Foraging areas used by the evening bat include forest stands, agricultural areas, and along waterways.

Clem (1993) evaluated the foraging habits of female evening bats at a maternity roost in Indiana, primarily focusing on the duration, maximum distance flown to foraging areas, and number of nightly foraging bouts. Carter (1998) monitored the spatial movements of evening bats in bottomland hardwood forests of South Carolina and estimated home ranges for 6 evening bats (5 females & 1 male). Duchamp et al. (2004) estimated home ranges for 11 female evening bats in a rural, but developing area of Indiana. The most recent and thorough investigation of evening bat foraging habits was conducted in a pine-dominated region of Southwest Georgia (Morris et al. 2011). Similar to the study conducted in Indiana (Duchamp et al. 2004), the study conducted in Southwest Georgia obtained a small sample size (n=14), requiring the pooling of data between sexes. Additionally, all of the aforementioned studies were conducted in landscapes consisting of a mosaic of habitat types, none of which were located in the western periphery of the species range. Thus, sex-specific information on the spatiotemporal movements of the evening bat in forest-dominated landscapes has not been previously addressed. Although the spatial movements of the evening bat have been evaluated in these previous studies, small sample sizes have prohibited the evaluation of sex-specific foraging habits. Furthermore, the evening bat is a prime candidate for a sex-specific foraging study because the species is considered to be relatively slow-flying in comparison to other sympatric species of forest-dwelling bats; and the evening bat is abundant in Arkansas, increasing the likelihood of obtaining adequate sample sizes. In this study, I radio-tracked evening bats from an abundant population in Arkansas to (1) estimate foraging range size of evening bats, and (2) assess year- and sex-specific foraging patterns (i.e., in size and number of core foraging areas). I predicted that foraging range sizes would not be consistent with previous studies and that male and female evening bats would exhibit different foraging habits due to differences in the energetic requirements and constraints associated with reproduction. Additionally, I predicted that males and females would exhibit foraging-site fidelity.

METHODS

Study Area

I conducted my research in the USDA Forest Service's Sylamore Ranger District, Ozark National Forest, specifically within Baxter and Stone counties (Figure 2.1). The district is located in the Ozark Highlands Ecoregion of north-central Arkansas. The low-elevation district (50-800 m) is an intensively managed forest primarily consisting of oak-hickory dominated stands. Forest comprised the majority of the district (90%) with gravel roads, small wildlife openings, and recreational areas scattered throughout (10%). The forest-dominated landscape and karst geology support a diversity of bat species and other wildlife. From June 1 to August 15 2013 and 2014, average total precipitation for the Sylamore Ranger District was 2.21 cm and average maximum temperature was 30.2°C (NOAA 2015).

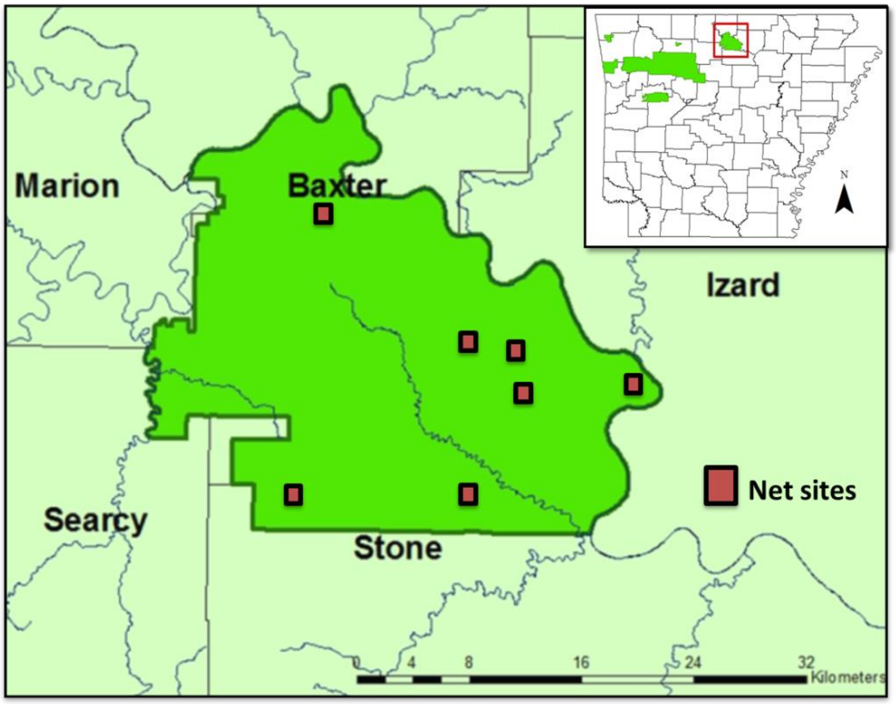

Figure 2.1. Location of net sites in the Sylamore Ranger District, Ozark National Forest.

Capturing and Tracking Bats

I captured evening bats during June, July, and August in 2013 and 2014 using triple-high and single-high mist nets placed strategically above, or in the vicinity of ponds and streams. Net site selection was based on water availability and accessibility. The following characteristics were recorded for all bat captures: sex, mass (g), relative age (juvenile or adult), forearm length (mm) and reproductive condition (females: non-reproductive (NR), pregnant (P), lactating (L), or post-lactating (PL); males: Scrotal (S) or non-reproductive (NR)). Additionally, I assessed the presence or absence of parasites, wing condition, and any physical abnormalities. I attached 0.33-g VHF transmitters (Model LB-2X, Holohil Ontario, Canada) to the back of male and female evening bats weighing ≥8 g using Perma-Type® or Skin Bond® surgical cement. To avoid additional stress, I did not attach transmitters to pregnant bats. To ensure transmitter adhesion, bats, once affixed with transmitters were held for 1-2 minutes before being released.

To avoid inhibiting foraging maneuverability, transmitter weight never exceeded 5% of the captured individual's body mass (Aldridge and Brigham 1988), and handling time never exceeded 15 minutes to minimize capture-related stress. Additionally, I did not start tracking until the following day to avoid monitoring abnormal behavior associated with capture-related stress. I radio-tagged and tracked 70 evening bats using Wildlife Materials TRX-1000s receivers and 5-element folding Yagi antennas. Bats were tracked daily to diurnal roosts and nightly during their initial foraging bout which began upon emergence and ended once all bats returned to their roosts. Bats were only monitored for approximately 3-7 days following capture and during the initial foraging bout, which lasted 1-3 hours per night. Although transmitters remained active for ~21 days, transmitter attachment to evening bats rarely exceeded 7 days. All methods and procedures were approved by the Arkansas State University Institutional Animal Care and Use Committee (IACUC protocol number: 451729-1).

Monitoring the spatial movements of nocturnal, flying mammals in steep mountainous terrain is physically demanding and logistically challenging. Therefore, to maximize tracking success, I attempted to locate diurnal roosts on a daily basis which aided in determining the best possible tracking stations. Stations were strategically positioned along roads and if possible located at the highest elevation points within the immediate tracking area. To estimate foraging locations, bats were located by 2-3 observers taking simultaneous bearings in no less than 2-minute intervals from pre-determined geo-referenced tracking stations. I attempted to use stations located at equal distances from other tracker locations to orient trackers in a triangle-like position around day roost locations; however, this was not always possible due to the lack of roads and trails in some areas. To obtain accurate bearings, orienteering methods include pointing the compass at a distant object, which is not always possible under night-time tracking conditions. To negate this problem, Yagi antennas were mounted to collapsible tripods giving trackers an object with which to align the compass as well as minimize accidental movement of the antenna. This method enabled us to obtain more accurate bearings, especially in low-light conditions. Due to the steep mountainous terrain and dense forest canopy, I was often unable to detect transmitter signals beyond 1 km. Similarly, the range of detection of the 2-way radios was frequently limited by aforementioned conditions which made coordinating simultaneous tracking of multiple bats increasingly difficult. One benefit of limited transmitter range is that the radio-tagged individuals from which we could obtain strong signals were often less than 500 m from tracker locations. Due to the close proximity of foraging bats to trackers, 2 bearings were sufficient for estimating foraging locations. To minimize tracker error, we only used 2 bearings to estimate an individual's location in the event that both trackers could obtain strong signals, and a third bearing could not be obtained. All location estimates were plotted using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

Data Analyses

To quantify the spatial movements of evening bats during their primary foraging bout, I used fixed kernel (FK) (Worton 1987) with least squares cross validation (LSCV) and minimum convex polygon (MCP) (Mohr 1947) methods. Independent locations are required to satisfy statistical assumption of kernel methods. Therefore, Morris and colleagues (2011) used locations that were a minimum of 30 minutes apart to meet this assumption of independence. However, the primary foraging bouts of evening bats rarely exceeded 120 minutes, so intervals of ≥30 minutes would result in only 3-4 locations per individual per night. Furthermore, complete removal of temporally-dependent locations (i.e., autocorrelated data) likely diminishes biologically relevant information, especially for data obtained at a constant time interval (De Solla et al. 1999). In another evening bat study, locations were deemed independent at intervals ≥4 minutes (Carter 1998). Evening bats in my study often traveled distances ≥1 km in less than 20 minutes, sometimes leaving the study area and foraging in adjacent hollows. Considering the time constraints at which individuals can be tracked, all bat locations ≥5 minutes apart from subsequent location estimates (3-5 minutes; Duchamp et al. 2004) were included in FK analyses. In addition to foraging locations, the capture and diurnal roost locations were included in analyses as one independent location each. All foraging range estimates were made with the default bandwidth settings and calculated in program R (R Core Team 2014) using the package "adehabitatHR" (Calenge 2006). Because radio-tracking data did not follow a normal distribution, a Wilcoxon rank sum test was used to compare 95% FK and 95% MCP foraging range estimates between sexes, as well as between years. All mean estimates are reported ± 1 SE and all median estimates are reported with first (Q1) and third (Q3) percentiles [Q1-Q3].

RESULTS

During summers 2013 and 2014, I captured 551 bats representing 11 species (*Eptesicus fuscus* [big brown bat; n = 42]; *Lasiurus borealis* [Eastern red bat; n = 133]; *Lasiurus cinereus* [hoary bat; n = 7]; *Lasiurus seminolus* [Seminole bat; n = 5] *Myotis grisescens* [gray bat; n = 16], *Myotis sodalis* [Indiana bat; n = 6]; *Myotis septentrionalis* [Northern long-eared bat; n = 157], *Myotis lucifugus* [little brown bat; n = 1]; *Myotis leibii* [Eastern small-footed bat; n = 1]; *Nycticeius humeralis* [evening bat; n = 165]; and *Perimyotis subflavus* [tricolored bat; n = 18]). I radio-tracked 70 of the 165 captured evening bats, obtaining sufficient number of independent locations (≥20) to estimate foraging range sizes of 24 (14 male & 10 female) evening bats.

Specifically, foraging ranges were estimated for 11 (9 male [3 scrotal; 6 non-reproductive] & 2 female [1 post-lactating; 1 non-reproductive]) and 13 (5 male [5 scrotal] & 8 female [3 lactating; 2 post-lactating; 3 non-reproductive]) evening bats during 2013 and 2014, respectively (Appendix A). Transmitter attachment varied substantially from 3-13 days with rain and extreme heat likely reducing duration of transmitter attachment. On one occurrence, 5 tagged bats all dropped transmitters on the same day, which occurred after a night of storms and substantial rainfall. Likewise, a similar event occurred to another group of 6 bats during a week of extreme heat (>34°C) and high levels of humidity.

The length of the first and primary foraging bout ranged from 47 to 144 minutes beginning approximately 30 min prior to sunset with some variation related to cloud cover and weather conditions. Individual evening bats used 1-7 core foraging areas ($\bar{x}= 1.8 \pm 0.3$; Figure 2.2). The medians for male (2.0 [1.0-2.75]) and female (1.0 [1.0-1.0]) core foraging areas during the combined summers 2013-2014 were significantly different ($W = 110$, $P < 0.01$).

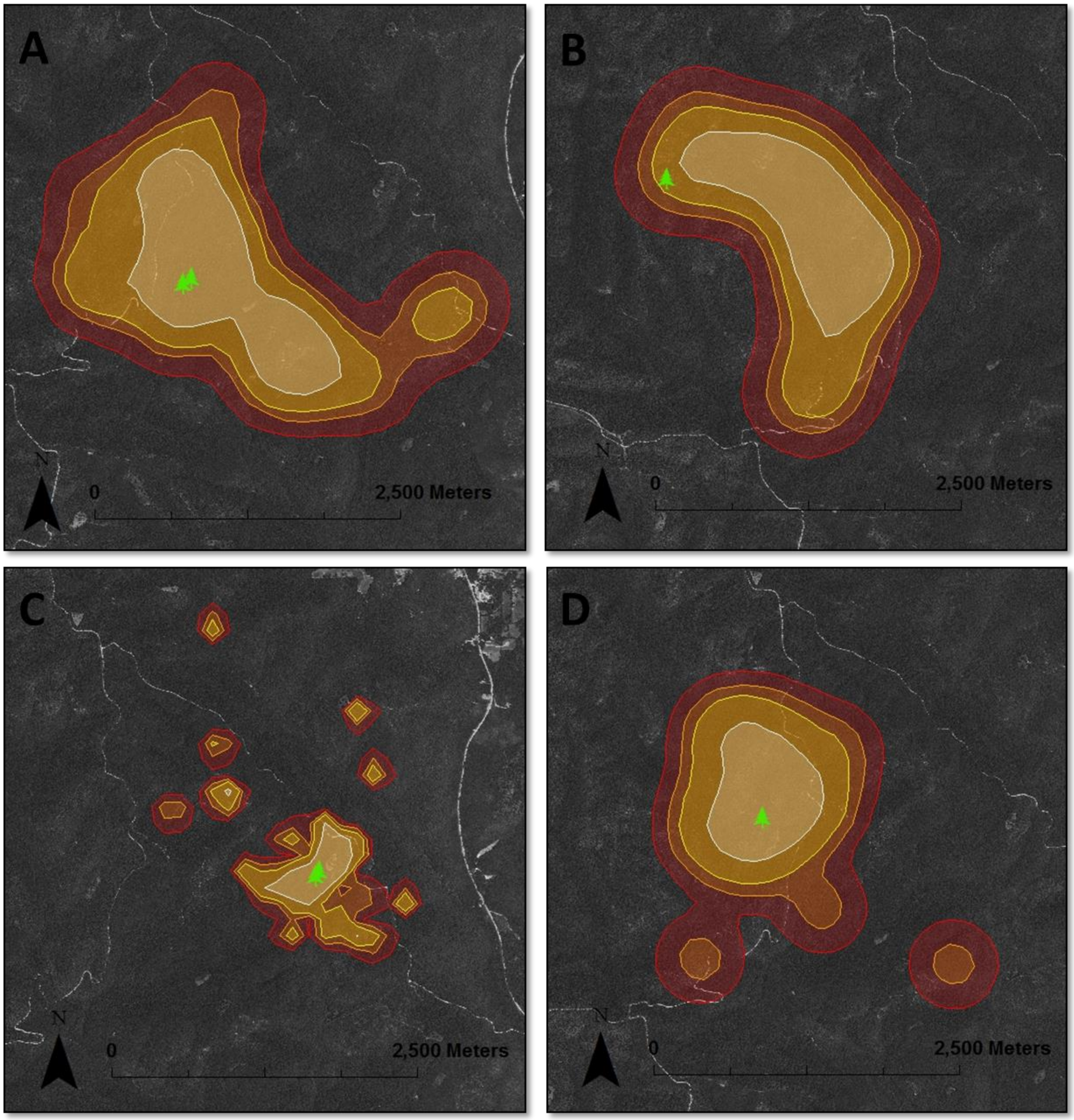

Figure 2.2. Fixed kernel foraging range of 4 representative evening bats tracked during summers 2013 and 2014 in the Sylamore Ranger District. Colored contours indicate from 50% (white) to 95% (red) of all foraging locations. Bats A (#014), C (#024), and D (#023) were males; bat B (#021) was female. Roost locations indicated by green tree icon. Individual variation in habitat use occurred among individuals with bats A and B having large continuous ranges, and bats C and D exploiting 3-7 core foraging areas. Map produced using ArcMap (ArcGIS Version 9.3).

Mean 95% FK foraging range size of evening bats was 548 ± 108 ha, with variability among individuals (from 48 ha to 2,239 ha; Appendix A), between sexes, and years (Table 2.1.).

Table 2.1. Mean 95% FK foraging range estimates for evening bats tracked during summers 2013 and 2014.

	95% FK					
	2013		**2014**		**Pooled**	
Male	305 ± 128 ha	n=9	380 ± 73 ha	n=5	332 ± 85 ha	n=14
Female	404 ± 132 ha	n=2	964 ± 230 ha	n=8	852 ± 198 ha	n=10
Both	323 ± 106 ha	n=11	739 ± 163 ha	n=13	548 ± 108 ha	n=24

The medians for male (202.0 ha, [109.6-400.8]) and female (556.4 ha, [497.7-1190.0]) 95% FK foraging ranges during the combined summers 2013-2014 were significantly different (W = 23, P = 0.005; Figure 2.3.A). The medians for male (363.4 ha, [354.7-413.3]) 95% FK foraging ranges were significantly smaller than female (615.8 ha, [543.2-13310.0]) 95% FK foraging ranges during summer 2014 (W = 4, P = 0.019; Figure 2.3.B). The medians for 95% FK foraging ranges for males and females combined was significantly larger in 2014 (550.6 ha, [413.3-669.2]) than in 2013 (163.2 ha, [100.8-403.5]; W = 29, P = 0.012; Figure 2.3.C).

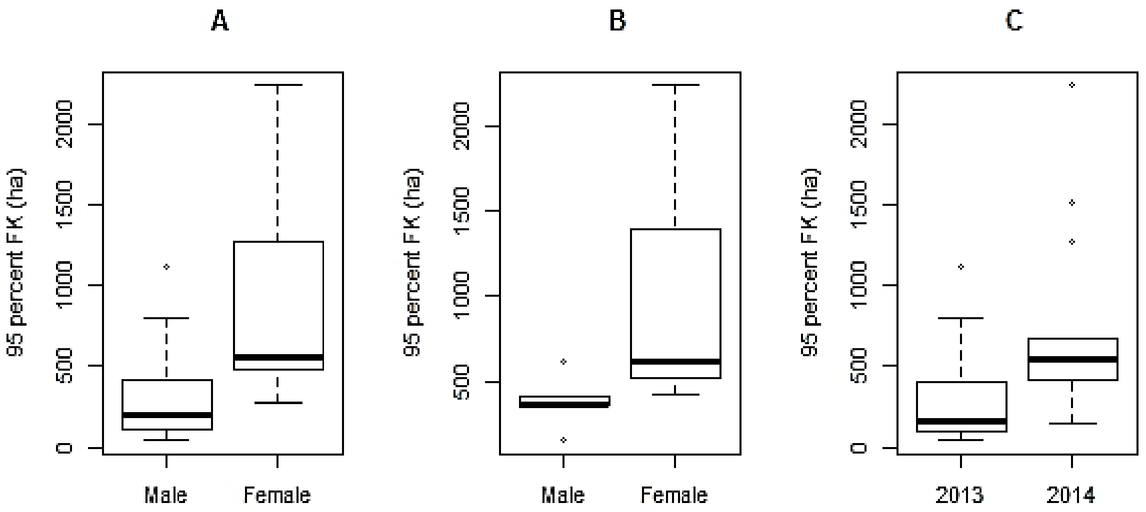

Figure 2.3. 95% FK foraging range estimates for (A) males and females during the combined summers 2013-2014, (B) males and females during summer 2014, and (C) both sexes during summers 2013-2014.

Mean 95% MCP foraging range of evening bats was 165 ± 38 ha, with variability among individuals (from 14 ha to 491 ha; Appendix A), between sexes, and years (Table 2.2.).

Table 2.2. Mean 95% MCP foraging range estimates for evening bats tracked during summers 2013 and 2014.

	95% MCP					
	2013		**2014**		**Pooled**	
Male	156 ± 59 ha	n=9	180 ± 26 ha	n=5	165 ± 38 ha	n=14
Female	130 ± 12 ha	n=2	273 ± 52 ha	n=8	244 ± 45 ha	n=10
Both	151 ± 48 ha	n=11	237 ± 35 ha	n=13	197 ± 30 ha	n=24

The median 95% MCP foraging range for females (194.4 ha, [13.5-328.8]) was not significantly different than for males (125.4 ha, [52.9-216.4]; W = 44, P = 0.138; Figure 2.4.A). No difference was detected between male (194.2 ha, [137.3-200.9]) and female (201.7 ha, [176.7-393.5]) 95% MCP foraging ranges during summer 2014 (W = 14, P = 0.44; Figure 2.4.B).

Median 95% MCP estimates were significantly larger in 2014 (197.6 ha, [137.3-259.9]) than 2013 (113.6 ha, [39.5-181.3]; W = 37, P = 0.047; Figure 2.4.C).

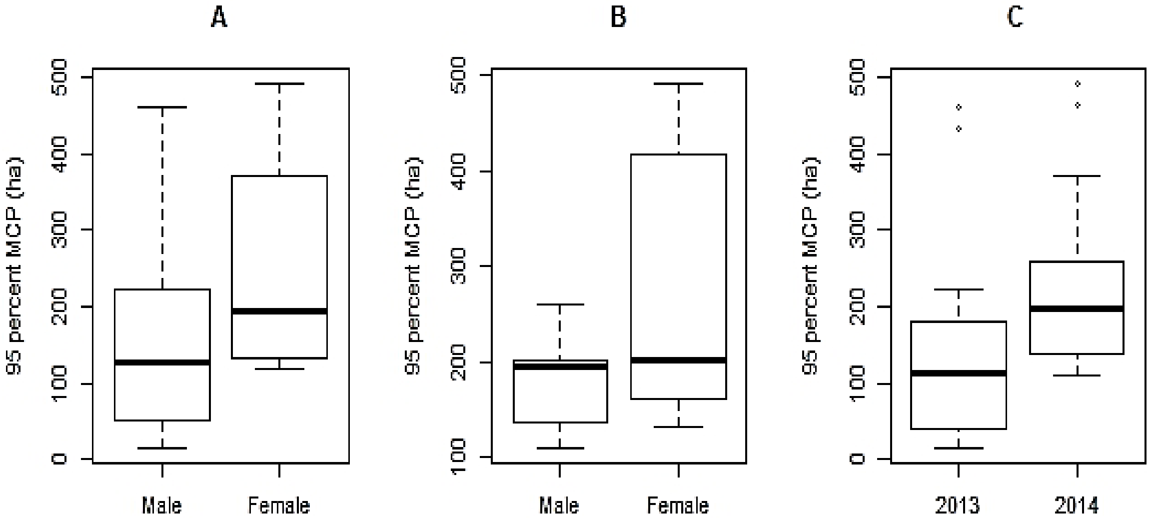

Figure 2.4. 95% MCP foraging range estimates for (A) male and females during summers 2013-2014, (B) males and females during summer 2014, and (C) 95% MCP foraging range estimates both sexes during summers 2013-2014.

The median 95% MCP foraging range for males during 2013 (59.2 ha, [27.5-221.6]) was not significantly different than for males during 2014 (194.2 ha, [137.3-200.9]; W = 15, P = 0.364; Figure 2.5.A). Similarly, median 95% FK foraging range for males during summer 2013 (123.7 ha, [96.7-240.8]]) and males during summer 2014 (363.4 ha, [354.7-413.3]) (W = 12, P = 0.190; Figure 2.5.B) was not significantly different. Though no difference was detected using either method, annual trends of FK and MCP range estimates were consistent between methods.

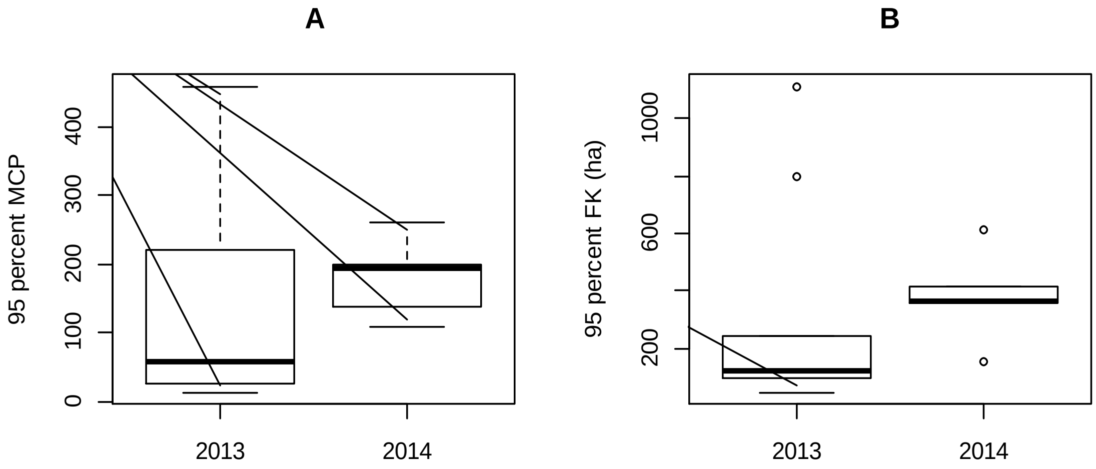

Figure 2.5. 95% MCP foraging range estimates for (A) males during summers 2013-2014, (B) and (B) 95% FK foraging range estimates for males during summers 2013-2014.

DISCUSSION

Understanding sex-specific habitat use and spatial requirements of forest bats is essential to the development of adequate forest management regimes, as they may necessitate sex-specific management approaches (Safi et al. 2007). Although a few studies have monitored the spatial movements of evening bats, none has thoroughly investigated differences between sexes (but see Morris et al. 2011). The present study represents the largest sample size of radio-tracked evening bats and the first to report differences in foraging habits between males and females in any bat species in the United States.

Sex-Specific Foraging Differences

The roosting habits of male and female evening bats differ during summer and likely reflect variations in physiological and behavioral pressures between sexes (Perry & Thill 2008).

Because male and female evening bats have different energetic requirements, specifically those associated with female reproduction and rearing pups, these differences should also be present in their foraging habits. As predicted, there were differences in the space-use patterns of male and female evening bats using the FK method (Appendix B), which were not detected by Morris et al. (2011) likely due to a small sample size (n=14; 5 females & 9 males) and inconsistent sampling among months.

Despite being considered a habitat generalist, specifically due to plasticity in roosting (Menzel et al. 2001) and foraging habits (Morris et al. 2011), evening bats might not be generalists in their foraging habits or diets. In my study, evening bats used multiple core foraging areas, which was in agreement with Morris et al. (2011). This foraging behavior suggests that these bats may forage for specific resources that may not be evenly distributed in the habitat. However, the number of core foraging areas differed between sexes, with males exploiting more core areas than females. This highlights sex-specific foraging habits that might be influenced by several factors (e.g., roost availability, insect abundance, inter-or intra-specific competition, distance to water, reproductive status). The relative role of these factors, in each sex, remains to be tested.

Previous studies (see Carter 1998; Duchamp et al. 2005; Morris et al. 2011) estimated foraging ranges via the Adaptive Kernel (AK) method. Further, Morris et al. (2011) compared AK foraging range estimates across studies and found that foraging range estimates were similar across studies. I employed the fixed kernel (FK) method with least squares cross validation as it provides more accurate and precise estimates than adaptive kernel methods (Seaman & Powell 1996). Because I did not use the AK method, the results from my study are not comparable to estimates provided by Carter (1998). However, generally speaking FK foraging ranges in this study are in the range of previously reported AK ranges. Although the FK method is preferred over other home range estimators such as MCP, FK estimates cannot be compared across studies (Harris et al. 1990). Therefore, I also employed the MCP method for comparative purposes. Based on 95% MCP estimates, foraging range of evening bats was 118.5 ha (n=14) in southwest Georgia (Morris et al. 2011) and 303.7 ha (n=11) in Indiana (Duchamp et al. 2004). Mean 95% MCP foraging range estimates in Arkansas (197 ± 30; n=24; my study) exceeded those of Morris et al. (2011) but were lower than those of Duchamp et al. (2004). These differences may reflect variation in bat community structure, habitat availability, and resource abundance at each study area. More specifically, the study conducted in Indiana occurred in an urban-rural landscape, i.e., predominantly rural and undergoing rapid housing development, differing in foraging habitat availability and quality from the more forested site in Southwest Georgia. Duchamp et al. (2004) found that evening bats foraged in a predictable direction from roosts, all of which were located in small, adjacent groups of wooded areas, and suggest that this directional preference is likely due to limited availability of quality foraging areas. Further, evening bats in Indiana avoided traversing large tracts of urban development to reach more suitable foraging habitat (Duchamp et al. 2004). In contrast, the availability of forest habitat of Southwest Georgia, albeit fragmented and pine-dominated, exceeded that of the urban-rural landscape in Indiana. Additionally, the study site in Southwest Georgia had substantially less urban development than Indiana. The Sylamore Ranger District was characterized by homogenous forest stands which spanned across a large tract of land and differed from the study site in Georgia where forested habitat was less widespread and expansive than in the Sylamore Ranger District. Specifically, the amount of forested area available at my study site was nearly five times the Southwest Georgia study site.

Although female evening bats used fewer core areas than males, they exploited a larger range during the combined summers 2013-2014. The present study is the first to investigate and show sex-specific foraging habits in a bat species in the U.S., but similar patterns have been documented worldwide in long-legged bats (*Macrophyllum macrophyllum*; Meyer et al. 2005) in Panama and western barbastelle bats (*Barbastella barbastellus*; Hillen et al. 2011) in Germany. Home ranges for females were larger than for males; however, this difference was not significant for *M. macrophyllum*. On the contrary, for Daubenton's bat (*Myotis daubentonii*; Encarnção 2012) in Germany and the big brown bat (*Eptesicus* fuscus; Wilkinson & Barclay 1997) in British Columbia, males had larger home ranges than females. Additional differences between sexes have been detected: males of the brown long-eared bat (*Plecotus auritus*; Entwistle et al. 1996) in Scotland selected foraging areas further from roost locations than females and male parti-colored bats (*Vespertilio murinus*; Safi et al. 2007) in Switzerland exhibited more flexibility in habitat use than females. Thus, there is no clear pattern across species and this might be because ecological, morphological, and behavioral differences exist among species (Safi et al. 2007). Also, habitat varies among regions, and differences between sexes may be region-specific.

Confounding Factors and Limitations

Variation in methodologies may have been contributing factors to differences among evening bat studies. For example, location sampling intervals, times to independence, sample sizes, and home range estimator used in analyses vary among studies. Specifically, Morris et al. (2011) used 20 random, independent locations to estimate AK foraging ranges for 14 bats, whereas my study estimated FK foraging ranges for 24 individuals with ≥20 independent locations. Additionally, the various software packages used for spatial analyses can yield different results (Lawson & Rodgers 1997), especially if analyses do not use identical parameters. For this reason, it is difficult to compare home range estimates across studies, even those that use identical analytical methods. Although the results of my study are representative of two study seasons, both of the previously mentioned studies (i.e., Duchamp et al. 2004; Morris et al. 2011) monitored evening bats for only one study season.

Differences between years could have been caused by sampling bias, specifically the larger number of females captured in 2014. Because females consistently had larger foraging ranges than males and estimates in 2014 were larger than in 2013, a large sample of females may have produced erroneous results. However, another likely explanation could be found in weather conditions with summer 2013 being hotter than in 2014. The male home range comparisons between years, although not significant, do indicate a trend for a foraging range larger in 2014 than in 2013.

Inter-annual variation in summer weather conditions might explain differences in foraging range between years in my study but also among studies. The total precipitation for the Sylamore Ranger District from June 1 to August 15 was 2.39 cm in 2013 and 2.03 cm in 2014. The total number of days that maximum temperatures exceeded 32.2°C was 25 in 2013 and 12 in 2014 (NOAA 2015). Hot summer conditions and limited water availability during summer 2013, likely due to increased evaporation rates, may have constricted the spatial movements of foraging bats to areas with lasting water sources whereas bats could rely on other more ephemeral bodies of water (i.e., ponds and small streams) in the wetter summer season of 2014. Previous studies did not report weather conditions or water availability. However, summer weather patterns influenced water availability, which likely affected bat habitat use, specifically the extent of their home ranges. For that reason, future research should address the effects of weather conditions and water availability on bat foraging habits to allow more sensible comparisons across studies. However, these endeavors should be given careful consideration: there are serious limitations for addressing water availability-related questions, especially in areas where water is ephemeral. For example, thorough evaluation of foraging ranges and distance to water sources requires knowledge of all available water during the entirety of the study.

The length of the initial foraging bout was consistent with the findings of three previous studies (Wilkinson 1992; Clem 1993; and Duchamp et al. 2004), with cloud cover and other weather factors influencing the start time. Evening bats, specifically lactating females, have been shown to exhibit bimodal foraging behavior, or subsequent foraging bouts which are often of much shorter duration than the initial foraging bout (Clem 1993); however, it is unknown whether males exhibit similar foraging habits. Because locating roosts and monitoring initial foraging bouts extensively drained receivers which required a minimum 4-5 hours of charge per hour of use, monitoring secondary foraging bouts was essentially unfeasible.

It is unclear why estimates of foraging range are different among evening bat studies. Confounding factors possibly contributing to sex-specific foraging habits include differences in parental investment of males and females (Safi et al. 2007), energetic requirements and social behavior (Encarnção 2012), intraspecific competition (Meyer et al. 2005), landscape type, population density and bat guild diversity. Although I obtained a larger sample size than in previous studies, sampling was not uniform among years or months, and it was still too small to test for the effects of reproductive status and age (i.e., adult vs. juveniles) on foraging range. Also, I could not test for differences between sexes during 2013 due to an insufficient number of females. The larger foraging range of females may reflect increased energetic needs associated with reproduction, especially when many females are pregnant or rearing young during May, June and July. Both Duchamp et al. (2004) and Morris et al. (2011) found that foraging ranges increased in August, and this behavior is thought to be associated with males becoming reproductively active; yet, it remains unknown if females exhibit a similar pattern.

Limitations (e.g., limited roads, steep terrain, and dense forest canopy) prevented the continuous tracking of individuals. Likewise, the movements of bats and the variables that influence these movements are difficult to predict; therefore, numerous foraging locations were taken opportunistically. Because bats commonly traveled to areas in which tracking was not possible (i.e., adjacent hollows), foraging range estimates, especially MCP, are likely conservative. Average linear error for location estimates was approximately 8 degrees, resulting in an estimated linear error of 140 m at 1 km (Fuller et al. 2005).

Conclusions

In conclusion, I detected differences in foraging ranges and use of core areas between males and females which supports my prediction that sex-specific foraging habits exist, and highlights the need to not neglect these differences in future studies of bats in the United States. Hereafter, I provide several recommendations. First, studies which pool data between sexes should interpret results with caution, as they may mask biologically relevant information specific to males or females. Second, future studies should exert more effort on obtaining larger sample sizes, preferably with uniform sampling among months and years. Third, effort on obtaining larger sample sizes should not only be expended to evaluate differences between sexes, but also to make comparisons among bats of different reproductive stages and ages. During my study, females were particularly difficult to capture in comparison to males. Increased effort of mist-netting at creeks than ponds could result in a much larger number of evening bat captures, increasing the female sample size (refer to Chapter IV for capture comparison at ponds and creeks). Alternatively, to increase female sample size, one could track radio-tagged females to maternity roosts; and strategically place mist-nets around these roosts. However, this approach needs to be assessed because it may result in pseudoreplication, especially if females from the same roost tend to always share the same roost.

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CHAPTER III

SEX-SPECIFIC ROOST CHARACTERISTICS OF THE EVENING BAT (*NYCTICEIUS HUMERALIS*) IN THE OZARK REGION OF NORTH-CENTRAL ARKANSAS

ABSTRACT

Roosting ecology is a top priority research topic and identifying sex-specific roosting requirements is crucial to develop appropriate habitat management plans. Here, I assessed sex-specific roost and habitat differences at 72 diurnal roost plots in the Ozark National Forest, Sylamore Ranger District in north-central Arkansas during June through August, 2013-2014, using 50 radio-tracked evening bats. Though the roosting ecology of the evening bat has been evaluated in a variety of landscapes, this study is the first to evaluate inter-sexual variation in roost-site selection at roost and plot levels. No differences were detected in variables at the roost-level between sexes. No differences were detected between roost and random plot variables for males or females. At the roost plot scale, males selected roost sites with a higher canopy cover and larger basal area than females, and males roosted at lower elevations. Additional research is needed to determine sex-specific habitat requirements in other species to insure management regimes provide adequate roosting habitat for both males and females in a community of forest-dwelling bats.

INTRODUCTION

Summer day roosts, also known as diurnal roosts, are resources critical to the fitness and survival of ephemeral-roosting and cave-dwelling forest bats (Kunz 1982). Alteration of forests for human development and resource exploitation influences roost abundance and distribution. Roost availability affects bat habitat use and lack of suitable roosts can be a limiting factor for bat populations (Fenton 1997). Although the summer roosting habits of forest bats generally vary among species, selection of diurnal roosts exploited during summer overlap among sympatric species (Timpone et al. 2010), which can be both common (e.g., evening bat) and imperiled (e.g., Indiana bat) species selecting similar roosts or roosts in areas with similar habitat characteristics. Although some forest-dwelling species use permanent roosts (i.e., caves, mines, bridges, and rock crevices) for all or part of their annual life cycles, ~75% of species endemic to eastern North America use ephemeral roosts (e.g., live trees, leaf litter, snags) for all or part of their annual life cycles. Many ephemeral-roosting species exploit numerous roosts over relatively short periods, some of which exhibit roost-switching every 1-2 days (e.g., evening bat; Hein et al. 2009). Although some strictly cave-obligate species (e.g., gray bat) exhibit similar habits, suitable roost sites for cave-obligate species are often more limited in availability deeming the roosting habits of these species relatively predictable, more so than ephemeral-roost-dependent species (Hutchinson & Lacki 2000). As a result, locating roost sites and identifying roost-site characteristics for ephemeral-roost-dependent species can be particularly difficult and bat conservation initiatives have placed much emphasis on evaluating the roosting habits of forest-dwelling species. For example, Bat Conservation International and Arkansas Game and Fish Commission have deemed the roosting ecology of Rafinesque’s big-eared bats and Southeastern Myotis top priority for research efforts in 2015 (BCI 2015). Likewise, the U.S. Fish and Wildlife

Service and USDA Forest Service continue to fund research and inventory endeavors focused on identifying and conserving roosting habitat for the Indiana bat (USFWS 2007).

For some imperiled species, ephemeral roosts serve as primary roost sites during summer, and the loss of such species may increase roosting habitat for non-imperiled sympatric species. With research efforts focused toward evaluating the roosting habits of imperiled species, many of which roost in caves or similar permanent roosts during part of their life cycles, non-imperiled species that are comparatively abundant often receive less research attention. Though the effects are largely unknown, the loss of imperiled species may affect sympatric species. For example, the extirpation of one species could allow other sympatric species to expand or reduce their niches which could alter ecosystem dynamics. Because imperiled species are often less abundant, using non-imperiled species might serve as better candidates for identifying quality roosting habitat. Likewise, studying species in locations where they are abundant would provide a more thorough understanding of roosting habits than in areas where they are scarce.

Among these ephemeral-roost-dependent species, the evening bat (*Nycticeius humeralis*) is a small insectivore endemic to the eastern U.S. (Watkins 1972; Reid 2006). Although the species is considered abundant throughout the western portions of its range, specifically Arkansas and Missouri, many populations throughout much of the eastern United States have faced declines in recent decades (Boyles & Robbins 2006). These declines are largely due to changes in habitat availability; specifically anthropogenic factors such as destruction of habitat for human development and agriculture.

The roosting habits of the evening bat have been evaluated for individuals using natural roosts, such as trees (Menzel et al. 2001; Boyles & Robbins 2006; Miles et al. 2006; Timpone et al. 2006; Perry & Thill 2008; Hein et al. 2009), and for maternity colonies using man-made structures (Watkins & Shump 1981). During summer, females aggregate into maternity colonies while males remain solitary. It is hypothesized that solitary males have different energy requirements than females (Hein et al. 2009), enabling them to be less selective than females. Moreover, since roost-site selection varies between sexes, landscapes comprised of homogenous habitat may not be equally beneficial to both male and female forest bats. Because both males and females rely on ephemeral roosts, it is hypothesized that promoting a heterogeneous forest landscape, dominated by mature trees (Hein et al. 2009) will likely provide both sexes with better quality roosting habitat than homogenous forest stands (Miles et al. 2006).

There is a need to determine sex-specific habitat requirements (Hein et al. 2009) of individual species (i.e., evening bats) roosting habits (Patriquin & Barclay 2003) and entire bat communities (Murphy et al. 2012). In this study, I radio-tracked evening bats in north-central Arkansas during summers 2013 and 2014 to (1) determine roost characteristics for male and female evening bats and (2) assess sex-specific roost characteristics. I predicted that male and female evening bats would select roosts based on specific characteristics and that these characteristics would differ between sexes, females being more selective than males.

METHODS

Study species

Evening bats roost in Spanish moss (*Tillandsia usneoides* (L.) L.)(Jennings 1958); underneath the exfoliating bark of mature trees (Menzel et al. 1999); within snags (Watkins 1972; Boyles & Robbins 2006) and vacant man-made structures (Watkins 1972). During summer, male and female evening bats select diurnal roosts independent of each other with males remaining solitary and reproductively-active females aggregating into maternity colonies

(Miles et al. 2006; Hein et al. 2009). Forked-top, also called bifurcated trees, are commonly used by reproductively-active female evening bats (Menzel et al. 1999; Miles et al. 2006; Hein et al. 2009). Additionally, two studies reported an adult male evening bat using an underground roost in Missouri during winter (Boyles et al. 2005) and in Arkansas during summer (Perry & Thill 2008).

Study area

The study area is located at the USDA Forest Service's Sylamore Ranger District, Ozark National Forest, approximately 10 km northwest of Mountain View, Arkansas (Figure 1.1). The district is composed of homogenous forest stands which span approximately 53,000 hectares, and encompasses the counties of Stone, Searcy, Marion, Baxter, and Izard in the Ozark Highlands Ecoregion of north-central Arkansas. The low-elevation district (50-800 m) is composed of intensively managed hardwood and pine forests, and characterized by steep, mountainous slopes consisting of limestone and sandstone ridges. The Sylamore Ranger District is primarily comprised of oak (*Quercus*) and hickory *(Carya)* forest stands. The area is managed via selective timber harvest and prescribed fire; and supports a highly-diverse guild of 16 bat species, 3 of which (i.e., Indiana bat, gray bat, and Ozark big-eared bat) are federally listed as endangered. From June 1 to August 15 2013 and 2014, average total precipitation for the Sylamore Ranger District was 221 mm and average maximum temperature was 30.2°C (NOAA 2015).

Capturing and tracking bats

I captured bats during June, July and August in 2013 and 2014 at various sites throughout the Sylamore Ranger District using mist-nets, both triple-high and single-high applications

(Figure 2.1). I placed mist-nets in sites suspected of abundant bat activity (e.g., trails, logging roads, near ponds, and above streams) to increase the likelihood of capturing evening bats. For each capture, measurements were recorded and transmitters attached to bats ≥8 g. For more details, refer to the Methods section of Chapter II. Bats were tracked to diurnal roost sites via the homing method using Wildlife Materials TRX-1000s receivers and 5-element folding Yagi antennas. I tracked bats to diurnal roosts each subsequent day following capture. Of the 70 radio-tagged evening bats, only 50 individuals were successfully tracked to at least one roost tree. I marked roost tree locations using a Garmin Map 62Stc GPS unit.

All suspected roost trees were identified to genus. For all roosts, I measured roost DBH (diameter at breast height) using metric fabric tape; estimated roost height (m) using a clinometer; and assessed roost condition (i.e., decay stage) identical to that of previous evening bat study (Table 3.1; Boyles & Robbins 2006). Additionally, I characterized 7 habitat variables in a 17.8-m radius or 0.1-ha plot surrounding each roost using similar criteria established in 2 previous evening bat studies (Boyles and Robbins 2006; Perry and Thill 2008). Specifically, for each roost plot, I estimated canopy cover (%) using a densiometer at 4 different locations equally spaced along the periphery of the plot; counted the number of small woody stems (SWS) >1 m tall and <5 cm DBH and number of large woody stems (LWS) >1 m tall and ≥5 cm DBH; estimated basal area (m^2/ha) using a forestry prism; and counted the number of snags. Additionally, I recorded relative overstory height in relation to the roost (1 = roost >1 m below surrounding canopy; 2 = roost height equivalent to surrounding canopy; 3 = roost >1 m above surrounding canopy) and classified roost decay stage (Table 3.1).

Table 3.1. Tree decay stages and description used to characterize evening bat day roosts. The following table was modified from Boyles & Robbins (2006).

Decay stage	Roost description	Bark remaining
1	Live tree	>75%
2	Dying or partially dead	75-50%
3	Mostly dead	50-25%
4	Dead	<25%

For each roost plot, I characterized a random paired plot (0.10 ha in radius as well) which was located ≥40 m away but not exceeding 100 m from the center of the roost plot. Random plot locations were derived using a random numbers table to generate both a distance (m) and bearing from the roost plot. I recorded the location of the random plots and characterized the same 7 habitat variables as for the roost plots. Because the orientation of roosts entrances could not be assessed visually, ArcMap (ArcGIS Version 9.3) was used to extract aspect and slope data from roost plot locations.

Data analyses

For both males and females, I determined factors influencing diurnal-roost selection by comparing habitat variables measured at roost and random paired plots (i.e., canopy cover, number of LWS, number of SWS, basal area, and number of snags) with Wilcoxon signed-rank tests. To determine differences between male and female roost characteristics, DBH, roost height, canopy cover, number of LWS, number of SWS, basal area, and number of snags were compared between male and female roost plots using Wilcoxon rank-sum test. A generalized Fisher’s exact test was used to test for differences in male and female roost conditions and relative overstory height. To determine differences among roost conditions and relative overstory height, data were pooled between sexes and years and analyzed using a G-test. Roost plot slope and aspect was converted from angular to circular data and compared between sexes using MANOVA. All analyses were conducted using program R (R Core Team 2014) and results were reported as medians with IQR and means ($\bar{x}$) ± S.E (α=0.05).

RESULTS

Captures

During June, July and August 2013 and 2014, I captured 551 bats representing 11 species (See chapter II for additional details). Of the 165 captured evening bats, 50 evening bats were successfully radio-tracked to 72 roosts during June, July and August 2013-2014. Specifically, I tracked 32 males to 57 roosts and 18 females to 15 roosts (Appendix C). Males often exploited numerous roosts enabling a larger sample size than females. In contrast, no females exploited more than one roost during my study, and on 2 occasions, multiple radio-tagged females used the same roost, hence the higher number of females fitted with transmitters than number of roosts. Although transmitter battery life was 21 days, transmitter attachment ranged from 3-13 days with weather conditions influencing the span of transmitter adherence.

Number and species of roost trees

Evening bats in the Sylamore Ranger District selected roosts belonging to 7 tree genera, with males exhibiting more plasticity in roost selection than females. Both males and females selected roosts belonging to the genus *Quercus* more than any other genus (Table 3.2). Roost types included snags and live trees. Females often selected snags or live trees that were forked-top while males roosted in snags and under exfoliating bark of live and dead trees. Male evening bats commonly switched roosts every 1-3 days with individuals exploiting 1-4 roosts ($\bar{x}$ = 1.7 ± 0.1). In contrast, females did not exhibit roost-switching and only used one roost each for the duration of the study.

Table 3.2. Total number of diurnal roosts used by males and females per genus during June-August, 2013 and 2014.

Genus	Male	Female
Cornus	0	1
Fraxinus	1	0
Juniperus	1	0
Carya	6	2
Quercus	34	10
Pinus	7	2
Sassafras	4	0
Unknown	4	0

Roost tree variables

No differences were detected between male and female roost for DBH and roost height (Table 3.3; Figure 3.1).

Table 3.3. Means, standard errors (SE), and medians of 3 variables measured at 72 roosts in the Sylamore Ranger District during June-August, 2013 and 2014.

	Male roost (*n* = 57)			Female roost (*n* = 15)			Wilcoxon test	
Variable	$\bar{x}$	SE	Mdn	$\bar{x}$	SE	Mdn	*V*	*P*
DBH (cm)	28.3	1.8	25.5	32.6	3.2	34.0	326.5	0.163
Roost height (m)	13.1	0.8	12.8	13.0	1.5	13.5	421.5	0.939

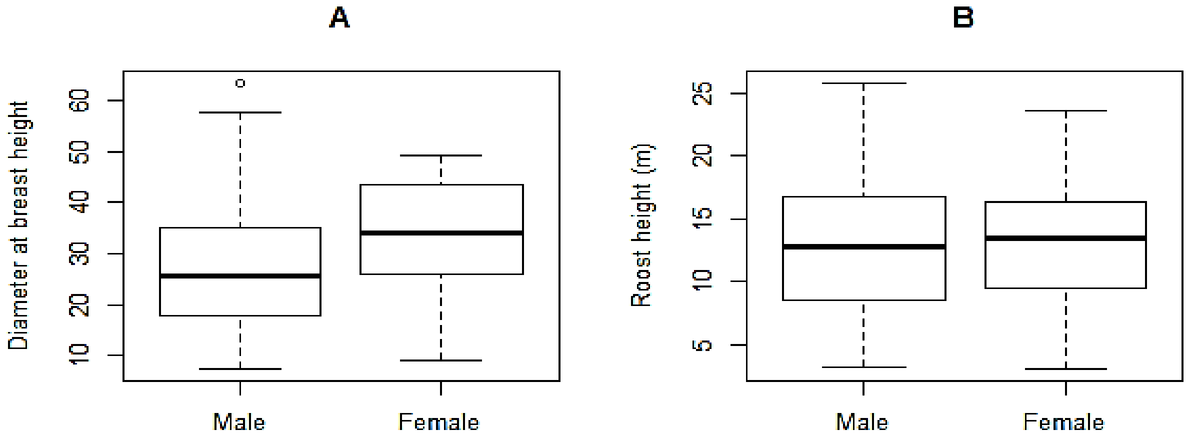

Figure 3.1. Comparison of 2 roost variables DBH (cm) and roost height (m) measured at 72 roosts (57 and 15 for males and females, respectively) in the Sylamore Ranger District during June-August, 2013 and 2014.

No difference in roost decay stage was detected between sexes (df = 3; P = 0.138; Figure 3.2.A). Evening bats used stage 1 (live) roosts more significantly than other decay stages and used stage 4 (dead) roosts less than any other stage (G_3= 61.9, P < 0.001; Figure 3.2.B).

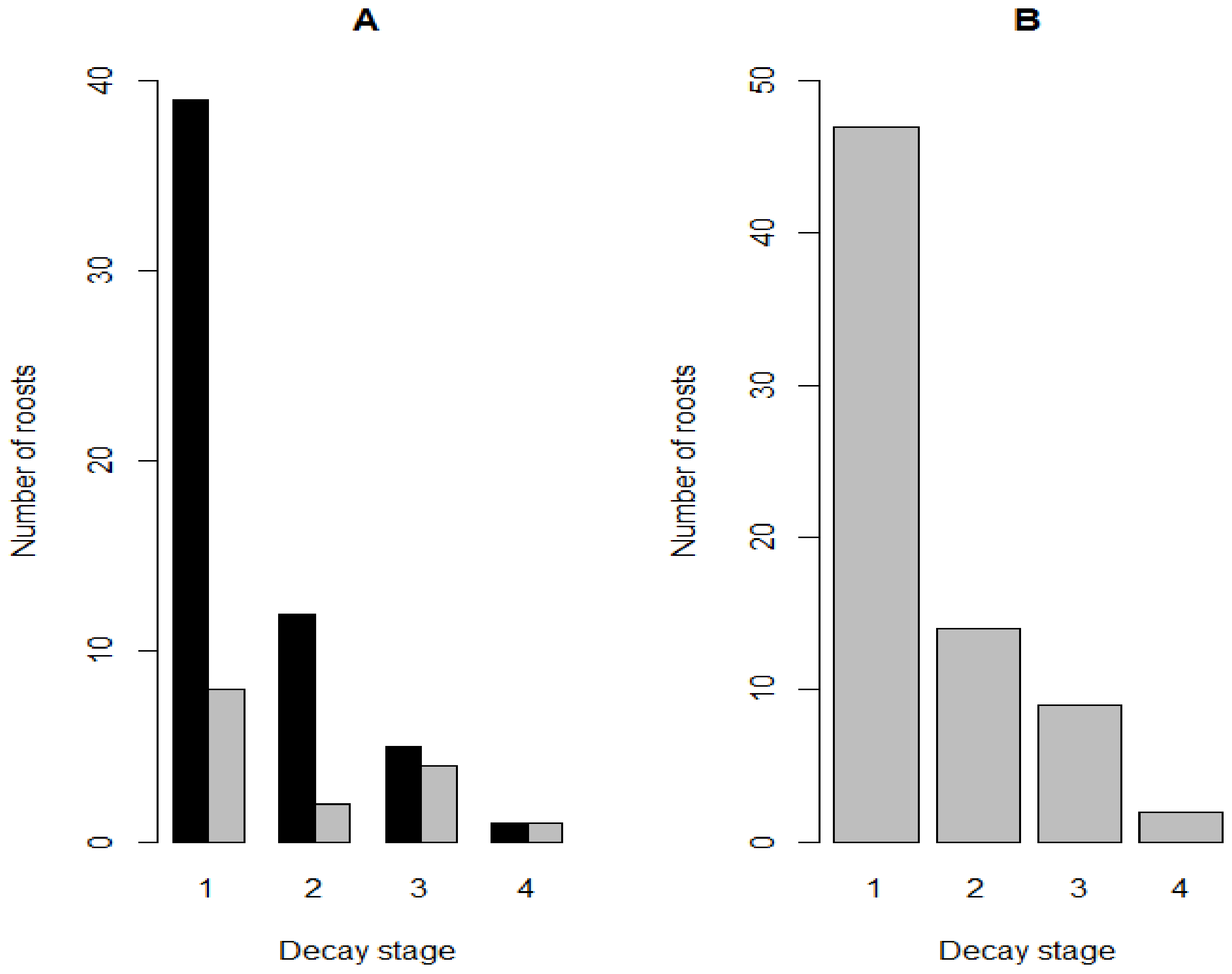

Figure 3.2. Number of roosts per decay stage (i.e., roost condition) by sex (A) and sexes pooled (B) roosts in the Sylamore Ranger District during June, July and August, 2013 and 2014. Decay stages are as follows: (1) = live tree, >75% bark remaining; (2) = dying or partially dead, 50-75% bark remaining; (3) = mostly dead, 25-50% bark remaining, and (4) = dead, <25% bark remaining.

Plot variables

No differences were detected for any of the tested plot variables between roosts and random paired plots for males (Table 3.4.A; Figure 3.3) or females (Table 3.4.B; Figure 3.4).

Table 3.4. Habitat characteristics of male (A) and female (B) evening bat roost and random paired plots in the Sylamore Ranger District during June-August, 2013 and 2014.

(A) Males

	Roost (n = 57)			Random (n = 57)			Wilcoxon test	
Plot Variable	$\bar{x}$	SE	Mdn	$\bar{x}$	SE	Mdn	V	P
Canopy cover (%)	83.0	1.4	86.2	78.8	1.8	82.5	1054.0	0.071
Large woody stems	67.8	5.8	59.0	63.6	4.9	57.0	883.5	0.653
Small woody stems	64.4	3.7	63.0	56.8	3.3	55.0	1101.0	0.143
Basal area (m^2/ha)	117.0	4.4	115.0	104.7	4.4	105.0	934.0	0.053
Snags	7.7	0.6	7.0	6.5	0.5	6.0	881.5	0.232

(B) Females

	Roost (n = 15)			Random (n = 15)			Wilcoxon test	
Plot Variable	$\bar{x}$	SE	Mdn	$\bar{x}$	SE	Mdn	V	P
Canopy cover (%)	71.4	5.0	79.2	77.4	3.3	79.0	40.0	0.276
Large woody stems	83.9	14.9	97.0	83.5	19.6	58.0	57.0	0.887
Small woody stems	62.8	6.5	65.0	62.1	7.4	60.0	59.5	1.000
Basal area (m^2/ha)	84.0	7.7	85.0	98.7	7.3	100.0	36.5	0.189
Snags	8.7	1.3	7.0	7.7	1.0	7.0	65.5	0.430

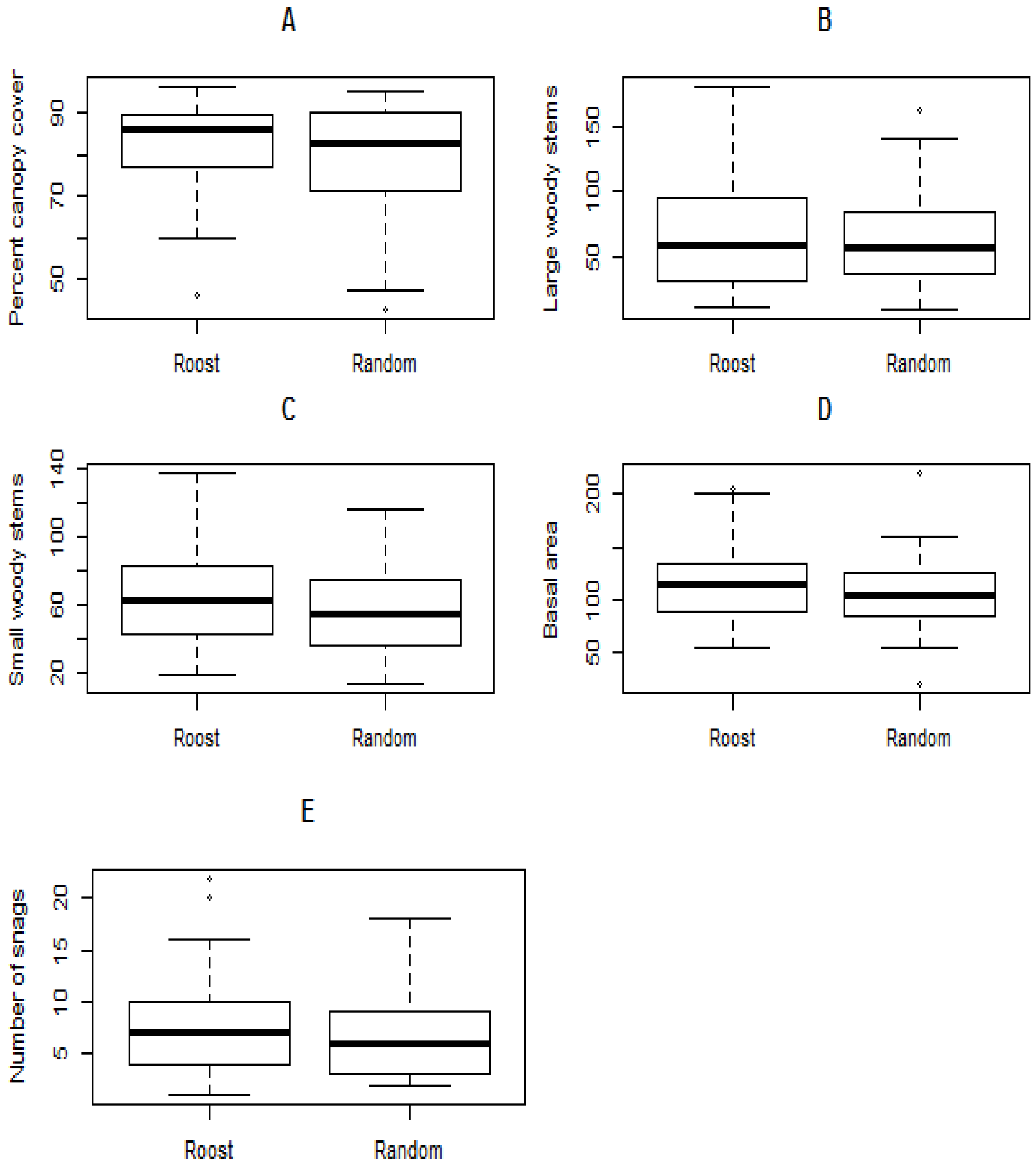

Figure 3.3. Male roost-site selection, (A) percent canopy cover, (B) number of LWS, (C) number of SWS, (D) basal area, and (E) number of snags measured at 57 male roost and random paired plots in the Sylamore Ranger District during June-August, 2013 and 2014.

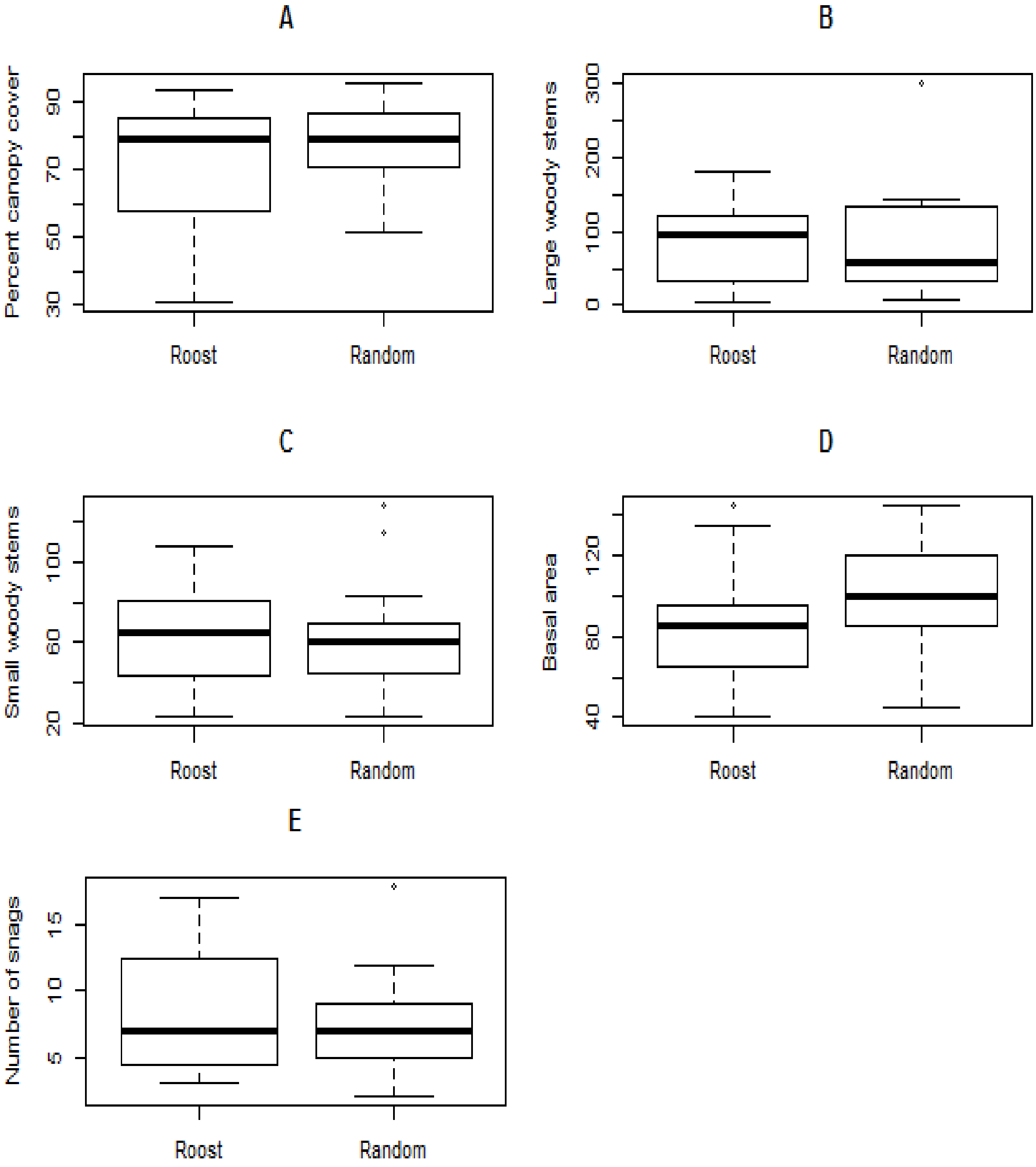

Figure 3.4. Female roost-site selection, (A) percent canopy cover, (B) number of LWS, (C) number of SWS, (D) basal area, and (E) number of snags measured at 15 female roost and random plots in the Sylamore Ranger District June-August, 2013 and 2014.

There was no significant difference in median number of LWS, SWS, and snags between male and female roost plots, but medians for canopy cover and basal area were significantly higher at male than female roost plots. Median for male roost elevation was significantly lower than females (Table 3.5; Figure 3.5).

Table 3.5. Means, standard errors (SE), and medians of 6 habitat variables measured at 72 roost plots in the Sylamore Ranger District during June-August, 2013 and 2014.

	Male Plot (n = 57)			Female Plot (n = 15)			Wilcoxon test	
Variable	$\bar{x}$	SE	Mdn	$\bar{x}$	SE	Mdn	V	P
Canopy cover (%)	83.0	1.4	86.2	71.4	5.0	79.2	588.0	0.026
Large woody stems	67.8	5.8	59.0	83.9	14.9	97.0	367.5	0.409
Small woody stems	64.4	3.7	63.0	62.8	6.5	65.0	435.0	0.922
Basal area (m^2/ha)	117.0	4.4	115.0	84.0	7.7	85.0	667.0	<0.001
Snags	7.7	0.6	7.0	8.7	1.3	7.0	380.5	0.517
Elevation (m)	235.0	9.2	236.0	284.3	13.1	301.0	252.0	0.015

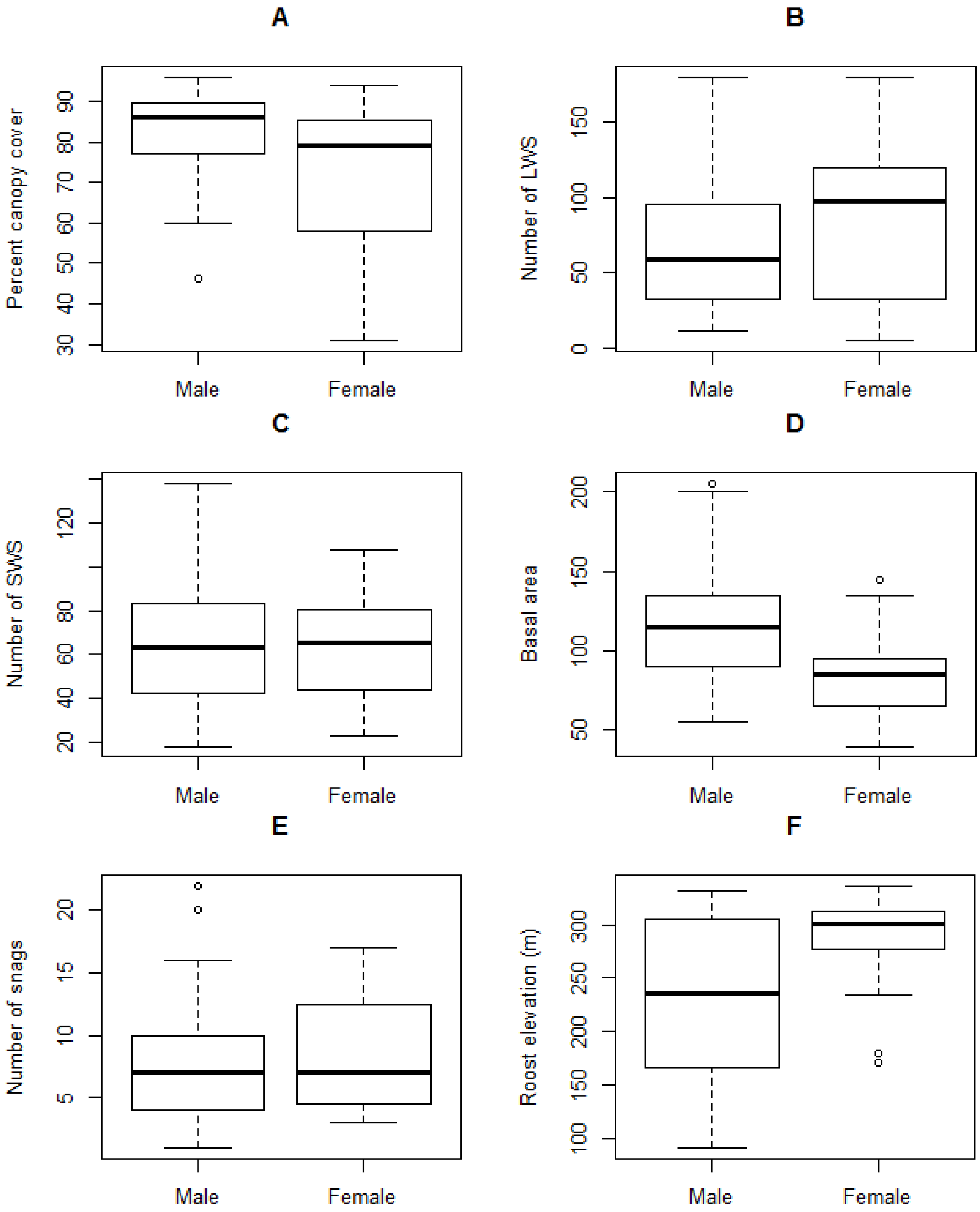

Figure 3.5. Sex-specific roost-site selection, (A) percent canopy cover, (B) number of LWS, (C) number of SWS, (D) basal area, (E) number of snags, and (F) elevation measured at 57 male and 15 female roost and random paired plots in the Sylamore Ranger District during June-August, 2013 and 2014.

There was no significant difference in relative overstory height between sexes (df = 2; $P = 0.420$; Figure 3.6.A). Evening bats used roosts below or at the same level as relative overstory height significantly more than roosts higher than relative overstory height ($G_2 = 29.0$; $P < 0.001$; Figure 3.6.B).

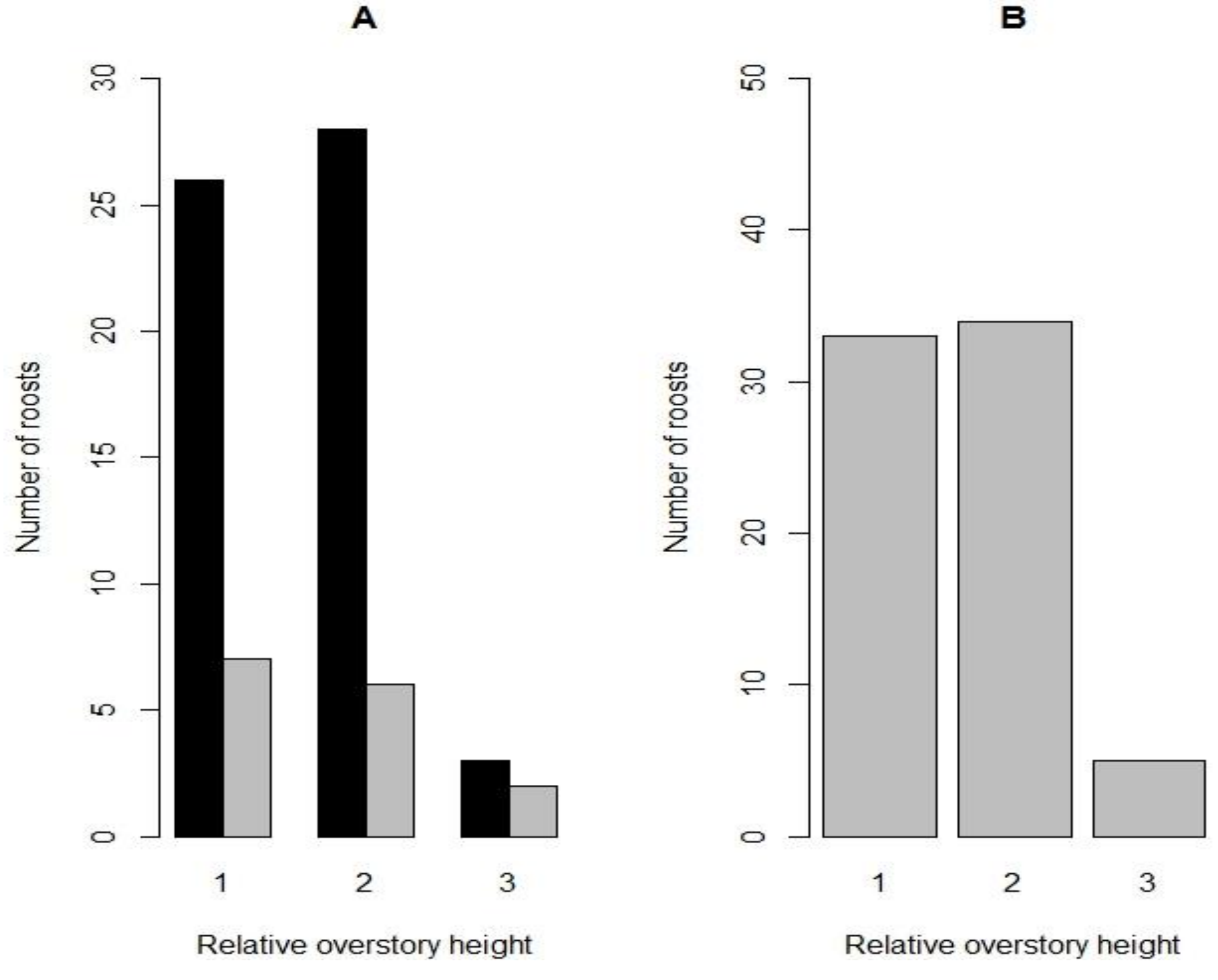

Figure 3.6. Relative overstory roost height (i.e., height of surrounding canopy) for male and female (A) and sexes pooled (B) in the Sylamore Ranger District during June-August, 2013 and 2014. Overstory height was classified as follows: (1) = roost >1 m below surrounding canopy; (2) = roost and canopy height equivalent; and (3) = roost >1 m above surrounding canopy.

There was no significant difference in roost aspect and slope between sexes (approx. $F_{1,66}$, df = 65; *P* = 0.789; Figure 3.7).

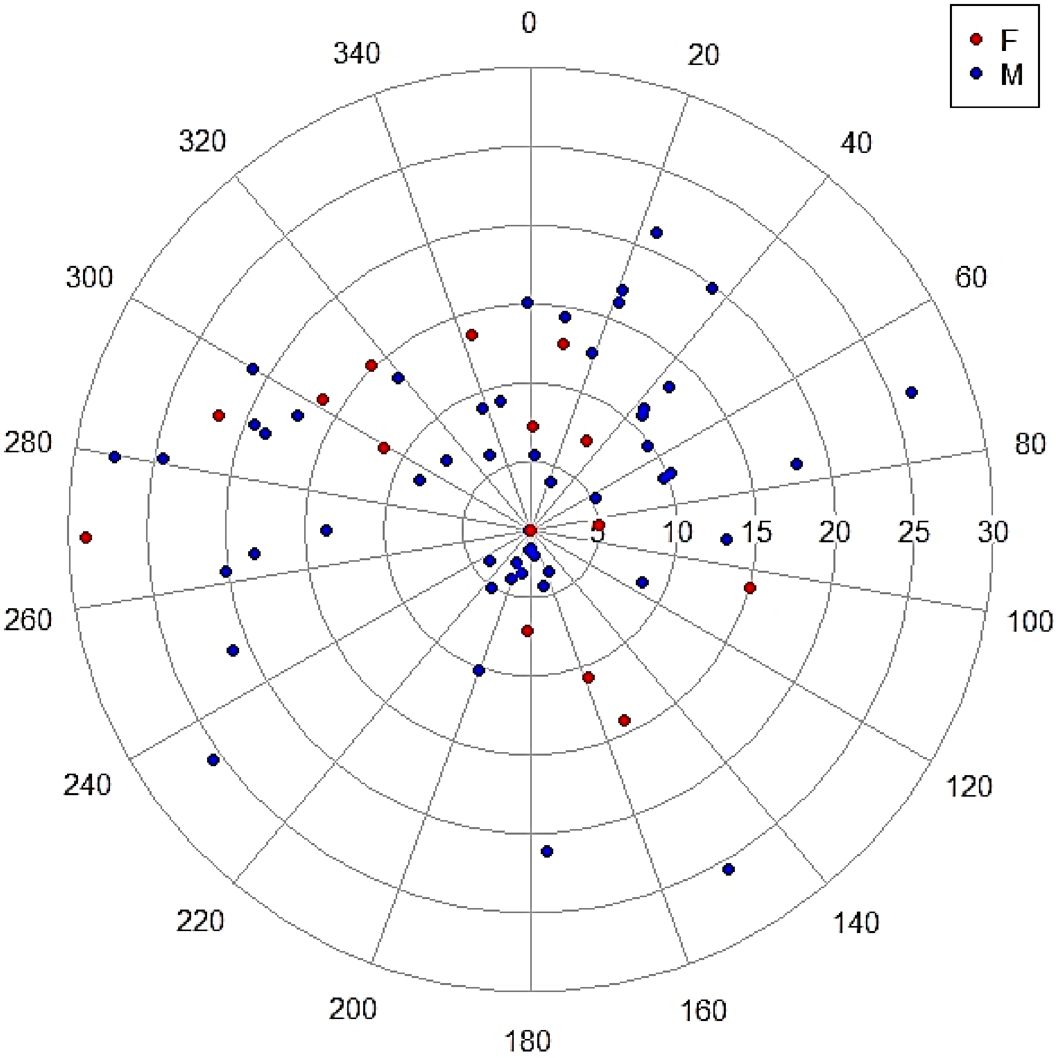

Figure 3.7. Polar plot illustrating roost aspect and slope of male and female roost plots in the Sylamore Ranger District during June-August, 2013 and 2014.

DISCUSSION

Sex-specific knowledge of forest bat roosting habits for non-imperiled species is needed to develop proficient habitat management plans and insure the longevity of forest-dwelling species. Though roosting ecology of forest bats is important, sex-specific differences are often neglected or sample sizes too small to compare inter-sexual differences. Because male and females differ in their physiological demands, these differences should be present in their roosting habits (Hein et al. 2009). The present study is the first to compare factors influencing evening bat roost-site selection between sexes at roost and plot levels.

Studies on diurnal-roost characteristics of evening bats have been conducted in pine-dominated landscapes in west-central South Carolina (Menzel et al. 2001), Southwest Georgia (Miles et al. 2006), central Arkansas (Perry & Thill 2008), and southeastern South Carolina (Hein et al. 2009); and in oak-hickory-dominated forests located in northeastern Missouri (Timpone et al. 2006) and southwestern Missouri (Boyles & Robbins 2006). Of the previous studies, Hein et al. (2009) is the only known study to evaluate differences in roost-site selection between sexes. Unlike this study, the previous study evaluated differences at the landscape level and not at the roost or plot levels.

Roosting habits

Consistent with observed habits of previous studies (Miles et al. 2006; Hein et al. 2009), male evening bats remained solitary while females aggregated into maternity colonies or remained solitary during summer. Similar to what Boyles & Robbins (2006) and Perry & Thill (2008) reported, male evening bats in the Sylamore Ranger District exhibited roost switching. Though females did not exhibit roost switching in the district, this behavior has been observed for both sexes in pine-dominated landscapes in Southwest Georgia (Miles et al. 2006) and southeastern South Carolina (Hein et al. 2009). Contradictory to females tracked in the Sylamore Ranger District, females exhibited roost switching and males mostly used one roost each for the duration of the tracking period in South Carolina (Hein et al. 2009).

Roost level characteristics

Because evening bats have been observed roosting in a plethora of tree species, they are commonly classified as roost generalists. In the Sylamore Ranger District, evening bats of both sexes used roosts belonging to the genus *Quercus*. Since the genus *Quercus* dominates the Sylamore Ranger District, evening bats may simply be using what is most abundant in the district. Similarly, in previous studies conducted in pine-dominated landscape, evening bats predominantly roosted in trees belonging to the genus *Pinus* (Miles et al. 2006; Perry & Thill 2008; Hein et al. 2009). Our results hence support the generalist tendency of this species.

In addition to genus, male and female evening bats selected roosts with similar characteristics (i.e., height, DBH, and decay stage). However, the small sample size of female roosts may have biased our results by not detecting differences in roost selection among females of different reproductive status. For example, DBH is likely an important parameter for females that are more restricted in their roosting habits than males. Reproductively active females in southeastern South Carolina selected roosts in predominantly mature forest stands containing ample snags and large-diameter trees (Hein et al. 2009). Males in the district used a wider range of diameter roosts than females, and though females aggregate into colonies, they are likely more limited to larger diameter roosts capable of supporting multiple bats.

Plot level characteristics

At the plot level, no differences were detected between roost and random plot variables for males or females, further supporting their generalist nature unless sex-specific roost selection was not detected as a result of a small sample of females. However, differences were detected for 3 of the 7 plot variables measured at male and female roosts. Male roosts were located in areas with higher canopy cover and larger basal area than females suggesting that males select roosts in areas of dense forest with increased shade and higher density of trees. Similar to Perry & Thill (2008), male evening bats commonly roosted in un-thinned forest stands with small-diameter trees.

I observed differences in roost-site locations, specifically the elevation at which males and females selected roosts. Females selected roosts in areas located along ridge tops while males commonly roosted in lower elevations, specifically along mountain slopes and at the bottom of hollows. These differences likely reflect thermoregulatory demands associated with reproduction. The energetic demands of females during reproduction exceed those of males and likely require females to select roosts favorable for rearing pups. The effects of elevation on roost-site selection have not been addressed for evening bats; however, females in the Sylamore Ranger District commonly selected roosts in areas at higher elevations than males. Results of other studies suggest that females forage and roost in areas at lower elevations than males in the Peruvian Andes (Graham 1983; Patterson et al. 1996), British Columbia (Grindal et al. 1999), South Dakota (Cryan et al. 2000), and Germany (Encarnção et al. 2005). In the Sylamore Ranger District, changes in elevation were relatively small (i.e., 100 – 300m) in comparison to previous studies which were conducted in larger, mountainous landscapes. In the Ozarks, lower elevations such as mountain hollows and creek beds were generally cooler at night than locations along ridge tops. In areas with larger range in elevation, temperature generally drops by 1°C every 100 m gained in elevation. Thus, seemingly contradictory results could be associated with differences in the range of elevation among study sites. Additionally, relative overstory height did not differ between sexes; however, evening bats in the Sylamore Ranger District typically selected roosts below or equal to the relative overstory height. Therefore, the amount of shade provided by surrounding overstory likely influences internal roost conditions (i.e., temperature), and evening bats may be selecting roosts which best accommodate their thermoregulatory requirements. Roosts with lower internal temperatures may provide better conditions favorable for bats that choose to minimize energy expenditures via torpor (Perry & Thill 2008), while roosts with higher internal temperatures may be more beneficial for sustaining the thermoregulatory processes of bats that are reproductively active females (Menzel et al. 2001).

Although evening bat roosts were segregated by elevation and location, they did not segregate by roost slope and aspect. Though slope and aspect of roost locations likely affect the amount of solar radiation available at roosts and this availability likely influences internal roost temperature, these factors did not seem to influence evening bat roost selection in the district. Instead, other factors such as elevation and forest stand characteristics were likely more influential on roost thermal conditions.

Management recommendations

Evening bats selected live trees (stage 1) more than snags and mean DBH for males and females was ≥ 28.3 cm. In agreement with the hypothesis of Hein et al. (2009), our results suggest that forest-stand age may influence evening bat roost-site selection with old trees providing more roosting opportunities than young trees. In other words, increasing the availability of mature trees would best provide ample roosting sites for both sexes. Future management efforts should promote forest-stand diversity in a manner that will increase old-growth forest conditions, as it will increase roost availability and be most beneficial to the conservation of this species. Likewise, maintaining habitat favorable for habitat generalists should also benefit species that are more specialists in nature, as well. Based on the results of this study, it is recommended that forest management regimes be implemented in a manner that promotes forest-stand maturation, as it will likely best provide suitable roosting habitat for the entire forest bat community.

Conclusions

In conclusion, my study supports the prediction that diurnal roost characteristics are sex-specific in the Sylamore Ranger District. Despite this obvious benefit, non-imperiled species, and particularly as generalists as the evening bat, continue to be considered of lesser importance than species classified as threatened or endangered. All forest-dwelling species, regardless of conservation status, should be considered of equal importance to land managers and biologists. Sex-specific studies are critical to habitat managers because practices used to promote habitat conditions favorable for females may not be equally beneficial to males (Perry & Thill 2008). Implications of such studies are critical to habitat managers because such information allows managers to evaluate current management plans and make improvements as needed. Future research should increase effort in obtaining larger sample sizes with equal representation between sexes, reproductive classes, and ages of bats.

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CHAPTER IV

CONCLUDING DISCUSSION

Overall Synthesis

The objectives of this thesis were to determine if the evening bat exhibited sex-specific foraging habits and selection of diurnal roost sites in the Ozark National Forest, Sylamore Ranger District of north-central Arkansas. To determine if the evening bat exhibits sex-specific foraging and roosting habits, I needed to obtain detailed knowledge of the spatial and temporal movements of evening bats. To do this, I employed VHF radio telemetry techniques to monitor evening bat foraging habits and locate diurnal roost sites to determine if sex-specific differences exist, and if so, use this information to provide general management recommendations that will best benefit the district's entire forest bat community. During June, July and August 2013 and 2014, I equipped 70 evening bats with VHF-radio transmitters and obtained sufficient data to estimate foraging range sizes of 24 evening bats (Appendix A), and successfully located and characterized 72 diurnal roosts (Appendix C).

In Chapter II, I estimated foraging range size of evening bats, and assessed year- and sex-specific foraging habits. Results supported my prediction that male and female evening bats exhibited different foraging habits during summer, and these differences likely reflect inter-sexual variation in physiological and behavioral pressures (Perry & Thill 2008). FK foraging ranges for females were larger than for males. Likewise, MCP estimates for females were generally larger than for males; however, MCP foraging range estimates were not significantly different between sexes. Additionally, differences in evening bat foraging ranges were detected between years. FK and MCP foraging range estimates were larger in 2014 than 2013, and these differences are possibly related to variation in annual precipitation and resource availability between years. Evening bats in the district exploited multiple core foraging areas, males using more than females. Although I did not assess habitat conditions at core foraging areas, these core areas were likely exploited due to the presence of critical resources (e.g., water and insects). Interestingly, males exploited more core foraging areas than females; yet females exhibited larger foraging ranges than males. The use of multiple core areas suggests that male evening bats are possibly more selective in their foraging habits than females which may be constrained by increased energetic requirements associated with reproduction. In areas where I was capable of tracking both males and females, there was little overlap in male and female foraging locations supporting that sexes remain sexually segregated to some extent (Appendix B). Since foraging ranges and use of core areas differed between sexes, it can be concluded that sex-specific foraging habits exist, and these difference should not be neglected in future studies, as studies that pool data between sexes may mask biologically relevant information.

In Chapter III, I quantified forest-stand characteristics at 72 roosts and random-paired plots to determine diurnal-roost characteristics for male and female evening bats, and assessed sex-specific roost characteristics. Evening bats roosted in both live trees and snags, and mostly selected roosts belonging to the genus *Quercus* which was the most abundant genus in the district. This tendency to exploit the most abundant genera as roost locations is consistent with previous studies (Miles et al. 2006; Perry & Thill 2008; Hein et al. 2009). Though no differences (i.e., DBH and roost height) were detected between sexes at the roost level, male and female evening bats exhibited some selectivity by exploiting live roosts (stage 1) more than snags (stages 2-4), selecting stage 4 least, and trees that had a large DBH. These findings indicate that live, mature trees are essential to fulfilling evening bat roosting requirements. A lack of female data may have biased our results by not detecting differences in roost selection among females of different reproductive status. At the plot level, no differences were detected between roost and random plot variables for males or females; however, differences were detected between sexes for 3 of the 7 plot variables supporting my prediction that male and females exhibit sex-specific roosting habits, females being more selective than males. Specifically, males and females selected roosts that varied in canopy cover, basal area and elevation. Canopy cover and basal area were typically higher at male roosts than at female roosts suggesting that males select areas with a higher density of trees and are more shade-tolerant than females. Unexpectedly, a difference was detected in roost elevation between sexes, with males typically selecting roosts at lower elevations than females. Females typically selected roosts in areas with decreased canopy cover and lower basal area, and these areas were typically located along mountainous ridges where sunlight and mature forest stands appeared to be most abundant. It is likely that these results reflect differences between male and female energetic requirements during reproduction. Results supported my prediction that evening bats selected roosts based on specific characteristics, and these characteristics differed between sexes.

In conclusion, combined results from Chapters II and III suggest that male and female evening bats do segregate spatially throughout the day (Appendix B). They exploit different foraging areas (in size, number, and location). Though there is some overlap in foraging locations on the map (Appendix B), there is an elevation effect in roosting habits which further separates sexes. Particularly, male and female roosts are at different elevations; however, roost aspect and slope do not seem to influence segregation. Though they use roosts with similar characteristics, they do not use the same roosts. Not only do sexes exhibit different habits, they do clearly segregate spatially which might be a result of differing physiological requirements and/or to minimize intra-specific competition. Unfortunately, I was unable to address these 2 hypotheses as mentioned in Chapter II.

Limitations and Future Directions

VHF-telemetry equipment is essential to monitor the space-use patterns of bats; however, the use of such technology poses technological and logistical limitations, especially for studies conducted in mountainous terrain. My research was most limited by the number of individuals used to monitor evening bat foraging bouts and field site conditions (i.e., steep, mountainous terrain and dense forests). Typically, triangulation methods require 3 individuals, all of which are capable of simultaneously detecting signals, and my study was conducted using the minimum required number of individuals. To increase tracking success, I suggest increasing the number of individuals, especially in logistically challenging terrain, as it would allow more thorough investigation of bat habitat use patterns.

Though this study increased the general knowledge of evening bat foraging habits, I was unable to address all objectives. Specifically, questions related to differences between sexes (e.g., number of foraging bouts, sexual segregation of habitat types) due to a small sample of females and lack of uniform sampling of females of different reproductive statuses. For example, comparison of differences among bats of different reproductive statuses requires equal sampling among sexes and months which I was unable to obtain. Further, questions concerning the influence of water availability and management practices on evening bat foraging habits were also impractical (Table 4.1). Thorough evaluation of distance to water sources requires knowledge of all available water during the entirety of the study which was impossible, especially in the district where water is ephemeral. To successfully address water-related research questions, study site selection should be done with caution, preferably by considering areas where water sources are prevalent throughout the summer. Additionally, evaluation of the effect of forest management practices on evening bat foraging habits requires in-depth, long-term data on the temporal and spatial movements of evening bats, as well as past forest management initiatives (e.g., when a given stand was last burned). Similarly, to best address the effects of management practices on bat foraging habits, future research would should delineate treatment and control areas (i.e., stand of varying management types) throughout the study area. Because females were so limited in our study area, future research should exert more effort on obtaining larger sample sizes, preferably with uniform sampling among months. Future studies should address the effects of weather conditions, management regimes, and water availability on bat foraging habits to allow more sensible comparisons across studies. However, these studies should be designed with caution, as there are serious limitations for addressing water availability-related questions. In general, results of this study suggest that differences in evening bat foraging and roosting habits exist; however, females were particularly limited compared to males. Although water availability likely influenced total bat captures, the type of water source (i.e., pond vs. stream) may have influenced total captures for each sex. For example, in 2013, net sites were primarily located over or in the vicinity of ponds, while net sites in 2014 were primarily located over or near creeks (Appendix C). In general, the likelihood of capturing evening bats, particularly females, was significantly higher at creeks than at ponds ($\chi^2 = 6.24$, $P = 0.013$). Because capture efforts primarily focused on pond sites, especially during summer 2013, female captures were limited. Unequal samples of males and females among months and years prohibited comparison of different reproductive stages and ages. A small sample of female roost data may have masked differences in roosting habits. Despite these constraints, this research exceeded the duration and sample sizes of previous evening bat foraging studies (Carter et al. 1998; Duchamp et al. 2004; Morris et al. 2011), and was the first to report sex-specific differences in foraging habits in any bat species in the United States. Though roost and foraging studies are generally conducted separately, the spatial relationship of these resources is critical to understanding how bats use forest habitats. Implications of such studies allow habitat managers to evaluate current management regimes and make adjustments as needed. Females are particularly important to protect due to their high level of parental investment associated with rearing pups, and this study shows that management decisions based solely on male-focused studies or data pooled between sexes does not guarantee adequate protection of females. In general, this research has increased the overall knowledge of evening bat foraging and roosting habits during summer emphasizing the fact that sex-specific studies should not be neglected from future studies.

Table 4.1. Summary of question-specific results. Questions and predictions not addressed are italicized.

QUESTIONS	
PREDICTIONS	**RESULTS**
Q1. Are home range estimates for *N. humeralis* consistent with previous studies?	
P.1.A. Foraging range estimates will not be consistent with previous studies.	Estimates were consistent with previous evening bat studies.
P.1.B. Foraging range size for males will be larger than for females.	No, foraging range estimates for females were greater than for males.
Q2. Do males and females use different forage sites? If so, what/where are they, how do they differ, how distant are they from each other? Otherwise, do males and females use the same sites at different times? Do males and/or females exhibit foraging-site fidelity?	
P.2.A. Males and females will predominantly forage in different habitat types during early summer (May) and less so as fall approaches.	*Different foraging sites although overlap, habitat type was largely homogenous and could not be addressed. Progression of season not addressed due to a small sample of females and lack of uniform sampling of among different reproductive statuses and months.*
P.2.B. Distance to foraging areas will be shorter during lactation than during post-lactation. *P.2.C. Lactating females will make more foraging trips than non-reproductive females.* *P.2.D. Distance traveled to foraging areas will be greater for males than females.* *P.2.E. Females will exhibit more foraging bouts per night than males.*	*Could not address due to a small sample of females and lack of uniform sampling of among different reproductive statuses and months.*
P.2.F. Males and females will exhibit foraging-site fidelity.	Yes, males more so than females, males using multiple core areas.

Q3. Do core foraging areas encompass or are close to water sources?	
P.3.A. Foraging activity (number of foraging locations) will decrease as distance to water sources increases. *P.3.B. Foraging occurs more at water sources than at random given what is available in the district.* *P.3.C. Roost-site locations and distances to water sources, both ponds and streams, will determine bat foraging locations, regardless of elevation. If the roost site is at equal distance to stagnant and running water bodies, stagnant water will be favored.*	*Water ephemeral so couldn't address this; however availability is likely important and future studies should pose water-related questions with much consideration to insure feasibility.*
Q4. Do forest management practices influence bat foraging habits?	
P.4.Foraging activity will not be distributed equally among stands of all management types.	*Could not address due to lack of management data, largely homogenous habitat, and inability to continuously track individuals.*
Q5. Do males and females select diurnal roosts with different characteristics? If so, what are these characteristics, how do they differ from each other?	
P.5. Evening bats will select roosts based on specific characteristics and that these characteristics would differ between sexes, females being more selective than males.	Yes, sex-specific differences exist, females being more selective than males.
CONCLUSION:	**Males and females exhibit different roosting and foraging behaviors.**

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Appendix A

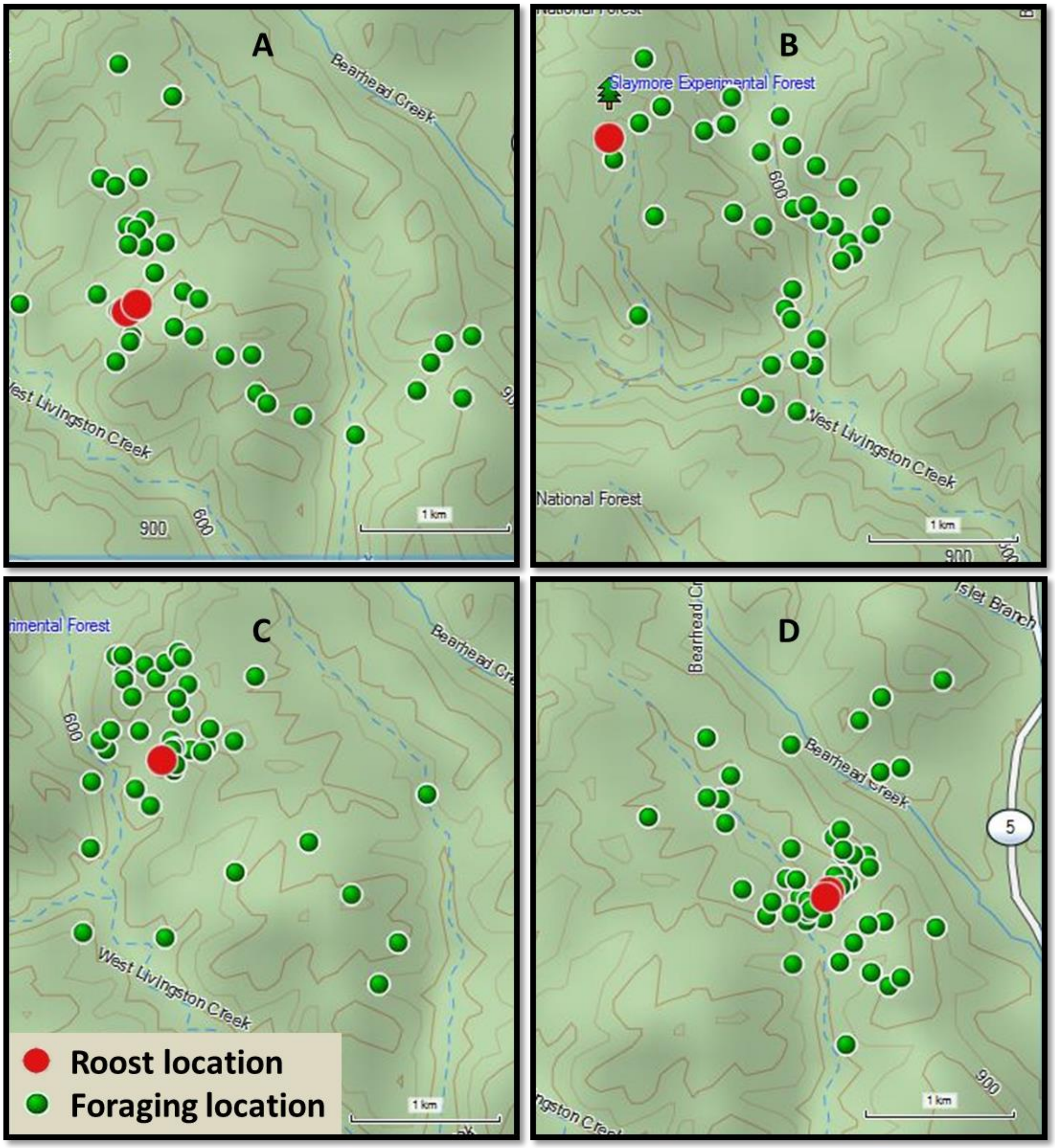
Estimated home range size of bats (n=24) tracked in the Sylamore Ranger District, Ozark National Forest during summers 2013 and 2014. Data include relative age (Juvenile (J) or Adult (A)); sex (male (M) or female (F)); month and year tracked; number of locations included in analyses; number of core foraging areas; and home range estimates in hectares for 95 and 50% fixed kernels with least squares cross validation and 95% minimum convex polygon methods.

Bat ID #	**Age**	**Sex**	**Condition**	**Month**	**Year**	**Locations**	**Core Areas**	**95% FK**	**50% FK**	**95% MCP**
001	A	M	S	July	2013	26	1	1114.6	164.7	460.0
002	A	F	PL	July	2013	23	1	535.3	56.9	141.0
003	A	M	NR	June	2013	21	2	47.6	97.1	24.9
004	A	M	NR	June	2013	23	2	48.0	323.1	14.2
005	A	M	NR	June	2013	29	3	123.7	130.9	59.2
006	A	M	S	July	2013	29	3	240.8	155.4	113.6
007	A	M	S	July	2013	29	5	163.2	207.0	221.6
008	A	M	NR	June	2013	20	1	96.7	71.2	27.5
009	J	F	NR	August	2013	27	1	271.7	9.3	118.1
010	A	M	NR	July	2013	32	1	801.4	22.3	433.6
011	A	M	NR	June	2013	31	1	104.9	171.5	50.8
012	J	F	NR	July	2014	23	1	1517.5	371.5	464.6
013	A	F	PL	July	2014	26	1	550.6	141.9	131.0
014*	A	M	S	July	2014	25	1	613.9	136.3	259.9
015	A	M	S	July	2014	28	2	363.4	311.2	137.3
016	J	F	NR	July	2014	26	1	669.2	125.4	205.8
017	J	F	NR	July	2014	20	2	2238.5	8.3	490.9
018	A	F	L	July	2014	26	1	415.3	21.7	133.1
019	A	F	L	July	2014	28	1	1269.4	48.8	369.8

Bat ID #	Age	Sex	Condition	Month	Year	Locations	Core Areas	95% FK	50% FK	95% MCP
020	J	M	S	July	2014	22	2	354.7	29.3	194.2
021*	A	F	L	July	2014	24	1	485.1	64.7	197.6
022	A	F	PL	July	2014	27	1	562.3	21.3	191.2
023*	A	M	S	July	2014	24	2	413.3	77.1	109.3
024*	A	M	S	June	2014	37	7	154.9	19.8	200.9

*Fixed kernel foraging range for bats 014, 021, 023, and 024 depicted in Figure 2.2.

Appendix B



Foraging and roost locations of 4 representative evening bats tracked during summers 2013 and 2014 in Big Spring Hollow of the Sylamore Ranger District. Bats A (#014), C (#024), and D (#023) were males; bat B (#021) was female. Maps produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

Appendix C

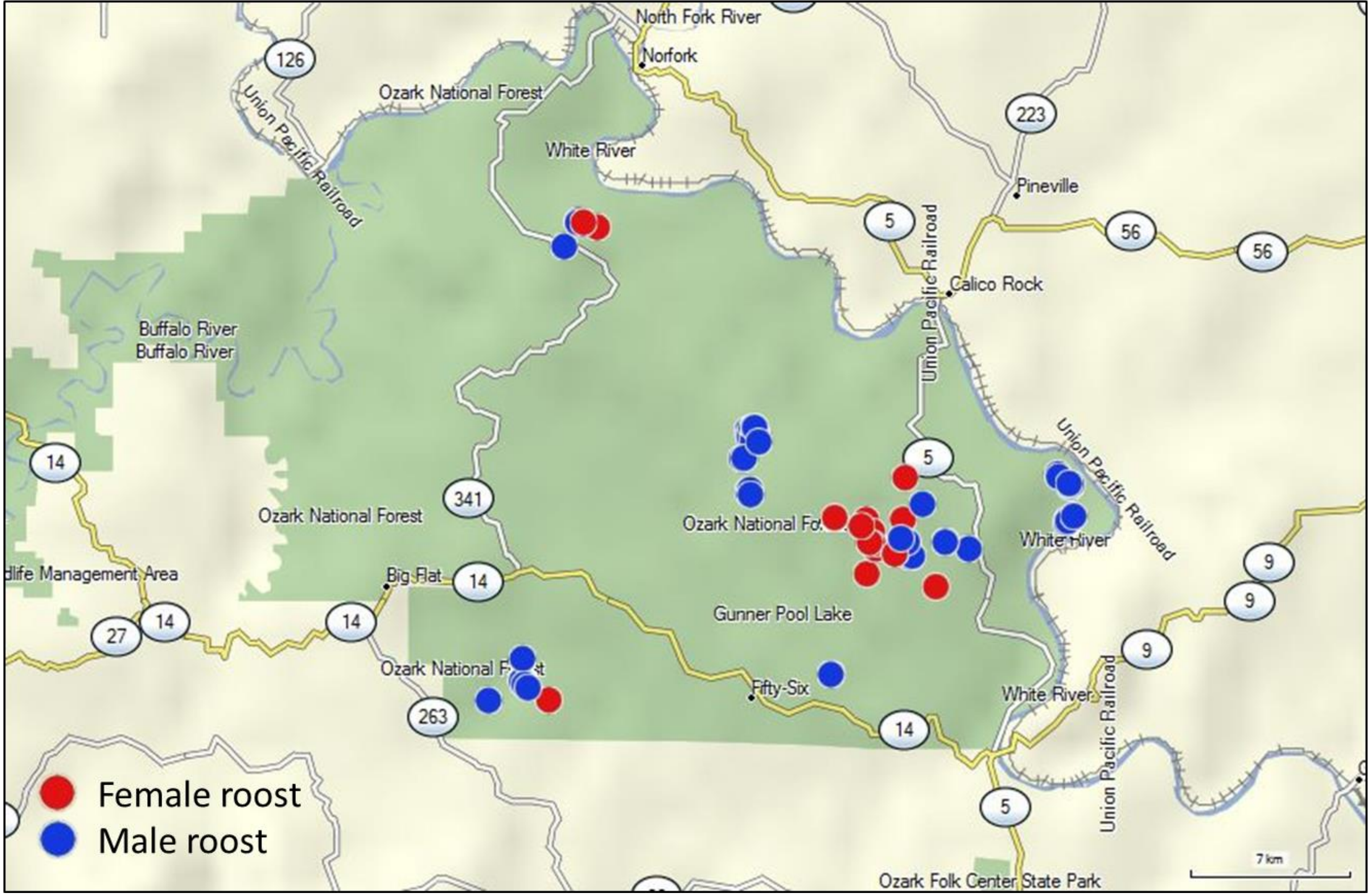


Figure C.1. All evening bat roost locations and study sites in the Sylamore Ranger District during summers 2013 and 2014. Map produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

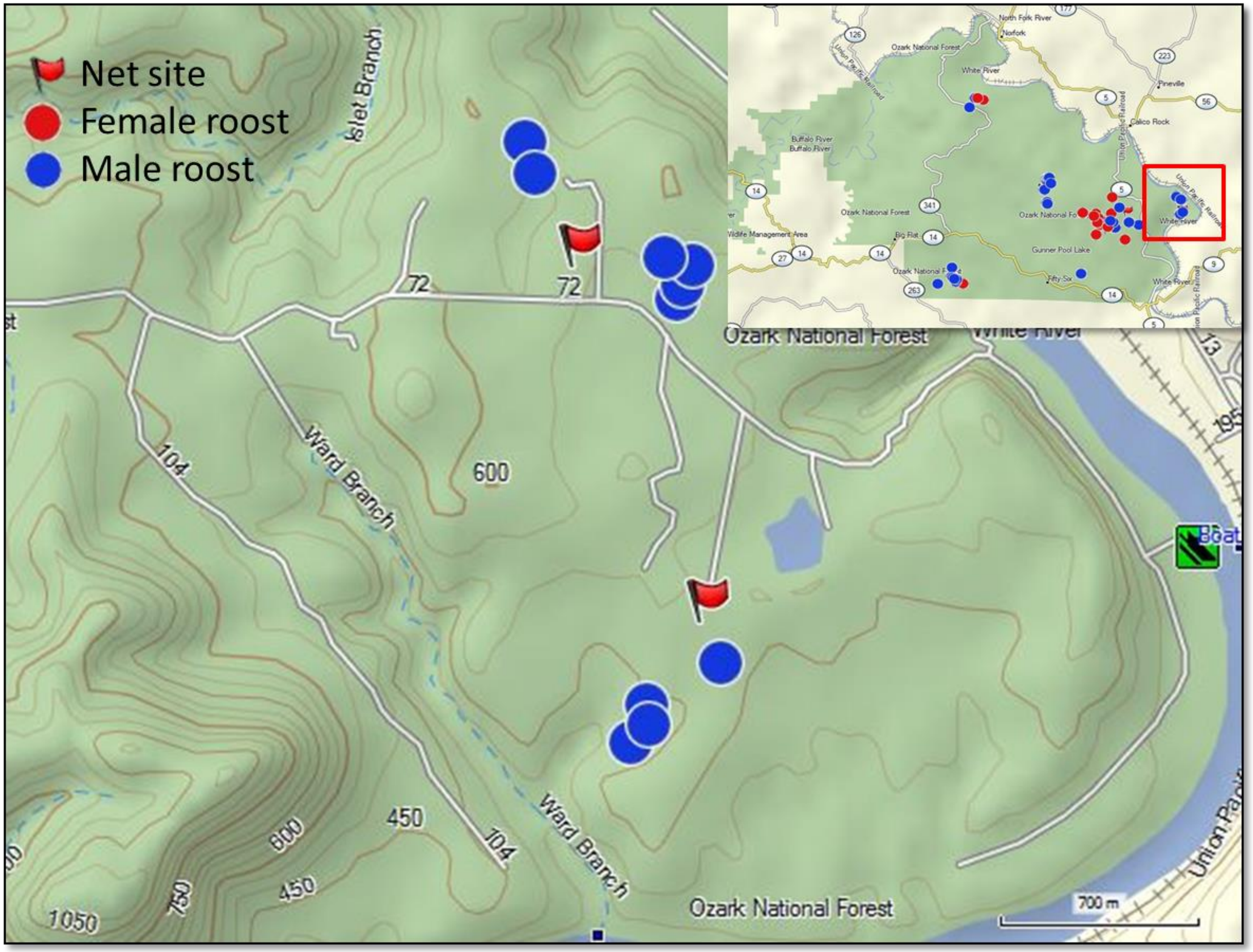


Figure C.2. Evening bat roost locations at Optimus study site in the Sylamore Ranger District during summers 2013 and 2014. Net sites were at ponds. Map produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

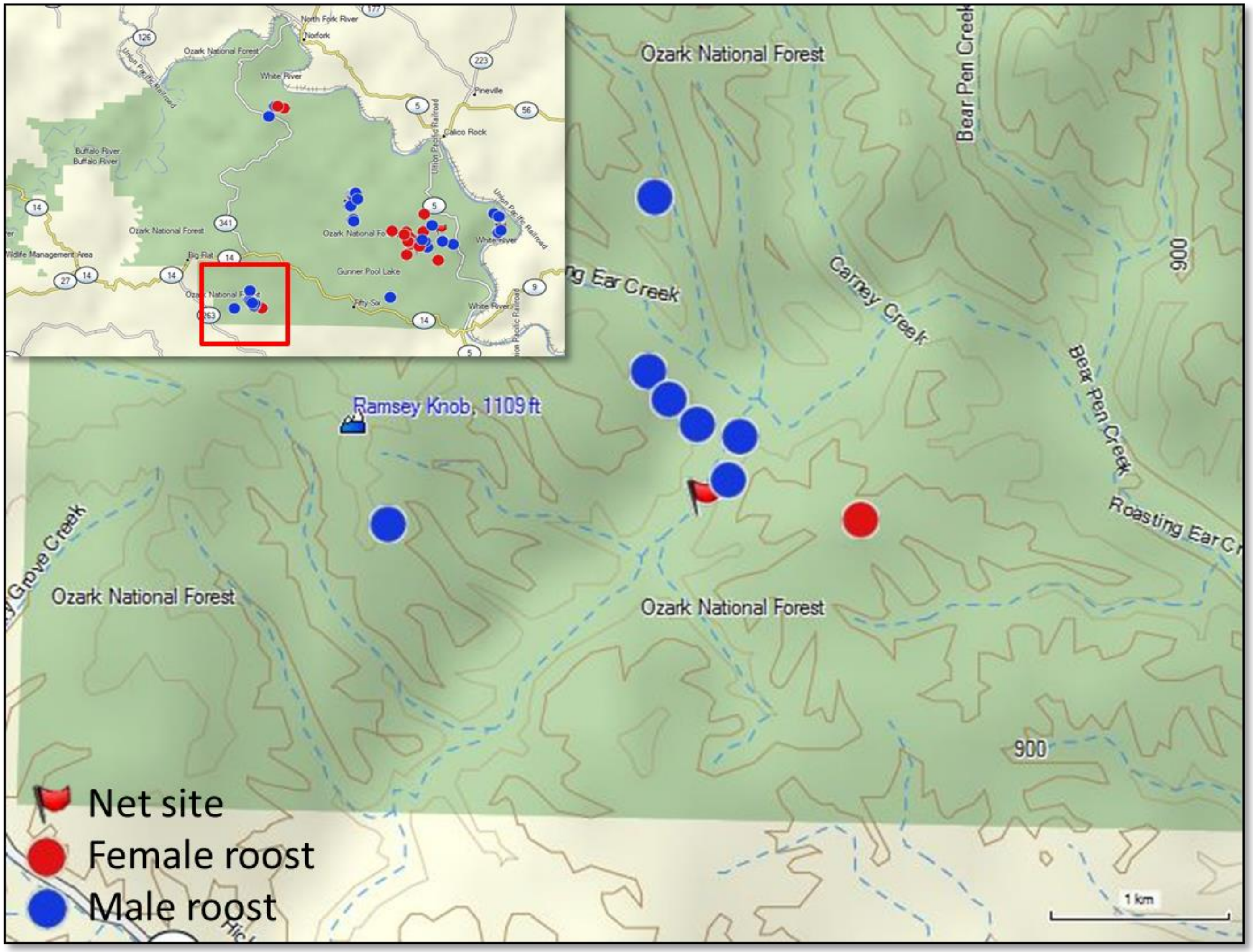


Figure C.3. Evening bat roost locations at Roasting Ear study site in the Sylamore Ranger District during summers 2013 and 2014. Net sites were at creeks. Map produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

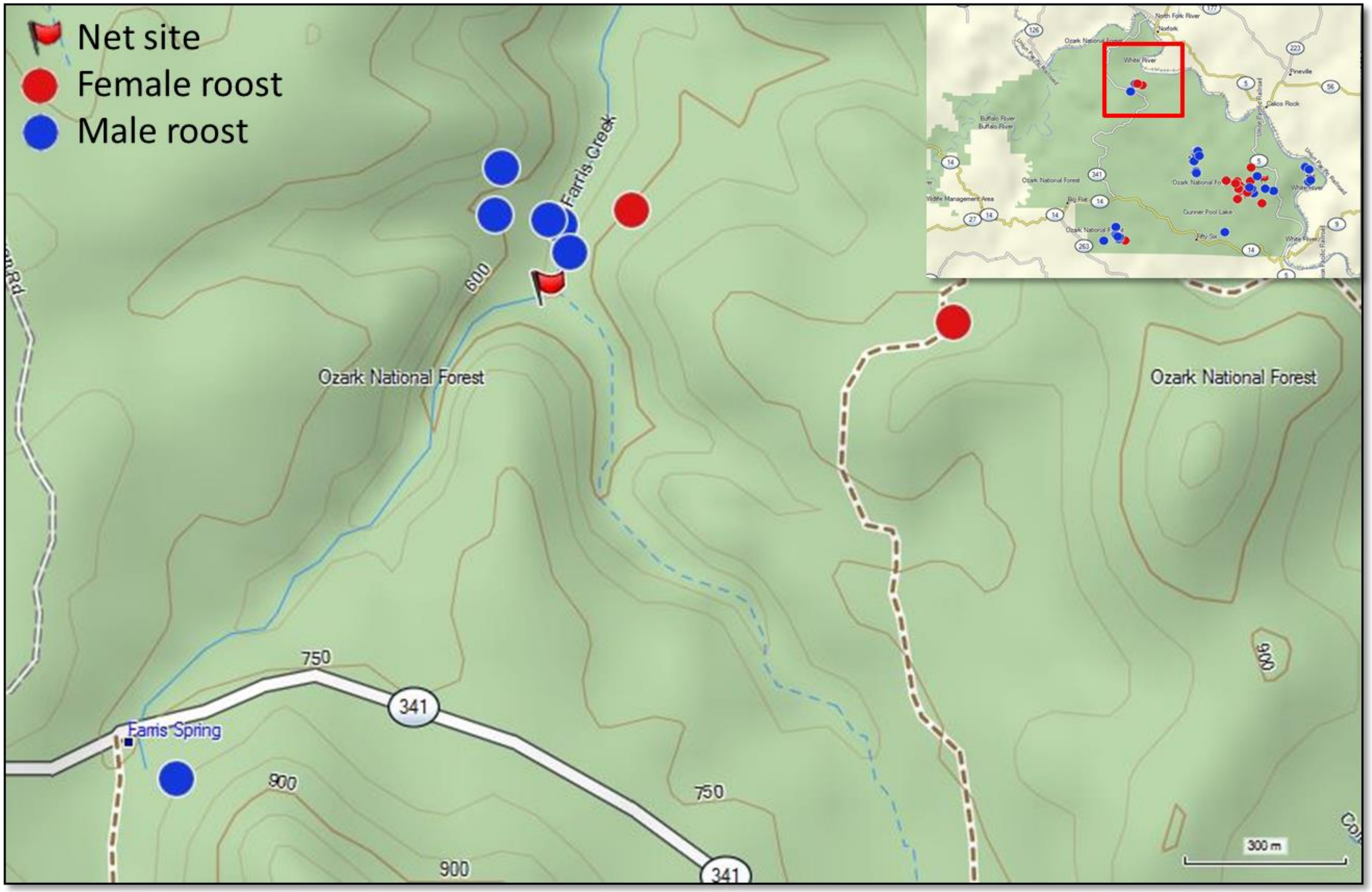


Figure C.4. Evening bat roost locations at Lone Rock study site in the Sylamore Ranger District during summers 2013 and 2014. Net sites were at creeks. Map produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

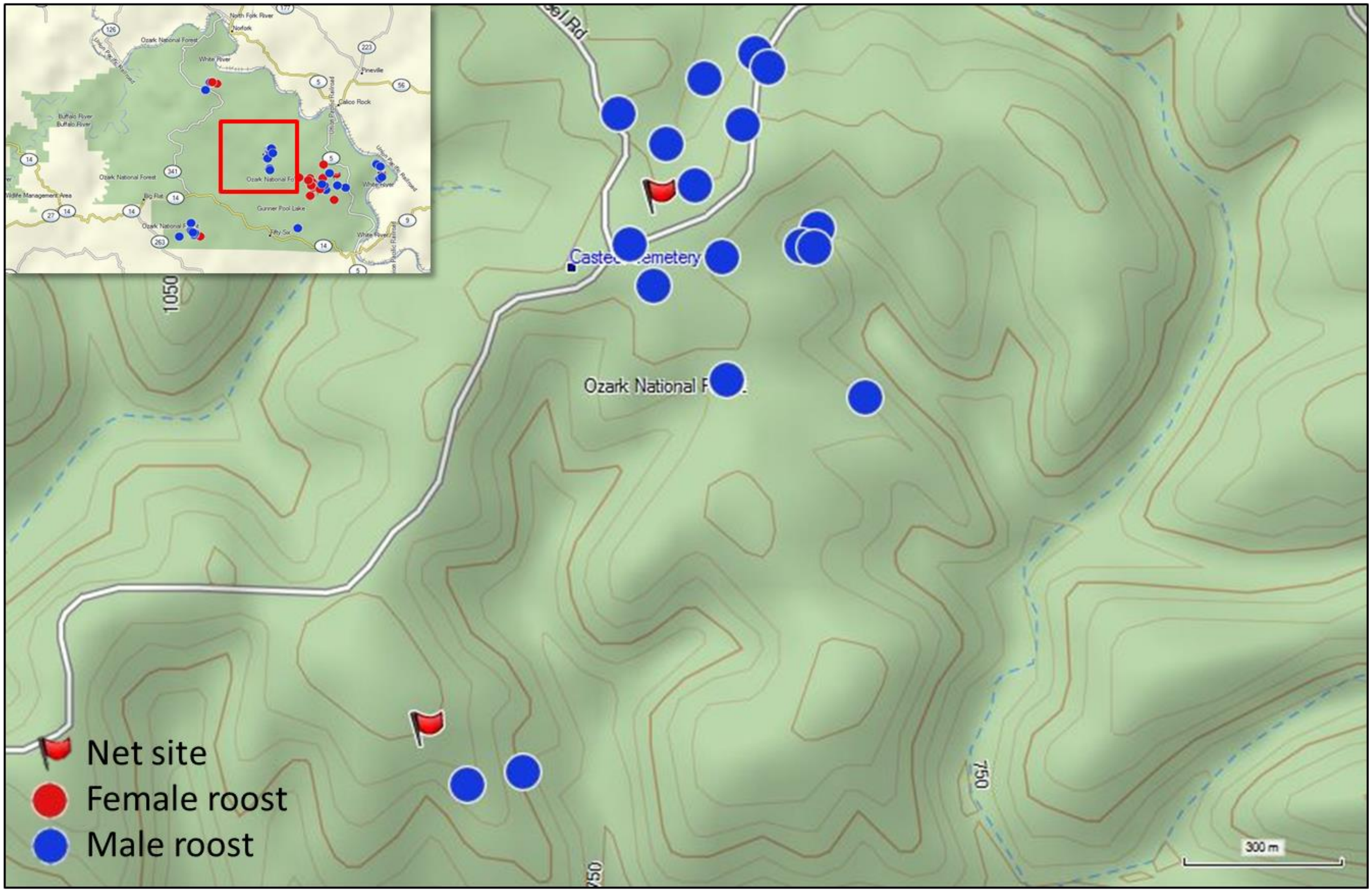


Figure C.5. Evening bat roost locations at Casteel study site in the Sylamore Ranger District during summers 2013 and 2014. Net sites were at ponds. Map produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.

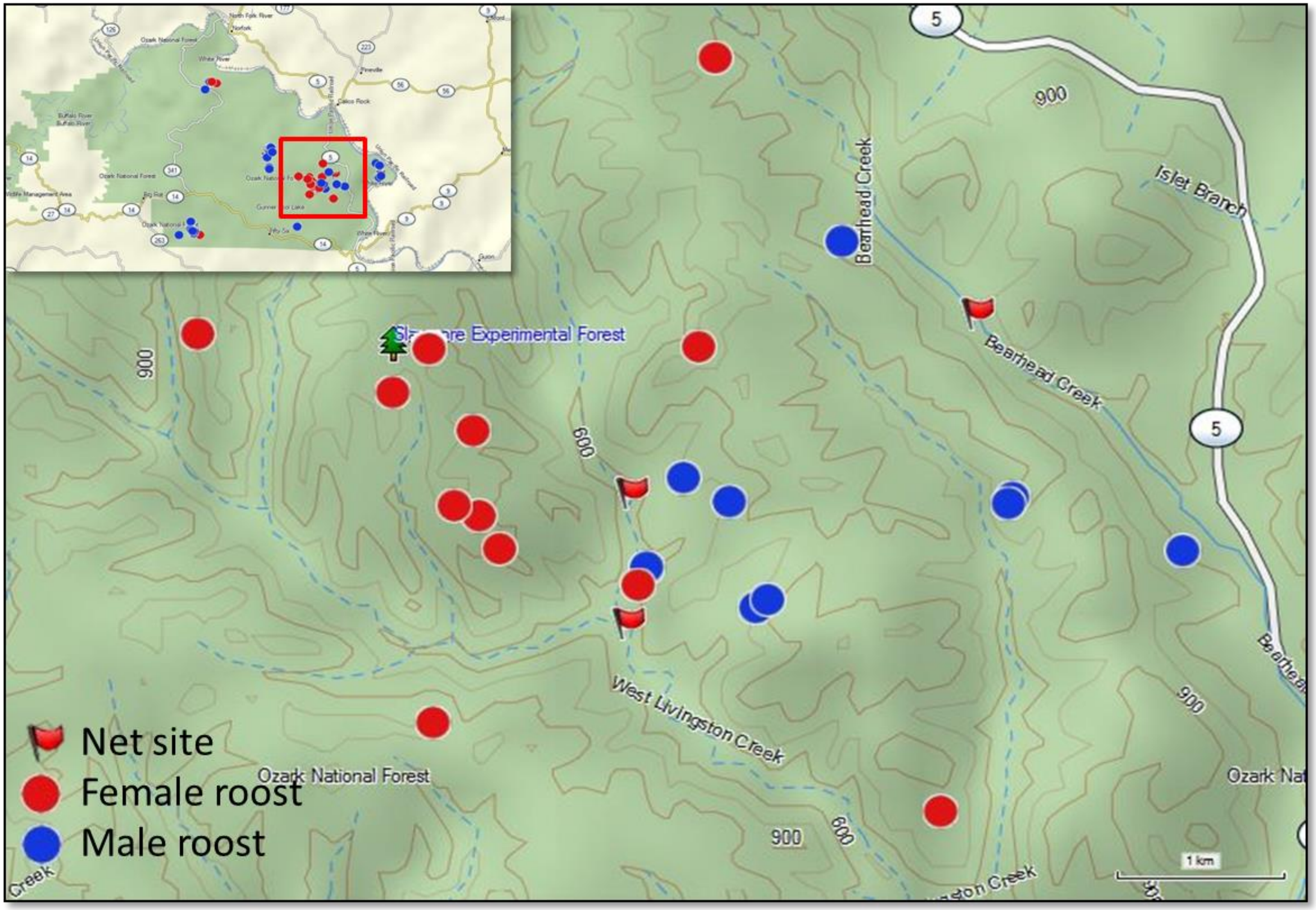


Figure C.6. Evening bat roost locations at Big Spring Hollow study site in the Sylamore Ranger District during summers 2013 and 2014. Net sites were at creeks. Map produced using Garmin Mapsource Version 6.16.3 ©1999-2010 Garmin Ltd.