



Sex-specific foraging habits and roost characteristics of *Nycticeius humeralis* in north-central Arkansas

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Sexual segregation is common in polygynous mammals, particularly in wild ungulates, but is less known in bats of North America. Yet, the declining bat populations caused by white-nose syndrome, wind energy facilities, and habitat loss throughout eastern North America require habitat management, which may be sex specific. We thus determined sex-specific roosting and foraging habits of evening bats (*Nycticeius humeralis*) in north-central Arkansas. During the summers of 2013 and 2014, we equipped 70 individuals with radiotransmitters to track their foraging movements and identify their roosts that we characterized with 3 tree-level and 7 plot-level variables. We found that evening bat males and females segregate spatially with females foraging over a larger area than males. Females' roosts were also higher in elevation. Although the roost itself had similar characteristics between sexes, its surrounding habitat was characterized by less canopy cover and a smaller basal area for females. Our results support sex-specific habits and sexual segregation in a forest-dwelling bat, which highlights the importance of sex-specific studies to inform management decisions that would benefit both sexes, including females for which parental investment is higher.

Key words: elevation, evening bat, foraging, *Nycticeius humeralis*, roost ecology, sexual segregation, spatial

Sexual segregation suggests differentiating habitat needs among sexes (Encarnação 2012). Most research on sexual segregation in mammals is limited to wild ungulates (Main and Coblenz 1996; Kie and Bowyer 1999; Alves et al. 2013) and has been little addressed in bats. Kie and Bowyer (1999) defined 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 include population density, intraspecific competition, energy requirements, body size, social structure, sex ratio, and risk of predation (Kie and Bowyer 1999).

Sexual segregation is common among polygynous species, especially those with a marked sexual dimorphism in body size (Kie and Bowyer 1999; Alves et al. 2013). 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. Although female bats of many species are known to form maternity colonies in roosts that do not contain any adult males (Kunz and Lumsden 2003), few studies quantified spatial segregation in bats. Most studies addressing sexual segregation in bats (Bradbury and Vehrencamp 1977; Cryan and Wolf 2003; Altringham and Senior 2005; Safi et al. 2007;

Encarnação 2012; Amichai et al. 2013) focused on latitudinal or altitudinal segregation.

In eastern North America, the synergistic effects of white-nose syndrome (WNS—Blehart et al. 2009), wind facility fatalities (Hayes 2013; Smallwood 2013), and habitat loss (Mickleburgh et al. 2002) have led to a decline in abundance of bat populations. As species susceptible to WNS decline, forest-dwelling species considered nonsusceptible to WNS become increasingly important to land managers because the loss of WNS-susceptible species may allow other sympatric species to expand their niches, which could alter ecosystem dynamics. Thus, knowing the spatial relationship between foraging areas and diurnal roosts of forest-dwelling bats in the Eastern United States is imperative to the establishment of successful conservation initiatives. Furthermore, landscapes as they are managed today may not benefit males and females equally. Therefore, assessing sex differences should be an integral part of foraging and roosting studies.

Many ephemeral-roost-dependent bat species remain sexually segregated throughout the summer. Females will commonly form maternity roosts while males remain solitary (Kunz and Lumsden 2003), which indicates spatial segregation.

Likewise, the distribution of roost sites throughout the landscape likely influences foraging location; thus, sexual segregation may also exist in foraging habits. It is unknown whether males remain spatially segregated from females solely during roosting. They may be spatially segregated during both roosting and foraging. 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).

Among the bat species of eastern North America, the evening bat (*Nycticeius humeralis*) is a prime study candidate to shed light on sexual segregation in forest-dwelling bats because the species is considered an easy-to-track species that is abundant in Arkansas, allowing for larger sex-specific sample sizes. The evening bat is a species in which WNS has not been detected and for which fatalities at wind-turbine facilities have not been documented in Arkansas (but see Good et al. 2012 for evening bat fatalities in Indiana). Most studies of evening bats have focused on identifying roosting requirements (e.g., Menzel et al. 2001; Miles et al. 2006; Perry and Thill 2008). Its spatial movements have also 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.

Using very-high-frequency (VHF) radiotelemetry equipment, our objectives were to 1) determine sex-specific roost requirements and foraging habits (e.g., home range) of evening bats and 2) evaluate spatial sexual segregation. It is hypothesized that males have lower energy requirements than females because of costs associated with reproduction (Hein et al. 2009). Therefore, we predicted that roosting and foraging habits would differ between sexes, with females being more selective and exploiting a different area (in location or size) than males.

MATERIALS AND METHODS

Study Species

The evening bat is a small insectivorous species that obtains food (primarily small beetles, moths, and leafhoppers) in flight by aerial hawking in forest stands, agricultural areas, and along waterways (Whitaker 2004). It exhibits a biphasic foraging pattern, i.e., foraging activity peaks a few hours around dusk and dawn (Reid 2006). The 1st and primary foraging bout begins soon after sunset (Wilkinson 1992), and generally does not exceed 2.5 h (Clem 1993).

Evening bats roost in Spanish moss (*Tillandsia usneoides* (L.) L.) (Jennings 1958); underneath the exfoliating bark of mature trees (Menzel et al. 1999); within hollow trees (Watkins 1972; Boyles and Robbins 2006); and vacant man-made structures (Watkins 1972; Clem 1993). 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). The cavity that forms at the base of the fork of forked-top, also called bifurcated, trees are commonly used for roosting by reproductively active female evening bats (Menzel

et al. 1999; Miles et al. 2006; Hein et al. 2009). Additionally, adult male evening bats may also use underground roosts (Boyles et al. 2005; Perry and Thill 2008).

Study Area

Our study was conducted at the USDA Forest Service's Sylamore Ranger District, Ozark–St. Francis National Forest, approximately 10 km northwest of Mountain View, in the Ozark Highlands Ecoregion of north-central Arkansas (Fig. 1). The 53,000-ha low-elevation (50–800 m) district is composed of homogeneous forest stands, intensively managed (via selective timber harvest and prescribed fire), primarily composed of oaks (*Quercus*) and hickories (*Carya*), and characterized by steep, mountainous slopes consisting of limestone and sandstone ridges. Forest comprised the majority of the district (90%) with gravel roads, small wildlife openings, and recreational areas scattered throughout (10%). The forest-dominated area and karst geology support a diverse guild of 12 bat species, 2 of which (i.e., Indiana bat *Myotis sodalis* and gray bat *Myotis grisescens*) are federally listed as endangered and the northern long-eared myotis (*Myotis septentrionalis*) that is federally listed as threatened. From 1 June to 15 August, total precipitation for the Sylamore Ranger District was 239 mm in 2013 and 203 mm in 2014, while the total number of days with a maximum temperature exceeding 32.2°C was 25 in 2013 and 12 in 2014 (National Oceanic and Atmospheric Administration [NOAA] 2015).

Field Methods

We captured evening bats in June–August of 2013 and 2014 using triple-high and single-high mist nets placed above, or in the vicinity of ponds and streams. The following characteristics were recorded for all bat captures: sex, relative age (juvenile or adult), and reproductive condition (females: nonreproductive, lactating, or postlactating; males: reproductive or nonreproductive). We attached 0.33-g VHF transmitters (Model LB-2X, Holohil, Ontario, Canada) to the back of bats using Perma-Type or Skin Bond surgical cement. Pregnant bats were excluded. To ensure transmitter adhesion, bats, once affixed with transmitters, were held for 1–2 min 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 min to minimize capture-related stress. Additionally, tracking only started the following day to avoid monitoring abnormal behavior associated with capture-related stress. Using TRX-1000s receivers (Wildlife Materials International Inc., Murphysboro, Illinois) and 5-element folding Yagi antennas, 2–3 observers tracked bats 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 monitored for 3–8 days following capture and during the initial foraging bout, which lasted 1–3 h per night. All methods and procedures were conducted following guidelines of the American Society of Mammalogists (Sikes et al. 2011) and approved by the Arkansas State University Institutional Animal Care and Use Committee (IACUC protocol number: 451729-1).

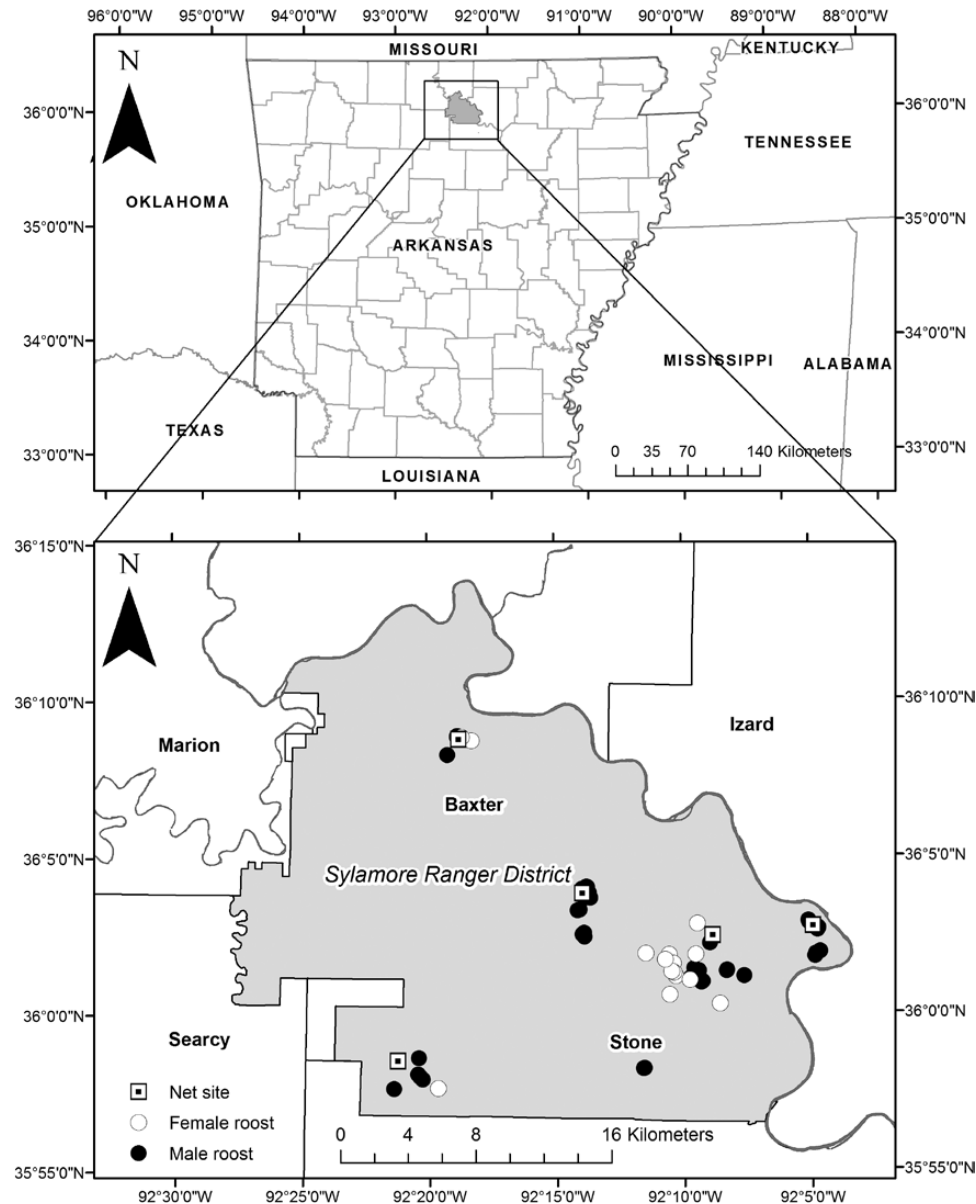


Fig. 1.—Location of net sites and roosts of evening bats (*Nycticeius humeralis*) in the Sylamore Ranger District, Ozark–St. Francis National Forest, Arkansas, during summers 2013 and 2014. See [Supporting Information S3](#) for more detailed maps of the roost locations with elevation contours and creeks.

Foraging habits.—Foraging locations were obtained by triangulation on 2-min intervals. Due to the steep mountainous terrain and dense forest canopy, transmitter signals were often not detected beyond 1 km, and radiotagged individuals from which we could obtain strong signals were often < 500 m from tracker locations. All bat locations were plotted in the field based on tracker locations and bearings, on a Garmin device with the Mapsource program 6.16.3 1999–2010 Garmin Ltd.

Roosting habits.—Bats were tracked to diurnal roosts each subsequent day following capture, and the location (GPS coordinates and elevation) of each roost tree was marked using a GPS unit. Additionally, aspect and slope were extracted using ArcMap (ArcGIS Version 9.3, ESRI). All suspected roost trees were identified to genus. At the roost level, we measured roost diameter at breast height (DBH), roost height using a

clinometer, and roost condition (i.e., decay stage; [Table 1](#)). At the plot level (0.1-ha plot surrounding each roost), we measured 1) canopy cover with a densiometer at 4 different locations equally spaced along the periphery of the plot, 2) number of small woody stems (> 1 m tall and < 5 cm DBH), 3) number of large woody stems (> 1 m tall and ≥ 5 cm DBH), 4) basal area with a forestry prism, 5) number of snags, and 6) relative overstory height (scale of 1–3 for roost > 1 m below, at the same height as, and > 1 m above surrounding canopy), following previous evening bat studies ([Boyles and Robbins 2006](#); [Perry and Thill 2008](#)). Additionally, for each plot with an identified roost tree (roost plot), we randomly selected a distance (between 40 and 100 m) and a direction (between 0 and 360°) to define a paired plot of the same size in which we recorded the same plot-level variables as in the roost plot.

Table 1.—Tree decay stages and description used to characterize evening bat (*Nycticeius humeralis*) day roosts. The following table was modified from [Boyles and 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%

Data Analyses

Foraging habits.—To quantify the spatial movements of evening bats during their primary foraging bout, we used both minimum convex polygon (MCP—[Mohr 1947](#)) and fixed kernel (FK—[Worton 1989](#)) with least squares cross-validation methods. FK requires independent locations, defined as allowing enough time for the animal to traverse its home range if desired ([White and Garrott 1990](#)). Given the speed of bat flight, we thus included all individuals with ≥ 20 locations ([Morris et al. 2011](#)) that were ≥ 5 min apart in FK analyses, following [Carter \(1998\)](#) and [De Solla et al. \(1999\)](#). In addition to foraging locations, the capture and diurnal roost locations were included in analyses as 1 independent location each. Because radiotracking 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.

Roosting habits.—For both males and females, we identified factors influencing diurnal-roost selection by comparing all roost- and plot-level variables measured at roost and random paired plots with Wilcoxon signed-rank tests. We used Wilcoxon rank-sum test to determine sex differences in roost characteristics. Sex differences in roost condition and relative overstory height were tested with a generalized Fisher's exact test. To determine frequency 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 were converted from angular to circular data and compared between sexes using a multivariate analysis of variance.

All roosting and foraging analyses were conducted using program R ([R Core Team 2014](#)). Foraging range estimates were made with the default bandwidth settings and calculated with the package “adehabitatHR” ([Calenge 2006](#)). Results are reported at $\alpha = 0.05$. All mean estimates are reported ± 1 SE and all median estimates are reported with 1st (*Q1*) and 3rd (*Q3*) percentiles [*Q1*–*Q3*].

RESULTS

During summers 2013 and 2014, we 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; $n = 5$]; *M. grisescens* [gray bat; $n = 16$]; *M. sodalis* [Indiana bat; $n = 6$]; *M. septentrionalis* [Northern long-eared bat; $n = 157$]; *Myotis lucifugus* [little brown bat; $n = 1$]; *Myotis leibii* [Eastern small-footed bat; $n = 1$]; *N. humeralis* [$n = 165$]; and *Perimyotis subflavus* [tricolored bat; $n = 18$]).

For evening bats, we captured 40 females and 95 males. They were captured significantly more in nets set over or near creeks than ponds (females: $\chi^2_1 = 36.1$, $P < 0.001$; males: $\chi^2_1 = 33.0$, $P < 0.001$). However, the proportion of captures at creeks versus ponds was significantly higher for females (97.5%) than for males (80%, $\chi^2_1 = 5.51$, $P = 0.019$). We radiotracked 70 of the 165 captured evening bats. Although transmitter battery life was 21 days, transmitter attachment lasted from 3 to 13 days with rain and extreme heat likely reducing duration of transmitter adherence. After 1 night of storms and substantial rainfall, 5 tagged bats all dropped transmitters on the same day. A similar event occurred to another group of 6 bats during a week of extreme heat ($> 34^\circ\text{C}$).

Foraging Habits

We recorded ≥ 20 independent locations for 24 (14 adult males and 10 adult and juvenile females) of the 70 radiotracked evening bats. Specifically, foraging ranges were estimated for 11 bats (9 males and 2 females) in 2013 and 13 (5 males and 8 females) in 2014 (see [Supporting Information S1](#)).

Individual evening bats used 1–7 core foraging areas ($\bar{X} = 1.8 \pm 0.3$; see [Supporting Information S2](#)). 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 ($W = 110$, $P < 0.01$). There was little spatial overlap among core foraging areas (see [Supporting Information S2](#)).

Mean 95% FK foraging range size of evening bats was 548 ± 108 ha, with variability among individuals (from 48 ha to 2,239 ha; see [Supporting Information S1](#)). The median 95% FK foraging range was lower for males (202.0 ha [109.6–400.8]) than females (556.4 ha [497.7–1190.0]) ($W = 23$, $P = 0.005$; see [Supporting Information S2](#)). Mean 95% MCP foraging range of evening bats was 165 ± 38 ha, with variability among individuals (from 14 to 491 ha; see [Supporting Information S1](#)) and between sexes. 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]; $W = 44$, $P = 0.138$; see [Supporting Information S2](#)).

Roosting Habits

Of the 70 radiotagged evening bats, 50 were successfully radiotracked to at least 1 roost tree, totaling 72 roosts identified during June–August 2013–2014. Specifically, we tracked 32 males to 57 roosts and 18 females to 15 roosts, and there seemed to be substantial spatial sexual segregation ([Fig. 1](#); see [Supporting Information S3](#)). Adult males and females were not found in the same roost. Males commonly switched roosts every 1–3 days with individuals exploiting 1–4 roosts ($\bar{X} = 1.7 \pm 0.1$). In contrast, females never exhibited roost-switching, only used 1 roost each for the duration of the study, and on 2 occasions, multiple radiotagged females used the same roost.

Number and genera 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 2). All but 1 females selected snags or live trees that were forked-top while males roosted in snags and under exfoliating bark of live and dead trees.

Roost tree variables.—No sex differences were detected for DBH and roost height (Supporting Information S4). No difference in roost decay stage was detected between sexes (Fisher's exact test: $P = 0.138$; Fig. 2A), but all evening bats used stage 1 (live) roosts significantly more than other decay stages and stage 4 (dead) roosts less than any other stage (G -test: $G_3 = 61.9$, $P < 0.001$).

Roost plot variables.—No differences were detected for any of the tested plot variables between roost and random paired plots for males or females (Supporting Information S4). There was no significant difference in median number of large or small woody stems, and snags between male and female roost plots, but medians for canopy cover (Fig. 3A) and basal area (Fig. 3B) were significantly higher at male than female roost plots. Median roost elevation was also significantly lower in males than females (Table 3; Fig. 3C). There was no significant difference in relative overstory height between sexes (Fisher's exact test: $P = 0.420$; Fig. 2B). Evening bats used roosts below or at the same level as relative overstory height significantly more than roosts higher than relative overstory height (G -test: $G_2 = 29.0$, $P < 0.001$). There was no significant difference in roost aspect and slope between sexes (approx. $F_{1,66} = 0.238$, $P = 0.789$; Fig. 4).

DISCUSSION

Understanding sex-specific foraging and roosting habitat 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). The present study, which represents the largest sample size of radiotracked evening bats, shows spatial sexual segregation in both foraging and roosting habits in this bat species, native of the United States.

Sex-Specific Foraging Habits

Because male and female evening bats have different energetic requirements, specifically those associated with female reproduction and rearing pups, foraging habits could differ between

Table 2.—Total number of diurnal roosts used by male and female evening bats (*Nycticeius humeralis*) per genus in the Sylamore Ranger District, Arkansas, during June–August, 2013 and 2014.

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

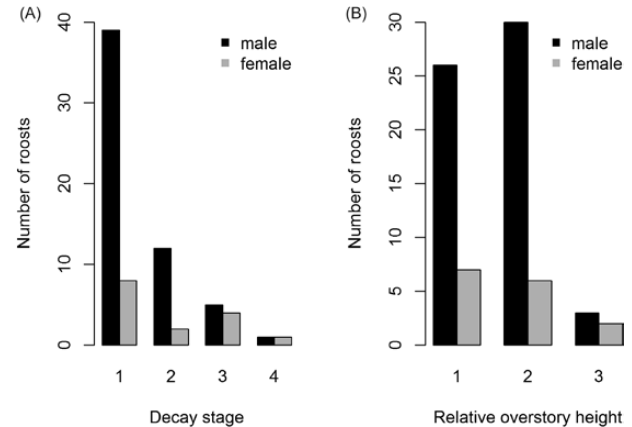


Fig. 2.—Roost and roost plot characteristics for male and female evening bats (*Nycticeius humeralis*) in the Sylamore Ranger District during June–August, 2013 and 2014. A) Number of roosts per decay stage (i.e., roost condition), with 1 for live tree (> 75% bark remaining), 2 for dying or partially dead (50–75% bark remaining), 3 for mostly dead (25–50% bark remaining), and 4 for dead (< 25% bark remaining). B) Relative overstory roost height (i.e., height of surrounding canopy), classified as 1 for a roost > 1 m below surrounding canopy, 2 for a roost at canopy height, and 3 for a roost > 1 m above surrounding canopy.

sexes. As predicted, there were differences in the space-use patterns of male and female evening bats, which were not detected by Morris et al. (2011) likely due to their smaller sample size ($N = 14$; 5 females and 9 males).

Female evening bats used fewer core areas than males but exploited a larger range. This difference 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 may be associated with males becoming reproductively active; yet, it remains unknown if females exhibit a similar pattern. Although our sample size was larger than in previous studies, it was still too small to test for the effects of reproductive status and age (i.e., adult versus juveniles) on foraging and roosting habits. The differing number of core areas and home range size between males and females suggest sex-specific needs, but the differing location of these core areas and the limited overlap of home ranges also suggest spatial segregation. Because of the reproductive-related energy requirements, females may have to select for predictable water sources, which is supported by our capture data, with females captured more at permanent than ephemeral water sources. We thus highly encourage future studies to thoroughly examine the influence of water availability and predictability on foraging habits of both sexes.

Our study shows sex-specific foraging habits in a bat species in the United States, but similar patterns have been documented elsewhere 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

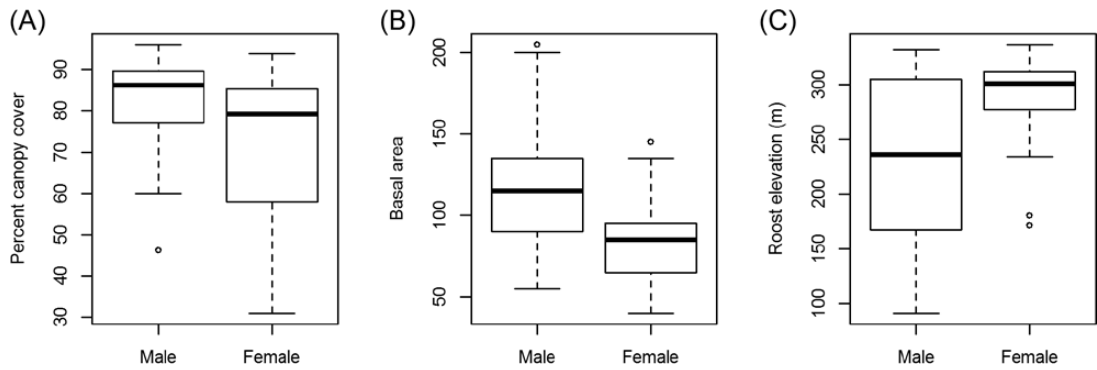


Fig. 3.—Sex-specific roost-site selection, A) percent canopy cover, B) basal area, and C) elevation measured at 57 male and 15 female evening bats (*Nycticeius humeralis*) in roosts and random paired plots in the Sylamore Ranger District during June–August, 2013 and 2014.

Table 3.—Means, *SEs*, and medians (*Mdn*) of 6 habitat variables measured at 72 roost plots in the Sylamore Ranger District during June–August, 2013 and 2014.

Variable	Male plot (<i>n</i> = 57)			Female plot (<i>n</i> = 15)			Wilcoxon test	
	\bar{X}	<i>SE</i>	<i>Mdn</i>	\bar{X}	<i>SE</i>	<i>Mdn</i>	<i>V</i>	<i>P</i>
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 (m²/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

contrary, for Daubenton’s bat (*Myotis daubentonii*—Encarnação 2012) in Germany and the big brown bat (*E. fuscus*—Wilkinson and 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 of ecological, morphological, and behavioral differences among species (Safi et al. 2007). Also, habitat varies among regions, and differences between sexes may be region specific.

Sex-Specific 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. Although we only tracked bats for an average of 4.32 days, we had a profound difference in roost-switching behavior between sexes. Similar to what Boyles and Robbins (2006) and Perry and Thill (2008) reported, male evening bats in the Sylamore Ranger District exhibited roost-switching. Females did not switch roosts during our study, unlike females in other populations (Bowles et al. 1996; Sparks et al. 1998; Miles et al. 2006; Hein et al. 2009). If females switched roost in our district, they did so much less frequently than males.

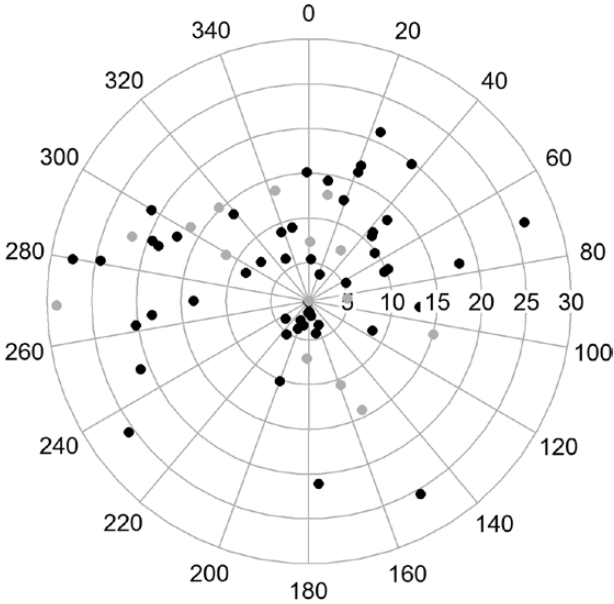


Fig. 4.—Polar plot illustrating roost aspect and slope of male (*n* = 53) and female (*n* = 15) roost plots of evening bats (*Nycticeius humeralis*) in the Sylamore Ranger District during June–August, 2013 and 2014.

Male and female evening bats selected roosts belonging to the most abundant genus (*Quercus*) in the District, with similar characteristics (i.e., height, DBH, and decay stage), which does not support the hypothesis of females being more selective than males. However, selective behavior may vary 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 with large-diameter trees (Hein et al. 2009). Males tracked during our study used a wider range of diameter roosts (from bark to cavity) than females (limited to cavities), and because females aggregate into colonies, they are likely more limited to larger diameter roosts capable of supporting multiple bats.

At the plot level, 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 and Thill (2008), male evening bats commonly roosted in un-thinned forest stands with small-diameter trees. 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. 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 (Encarnação et al. 2005). In the Sylamore Ranger District, changes in elevation were relatively small (i.e., 100–300 m) in comparison to previous studies conducted in landscapes with higher elevations. In the Ozarks, lower elevations such as mountain hollows and creek beds were generally cooler at night than locations along ridge tops. Temperature drops by 0.65–1°C every 100 m gained in elevation (Bharatdwaj 2006). Thus, seemingly contradictory results could be associated with differences in the range of elevation among study sites. Evening bats in the Sylamore Ranger District typically selected roosts below or equal to the relative overstory height. Assuming that the amount of shade provided by surrounding overstory influences internal roost conditions (e.g., temperature), the combination of low relative overstory height and high elevation may be associated with internal temperatures more beneficial for sustaining the thermoregulatory processes of reproductively active female bats (Menzel et al. 2001). Although slope and aspect of roost locations likely affects internal roost temperature through the amount of solar radiation received, these factors did not seem to influence sex-specific roost selection in the district.

Our results suggest that male and female evening bats segregate spatially, completely during the day (see Supporting Information S2) and less at night (see Supporting Information S3). Despite some overlap, they mostly exploit different foraging areas (in size, number, and location), with females avoiding ponds. There is an elevation effect in roosting habits that further separates sexes. However, roost aspect and slope did not seem to play a role in sexual segregation. Males and females also select roost trees with similar characteristics, but not only are they at different elevations, the surrounding habitat also differs in canopy cover and basal area. So, not only do sexes exhibit different habits, they do clearly segregate spatially. Further research should examine factors that drive sexual segregation,

e.g., parental investment (Safi et al. 2007), energetic requirements and social behavior (Encarnação 2012), intraspecific competition (Meyer et al. 2005), landscape type, population density, or bat guild diversity.

Though roost and foraging studies are generally conducted separately, the spatial relationship of these resources is critical to understanding how bats use forest habitats. A sex-specific evaluation is also critical because practices used to promote habitat conditions favorable for males may not be equally beneficial to females (Perry and Thill 2008). Yet, females are particularly important to protect due to their high level of parental investment associated with rearing pups. Our study emphasizes that management decisions based solely on male-focused studies or data pooled between sexes does not guarantee adequate protection of females.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Summary of capture and foraging data from all radiotracked evening bats providing relative age (adult versus juvenile), sex, month and year captured, number of independent locations, number of core foraging areas, and home range size of all evening bats ($n = 24$) radiotracked in the Sylamore Ranger District, Ozark–St. Francis National Forest during summers 2013 and 2014.

Supporting Information S2.—Foraging range and roost locations of all tracked evening bats tracked during summers 2013 and 2014, in the Sylamore Ranger Forest District, Arkansas.

Supporting Information S3.—Net sites and sex-specific roost tree locations in the Sylamore Ranger Forest District, Arkansas.

Supporting Information S4.—Roost and roost plot characteristics of evening bats, Sylamore Ranger Forest District, Arkansas.

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