Roost tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois

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Abstract

Roost trees used by female Indiana bats (*Myotis sodalis*), a federally endangered species, and sympatric northern long-eared bats (*Myotis septentrionalis*) at two locations in southern Illinois greatly impacted by past flooding were located using radiotelemetry. For 30 Indiana bats, we located 49 roosts in 7 species of trees. Green ash snags (*Fraxinus pennsylvanica*) and pin oak snags (*Quercus palustris*) were used more than expected and sweetgum snags (*Liquidambar styraciflua*) less than expected based on availability. Ten adult female northern long-eared bats were tracked to 19 different trees of 5 species. We used logistic regression to predict use of roost versus random trees for both species, and to compare roosts of Indiana bats versus northern long-eared bats. Indiana bats typically roosted in areas of low vegetative obstruction (clutter) on the forest edge ($\chi^2 = 10.28$, d.f. = 2, $P = 0.006$). Compared to random trees, roosts of northern long-eared bats were within intact forests ($\chi^2 = 10.56$, d.f. = 1, $P = 0.001$). Amount of obstruction and decay differed; roosts of *M. sodalis* typically were less cluttered and more decayed than those of *M. septentrionalis* ($\chi^2 = 38.63$, d.f. = 2, $P < 0.001$). Indiana bats roosted almost exclusively under exfoliating bark of bottomland snags, whereas northern long-eared bats also made extensive use of cavities and crevices. Indiana bats cannot be expected to remain in an area indefinitely if snag creation is not sustained, and natural forest succession should be considered in long-term management of this endangered species.
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1. Introduction

Northern long-eared bats (northern myotis, *Myotis septentrionalis*) use similar habitat as Indiana bats (*Myotis sodalis*). Both species use forest during summer and hibernate in caves and mines during winter (Foster and Kurta, 1999). They are commonly sympatric, but while northern long-eared bats are common, Indiana bats are federally endangered and declining throughout their range.

The general roosting ecology of Indiana bats has been described (Gumbert et al., 2002; Kurta et al., 2002; Miller et al., 2002; Whitaker and Brack, 2002; Britzke et al., 2003; Menzel et al., 2005; Ritzi et al.,

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2005; see Menzel et al., 2001 for review of earlier literature) as has the roosting ecology of northern long-eared bats (Sasse and Pekins, 1996; Foster and Kurta, 1999; Lacki and Schwierjohann, 2001; Menzel et al., 2002; Owen et al., 2002). Although reports of roosts of Indiana bats are sometimes conflicting, some underlying patterns associated with roosting observations have been noted. Kurta et al. (1996) and Callahan et al. (1997) have shown that individuals that form maternity colonies collectively may use several trees to provide the total resources needed for roosting (including cover and correct temperature) during varying environmental conditions. Colonies usually have from one to a few "primary" trees (Callahan et al., 1997) or "focal" trees (O'Donnell and Sedgeley, 1999) that provide proper roosting conditions most of the time. These often are large snags with exfoliating bark exposed to ample sunlight. "Alternate" roosts are used to a lesser degree usually by fewer bats at any given time. These roosts may be used during adverse environmental conditions, such as in rain, wind, and temperature extremes (Humphrey et al., 1977) to reduce parasite loads, access foraging grounds, minimize predation, or assess alternative roosts as a precaution against loss of primary trees (Kurta et al., 2002).

To better understand characteristics of summer maternity roosts of Indiana bats in southern Illinois, where severe floods during the 1990s created abundant snags in bottomland forest habitats, our objectives were to quantify habitat characteristics of maternity roosts and compare characteristics of the roost trees of Indiana bats with those of northern long-eared bats.

2. Materials and methods

2.1. Study area

We studied Indiana bat maternity colonies within the greater Mississippi River Floodplain at two locations in southern Illinois. The first colony used Oakwood Bottoms, an 80-year-old closed-canopy bottomland forest near the town of Grand Tower, Jackson County, Illinois. Oakwood Bottoms is dominated by pin oak (*Quercus palustris*) and other species of oaks, as well as various species of maple (*Acer*), elm (*Ulmus*), and ash (*Fraxinus*). Severe flooding in 1993 and 1995 caused

extensive tree mortality (25–30%) and abundant numbers of snags in Oakwood Bottoms and the surrounding area (for details of the flooding see Jacobson and Oberg, 1997). This colony also used the adjacent floodplain forest that extended east from Oakwood Bottoms 1–2 km to the Big Muddy River. Because this area was not protected by the large levee system, the tree mortality from floods was about 80%. This resulted in two distinctly different structural types of bottomland habitat available to bats. Oakwood Bottoms is a more intact forest with a mostly closed-canopy, whereas the floodplain is open canopy (<50% cover). Occasionally, this colony also used the adjacent floodplain of Cedar Creek, a tributary of Big Muddy River. This tributary has cut a large valley out of the upland bluffs along the edge of the Mississippi Floodplain 5–10 km northeast of Oakwood Bottoms, near the town of Pomona, Jackson County, Illinois. This floodplain has fewer snags and is narrower, resulting in a greater component of upland habitats compared to Oakwood Bottoms.

The second Indiana bat colony is located in Bluff Lake Swamp near the town of Millcreek, Union County, Illinois, along the eastern edge of the Mississippi River Floodplain, about 30 km south of the Oakwood Bottoms colony. This site includes uplands, various bottomlands, agricultural, and large wetland areas. Roosting bats primarily used a swamp with high densities of snags along its edge, a consequence of extensive damming by beaver (*Castor canadensis*) that continually elevated water levels. Forest on the southwest and west side of the swamp is 60–80-year old. The forest on the southeastern side of the swamp is relatively young (20–40 years) and contains few snags. The northern and eastern sides of the swamp abut the base of bluffs at the edge of the Mississippi River Floodplain. Elevation increases 120 m in 0.3 km. Tree species on the bluffs are typical of upland forest found throughout this area.

2.2. Data collection

At each location, bats were captured using high mistnet systems (Gardner et al., 1989; Avinet, Dryden, New York). Width and height of nets varied according to location. Nets were placed in areas of anticipated high activity of bats, such as flight corridors. Occasionally, nets were placed around known roost

trees to capture bats as they exited in evening to forage. After capture, selected bats were fitted with 0.48 g radiotransmitters (Model LB-2, Holohil Systems Ltd., Carp, Ont., Canada) affixed to their back with Skin-Bond surgical glue (Smith and Nephews United Inc., Largo, FL, USA). Bats were tracked to their roosting sites each day until the transmitter was shed or the battery died, typically 4–5 days. For comparison with Indiana bats, female northern long-eared bats at Oakwood Bottoms also were captured and tracked using the same techniques.

At each roost tree, we measured 10 microhabitat variables (Appendix A). Around each known roost, a 0.04 ha circular plot was established and five other habitat characteristics were measured (Appendix B). For comparison with known roost trees, habitat variables also were measured on random trees from within the same stand. This represented a sample of trees available for bats to roost in. Because bats could use these trees, we considered them random samples of trees rather than "not used." Random trees were located using a random bearing and random distance from each known roost and selecting the closest tree that met our criteria. Random trees for Indiana bat analyses were restricted to snags with diameters at breast height (dbh) $\geq$ 9 cm (MacGregor et al., 1999), and $\geq$10 m high (Kurta et al., 1996). This represents the smallest diameter and the average roost height of published roost records. For northern long-eared bats, we also measured habitat variables of random trees selected for comparison to known roosts. We did not restrict the selection of "random" trees for northern long-eared bats because they used a variety of understory snags, as well as large living trees with cavities. Trees without cavities were also considered because on actual roost trees the cavities were not always obvious without considerable searching and or witnessing bats exiting the tree.

Values for landscape-level variables were calculated with Geographic Information Systems (GIS; ArcView 3.2, ESRI, Redlands, CA). The coordinates of each roost tree were recorded with a global positioning system (GPS) unit and entered into the GIS. Habitat coverages used in the analysis included digitized aerial photographs, digitized topography maps, and the Critical Trends Assessment Land Cover Database of Illinois, 1991–1995. All were obtained from the Illinois Natural Resources Geospatial Data Clearinghouse (http://www.isgs.uiuc.edu/nsdihome/ISGSindex.html). Distances between roosts were calculated using the measuring tools in ArcView 3.2. The extension animal movements (Hooge and Eichenlaub, 1997) was used to calculate core areas used by the maternity colonies for roosting. Here, we report 90% contour areas from the Adaptive Kernel estimator for each colony separately.

2.3. Statistical analysis

Likelihood ratio χ^2 tests were used to determine if species of roost tree were chosen in proportion to availability. Case–control logistic regression (Hosmer and Lemeshow, 1989) was used to examine habitat differences between the roosts of Indiana bats and random trees, northern long-eared bats and random trees, and Indiana bats and northern long-eared bats. Because number of variables in a logistic regression model should not exceed 1 for every 10 samples (Hosmer and Lemeshow, 1989), we reduced variables by beginning with a univariate analysis of each habitat variable. All variables with a P-value < 0.25 were included in a subsequent multivariate analysis. A P-value of 0.25 was used because Bendel and Afifi (1977) documented that more conservative levels (i.e., 0.05) often eliminated variables that later proved to be important when combined with other variables. Final models were constructed using only those variables from the multivariate analysis that had a final P-value ≤ 0.05.

3. Results

We attached transmitters to 30 adult female Indiana bats and 10 adult female northern long-eared bats from 1999 to 2002. We tracked Indiana bats to 49 roost trees; vegetation sampling was conducted around 47 of these. Indiana bats were tracked for an average of 4.4 nights (range 0–11); they switched roosts an average of 2.8 times (range 0–7). The greatest number of consecutive nights per tree was 4. We tracked 10 northern long-eared bats to 19 roost trees. Northern long-eared bats were tracked for an average of 3.9 nights (range 0–7) and switched roosts an average of 2.5 times (range 0–5). The longest a northern long-eared bat used the same tree was 3 consecutive nights.

A total of 2732 individual trees was identified from both study areas from 0.04 ha circular plots around roost and random trees. Common overstory trees were elm (28%), unidentified snags (26.5%), green ash (*Fraxinus pennsylvanica*; 9.7%), pin oak (6.8%), and sweetgum (*Liquidambar styraciflua*; 6.4%). All other species accounted for <5% each. Of 28 species of overstory trees recorded on the study area, 23 species were large enough to be used by Indiana bats for roosting; however, only seven species were actually used. All roosts of Indiana bats discovered during this study were in snags. Relative to their abundance on the study area, Indiana bats selected green ash snags (*n* = 16) and pin oak snags (*n* = 8) more than expected, and sweetgum snags (*n* = 0) less than expected. Roosts also occurred in unidentified snags (*n* = 10), and snags of elm (*n* = 8), silver maple (*Acer saccharinum*; *n* = 4), cottonwood (*Populus deltoides*; *n* = 2), and shagbark hickory (*Carya ovata*; *n* = 1). Northern long-eared bats used five identified species of trees for roosting; nine roosts were in pin oak, five in elm, two in unidentified snags, and one each in sweetgum, oak, and hawthorn (*Cratagus* spp.). Green ash was abundant on the study areas as was willow (*Salix*; 3.7% of trees on the area) but neither were used by northern long-eared bats. Eight (42%) roosts of northern long-eared bats were in hollow boles or branches of living trees, including elm, sweetgum, and pin oak.

Indiana bats roosted under exfoliating bark, except for two roosts that were in crevices of snags, one of which was partially covered by bark. Northern long-eared bats used bark, cavity, and crevice roosts. Percentage bark coverage did not differ between roosts and random trees for *M. sodalis* (Table 1) or *M. septentrionalis* (Table 2).

Two variables distinguished between Indiana bat roosts and a random sample of snags (χ^2 = 10.284, d.f. = 2, *P* = 0.006). Amount of roost obstruction around random snags was higher than around Indiana bat roosts (χ^2 = 8.265, d.f. = 1, *P* = 0.004), and roosts were closer to the contiguous forest than random snags (χ^2 = 5.002, d.f. = 1, *P* = 0.025). The logistic regression model was:

$$x = 2.097 - 0.856\,(\text{degree of roost obstruction})$$
$$- 0.023\,(\text{distance to forest})$$

with the probability of a tree being an Indiana bat roost = $1/1 + e^{-x}$.

One variable, distance to forest, distinguished between roosts of northern long-eared bats and random trees (χ^2 = 10.562, d.f. = 1, *P* = 0.001). Northern long-eared bat roosts were closer to intact forests than were random trees. The logistic regression model was:

$$x = -0.374 - 0.154\,(\text{distance to forest})$$

with the probability of a tree being a northern long-eared bat roost = $1/1 + e^{-x}$.

Comparing roosts of Indiana bats and northern long-eared bats (Table 3), two variables were significant (χ^2 = 38.633, d.f. = 2, *P* < 0.001). Degree of roost obstruction was greater around northern

Table 1

Comparison of Indiana bat (*Myotis sodalis*) roost trees and random trees in southern Illinois, 1999–2002

	Indiana bat (*n* = 47)		Random trees (*n* = 37)		Univariate logistic regression statistics	
	Mean (range)	S.E.	Mean (range)	S.E.	χ^2-value	*P*-value
Percentage cover of bark	47.0 (0–95)	3.9	55.0 (0–100)	5.8	1.432	0.231
Percentage closure (at base) of canopy	36.3 (0–85)	4.1	36.6 (0–95)	5.8	0.001	0.980
Percentage closure (at roost) of canopy	17.7 (0–65)	3.0	17.6 (0–85)	3.7	0.000	0.993
Obstruction of roost (visual)	1.3 (1–3)	0.1	1.9 (1–5)	0.2	6.264	0.012
DBH (cm)	39.0 (18.5–82)	2.0	37.7 (14.5–72.5)	2.2	0.159	0.690
Decay class	2.8 (1.5–3.75)	0.1	3.2 (1.25–4)	0.1	0.697	0.404
Distance to forest (m)	14.2 (0–50)	2.6	20.1 (0–150)	5.4	1.524	0.217
Height of roost (m)	10.0 (2.5–28.4)	0.8				
Height of roost tree (m)	17.5 (3–35)	1.0	15.7 (5.1–29.8)	1.0	1.805	0.179
Average DBH (cm)	23.3 (11.9–46)	1.2	22.8 (12.3–35.8)	1.0	0.083	0.774
Average height (m)	9.7 (2.4–21)	0.6	10.1 (4.3–18.2)	0.6	0.214	0.644

Table 2

Comparison of northern long-eared bat (*Myotis septentrionalis*) roost trees and random trees in southern Illinois, 1999–2002

	Northern long-eared bat ($n = 19$)		Random trees ($n = 46$)		Univariate logistic regression statistics	
	Mean (range)	S.E.	Mean (range)	S.E.	χ^2-value	P-value
Percentage cover of bark	79.2 (0–100)	7.1	63.8 (0–100)	5.7	2.634	0.105
Percentage closure (at base) of canopy	61.3 (0–95)	6.5	44.0 (0–95)	5.3	3.540	0.060
Percentage closure (at roost) of canopy	44.0 (0–90)	7.2	24.8 (0–90)	4.1	5.514	0.019
Obstruction of roost (visual)	3.2 (1–5)	0.3	2.3 (1–5)	0.3	4.055	0.044
DBH (cm)	37.3 (12–68)	4.7	34.9 (11.5–72.5)	2.2	0.277	0.599
Decay class	1.4 (0–3.75)	0.3	2. (0–4)	0.3	3.411	0.065
Distance to forest (m)	4.0 (0–70)	3.7	17.0 (0–150)	4.9	10.562	0.001
Height of roost (m)	9.2 (1.5–22)	1.4				
Height of roost tree (m)	15.8 (3–30.8)	2.0	14.9 (5.1–29.8)	0.9	0.227	0.634
Average DBH (cm)	18.9 (12.4–29)	1.1	22.0 (12.3–35.8)	0.8	4.400	0.036
Average height (m)	10.6 (4.6–16.6)	0.6	10.5 (4.3–18.5)	0.5	0.049	0.824

long-eared bat roosts than around Indiana bat roosts ($\chi^2 = 14.954$, d.f. = 1, $P < 0.001$), and *M. septentrionalis* roosts were less decayed than those of *M. sodalis* ($\chi^2 = 4.876$, d.f. = 1, $P < 0.027$). The logistic regression model was:

$$x = -1.276 + 1.214 \,(\text{degree of roost obstruction})$$
$$- 0.921 \,(\text{decay class})$$

with the probability of a tree being a northern long-eared bat roost = $1/1 + e^{-x}$.

Average dbh for Indiana bat roosts was 39 cm (Table 1), and 37 cm for northern long-eared bats (Table 2). Neither was different than that of random trees available in the study areas. Average roost height for Indiana bats was 10 m. It was 9 m for northern long-eared bats. Roost tree height did not differ from the height of the surrounding trees. Indiana bats used roosts with low canopy closure levels (Table 1), although not different from that of random trees. Northern long-eared bats roosted in areas with higher canopy closure than in random plots (Table 2).

For both species, all roost trees were in bottom-land and floodplain habitat that was flooded ≤1 m at some point during the study. Many trees remained flooded throughout the entire study. During driest periods, fresh water was located a maximum of 750 m from used roosts.

Table 3

Comparison of Indiana bat (*Myotis sodalis*) and northern long-eared bat (*Myotis septentrionalis*) roost trees in southern Illinois, 1999–2002

	Indiana bat ($n = 47$)		Northern long-eared bat ($n = 19$)		Univariate logistic regression statistics	
	Mean (range)	S.E.	Mean (range)	S.E.	χ^2-value	P-value
Percentage cover of bark	47.0 (0–95)	3.9	79.2 (0–100)	7.1	16.169	0.000
Percentage closure (at base) of canopy	36.3 (0–85)	4.1	61.3 (0–95)	6.5	9.912	0.002
Percentage closure (at roost) of canopy	17.7 (0–65)	3.0	44.0 (0–90)	7.2	13.386	0.000
Obstruction of roost (visual)	1.3 (1–3)	0.1	3.2 (1–5)	0.3	31.959	0.000
DBH (cm)	39.0 (18.5–82)	2.0	37.3 (12–68)	4.7	0.162	0.687
Decay class	2.8 (1.5–3.75)	0.1	1.4 (0–3.75)	0.3	23.679	0.000
Distance to forest (m)	14.2 (0–50)	2.6	4.0 (0–70)	3.7	5.924	0.015
Height of roost (m)	10.0 (2.5–28.4)	0.8	9.2 (1.5–22)	1.4	0.304	0.581
Height of roost tree (m)	17.5 (3–35)	1.0	15.8 (3–30.8)	2.0	0.867	0.352
Average DBH of plot (cm)	23.3 (11.9–46)	1.2	18.9 (12.4–29)	1.1	5.498	0.019
Average height of plot (m)	9.7 (2.4–21)	0.6	10.6 (4.6–16.6)	0.6	0.795	0.373

The roosting area encompassed by Indiana bats at Oakwood Bottoms was 1322.0 ha, which was seven times larger than the area used by sympatric northern long-eared bats (186.3 ha). The greatest straight-line distance traveled between consecutive roosts for Indiana bats was 4650 m, traveled by two bats on separate occasions. Although we do not know the density of Indiana bat populations at Oakwood Bottoms and Bluff Lake, our emergence counts suggest they are about equal in size. However, Indiana bats at the Bluff Lake colony used an area 479 ha in size, only 36.2% of the roosting area used at Oakwood Bottoms. The longest distance moved in consecutive nights by an Indiana bat at Bluff Lake was about 1000 m; the shortest distance moved was 20 m. Northern long-eared bats also moved relatively shorter distances between consecutive roosts. Most roosts were <100 m apart. The longest distance traveled between roosts was 860 m. One northern long-eared bat moved 1390 m between the capture location and its roost the next day.

Because the smallest dbh and minimum height of roost trees used by Indiana bats was 18.5 cm and 10 m, respectively, we considered snags with those dimensions or larger as potential roost trees. Given these criteria, the study areas had a density of about 45.3 suitable snags/ha. However, this is likely an elevated estimate as all these probably did not have suitable canopy closure or bark cover.

4. Discussion

The amount of roost switching we observed by maternal Indiana bats was similar to that in other studies (Kurta et al., 1996; Kurta et al., 2002). Likewise, northern long-eared bats switched roosts an average of every 2 days in Michigan (Foster and Kurta, 1999), 2.2 days in New Hampshire (Sasse and Pekins, 1996), and every 3 days in West Virginia (Owen et al., 2002). It is unknown why either species switches roosts. Likely factors include temperature, precipitation, predator pressure, parasitism, and ephemeral roost sites. It is unlikely that weather is the sole driving factor because many roost trees were used in a variety of temperature and precipitation conditions. Likewise, parasitism is unlikely to be the only factor because most roosts continued to be used by some bats.

Switching roosts would do little to reduce ectoparasite loads unless all the bats moved together, eliminating hosts at a roost and eventually causing parasites to die or vacate. Additionally, many ectoparasites of the fur and skin would infest new roosts with the bats. Predation pressure could lead to abandonment of a roost. However, potential predation should cause bats to abandon simultaneously, but this was not seen. It would seem that maintaining knowledge of alternate roost sites could be the main driving force leading Indiana bats and northern long-eared bats to switch roosts. About 25–30% of the roost trees we located fell within 1 year of discovery, some within weeks. Additionally, exfoliating bark frequently is shed. Many trees in our study had the piece of bark where bats roosted fall off within months of discovery. Thus, it would be highly adaptive for individuals to be familiar with the location and current condition of several alternate roosts (Kurta et al., 2002).

In addition to knowledge of alternate roost sites, social interactions likely are involved in roost switching because it was highly fluid and dynamic. Often, bats with transmitters would switch to the same tree, or another bat would be found at a new roost a few days after the first switched. The Indiana bat colony did not move as a discrete unit, but shifted group composition and roosts over a period of days or weeks. During most of the study the colony was dispersed over multiple roosts. This fission–fusion group movement pattern was described by Kerth and König (1999) and observed in Indiana bats in Michigan (Kurta et al., 2002) and Kentucky (Gumbert et al., 2002).

Typically, roosts of Indiana bats are in dead trees (Gardner et al., 1990; Kurta et al., 1996; Callahan et al., 1997; Foster and Kurta, 1999). Although use of live trees for roosts has been noted, primarily shagbark hickories (Humphrey et al., 1977), we found no roosts in live trees during our study. Two factors may have contributed to this. First, live shagbark hickories were uncommon—only 0.4% of trees in the study area. Second, the exceptionally high densities of snags may have reduced the need to use living trees. Live trees may not provide favored microclimate and appear to be a poor-quality roosting resource for Indiana bats in southern Illinois. Considering average size of slabs of exfoliating bark these bats used, it would be surprising to find a live,

healthy tree with enough exfoliating bark to accommodate this highly gregarious species.

Northern long-eared bats roost in a greater variety of tree species and roost types than do Indiana bats, including thin-barked species and living trees as well as snags. Additionally, because northern long-eared bats often form smaller groups than Indiana bats, they commonly are found in smaller trees. For example, we found one northern long-eared bat that roosted in a cavity <2 m off the ground in a 12-cm dbh hawthorn snag. Conversely, green ash, often used by northern long-eared bats in other studies (Foster and Kurta, 1999), was not found to be used in our study area, although they were abundant. As studies continue to examine the roosting habits of this species, the list of tree species "used" will likely increase. Given the differences observed between study areas it is likely that structural complexity of the habitat or the available roosting resources are more important habitat factors than actual tree species.

Differences in roost selection by Indiana bats and northern long-eared bats can be attributed to differences in bark, cavities, and other structural characteristics of trees. With few exceptions, Indiana bats roosted under exfoliating bark. Many common tree species in the study area have thin bark such that when a tree dies, its thin, fragile bark does not form the large sheets needed by Indiana bats for roosts. An exception was pin oak, which has thin, flaky bark, but was used extensively by Indiana bats. In our study area, the bark of pin oaks did not exfoliate in the typical manner; instead, it remained attached to the outer layer of cambium. This layer, 1–3 cm thick, would separate and form slabs. These slabs essentially acted as large plates of bark that Indiana bats would roost under. We believe formation of slabs is not typical of pin oaks, but is caused by trees dying from summer flooding.

Differences in the size of roosting areas of the two bat species may have resulted from differences in habitat quality related to roosting requirements, as well as number of bats tracked in each group. Because Indiana bats mainly are restricted to exfoliating bark, the use of a larger area may reflect their search for suitable snags. Because snags appeared to be plentiful in the study area, however, it is unlikely that they would need to search a large area to find suitable roosts. Rather, the relatively large roosting area of Indiana bats at Oakwood Bottoms compared to Bluff Lake may have resulted from individuals that spread their roost locations throughout what was available to optimize knowledge of alternate roosts, to reduce travel time to foraging areas, or to reduce potential foraging competition. The Indiana bats at Bluff Lake used a much smaller roosting area, probably because available roosting habitat was more limited. Although snag density at Bluff Lake was high, most snags were around the periphery of the swamp. Additionally, much of the surrounding area, although excellent foraging habitat, was either agricultural or immature forest too young to produce suitable snags. Small roosting areas obviously are sufficient as long as minimal roosting requirements are met. For example, an Indiana bat colony in Michigan restricted its roosting to a 5-ha wetland (Kurta et al., 1996). Northern long-eared bats commonly occur in more obstructed, interior bottomland forest habitats (Carroll et al., 2002). We found that their roosting requirements were met in an area similar in size to that used by Indiana bats at Bluff Lake. However, in Michigan, Foster and Kurta (1999) found that the area used by 12 northern long-eared bats was larger than that of Indiana bats, suggesting size of roost areas is site-specific.

Habitat features that differentiated between used and available roost trees in other studies of Indiana bats, such as dbh or canopy cover, did not appear to be as important in our study, possibly because of the large number of snags present. Nonetheless, we found general roost characteristics of *M. sodalis* were similar to those in other studies. For instance, Callahan et al. (1997) and Kurta et al. (2002) found that Indiana bats use large snags, with large amounts of bark cover, exposed to high levels of solar radiation. Although Kurta et al. (1996) found that percentage bark cover was not important, they reported that Indiana bats used large diameter snags with high solar exposure. We found Indiana bat roosts were in large snags with moderate to high bark cover and high solar exposure (canopy closure; Table 1), similar to the large number of available snags. A primary feature that was important in roost selection for both species was distance to forest. Many available snags were considerable distances out into open areas, including the middle of the swamp. These snags were rarely used. Most snags were either located within a small

opening in contiguous forest or within 50 m of forest edge. During all exit counts on these open-area roosts, when bats left the roost they flew directly into the nearest forest edge. We never observed Indiana bats leaving the roost and flying out to forage over open terrain. Murray and Kurta (2004) documented similar observations in Michigan. Also, around roosts that were away from forest, we never observed "checking" behavior (after exiting, bats circle the roost, briefly land, and then continue to circle) first described by Humphrey et al. (1977). Checking was common in our study around roosts within contiguous forest. Predator pressure may be a driving force leading bats to quickly leave the area of exposed roosts. If so, roost suitability would decrease with increasing distance from contiguous forest.

It is hypothesized that Indiana bats use roosts with high levels of solar exposure because high roost temperatures lead to more rapid fetal and juvenile growth and development (Racey, 1973; Callahan et al., 1997). Although we found levels of canopy closure for roost sites did not differ from those of random trees (Table 1), all were low (Table 1), with resulting high levels of solar exposure.

Features of northern long-eared bat roosts were similar to those documented elsewhere. Because *M. septentrionalis* use resources other than exfoliating bark, including cavities, they can use a greater variety of trees, reflecting major differences in roosting patterns from Indiana bats. In some studies, mean dbh of roost trees used by northern long-eared bats was larger than random trees (Sasse and Pekins, 1996; Foster and Kurta, 1999). Like Menzel et al. (2002) in West Virginia, we found that mean dbh and roost tree height for northern long-eared bats were not different from that of random trees (Table 2). Northern long-eared bats use roost trees with lower levels of solar exposure than do Indiana bats. With the exception of a study in northern Michigan (Foster and Kurta, 1999), all reported levels of solar exposure have been low (Sasse and Pekins, 1996; Lacki and Schwierjohann, 2001; Menzel et al., 2002) as in our study.

In many species of bats, individuals roost in a relatively small portion of their home (foraging) range (Menzel, 1998; Foster and Kurta, 1999; Menzel et al., 1999; Hutchinson and Lacki, 2000; Gumbert et al., 2002). Most Indiana bats in our study did not travel long distances, again a possible reflection of excellent habitat provided by abundant snag density. An exception was a single roost tree far outside the normal roosting area in the Oakwood colony. This lone roost was in an area considered a separate colony until two bats traveled between the Oakwood colony and this roost on two separate occasions. These roosts were 4650 m apart, on opposite sides of a large rocky bluff. The bats were never tracked above the shear rock walls of the bluffs (elevation increase of >120 m). Although they could easily have flown over the bluffs, we believe they flew around them and up the valley, a minimum distance of 5950 m. If the bats followed the river corridor through the floodplain they would have traveled 15,500 m between consecutive roosts.

5. Conclusions

We found both Indiana bat colonies in bottomland hardwood communities, as have most previous studies (see Menzel et al., 2001; Kurta and Kennedy, 2002). This may occur because bottomland communities are prone to large-scale disturbance events, such as flooding, that create large numbers of standing dead trees—a necessary resource for roosting. Conversely, most disturbance events in upland forests, such as windstorms, are either small in scale or do not leave many standing dead trees. For our areas, snag density represented >25% of the trees in the forest, and in some places, about 80%. Our sites cannot sustain such high snag densities over extended periods. Although they provide high-quality habitat for Indiana bats, these areas eventually will become unsuitable as snags deteriorate and fall at a greater rate than they are created by disturbances. Thus, in the long term, Indiana bat colonies may be forced to new areas as succession makes current areas unsuitable. If the necessary level of snag creation is not sustainable in an area, Indiana bats cannot be expected to remain there indefinitely. This successional dynamic should be considered for long-term management of this endangered species.

Appendix A. Habitat variables measured at roost trees used by Indiana bats (*Myotis sodalis*) and northern long-eared bats (*M. septentrionalis*) in southern Illinois, 1999–2001

Height of roost (*m*): Estimated with telemetry and visually locating suitable roosting bark and listening for vocal bats. Location often was confirmed with an exit count that same evening as bats left to forage. Actual height was determined using a clinometer (Suunto, Helsinki, Finland).

Height of roost tree (*m*): Determined using a clinometer.

Diameter of roost tree (*cm*): Diameter at breast height (dbh) measured using a diameter tape (Forestry Suppliers Inc., Jackson, MS).

Substrate of roost: Established with both visual and auditory confirmation of bats under the bark, in crevice or cavity, or with an exit count in the evening.

Degree of obstruction of roost (*clutter*): Visually estimated within five categories: open, light, moderate, cluttered, and very cluttered.

Percent cover of bark: The total amount of bark remaining on the tree. Estimated individually by both observers and an average value recorded.

Percent closure of canopy: Because bats often were roosting at or above the general tree canopy, this variable was estimated both at the base of the tree and at the roost. Percentage of area above observer covered by canopy was estimated. Observers visualized a 45° cone from base of tree and at roost and estimated percent canopy. Averages were taken; generally, variation among estimators was low.

Distance to water (*m*): Nearest permanent water, while tree was occupied.

Condition of roost: Rated between 0 (live) and 4 (devoid of bark and branches). Categories were slightly modified from Thomas et al. (1979).

Distance to forest (*m*): Distance from roost tree to nearest patch of closed-canopy forest. For most trees, this distance was zero because roosts were located within an intact forest.

Appendix B. Measurements from a 0.04 ha (11.3 m radius) circular plot established around each roost tree and all corresponding random trees in southern Illinois, 1999–2001

Measurements of overstory: Species, dbh, and height of trees with dbh ≥ 7 cm. The dbh (cm) was measured using a diameter tape and height (m) was measured with a clinometer.

Depth of overstory canopy (*m*): Range from top of tallest live tree to height of lowest major branches.

Measurements of understory: Number of stems of each species of woody vegetation with a dbh > 1.25 and < 7 cm.

Depth and height of understory (*m*): Range from the top of tallest understory tree (< 7 cm dbh), to bottom of understory—usually, the ground.

Density of understory: Recorded as one of five categories: open, light, moderate, moderate-heavy, and heavy by the same observer in all samples.

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