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*Original Article*

# Selection of Tree Roosts by Male Indiana Bats During the Autumn Swarm in the Ozark Highlands, USA

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**ABSTRACT** We identified 162 roosts for 36 male Indiana bats (*Myotis sodalis*) across 3 study areas in the Ozarks of northern Arkansas, USA, during the autumn swarm (late Aug to late Oct, 2005 and 2006). Bats utilized 14 tree species; snags of shortleaf pine (*Pinus echinata*) were the most utilized (30% of roosts) and pines were selected over hardwoods. Diameter of trees and snags used for roosting ranged from 7.8 cm to 68.6 cm diameter at breast height (dbh), but bats used trees ≥20 cm dbh at a greater proportion than their availability. Roosts were located in a number of different forested cover classes, including shelterwood and group selection stands that had undergone partial harvesting. Roosts in 2 of 3 study areas showed no differences in proportional use of forest cover classes versus availability of those classes. However, in one study area, mature forests (≥50 yr old) that had been burned once recently and stands burned multiple times over the past 10 years were used at a greater proportion than their availability, whereas mature forests that were not burned were used at a lower proportion than their availability. An examination of stand age data indicated that 98% of all roosts were located in stands ≥38 years old, suggesting that this is an important age threshold for roost selection in the Ozark Mountains. Bats in 2 study areas roosted at lower slopes in the higher elevation portions of the study areas, whereas no selection for topographic aspect were observed in all 3 study areas. Our data indicate that perceived habitat selection by a species may differ within the same geographic region and these differences could be due to factors such as differing selection among individuals, differences in juxtaposition of landscape components and cover types, and differing biological components such as the distribution of predators and predator densities. Published 2016. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** Arkansas, autumn swarm, fall, forest management, hibernacula, Indiana bat, Ozarks, roost selection.

The federally endangered Indiana bat (*Myotis sodalis*) is an insectivorous species of the eastern United States that hibernates in caves, mines, and other structures during winter, but generally roosts in trees and snags in forests during summer. Prior to the introduction of the fungus *Pseudogymnoascus destructans* and the onset of white-nose syndrome (WNS), populations of Indiana bats in eastern portions of their range were increasing, whereas western populations were decreasing (Thogmartin et al. 2012). With the onset of WNS, this species has exhibited an annual decline, which has reversed population gains made in recent years (Thogmartin et al. 2012). Because bats with greater fat accumulation at the onset of hibernation may have better survival from WNS (Turner et al. 2014), providing adequate forest habitat during autumn may help maximize fat accumulations and could potentially reduce mortality from WNS (Perry 2013*a*). Consequently, managers need information on habitat use and selection by Indiana bats during autumn to ascertain what characteristics of forests are important for the continued existence of this species.

Roosts and food are the 2 most important resources known to affect the distribution and abundance of bats (Kunz and Lumsden 2003). Male Indiana bats reach their peak mass gain in October, just prior to entering hibernation (LaVal and LaVal 1980), and this fat accumulation is used to maintain bats through the winter hibernation. Mass gain by bats during the prehibernation period may be obtained more through the efficient use of torpor than increases in food consumption (e.g., Speakman and Rowland 1999, McGuire et al. 2009). Furthermore, deeper, energy-saving torpor may be obtained at cooler day-roost sites, and roosting at cooler temperatures during the prehibernation period may result in greater energy savings (Speakman and Rowland 1999).

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Therefore, selection of adequate roost sites may be equally or even more important than quality foraging sites during autumn for building fat stores that allow overwinter survival.

For Indiana bat roosting, multiple studies have examined hibernacula (e.g., Humphrey 1978, Tuttle and Kennedy 2002) and summer roost-site selection (e.g., Kurta et al. 1993, Callahan et al. 1997, Britzke et al. 2003), with most studies focusing on females. Only a handful of studies have examined male roost selection during autumn (Kiser and Elliott 1996, MacGregor et al. 1999, Brack 2006, Johnson et al. 2010). During autumn, Indiana bats swarm and mate near the entrances of hibernacula at night (Parsons et al. 2003). Females may roost in caves, but males continue to roost in trees during the day (LaVal and LaVal 1980). Female bats typically enter hibernation with greater mass than males (e.g., Jonasson and Willis 2011, Storm and Boyles 2011), and females may have greater survival through hibernation than males (e.g., Johnson et al. 2014). Therefore, information on autumn roost-site selection by males is important for understanding potential survival of the species.

We characterized roost trees and forested cover classes used by male Indiana bats during the autumn swarm in 3 separate study areas. We identified the sizes and species of trees used for roosting along with the forest cover classes where roosts were located. Our goal was to determine size and species of trees used for roosting and how forest age, timber harvest, and prescribed burning affects roost selection across multiple study areas.

## STUDY AREA

Our study was conducted on 2 Ranger districts (~88 km apart) of the Ozark National Forest in the Ozark Highlands of northern Arkansas, USA. We established 2 study areas (Amphitheater and Gustafson) on the Sylamore Ranger District in Stone County. These 2 areas were located in the White River Hills subsection of the Ozark Highlands, which was characterized by karst hills and valleys (180−500 m in elevation) and underlain by dolomite (Foti and Bukenhofer 1998). The third study area was located on the Big Piney Ranger District, located in Newton County, Arkansas. The Big Piney study area was in the Upper Boston Mountain subsection of the Ozark Highlands, which was characterized by low mountains (300−825 m in elevation) and underlain mainly by sandstone (Foti and Bukenhofer 1998). Vegetation in the Ozark Highlands region was primarily hardwood forest (mixed oak [*Quercus* spp.] and hickory [*Carya* spp.]) and mixed hardwood–pine (*Pinus echinata*) forests; however, pine-dominated forests, cedar (*Juniperus virginiana*) forest, and cedar glades were also present. Open pastures of tall fescue (*Schedonorus arundinacea*) and wildlife openings were present in all 3 study areas. The 3 study areas differed in the proportion of pine-, hardwood-, and cedar-dominated forest, with Amphitheater having the most pine- and cedar-dominated forest and Big Piney having the least (Table 1).

**Table 1.** Percent composition of 4 forest cover types for 3 study areas including Indiana bat roosts in the Ozark Highlands of Arkansas, USA during 2005–2006.

| Cover type | Amphitheater | Gustafson | Piney |
|---|---|---|---|
| Hardwood-dominated | 65 | 77 | 84 |
| Pine-dominated | 22 | 14 | 11 |
| Cedar-dominated | 10 | 4 | <1 |
| Grass, pasture, and farms | 1 | 2 | <1 |

Each study site was associated with one cave hibernaculum where bats were captured. The Amphitheater and Gustafson hibernacula were approximately 4.5 km apart. A portion of both of these 2 study sites included the Sylamore Experimental Forest. This area had been subjected to controlled burning 6 times during the previous 10 years on a 1–3-year rotation. Additional controlled burning had been conducted in all study areas; previous harvest and thinning treatments were found throughout all 3 study areas. Each cave was a priority 3 hibernaculum, with estimated populations (in the year 2000) of about 67 bats at the Big Piney site (Wolf Creek Cave), 360 at Amphitheater, and 525 at Gustafson (USFWS 2007).

## METHODS

### Bat Capture and Radiotracking

We captured Indiana bats periodically at cave entrances in the Amphitheater and Gustafson areas (23 Aug−14 Oct 2005), and at the Big Piney area (7 Sept−8 Oct 2006) using harp traps and mist nets. During trapping, we monitored traps continuously because of high capture rates. We expected low numbers of female captures during late summer–autumn in this region; therefore, we selected only males for study. We affixed captured males with 0.35–0.50-g transmitters (Model LB-2N; Holohil Systems Ltd., Carp, ON, Canada; Model LT6-337, Titley Scientific, Columbia, MO) with an expected lifespan of 12−21 days. Mean mass of captured males was 7.1 g (range = 6.3−8.5), and transmitters represented approximately 4.1−7.0% of bat body mass. We attached transmitters to the mid-scapular region using surgical adhesive (Skin-Bond, Smith and Nephew. Inc., Largo, FL). We followed the guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee 1998). All activities were conducted under federal endangered species permit TE75913-1 and Arkansas Game and Fish Commission permit 081620041.

We radiotracked bats the day after transmitters were affixed and monitored bats until no signal was received or the expected life of the transmitter was exceeded. We tracked bats daily to their roost trees on the Amphitheater and Gustafson areas from 24 August to 8 November (2005), and from 10 September to 22 October (2006) in the Big Piney area. We determined individual roost trees via triangulation of radio signals around the base of the tree.

### Roost and Site Characterization

For each roost tree, we recorded tree species, diameter at breast height (dbh), and measured tree height with a clinometer. To characterize sites where roosts were located and determine availability of trees, we measured diameter of all trees and snags ($\geq$5.0 cm dbh) and identified each tree or snag to species in a 10-m radius (0.03 ha) plot surrounding each roost. We measured canopy cover at 4 locations (90° apart) along the outer edge of each plot using a spherical densiometer and averaged these measures for the plot. We also measured canopy cover at the base of each roost tree in 4 cardinal directions with the observer's back against the trunk; these measures were averaged for each roost tree.

**Forest Stand Availability and Use**

We used coarse-level stand maps that included forest type, stand age, and management history obtained from Ozark National Forest inventory data to initially classify forest stand availability. Stand boundaries were modified and stand classifications were revised using year 2009 digital orthophoto quarter quads (DOQQs) obtained from the U.S. Department of Agriculture Farm Service Agency, National Aerial Imagery Program. Using these DOQQs and other cover layers (e.g., glade restoration areas, burn blocks) supplied by the Ozark National Forest, we added additional vegetation classes, including openings (wildlife food plots, pastures, and utility right-of-ways) and glades. For some stands (especially those on private lands), exact age was unknown so we estimated age using aerial photos (e.g., comparing the length of tree bole shadows and diameter of tree crowns with those of known-age stands in a photo). Although this method did not allow for precise estimates of stand age, the majority of these stands appeared mature and we classified them as >50 years old. Nevertheless, these stands comprised only 5.9% of the Amphitheater study area, 6.6% of the Gustafson study area, and 5.4% of the Big Piney study area. We classified open habitats (pastures, utility right-of-ways, etc.) as 0 years old. We also obtained burn maps and burn history information from the Ozark National Forest. We initially identified 22 different cover classes available in the study areas. However, because statistical power of habitat-use analyses are reduced with greater numbers of classes, we combined cover classes and burn history to derive 9 primary cover classes for analysis (Table 2). For burn history, we included 3 designations: 1) No burn = no history of burns or records indicated preceding burns were >5 years before the study; 2) One recent burn = burned once in the past 5 years; and 3) Multiple burns = burned multiple times ($\geq$5) in the past 10 years.

**Analysis**

We compared distance from roosts to hibernacula swarm sites where bats were captured among the 3 study areas using analysis of variance and Tukey's tests for pairwise comparisons. We compared the proportion of roosts in trees <20 cm dbh and $\geq$20 cm dbh with the availability of those 2 size classes using $\chi^2$ test for homogeneity (Marcum and Loftsgaarden 1980). Likewise, we used a similar test to compare proportion of roosts in pines and hardwoods (all species combined) with the proportional availability of those 2 groups. We compared densities of live trees and snags (by size classes) among the 5 primary cover types (based on percent of the landscapes) using mixed-model analysis of variance (PROC MIXED; SAS Institute Inc. 2014); we evaluated pairwise comparisons using Tukey tests (SAS Institute Inc. 2014). We evaluated all tests at $\alpha = 0.05$.

To determine use of forest cover classes, we collected global positioning system (GPS) coordinates for each roost location and overlaid these on vegetation maps in a geographic information system (ArcGIS) to determine the proportion of roosts in each cover type. Instead of using an arbitrarily defined study area to define available habitat, we estimated available cover classes that included only areas that bats had likely encountered. For each bat, we connected lines among all roost locations and the hibernaculum where the bat was captured to create a polygon. We then combined all polygons for bats captured at that hibernaculum and buffered this area by 100 m (Fig. 1). Total area included in polygons was

**Table 2.** Cover classes used for analysis of male Indiana bat roosts in the Ozark Highlands of Arkansas, USA (2005–2006), which include combined forest types, ages, and burn history.

| Cover class | Description |
|---|---|
| Mature, no burn | Mature ($\geq$50 yr old) hardwood, mixed hardwood–pine, pine, and cedar forest that had not been burned or was burned >5 yr previously. |
| Mature, one burn | Mature ($\geq$50 yr old) hardwood, mixed hardwood–pine, pine, and cedar forest that had been burned once in the past 5 yr. |
| Mature, multiple burns | Mature ($\geq$50 yr old) hardwood, mixed hardwood–pine, pine, and cedar forest that had been burned multiple times (>5 times in the past 10 yr). |
| Partial harvest, no burn | All forest stands that had been partially harvested using single-tree selection, seed-tree, group-selection, or shelterwood harvesting (regardless of forest type) that had not been burned or had been burned >5 yr previously. |
| Partial harvest, one burn | All forest stands that had been partially harvested using single-tree selection, seed-tree, group-selection, or shelterwood harvesting (regardless of forest type) that had been burned once in the past 5 yr. |
| Immature, no burn | Immature (16–49 yr of age) forests, including cedar, hardwood, pine, and mixed hardwood–pine that had not been burned or had been burned >5 yr previously. |
| Immature, one burn | Immature (16–49 yr of age) forests, including cedar, hardwood, pine, and mixed hardwood–pine that had been burned once in the previous 5 yr. |
| Open areas | Open areas with no mature trees. Included pastures that were primarily monotypic stands of tall fescue, farms, buildings, yards, and other landforms associated with human habitation. Also included wildlife food plots planted with various wildlife foods such as *Lespedeza*, *Triticum*, or *Secale*, and early successional forest (pine, hardwood, or cedar $\leq$15 yr of age, including overgrown fields dominated by woody plants). |
| Open with mature trees | Open areas with scattered mature trees, included pastures or food plots with trees and cedar glades, regardless of previous burns. |

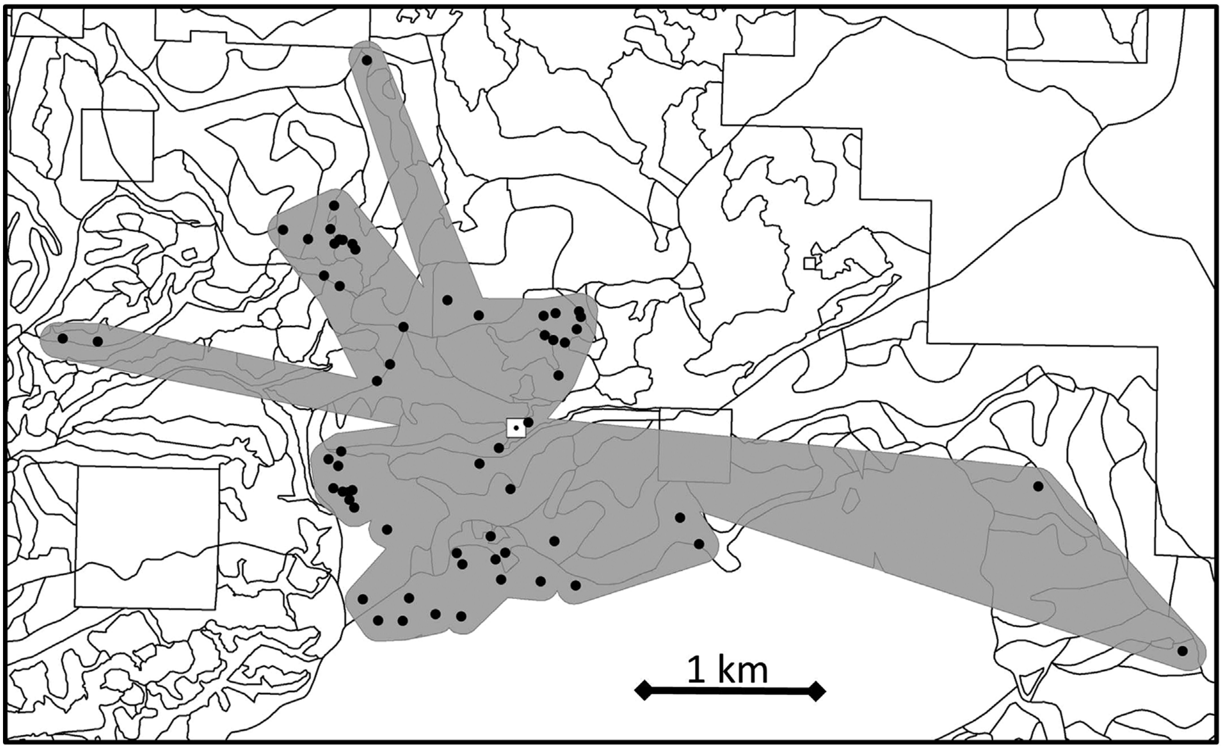


**Figure 1.** Example of available area for 1 of 3 study areas in the Ozark National Forest of Arkansas, USA, used for roosting by male Indiana bats during autumn, 2005–2006. Black circles represent roost location, the white square indicates swarming site (hibernacula) where bats were captured, dark lines indicate stand boundaries, and gray-shaded area is the designated area of available habitat.

1,039 ha for Amphitheater, 595 ha for Gustafson, and 833 ha for Big Piney. Two bats roosted substantial distances from the hibernacula where they were captured (9.8 and 11.6 km). Thus, roosts for these 2 bats were removed to reduce the vast area that would have been considered available if they were included. For each study area, we compared the proportion of roosts in each cover class with the proportion of available cover (based on area) using individual binomial tests. For each study area, we maintained the experiment-wise error rate for this analysis at 0.05 using the Benjamini–Hochberg method to control the positive false discovery rate (Benjamini and Hochberg 1995, Waite and Campbell 2006).

We compared topographic settings of roost locations with random locations to determine whether roosts differed in elevation, aspect, or slope position from random placement across the landscape. The GPS coordinates for roosts and random locations were overlaid on a 10-m digital elevation model in GIS. We generated 100 random locations within the available area for each of the 3 study areas using Geospatial Modeling Environment software (http://www.spatialecology.com/gme/), and obtained topographic variables for each roost and random coordinates using this software. We converted slope position into a continuous numeric variable, with bottomland = 1, lower slope = 2, middle slope = 3, upper slope = 4, and ridgetop = 5. We converted aspect (a circular variable) into a linear dimension using 2 variables: northness (cosine [aspect]) and eastness (sine [aspect]). Values for northness ranged from north = 1 to south = −1, whereas values for eastness ranged from east = 1 to west = −1 (Roberts 1986). We modeled these 4 topographic variables (elevation, slope position, northness, and eastness) using logistic regression (Hosmer and Lemeshow 2000) for each study area separately. We determined the most parsimonious models among 8 candidate models based on values of Akaike's Information Criteria for small samples ($AIC_c$; Burnham and Anderson 2002). We excluded models from the best set ($\Delta AIC_c \leq 2.0$) that contained parameters in which the 95% confidence interval for its odds ratio included 1 (uninformative parameters; Arnold 2010).

## RESULTS

We radiotagged 43 male Indiana bats. Transmitter signals were not located for 6 bats and 1 bat roosted exclusively in the cave hibernacula. Thus, we tracked 36 bats (13 at the Amphitheater site, 11 at the Gustafson site, and 12 at the Big Piney site) to 162 forest roost locations (58 at Amphitheater, 61 at Gustafson, and 43 at Big Piney). Mean number of roosts located for each bat was 4.6 (±0.4 SE) and ranged from 1 to 10. Average distance from forest roosts to swarming sites at cave entrances where bats were captured was 2.36 (±0.17) km and ranged from 34 m to 11.6 km. Distance from forest roosts to hibernacula swarm sites differed among the 3 study areas ($F_{2, 160} = 18.11$, $P < 0.001$). Mean distance from forest roosts to the Gustafson hibernaculum (1.11 ± 0.08 km) was less than those at the Amphitheater (3.22 ± 0.31 km) and Big Piney (2.96 ± 0.42 km) areas ($P < 0.001$). Three bats roosted substantial distances from the hibernacula where they were captured (6.9, 9.8, and 11.6 km). Another roost location was triangulated approximately 5.5 km from the swarm site, but we did not locate this roost.

## Roost Trees

Of the 162 roosts located, 157 were in trees or snags and 5 were in utility poles. Of the 157 roosts located in trees or snags, no plot data were collected for 15 ($n = 142$ tree roosts with surrounding plot data). Bats roosted in 14 tree species (Table 3). The tree species used most for roosting was shortleaf pine (30%), which comprised 22% of available trees. Based on proportion of pines and hardwoods used versus those available, pines were selected over all hardwood species combined ($\chi_1^2 = 13.4$, $P < 0.001$). Although shagbark hickory (*Carya ovata*) comprised <1% of available trees, 13% of roosts were in this species and most (89%) of those were live trees. Five tree types (shortleaf pine, white oak [*Quercus alba*], red oak [*Q. rubra*], maples [*Acer rubra* and *A. saccharum*], and shagbark hickory) comprised 77% of tree roosts. Most roosts (64%) were located in snags, which comprised only 16% of available trees, and the most frequently used substrate for roosting were shortleaf pine snags (30% of all roosts), which comprised <4% of available trees.

Mean diameter of roost trees was 29.0 ± 1.1 cm and ranged from 7.8 cm to 68.6 cm dbh (Table 3). The majority of roosts (54%) fell in the 10–30-cm dbh size range, but 31% of roost trees and snags were <20 cm dbh (Fig. 2). Nevertheless, trees <20 cm dbh were used less than their availability and trees ≥20 cm dbh were used more than their availability ($\chi_1^2 = 83.1$, $P < 0.001$). Mean height of live trees used for roosting was 22.3 m (±0.9; range = 4.3–33.3 m) and mean height of snags used for roosting was 13.5 m (±0.6; range = 1.4–34.6 m).

## Roost Stands

Forest stands used for roosting ranged from 25 to >100 years of age. However, an examination of stand age data where roosts were located indicated that 98% of all roosts were in stands dominated by an overstory ≥38 years old. These stands included pine stands, hardwood stands, and mixed pine–hardwood stands. We found 2 roosts in shelterwood stands and 1 roost in a group-selection stand, which comprised only 0–4% of the available stands, depending on study area (Table 4). We found no significant differences in proportional use and availability among forest cover classes in the Big Piney and Gustafson study areas (Table 4). However, in the Amphitheater area, mature forests (≥50 yr old) that had been burned once recently or burned multiple times over the past 10 years were used more than their availability and mature forests that were not burned were used less than their availability (Table 4). The majority of all roosts in all areas (54% of 154 roosts) were in mature stands that had not been burned recently, but this cover class comprised the majority of forest in all 3 study areas.

Sites of roosts in the 5 most abundant cover classes did not differ in the density of trees or snags ≥30 cm dbh (Table 5). Roost locations in immature forest stands that had not been burned had the greatest overall live-tree densities, and greater density of live midstory trees (5–14.9 cm dbh) than mature cover types. Mature and immature stands that had undergone a single recent burn generally had greater densities of medium-sized snags (15–29.9 cm dbh) than other cover types. Mean canopy closure in plots surrounding roost trees was 87.5% (±0.9%; range = 7–96%), and mean canopy cover at the roost tree was 87.3% (±0.9%; range = 14–96%).

## Elevations and Slope Position

For the Amphitheater and Gustafson study areas, only the top model contained informative parameters (95% CI for odds ratios did not include 1), and none of the top 3 models ($\Delta AIC_c < 2.0$) for the Big Piney area contained informative

**Table 3.** Percent of available trees from plots (% Available), number (and percent of total) of live trees and snags used for roosting by male Indiana bats, and size range (cm dbh) of tree species used for roosting in 3 study areas in the Ozark Highlands of Arkansas, USA, 2005–2006. Only trees ≥5.0 cm dbh were included in available tree proportions.

| | | No. of roosts (%)[b] | | | |
|---|---|---|---|---|---|
| Species | % Available[a] | Live | Dead | Total | Roost-tree size range (cm dbh) |
| Shortleaf pine (*Pinus echinata*) | 22 | 1 (<1) | 42 (30) | 43 (30) | 10.5–68.6 |
| White oak (*Quercus alba*) | 18 | 15 (11) | 8 (6) | 23 (16) | 14.2–65.0 |
| Hickory (*Carya* spp.; 4 spp.) | 11 | 4 (3) | 3 (2) | 7 (5) | 7.8–49.7 |
| Flowering dogwood (*Cornus florida*) | 9 | 1 (<1) | 2 (1) | 3 (2) | 9.5–11.8 |
| Red oak (*Quercus rubra*) | 6 | 5 (4) | 8 (6) | 13 (9) | 12.1–44.1 |
| Maple (*Acer rubra/saccharum*) | 6 | 3 (2) | 9 (6) | 12 (8) | 9.5–20.5 |
| Blackgum (*Nyssa sylvatica*) | 4 | 1 (<1) | | 1 (<1) | 23.3 |
| Ash (*Fraxinus pennsylvanica/americana*) | 3 | 1 (<1) | 2 (1) | 3 (2) | 35.5–44.0 |
| Black oak (*Quercus velutina*) | 3 | | 4 (3) | 4 (3) | 13.5–27.5 |
| Elms (*Ulmus* spp.) | 3 | 1 (<1) | 4 (3) | 5 (4) | 19.5–47.8 |
| Unknown hardwood snag | 3 | | 5 (4) | 5 (4) | 18.7–36.0 |
| Sassafras (*Sassafras albidum*) | 2 | 1 (<1) | 2 (1) | 3 (2) | 11.0–21.4 |
| Sweetgum (*Liquidambar styraciflua*) | 2 | 1 (<1) | | 1 (<1) | 46.5 |
| Shagbark hickory (*Carya ovata*) | <1 | 17 (12) | 2 (1) | 19 (13) | 23.0–58.0 |
| Other (22 tree species) | 7 | | | | |
| All species | 100 | 51 (36) | 91 (64) | 142 (100) | 7.8–68.6 |

[a] Percent based on 3,836 live trees and snags ≥5.0 cm dbh located in surrounding plots.
[b] No. (and percent) of 142 roosts located in trees or snags; excludes 5 roosts located in utility poles and 15 roost trees without surrounding plot data. These 15 roosts included 4 red maples, 1 hickory, 1 flowering dogwood, 1 ash, 4 shortleaf pines, 3 oaks, and 1 black locust (*Robinia pseudoacacia*).

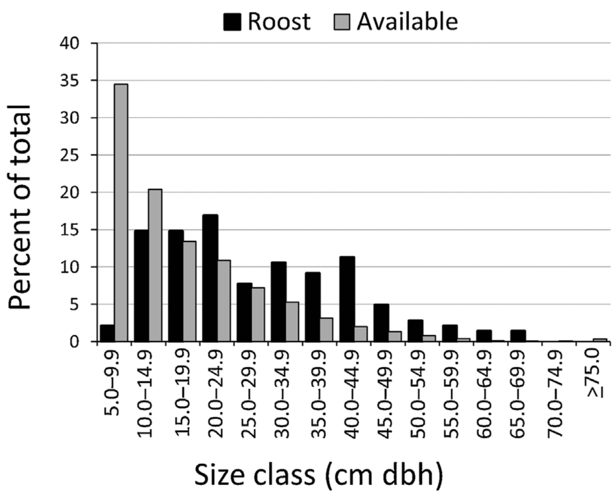


**Figure 2.** Size distribution (cm dbh) of available trees and snags versus percent of 142 roost trees and snags used by male Indiana bats during autumn in 3 study areas of the Ozark Highlands of Arkansas, USA, 2005–2006. Percent available was based on 3,836 total trees and snags in plots.

parameters (Table 6). In both the Amphitheater and Gustafson areas, the single best model contained slope position and elevation. These 2 models indicated bats were slightly more likely to roost at higher elevations, but more likely to roost at lower slope positions (Table 7). These models suggested that bats in 2 of the study areas tended to roost in the higher elevation portions within the study area, but roosted at lower slope positions in those areas. Aspect on the landscape (northness and eastness) did not appear to significantly affect roost placement in any of the study areas.

## DISCUSSION

Adult male Indiana bats exhibited flexibility in both the tree size (7.8–68.6 cm dbh) and tree species (14 species) selected for roosting during late summer and autumn, but bats generally selected pine snags and trees ≥20 cm. Tree diameters used for summer roosting by females in other regions of the United States, including Indiana, Missouri, and Michigan, are generally large ($\bar{x} = 41-62$ cm; USFWS 2007). Although average tree diameter used by males in this study (29.0 cm) was smaller than those used by females during summer, diameters were comparable to other studies of male roosting during autumn (e.g., average of 27.4 cm; Kiser and Elliott 1996).

Two tree species (shortleaf pine and shagbark hickory) comprised 42% of all roosts. Indiana bats are commonly found roosting in pine snags in southerly portions of their range (Kiser and Elliott 1996, MacGregor et al. 1999, Britzke et al. 2003). Further, the similarly roosting species, northern longed-eared bat (*Myotis septentrionalis*), also selected pine snags over hardwood snags in Arkansas (Perry and Thill 2007). The exfoliating bark on snags likely provides roosting habitat for only a short period (<3 yr). For example, Gardner et al. (1991) found 54% of hardwood snags used for roosting by Indiana bats were unusable 2 years later. Although shagbark hickory was relatively rare in our study areas (<1% of available trees), it comprised 12% of roosts. The peeling bark on live shagbark hickories could provide roosting habitat for decades, and roost stability could explain why shagbark hickories are widely used throughout the range of the Indiana bat during summer (e.g., Gardner et al. 1991, Callahan et al. 1997, Ford et al. 2002, Brack and Whitaker 2004).

We found a small number of roosts in utility poles and this behavior appears to be relatively common in cavity-roosting species, including Indiana bats. Similar utility-pole roosts were used by Indiana bats in northern Arkansas (Harvey 2002) and elsewhere (Hendricks et al. 2004, Stone and Battle 2004), and used by other bat species including northern long-eared bats (Sparks et al. 2004) and big brown bats (*Eptesicus fuscus*; Winterhalter 2004).

We found most roosts of males during autumn were in areas with relatively moderate canopy, with mean canopy

**Table 4.** Percent of each cover class available (% Avail.), number of Indiana bat roosts in that class (No.), percent of roosts in that class (%), and unadjusted *P*-values based on multiple binomial tests comparing use to availability in 3 study areas (Amphitheater, Gustafson, and Big Piney) of the Ozark National Forest of Arkansas, USA, 2005–2006.

| | Amphitheater ($n = 53$)[a] | | | | Gustafson ($n = 61$) | | | | Big Piney ($n = 40$)[a] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Roosts | | | | Roosts | | | | Roosts | | |
| Cover class | % Avail. | No. | % | *P* | % Avail. | No. | % | *P* | % Avail. | No. | % | *P* |
| Mature, multiple burns | 36.86 | 31 | 58.49 | 0.001* | 18.32 | 11 | 18.03 | 0.954 | | | | |
| Mature, one burn | 2.50 | 4 | 7.55 | <0.001* | 7.56 | 1 | 1.64 | 0.080 | 4.68 | 5 | 12.50 | 0.019 |
| Mature, no burn | 41.00 | 7 | 13.21 | <0.001* | 60.84 | 45 | 73.77 | 0.039 | 82.23 | 32 | 80.00 | 0.714 |
| Partial harvest, no burn | | | | | 3.87 | 2 | 3.28 | 0.811 | | | | |
| Partial harvest, one burn | 0.38 | 1 | 1.89 | 0.075 | | | | | | | | |
| Immature, no burn | 9.62 | 10 | 18.87 | 0.022 | 6.55 | 0 | 0.00 | 0.039 | 9.96 | 3 | 7.50 | 0.603 |
| Immature, one burn | 0.38 | 0 | 0.00 | 0.653 | 1.34 | 2 | 3.28 | 0.188 | | | | |
| Open with mature trees | 6.74 | 0 | 0.00 | 0.050 | 0.17 | 0 | 0.00 | 0.747 | | | | |
| Open areas[b] | 2.50 | 0 | 0.00 | | 1.34 | 0 | 0.00 | | 3.12 | 0 | 0.00 | |

[a] Did not include 5 roosts in the Amphitheater area from one bat that roosted 9.8 km from the hibernaculum (all 5 roosts in an immature stand burned once) and 3 roosts from another bat in the Big Piney study area that roosted 11.6 km from the hibernaculum (2 roosts in an immature stand burned once and 1 roost in a mature stand burned once). These roosts were not included in analyses to reduce vast areas that would have been considered available habitat. Missing cover classes in table were considered not available in that study area.

[b] Not included in analyses because of lack of roosting habitat in that cover class.

* *P*-value significant at $\alpha = 0.05$ after controls to maintain experiment-wide error (false discovery rate) within each study area.

**Table 5.** Comparison of mean (± SE) snag and live-tree densities (number/ha) by size class in 5 primary forested cover classes (Mat. = mature [≥50 yr old] and Imm. = immature [16–49 yr old]) distributed among 3 study areas in the Ozark National Forest of Arkansas used for roosting by male Indiana bats during fall, 2005–2006.

| | | Snag size classes (cm dbh) | | | | | | | | Live tree size classes (cm dbh) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 5–14.9 | | 15–29.9 | | ≥30 | | Total | | 5–14.9 | | 15–29.9 | | ≥30 | | Total | |
| Cover class[a] | $n$[a] | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE |
| Mat. >1 burn | 40 | 103AB[b] | 13 | 36A | 5 | 13 | 3 | 152A | 14 | 353A | 54 | 252A | 19 | 100 | 9 | 706AB | 59 |
| Mat. 1 burn | 10 | 92AB | 21 | 80AB | 28 | 16 | 7 | 188AB | 36 | 188A | 45 | 92B | 24 | 127 | 22 | 407A | 69 |
| Mat. no burn | 70 | 63A | 9 | 48A | 9 | 17 | 3 | 128A | 16 | 292A | 23 | 165B | 12 | 125 | 9 | 582A | 28 |
| Imm. 1 burn | 9 | 138AB | 63 | 138B | 34 | 11 | 8 | 286B | 59 | 502AB | 84 | 407C | 76 | 74 | 17 | 983BC | 104 |
| Imm. no burn | 11 | 151B | 46 | 29A | 13 | 6 | 4 | 185AB | 51 | 848B | 202 | 454C | 92 | 116 | 34 | 1,418C | 258 |

[a] Includes only roosts with surrounding plot data ($n = 140$ roosts); partially harvested stands were not included in analysis because of low sample size ($n = 2$ roosts with plot data and 1 roost without plot data). No roosts were located in open or open with mature tree cover classes.

[b] Within columns, means followed by like letters were not significantly different based on ANOVA and post hoc Tukey's tests at $\alpha = 0.05$.

closure at the roost tree of 87%. Compared with other studies (summarized in USFWS 2007), canopy closure at roost sites in this study was substantially greater than most (including many studies of males), but similar to results found by Schultes (2002) for males (81%). Reproductive female bats during summer may select trees with sparse canopy cover, which may allow sun exposure and warmer temperatures for development of young (Racey 1982, Callahan et al. 1997, Britzke et al. 2003); whereas, males may seek roosts with cooler temperatures to conserve energy (Callahan et al. 1997). Because male Indiana bats achieve maximum mass gain in October prior to hibernation (LaVal and LaVal 1980), shadier roosts may provide cooler temperatures for males in the autumn, which would allow deeper torpor, greater energy savings, and increased fat reserves for hibernation.

Distances from swarm site to roosts for 3 bats (6.9–11.6 km) were greater than what others have reported for male Indiana bats during autumn. Maximum distances between roosts and swarm sites for males reported by others are approximately 2.4–3.4 km (e.g., Kiser and Elliott 1996, Kurta 2000). Male Indiana bats may travel long distances between day roosts and swarming sites (USFWS 2007). Further, male Indiana bats visit multiple hibernacula during the autumn swarm (Cope and Humphrey 1977), and bats likely visit some swarming sites that are significant distances from their roost locations during autumn. Nevertheless, traveling these greater distances may have been attributed to

**Table 6.** Akaike's Information Criteria for small samples ($AIC_c$), difference ($\Delta AIC_c$) between $AIC_c$ and the best-approximating model, and generalized $R^2$ for logistic regression models comparing topographic parameters of roost and random locations for Indiana bats in 3 study areas of the Ozark Highlands of Arkansas, USA, 2005–2006. None of the top 3 models for the Big Piney area contained informative parameters (95% CI for all odds ratios included 1).

| Study area | Model | $AIC_c$ | $\Delta AIC_c$ | $R^2$ |
|---|---|---|---|---|
| Amphitheater | | | | |
| | Elevation + slope position | 163.12 | 0.00 | 0.271 |
| | Elevation + slope position + northness | 163.93 | 0.81 | 0.280 |
| | Elevation + slope position + eastness | 164.99 | 1.87 | 0.272 |
| | Elevation + slope position + northness + eastness | 165.67 | 2.56 | 0.282 |
| | Elevation | 181.46 | 18.34 | 0.111 |
| | Slope position | 193.47 | 30.35 | 0.005 |
| | Northness | 195.69 | 32.58 | 0.023 |
| | Eastness | 197.20 | 34.08 | 0.009 |
| Gustafson | | | | |
| | Elevation + slope position | 198.34 | 0.00 | 0.114 |
| | Elevation + slope position + eastness | 199.39 | 1.05 | 0.122 |
| | Elevation + slope position + northness | 200.39 | 2.06 | 0.114 |
| | Elevation + slope position + northness + eastness | 201.47 | 3.13 | 0.122 |
| | Slope position | 208.56 | 10.22 | 0.014 |
| | Elevation | 209.23 | 10.89 | 0.008 |
| | Eastness | 218.42 | 20.09 | 0.001 |
| | Northness | 219.55 | 21.21 | 0.001 |
| Big Piney | | | | |
| | Slope position | 163.66 | 0.00 | 0.271 |
| | Elevation | 164.06 | 0.40 | 0.280 |
| | Elevation + slope position | 165.59 | 1.93 | 0.272 |
| | Elevation + slope position + northness | 166.55 | 2.89 | 0.111 |
| | Elevation + slope position + eastness | 167.15 | 3.49 | 0.282 |
| | Elevation + slope position + northness + eastness | 168.16 | 4.49 | 0.005 |
| | Eastness | 170.20 | 6.54 | 0.015 |
| | Northness | 171.20 | 7.54 | 0.005 |

**Table 7.** Parameter estimates, standard error of the estimate (SE), odds ratios, and 95% confidence intervals for the odds ratios for parameters included in the best model comparing topographic properties of Indiana bat roost locations with random locations in 2 study areas of the Ozark Highlands, Arkansas, USA, 2005–2006. No parameters were significant in models for the Big Piney study area.

| Study area | Parameter | Odds ratio estimate | SE | Odds ratio | 95% CI |
|---|---|---|---|---|---|
| Amphitheater | | | | | |
| | Elevation | 0.033 | 0.007 | 1.033 | 1.020–1.047 |
| | Slope position | −1.217 | 0.300 | 0.296 | 0.165–0.533 |
| Gustafson | | | | | |
| | Elevation | 0.030 | 0.009 | 1.030 | 1.012–1.049 |
| | Slope position | −1.139 | 0.341 | 0.320 | 0.164–0.624 |

a lack of adequate swarming sites in the vicinity where the bats roosted.

We found bats roosting in all forested cover classes except for open areas with or without scattered trees (pastures, wildlife food plots, early successional forests, and cedar glades). Consequently, male Indiana bats during autumn did not appear to be particularly selective as long as relatively mature trees and snags were available. Although 14% of roosts were in immature stand classes (<50 yr old), nearly all roosts (98%) were in stands ≥38 years old, suggesting that this age appears to be an important threshold for roost selection by male Indiana bats during autumn. Indiana bats are often found roosting in a variety of managed forest habitats during autumn, including selective cut, clearcut, shelterwood stands, and burned woodlands (MacGregor et al. 1999, Brack 2006). MacGregor et al. (1999) suggested that timber harvesting using 2-age shelterwood cutting, along with retention of abundant snags, can provide favorable roosting habitat for males during autumn. Although partially harvested stands represented a small proportion of available habitat (0–4% depending on the area) in our study, we found a similar proportion of roosts (2%) in these partially harvested stands, suggesting male Indiana bats during autumn freely roosted in these partially harvested stands.

Our results indicted male Indiana bats responded to burned stands either positively (Amphitheater area) or showed no selection (Gustafson and Big Piney areas). Biological reasons for selecting areas burned multiple times are unclear for males during autumn. Large-snag (≥30 cm dbh) densities and overall snag densities were similar among the mature forest classes and midstory (5–14.9 cm dbh) tree densities (which contribute to clutter in a stand) were intermediate among the cover classes. Similarly, MacGregor et al. (1999) found male Indiana bats during autumn roosted twice as often as expected in an area burned frequently for red-cockaded woodpeckers (*Picoides borealis*) during 1 of 2 years of sampling. Johnson et al. (2010) suggested burning provoked minimal responses in roosting by male Indiana bats but likely created additional roost resources such as snags. It should be noted that the areas burned multiple times in this study were not subjected to thinning. Thinning may have a greater influence on overall bat activity than burning alone (Loeb and Waldrop 2008). Close proximity to areas of abundant insect production may have affected selection of these sites because frequently burned areas could be conducive to greater densities of flying insects. For example, Lacki et al. (2009) found a 34% increase in nocturnal insects used by bats in burned areas during the first year following spring burns in Kentucky.

Others have suggested that Indiana bats select ridge tops and upper slopes for roosting (Kiser and Elliott 1996, USFWS 2007). However, we found male Indiana bats during autumn did not appear to select upper slope positions for roosting, but tended to be more concentrated in lower slope areas in the higher elevation portions of the study areas. Other studies suggest Indiana bats may roost closer to streams than random (e.g., Kurta et al. 2002, Johnson et al. 2010), and lower slopes in our study areas were closer to streams than to upper slope areas. Furthermore, slope air drainage often creates cooler lower slope areas across a landscape (Perry 2013*b*), which could provide cooler areas where torpor depth can be maximized.

Separate studies on habitat use by the same bat species often show differences in habitat use and selection. For example, Broders and Forbes (2004) found female northern long-eared bats selected roosting in mature, shade-tolerant deciduous stands in New Brunswick, Canada, whereas Perry and Thill (2007) found they selected open pine stands for roosting in Arkansas. Differences such as these are often attributed to differences in ecosystems found among regions where the studies occurred, such as the dominant forest types, latitude, or climate. We found differences in habitat selection existed among our 3 study areas, which were all similar in latitude and forest type. The reasons that these differences occurred are unknown, but could have been attributed to selection of individual bats within each study group; differences in juxtaposition of various landform components, such as streams, mountains, open areas, mature forests, roads, and utility right-of-ways in each study area; differences in biological components such as predator abundance among study areas; or selection may have been a statistical artifact. Nevertheless, researchers should be cognizant of the potential for differences in habitat use or seemingly different use among areas separated by only a few kilometers.

## MANAGEMENT IMPLICATIONS

During the autumn swarm, male Indiana bats in the Ozarks did not appear to be particularly selective for forest cover classes as long as relatively mature trees and snags were available in lower slope areas. Large and small pines, hardwoods, snags, and live trees were used for roosting. However, larger pine snags (>20 cm dbh) and mature shagbark hickory appear to be important species for roosting in this region. Bats used various forested cover classes, including stands that were partially harvested and immature (<50 yr old) stands, and bats commonly roosted in stands that had undergone controlled burning; bats used burned forest more than its availability in one study area. Consequently, maintaining stands ≥38 years old and/or stands with abundant mature trees (≥20 cm dbh) in close proximity to hibernacula will likely provide suitable habitat for male Indiana bats during the autumn swarm and could reduce energy expenditure associated with travel between swarming sites and roost sites.

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