Overlap in Roosting Habits of Indiana Bats (Myotis sodalis) and Northern Bats (Myotis septentrionalis)

JOHN C. TIMPONE,1 JUSTIN G. BOYLES,2 KEVIN L. MURRAY,3 DOUG P. AUBREY4 AND LYNN W. ROBBINS
Biology Department, Missouri State University, Springfield, Missouri 65897

ABSTRACT.—Roosts are an integral habitat component for species of bats and may affect their survival and fitness. Conversion of forests to agricultural and urban areas may decrease available roosting habitat for the endangered Indiana bat (Myotis sodalis). Furthermore, the effects of habitat loss could be exacerbated if sympatric species favor and compete for similar roost-sites. We used radio-telemetry to study roosting habits of two species of Myotis in northeastern Missouri. We did not directly test for competition between these species for maternity roosts; rather, our goal was to determine if similarities in roost site characteristics were strong enough to warrant further investigation into competition for maternity roosts. Of 118 roosts located throughout the study, 79 were used by Indiana bats and 39 by northern bats (M. septentrionalis). Differences in roost structure (natural vs. manmade), tree status (live vs. snag), roost type (bark vs. cavity/crevice) and canopy coverage indicate that subtle, but biologically important differences exist in roost selection. Northern and Indiana bats both relied heavily on trees as roost sites; however, Indiana bats roosted in trees with lower canopy cover and less often in cavities and live trees than northern bats. Our results suggest that niche separation in roost selection exists between northern and Indiana bats.

INTRODUCTION

The availability of adequate roosts is critical for bats and may affect population size and species distributions (Humphrey, 1975; Kunz, 1982). Roosting habitat in the form of caves, mines or bridges is relatively easy to identify and protect (Tuttle and Kennedy, 1999), but this only partially protects many species of bats. Many North American species occupy caves only during hibernation, emerging in spring and dispersing to forest habitat where they form maternity colonies in trees.

Due to similarities in characteristics of tree-roosts used by forest-dwelling species of bats (Vonhof and Barclay, 1996; Timpone et al., 2006), there is potential for niche-overlap (MacArthur and Levins, 1967). Studies examining resource partitioning among bats have focused primarily on feeding (Belwood, 1979; Hickey et al., 1996; Carter et al., 2004), although it has been suggested that distributions of species of bats may be influenced by competition for roosts (Perkins, 1996). This could have implications for management of endangered Indiana bats, who may be roost specialists (Humphrey et al., 1977; Gardner et al., 1991; Kurta et al., 1996; Callahan et al., 1997; Kurta and Murray, 2002), and whose tree-roosts often occur in agricultural areas with highly fragmented forests (Menzel et al., 2005).

The Indiana bat was listed as federally endangered in 1967. While recent surveys indicate that Indiana bat populations are increasing in many states (USFWS, 2007), those in Missouri continue to decline. Data from the latest statewide census show an overall decrease of 95% since 1979 (Elliott, 2008). The northern bat is widely distributed in the eastern and north-
central United States and southern Canada. Both Indiana and northern bats are obligate forest species, where they rely heavily on trees as roosts (Sasse and Pekins, 1996; Foster and Kurta, 1999; Menzel et al., 2002; Carter and Feldhamer, 2005).

Concurrent comparisons of roosting habitat used by sympatric species can provide valuable knowledge concerning potential for interspecific interactions (Vonhof and Barclay, 1996; Foster and Kurta, 1999; Cryan et al., 2001; Carter and Feldhamer, 2005; Vonhof and Gwilliam, 2007). Indiana and northern long-eared bats commonly are sympatric and use similar trees as maternity roosts (Gardner et al., 1991; Sasse and Perkins, 1996; Callahan et al., 1997; Foster and Kurta, 1999; Cryan et al., 2001; Carter and Feldhamer, 2005). To date, two studies have compared the roosting habits of these two sympatric species (Foster and Kurta, 1999; Carter and Feldhamer, 2005). These studies showed that Indiana bats often choose roosts with very specific characteristics (e.g., high solar exposure, sloughing bark), whereas northern bats were more flexible in roost selection.

The purpose of this study was to characterize summer roost trees used by Indiana and northern bats to evaluate the degree of overlap in roost-site selection. Specifically, we were interested in determining if roost selection of these two species is similar enough that competition may occur if roosts become a limiting resource.

**STUDY AREA**

**MATERIALS AND METHODS**

We conducted this study on Deer Ridge Conservation Area (DRCA; 40°10′N, 91°49′W) and surrounding private lands in Lewis County, Missouri. Over 75% of DRCA’s 2800 ha were forested, whereas remaining habitat included old fields and wetlands. The majority of forested areas (90%) were upland hardwoods, including white oak (*Quercus alba*), northern red oak (*Quercus rubra*) and several species of hickory (*Carya spp.*). The remaining forests were bottomland hardwoods comprised largely of silver maple (*Acer saccharinum*), American elm (*Ulmus americana*), pin oak (*Quercus palustris*), sycamore (*Platanus occidentalis*), cottonwood (*Populus deltoides*) and swamp white oak (*Quercus bicolor*). DRCA harbors one of the largest tracts of remnant bottomland forest in northeastern Missouri, with river-to-upland floodplains 350–600 m wide (Root et al., 2003).

Upland forest habitat is managed by timber stand improvement and selective tree harvests which create a mixed-age stand with scattered canopy openings. Experimental clearcuts (CC) and basal-area-retention harvest plots (BAR) were created during late summer 1999 and winter 2000 on 50 ha of bottomland forest (Missouri Department of Conservation, 2000). In clearcuts, all stems >2.5 cm diameter at breast height (dbh) were cut. In BAR harvest plots, approximately 4.6 m² basal area/ha of “desirable” species (e.g., a mix of oak, maple, hackberry (*Celtis spp.*), ash (*Fraxinus spp.*)) was retained, whereas all stems >11.4 cm dbh were cut.

**DATA COLLECTION**

We captured bats in mist nets (10 m high, 6–18 m wide) placed over streams, ponds, sloughs, horse-trails and service roads from mid-May to mid-Aug. 2001 and 2002. Capture periods began at sundown and usually lasted until 0100 h. Individuals were identified to species, sexed and aged based on the degree of epiphyseal ossification (Anthony, 1988). We determined pregnancy by palpation of the abdomen and lactation and post-lactation by condition of teats and the ability to exude milk. We affixed a numbered aluminum band (Tennessee Tech University) around the forearm of all bats and attached radio-transmitters (0.51 g, LB-2, Holohil Systems Ltd., Carp River, Ontario, Canada) to the interscapular
region with surgical adhesive (Skin-Bond Cement, Smith and Nephew United, Largo, FL). We tracked radio-tagged bats to their day-roosts each successive day with a receiver (R1000, Communication Specialists, Inc., Orange, CA) and three-element Yagi antenna (TRX-2000S, Wildlife Materials, Murphysboro, IL).

We conducted exit counts to verify use of each day-roost, estimate colony size and determine roost type (bark, cavity or crevice). We recorded tree species, condition (live/snag), tree height, exit height, canopy cover and diameter at breast height (dbh) for each roost tree. Two species that were difficult to distinguish, black oaks (Quercus velutina) and northern red oaks, were placed into a single red oak group. Following Foster and Kurta (1999), snags were defined as having <50% live branches. We measured tree height and exit height using a clinometer (PM-5/360, Suunto Company, Espoo, Finland). Canopy height was estimated from mean height of five dominant trees in the immediate area of the roost tree (Weller and Zabel, 2001). A global positioning system unit was used to record the location of each tree and to determine distances moved between roosts. Each tree was classified into a bark class according to the amount of exfoliating bark present: high = ≥25% of tree covered in exfoliating bark; moderate = 10–25%; low = <10%; none = devoid of loose and peeling bark (Gardner et al., 1991). Each roost tree was classified as either a primary or alternate roost. Primary roosts harbored 30 or more bats on more than one occasion, and alternate roosts were used by fewer than 30 individuals (Callahan, 1993). We estimated percent canopy coverage with a convex densiometer (Forest Densiometers, Bartlesville, OK) by averaging readings made at the base of the tree and 3 m from the tree in each of the cardinal directions.

**STATISTICAL ANALYSES**

We used chi-square tests to determine the amount of dissimilarity in categorical variables (roost tree species, roost tree condition, tree bark class and roost type) between Indiana and northern long-eared bat roosts. We used logistic regression to examine differences in continuous roost variables (tree height, exit height, tree dbh, percent canopy cover and average canopy height) between roosts of Indiana and northern bats. Measurements of percent canopy cover were arcsine square root transformed to achieve normality (Zar, 1996). The logistic regression model included all of the above mentioned continuous variables. Statistical tests were performed by use of SAS (Version 8.1, SAS Inc., Cary, NC, USA) with an alpha of 0.05, and data are expressed as \( \bar{x} \pm SE \).

**RESULTS**

**Indiana bats.**—We affixed radiotransmitters to 29 Indiana bats that were subsequently tracked to 79 roosts, all in trees (Table 1). Indiana bats were tracked for an average of 7.2 ± 0.5 d (range 2–12). Average number of roosts used per bat was 3.4 ± 0.3 (range 1–6). The most consecutive nights a bat spent roosting in the same tree was four. Average distance from capture sites to roost trees was 1.0 ± 0.2 km (0.120–2.9 km), whereas average distance traveled between roost trees used on consecutive days was 0.62 ± 0.1 km (0.003–4.3 km).

Indiana bats used eight species of trees as day roosts. Pin oak was the most commonly used species (33%), followed by silver maple (25%), American elm (23%) and shagbark hickory (Carya ovata; 11%). The remaining roosts were of the red oak group (3%), white oak (3%), honey locust (Gleditsia triacanthos; 1%) and cottonwood (1%). Eighty-nine percent of roosts were located in snags and 87% were under exfoliating bark (Table 1). Eighty-five percent of roost trees were located in riparian forest and 15% were found in upland forest. Twenty five percent (17 of 67) of bottomland roosts were located in clearcuts or BAR plots, and of these, 79% (13 of 17) were in trees girdled during the 1999/2000 harvest.
Nine Indiana bat primary roost trees were identified during this study. Four primary roosts were in pin oaks, two were in American elms, and a single roost was in shagbark hickory, cottonwood and silver maple. Eight primary roost trees were on or near (<60 m) forest edges. The remaining tree was located in a forest opening. Six primary roosts were located in bottomland riparian forests and three were in upland forest. Bats roosted under exfoliating bark at all nine primary roost trees.

Six trees (13%) used by Indiana bats during summer 2001 were used again in 2002. One of these trees was a primary roost used frequently throughout both seasons, and two had been classified as alternate roosts in 2001 served as primary roosts in 2002. Three roost trees identified during summer 2001 were reused by three bats carrying transmitters later within the season. In 2002, seven trees were reused by bats carrying transmitters later within the season.

Northern bats.—We radiotracked 13 northern bats to 39 roosts (37 trees, 2 manmade structures). Northern bats were radiotracked for an average of 4.9 ± 2.9 d (range 1–13) and the average number of roosts used per bat was 3.1 ± 0.4 (range 1–5). The greatest number of consecutive nights a bat spent roosting in a tree was three, whereas bats spent up to 11 nights roosting in a manmade structure. Mean distance between capture sites and roosts was 1.7 ± 0.4 km (range 0.071–4.8 km), whereas the average distance traveled between roost trees was 0.67 ± 0.1 km (range 0.050–3.9 km).

Table 1.—Roost site characteristics of Indiana bats (Myotis sodalis) and northern bats (Myotis septentrionalis) bats in Missouri, Illinois, and Michigan

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Indiana bats</th>
<th>Northern long-eared bats</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>*Current study</td>
<td>*Current study</td>
</tr>
<tr>
<td>Number of roosts</td>
<td>79</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>47</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>32</td>
</tr>
<tr>
<td>Roost Type (Bark / Cavities &amp; Crevices)</td>
<td>69/10</td>
<td>19/12 **</td>
</tr>
<tr>
<td></td>
<td>45/2</td>
<td>11/8</td>
</tr>
<tr>
<td></td>
<td>23/0</td>
<td>15/14</td>
</tr>
<tr>
<td>Tree Condition (Live/Snag)</td>
<td>9/70</td>
<td>12/25</td>
</tr>
<tr>
<td></td>
<td>0/47</td>
<td>8/11</td>
</tr>
<tr>
<td></td>
<td>0/25</td>
<td>14/15</td>
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<tr>
<td>DBH (cm)</td>
<td>46 ± 1.7</td>
<td>43 ± 2.3</td>
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<tr>
<td></td>
<td>39 ± 2.0</td>
<td>37 ± 4.7</td>
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<tr>
<td></td>
<td>41 ± 1.0</td>
<td>63 ± 6.0</td>
</tr>
<tr>
<td>Canopy Coverage %</td>
<td>25</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>23/0 ***</td>
<td>17/12 ***</td>
</tr>
<tr>
<td>Exit Height (m)</td>
<td>9.1 ± 1.5</td>
<td>9.6 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>10.0 ± 0.8</td>
<td>9.2 ± 1.4</td>
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<tr>
<td></td>
<td>9.9 ± 0.9</td>
<td>10.5 ± 0.9</td>
</tr>
<tr>
<td>Tree Height (m)</td>
<td>17.7 ± 2.0</td>
<td>15.7 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>17.5 ± 1.0</td>
<td>15.8 ± 2.0</td>
</tr>
<tr>
<td></td>
<td>25.1 ± 1.6</td>
<td>23.0 ± 0.2</td>
</tr>
</tbody>
</table>

* Order of numbers (top to bottom) 1Current study, 2Carter and Feldhamer (2005), 3Foster and Kurtta (1999)

** Exit counts at 31 of 37 trees

*** 0–50%/51–100%

Nine Indiana bat primary roost trees were identified during this study. Four primary roosts were in pin oaks, two were in American elms, and a single roost was in shagbark hickory, cottonwood and silver maple. Eight primary roost trees were on or near (<60 m) forest edges. The remaining tree was located in a forest opening. Six primary roosts were located in bottomland riparian forests and three were in upland forest. Bats roosted under exfoliating bark at all nine primary roost trees. Six trees (13%) used by Indiana bats during summer 2001 were used again in 2002. One of these trees was a primary roost used frequently throughout both seasons, and two had been classified as alternate roosts in 2001 served as primary roosts in 2002. Three roost trees identified during summer 2001 were reused by three bats carrying transmitters later within the season. In 2002, seven trees were reused by bats carrying transmitters later within the season.
Northern bats used at least eight tree species as roosts: the red oak group (35%), silver maple (24%), pin oak (11%), American elm (11%), cottonwood (8%), honey locust (5%), shagbark hickory (3%) and shellbark hickory (Carya laciniosa; 3%). Upland forest contained 45% of roost trees, whereas riparian forests contained 55%. We conducted exit counts and located the roost site at 80% of trees used by northern bats. The roost site was under exfoliating bark at 59% of roosts and in crevices or cavities at 41% of roosts. The manmade structures used as roosts by northern bats were an abandoned barn and adjacent shed.

Species comparisons.—The overall model indicates that roost trees used by Indiana bats and northern bats were significantly different based only on continuous variables ($\chi^2 = 26.90$, df = 5, $P < 0.0001$). Specifically, Indiana bats roosted in taller trees ($\chi^2 = 5.34$, df = 1, $P = 0.021$) with less canopy cover ($\chi^2 = 9.96$, df = 1, $P = 0.002$) than northern bats. No significant differences were detected in dbh, exit height, or average canopy height of roost trees. Categorical variables indicated some biologically important differences as well. Northern bats roosted in live trees ($\chi^2 = 7.52$, df = 1, $P = 0.006$), cavities or crevices ($\chi^2 = 9.44$, df = 1, $P = 0.002$), and in trees in lesser stages of decay ($\chi^2 = 28.84$, df = 3, $P < 0.0001$) more often than Indiana bats. Roost tree distribution was similar for both species. The majority of roosts were located within the boundaries of DRCA in bottomland habitat although Indiana bats and northern bats both roosted in uplands as well. In one small (25 ha) tract of bottomland forest north of DRCA we located 19 Indiana bat and 13 northern bat roosts. Two trees in this tract used by Indiana bats also were used by northern bats although the two species were never observed in the same tree at the same time. Indiana bats were not observed roosting in manmade structures, but a small proportion of northern bats radiotracked (=2) were observed roosting in an abandoned barn and a shed.

DISCUSSION

Characteristics of Indiana bat roosts identified in this study are consistent with those reported elsewhere (Gardner et al., 1991; Callahan et al., 1997; Carter and Feldhamer, 2005). Indiana bats roosted almost exclusively underneath the exfoliating bark of dead trees having little to no canopy cover and changed roosts roughly every 2 d. The greatest number of roost trees found to be used by a single maternity colony in a season was 21 (18 alternate, 3 primary), and bats displayed both intra- and interannual fidelity to particular trees as noted by several authors (Callahan et al., 1997; Kurta and Murray, 2002).

Indiana bat maternity colonies will return to a specific tree as long as it is suitable (Gardner et al., 1991); however, given the ephemeral nature of roost trees, bats must be able to shift locations. Several hypotheses exist concerning why bats use alternate roosts (Kunz, 1982; Lewis, 1995), but one possibility is the need to proactively investigate new trees before their current roost-site becomes uninhabitable (Kurta et al., 2002). By the completion of this study, we documented the loss of 13% of all Indiana bat roosts due to bark loss or treefall. Gardner et al. (1991) reported a 30% loss of roost trees in just 1 y. Indiana bats, and other species with a strong reliance on ephemeral bark roosts, may benefit by maintaining a constant awareness of many potential roosts in the immediate area.

As documented in other studies, northern bats roosted in cavities or underneath the bark of both live trees and snags (Sasse and Pekins, 1996; Foster and Kurta, 1999; Carter and Feldhamer, 2005; Perry and Thill, 2007). They moved roosts about every 2 d, and showed intra-annual fidelity to at least one tree. However, northern bats were not limited to trees as roosts and also were radiotracked to man-made structures. An abandoned barn, occupied as a maternity colony in conjunction with another sympatric congener, the little brown bat (Myotis lucifugus), and equipment shed were used as roosts by northern bats. An exit count
at this structure yielded over 700 bats, and additional harp-trapping indicated a 3:1 ratio of little browns to northern bats.

Two prior studies have compared the roosting requirements of Indiana and northern bats in sympatry (Foster and Kurta, 1999; Carter and Feldhamer, 2005). Results from these studies and the present study include 149 roosts for Indiana bats and 88 for northern bats (Table 1), and provide a good opportunity for assessing similarities and differences in roost selection over a wide geographical area. Overall, there appears to be some overlap in characteristics of roost trees used by the two species, but the cause of differences in roost selection is unknown. Well designed experimental studies are needed to determine if these differences are the result of competition for roost sites leading to shifts in roosting niches or if inherent differences in the natural history shaped by selective pressures other than competition lead each species to choosing slightly different roosts.

Several trends appear to hold for Indiana bats and northern bats in sympatry, regardless of location. For example, a common difference between Indiana and northern bat roost trees is the amount of solar exposure they receive. Although methods for collecting these data are not standardized and can be misleading in the estimation of canopy cover at the actual roost site (Kurta et al., 2002; Britzke et al., 2003; Boyles, 2007), general trends still can be inferred. In all three studies, canopy cover at Indiana bat roosts was \( \leq 25\% \) compared to roughly 50\% for northern bats (Table 1). This disparity is in part a reflection of tree location. Indiana bats typically roost in “open” areas (U.S. Fish and Wildlife Service, 2007), whereas northern bat roosts commonly are found within or below the forest canopy (Sasse and Perkins, 1996; Foster and Kurta, 1999; Menzel et al., 2002; Carter and Feldhamer, 2005).

Another discrepancy in roost characteristics between Indiana and northern bats is the ratio of live trees and snags used as roosts. In Michigan (Foster and Kurta, 1999), Illinois (Carter and Feldhamer, 2005) and Missouri, snags constituted 47, 58, and 68\% of all roost trees used by northern bats, respectively (Table 1). In contrast, Indiana bats used no live trees in Michigan (Foster and Kurta, 1999) or Illinois (Carter and Feldhamer, 2005) and only 13\% of trees used in this study were live. In studies conducted on northern bats where reproductively active female Indiana bats are absent or rare, northern bats roost more often in snags. Northern bats roosted in snags 81\% of the time in South Dakota (Cryan et al., 2001), 83\% of the time in New Hampshire (Sasse and Perkins, 1996), 67\% of the time in West Virginia (Menzel et al., 2002) and 77\% of the time in Kentucky (Lacki and Schvierjohann, 2001). In the Ouachita Mountains of Arkansas, where northern bats were the most frequently encountered species, 90\% of all roosts were in snags (Perry and Thill, 2007). While this is an entirely qualitative observation, it suggests that northern bats are flexible enough in roost selection that their roosting niche may be expanded or shifted when sympatric with Indiana bats.

Our results indicate slight niche-overlap among these two species of *Myotis* in northeastern Missouri, but we found biologically important differences that separate the roosts used by the species and should allow for coexistence where roosts are abundant. Indiana bats roosted mostly in snags with exfoliating bark and low canopy cover. Northern bats roosted in snags with these characteristics, but did not exhibit as much dependence as Indiana bats on trees of this type. Northern bats roosted mainly in trees, but most were shorter and had higher canopy cover than trees used by Indiana bats.

Little information has been provided regarding the effects of active forest management on Indiana bat roosting behavior (U.S. Fish and Wildlife Service, 2007). Baseline (pre-treatment) data for Indiana bat populations at DRCA are unknown. However, a lactating female was captured in 1977, suggesting that maternity colonies were present in the vicinity
(Clawson, 1986). During this study, which began 2 years after completion of silvicultural treatments, we found Indiana bats roosting in both clearcuts and BAR plots. The majority of these roosts (13/17) were in girdled trees left in harvested blocks. Girdling a tree, compared to other methods of snag creation, creates a taller snag (Lewis, 1998) which some bat species appear to choose preferentially as roosts (Vonhof and Barclay, 1996; Betts, 1998; Ormsbee and McComb, 1998). This suggests that Indiana bats may adapt to forest management techniques if care is taken to leave adequate standing trees as potential roosts.

In West Virginia, all northern bat roosts located by Menzel et al. (2002) occurred in a stand subjected to a harvest within the previous 10 y. Most female roosts found in Arkansas occurred in partial harvested areas (Perry and Thill, 2007), and in South Dakota, 18 of 21 northern bat roost plots showed signs of recent (<5 y) harvests (Cryan et al., 2001). This apparent plasticity in roosting habits suggests that northern bats may be adaptable to managed forests allowing them to avoid competition with more specialized species (Menzel et al., 2002; Schmidt, 2003).

Although data indicate biologically important differences in roost selection and that northern bats are more opportunistic in roost selection than Indiana bats, some overlap in roost selection occurs. Therefore, we suggest that when possible, management plans be crafted to minimize niche-overlap between these species as suitable forest habitat continues to diminish. Managing for multiple species may be the best option where roosting niches even slightly overlap. For example, leaving suitable areas of intact forest with high canopy cover and cavity-susceptible tree species will benefit northern long-eared bats whereas snag formation and retention would benefit Indiana bats.

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LITERATURE CITED


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