SUMMER HABITAT USE OF ROOST TREES BY THE ENDANGERED INDIANA BAT (*MYOTIS SODALIS*) IN THE SHAWNEE NATIONAL FOREST OF SOUTHERN ILLINOIS

By

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Roost trees of Indiana bats (*Myotis sodalis*) and northern myotis (*Myotis septentrionalis*) were located using radio telemetry in two locations in southern Illinois. Fifty-three roost trees were located for 31 Indiana bats. Ten adult female northern myotis were tracked to 19 different trees. Indiana bats used seven different tree species and northern myotis used six. Indiana bats used green ash (*Fraxinus pennsylvanica*) and pin oaks (*Quercus palustris*) more than expected and sweetgum (*Liquidambar styraciflua*) less than expected. Logistic regression was used to create models to predict use between Indiana bats and random trees, northern myotis and random trees, and Indiana bats and northern myotis. Indiana bat roosts differed from available trees by typically being in areas of low roost obstruction (clutter) that were close to intact forests (X^2 = 10.284, df = 2, p = 0.006). When compared to random trees, roosts of northern myotis were closer to intact forests (X^2 = 10.562, df = 1, p = 0.001). The amount of roost obstruction (clutter)

around the roost and decay class of tree were important in distinguishing between the roosts of the two species ($X^2 = 38.633$, df = 2, $p < 0.001$). Northern myotis roosts were typically more cluttered and not as decayed as those of Indiana bats. Northern myotis also made extensive use of exfoliating bark, cavities and crevices, whereas Indiana bats almost exclusively used exfoliating bark. Indiana bats used a larger area for roosting than did the northern myotis. Additionally, Indiana bats traveled greater distances between roosts than did northern myotis.

I suggest that Indiana bat colonies are ephemeral in a given area because of short-term persistence of their roosting requirements. This makes long-term management of a given site problematic. Land managers may be able to use bat houses to help sustain colonies between natural disturbances that create the necessary roosting habitat.

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INTRODUCTION

Bats play important roles in ecosystems across the globe. Many bat species are important pollinators of many ecologically and economically vital plants (Subramanya and Radhamani 1993, Fleming et al. 2001, Muchhala and Jarrin 2002). Others are important seed dispersers (Heithaus 1982, Fleming et al. 1993). All bats in temperate regions of North America are insectivorous. Similar to bats in other areas, these animals play important roles in the control of insect populations (Ross 1967; Whitaker 1972; Kunz et al. 1995). However, of the 45 bats species found in the U.S., 6 are currently listed as endangered or threatened. Approximately 20 additional species are of "special concern" or candidates for listing in the future (Harvey et al. 1999). These trends in North America are similar to those for bats throughout the world (Nowak 1994). The Indiana bat (*Myotis sodalis*) is one of the federally listed endangered species in the U.S. This species hibernates in large colonies. Eight-five percent of all Indiana bats hibernate in only nine locations (USFWS 1999a). Because of a >50% population decline in 40 years and the vulnerability of such a large proportion of the species in a few areas, the Indiana bat was listed as endangered in 1967 (USFWS 1999a, Clawson 2002). Since its listing, their wintering habitat has been protected from disturbance by: 1) reducing human use of caves and mines used as hibernacula by construction of gates, and 2) education of the public. As part of the effort to restore the population of Indiana bats, researchers have strived to learn more about their natural history to better understand how management decisions affect this species. The vulnerability of these bats during winter was the leading factor for their listing. Despite habitat protection and public education, populations continue to decline (USFWS 1999a). Information on summer habitat use by this species is lacking. It is now thought that population declines may be a result of many factors including those affecting the availability and characteristics of summer habitat. In contrast, northern myotis (*Myotis septentrionalis*) use many of the same habitats as the Indiana bat; they use forest during the summer and hibernate in caves and mines during the winter. These two species are commonly sympatric, but while Indiana bats continue to decline, northern myotis are relatively common.

LITERATURE REVIEW – SUMMER HABITAT USE

General Roosting Ecology

Female Indiana bats form small maternity colonies (usually <100 bats) under exfoliating bark during the summer (Whitaker and Hamilton 1998). A single young is born in early summer (Mumford and Calvert 1960). Maternity colonies usually are composed only of females and young (Humphrey et al. 1977) with the males roosting separately (Hall 1962). Young usually are volant by early to mid July (Humphrey et al. 1977). Maternity roosts most commonly are located in bottomland or riparian areas (Gardner et al. 1991b, Callahan et al. 1997). However, maternity roosts occasionally have been found in other areas including pastures and upland hardwoods (Kurta et al. 1993a, Whitaker and Hamilton 1998). Summer roosts of males occur in a variety of locations. Bachelor colonies of approximately 1000 to 1500 bats have been seen in an abandoned mine in Illinois. Other roosts of males have been found under exfoliating bark similar to those used by females (Gardner et al. 1991b).

Indiana bat roosts used during spring, summer, and autumn can be placed into one of two categories: primary or alternate (Callahan et al. 1997). Primary roosts were defined by Callahan as trees that are used by >30 bats on more than one occasion. Alternate roosts are used by fewer individuals. Both roost types are essential for meeting Indiana bat maternity requirements. Although a 30-bat threshold may not be applicable to all colonies (especially to those with <30 bats), the concept of primary and alternate roosts will be maintained throughout this section.

Northern myotis differ in that they generally do not form large maternity colonies. They are generally found in groups of <30 individuals. Additionally, northern myotis will use a variety of roost types. They have been found in cavities, crevices, under exfoliating bark, and in human-created structures such as bat houses, bridges and old barns (Fitch and Shump 1979, Sasse and Pekins 1996, Burke 1999, Foster and Kurta 1999, Lacki and Schwierjohann 2001, Menzel et al. 2002, Feldhamer et al. 2003).

INDIVIDUAL TREE SCALE

Tree Species Used/Preferred

One of the earliest reported Indiana bat maternity roosts was a primary roost in a bitternut hickory (*Carya cordiformis*) snag and an alternate roost in a live shagbark hickory (*C. ovata*; Humphrey et al. 1977). Roosts in living trees most commonly are found in shagbark hickory (Gardner et al. 1991a, Callahan et al. 1997). Indiana bats have been documented roosting in snags of a plethora of tree species including red (*Acer rubrum*), silver (*A. saccharinum*), and sugar maple (*A. saccharum*), bitternut, shagbark, and pignut hickory (*C. glabra*), cottonwood (*Populus deltoides*), white (*Fraxinus *americana*), black (*F. nigra*), and green ash (*F. pennsylvanica*), American sycamore (*Platanus occidentalis*), white (*Q. alba*), scarlet (*Q. coccinea*), shingle (*Q. imbricaria*), northern red (*Q. rubra*), and post oak (*Q. stellata*), sassafras (*Sassafras albidum*), American (*Ulmus americana*), and slippery elm (*U. rubra*; Brack 1983, Gardner et al. 1991a, King 1992, Kurta et al. 1993a, b, 1996, Caryl and Kurta 1996, Salyers et al. 1996, Callahan et al. 1997, Britzke et al. 2003). Most recently, Britzke et al. (2003) found maternity colonies in conifers. An eastern hemlock (*Tsuga canadensis*) was used in North Carolina, pitch pine (*Pinus rigida*) and other non-specified pines (*Pinus* sp.) were used in the Great Smoky Mountains National Park, TN. Autumn and early spring roosting studies in Kentucky also have documented Indiana bats roosting in conifers such as Virginia pine (*Pinus virginiana*) and shortleaf pine (*P. echinata*); females also used sourwood (*Oxydendum arboreum*; Kiser and Elliott 1996, MacGregor et al. 1999).

Some biologists currently consider these trees to be the "acceptable species" (Gardner et al. 1991b, Rommé et al. 1994). However, new tree species are frequently being added to this list (e.g. MacGregor et al. 1999), and it is premature to consider this tree list as definitive. With the exception of Kurta et al. (1996), all currently known reports of roost tree species are observational. Most studies did not use statistical designs to test roost tree preference. However, Kurta et al. (1996) demonstrated that Indiana bats preferred green ash to silver maple. However, silver maple has been documented as a roost tree in other studies (Gardner et al. 1990, Callahan et al. 1997). Therefore, "preference" in roost tree selection by Indiana bats may be regional or even site-specific.

Some biologists think that Indiana bat use of snags is strongly influenced by bark characteristics. Because the vast majority of maternity roosts are found under exfoliating bark, the physical characteristics of the snag on which the bark is present may be more important than the tree species (Rommé et al. 1994).

Indiana bats will use artificial roost structures. Salyers et al. (1996) documented two male Indiana bats roosting in a bat box in central Indiana. Using radio telemetry, they tracked one bat to other bat boxes and a cedar shake garland. Wilhide et al. (1999) documented a male Indiana bat roosting under the metal brackets of a utility pole top in the Ozark National Forest, Arkansas. Mumford and Cope (1958) make two references to Indiana bats (males) roosting under bridges in Indiana. Additionally, male Indiana bats have been observed roosting in an abandoned mine during the summer along with northern myotis (Carter et al. 2002) and southeastern myotis (*M. austroriparius*). These reports suggest that male Indiana bats may be cosmopolitan in roost types used.

Northern myotis roost in many different types of trees, because they use a variety of different roost types (e.g. bark, cavities). In Kentucky, 12 species of trees were used. Sourwood and shortleaf pine were the most commonly used (Lacki and Schwierjohann 2001). However, in Michigan only three tree species were used. Eighteen roosts were in silver maple, 13 in green ash and one in red maple (Foster and Kurta 1999). Although American elms were abundant they were not used in the Michigan study (Foster and Kurta 1999). The species of trees used in New Hampshire were similar to the forest composition (Sasse and Pekins 1996). In West Virginia, northern myotis used seven species of trees. Thirty-three percent were found in black locust, which is more than expected based on availability (Menzel et al. 2002). Northern myotis readily use artificial roost structures (Burke 1999, Feldhamer et al. 2003).

Tree Condition

Although some alternate roosts have been located in living trees (primarily shagbark hickories), most Indiana bat roosts are in dead or dying trees. One of the two roost trees reported by Humphrey et al. (1977) was a live shagbark hickory. Approximately 10% of the roost trees from Illinois reported by Gardner et al. (1991b) and 28% of the trees reported by Callahan et al. (1997) were classified as live. Kurta et al. (1996) reported that many roost trees used were "mostly dead," thereby suggesting that they were still alive. Although most of the reported roosts have been in snags, live trees may be an important component of Indiana bat roosting ecology. Live and dead trees may differ in terms of protection from rain and solar radiation provided by their canopy as well as rates of heat loss (Humphrey et al. 1977, Gardner et al. 1990, Callahan et al. 1997).

Northern myotis use both living and dead trees. They roost under the exfoliating bark of snags or in the cavities of dead or living trees (Sasse and Pekins 1996, Lacki and Schwierjohann 2001, Menzel et al. 2002). Previous studies suggest that larger colonies usually occur in either cavities or under the bark of snags (Sasse and Pekins 1996). It is unclear if this trend is because larger cavities are most often found in snags or if they prefer some other characteristic of snags.

Structural Characteristics Of Roost Trees

Few maternity colonies of Indiana bats have been located in tree cavities. Rather, most primary maternity roosts have been located under exfoliating bark. The ability of a tree species to produce exfoliating bark probably influences Indiana bat use (Rommé et al. 1994, Callahan et al. 1997). However, studies from Michigan and Missouri that have compared the amount of exfoliating bark and Indiana bat use found no relationship; snags with more exfoliating bark were not used more often than were snags with little exfoliating bark. Both Kurta et al. (1996) and Callahan et al. (1997) found that the quantitative amount of loose, peeling bark did not differ between roost trees used and random snags presumably not used. However, these studies did not address the qualitative features of exfoliating bark.

Although most roosts have been in large trees, the size of roost trees varies. The average diameter for all roosts described by Garner et al. (1991b) was 36.7 cm with a range of 8-83 cm; the four roosts with the largest numbers of bats averaged 40 cm dbh. Primary roost trees described by Callahan et al. (1997) averaged 58.4 ± 4.5 cm dbh. Alternate roosts averaged 53.0 ± 4.1 cm dbh. Callahan et al. (1997) found no size difference between alternate and primary roosts or between roost snags and random snags. Kurta et al. (1996) found that average diameter of Indiana bat tree roosts (meaṇ= 40.9 ± 1.2 cm, range 30 to 52 cm) was significantly less variable than average diameter of random trees (meaṇ= 33.4 ± 1.4 cm, range 11 to 70 cm).

Study results examining roost tree size affect on selectivity are conflicting (Kurta et al. 1996, Callahan et al. 1997). Gardner et al. (1991b) arbitrarily concluded from 48 roost trees that snags of at least 22 cm dbh provide essential Indiana bat roosting habitat. Indiana bats have been observed roosting in snags < 22 cm dbh (Kurta et al. 1996, Callahan et al. 1997).

Roosts in spring and autumn for male Indiana bats do not differ in size from those used during summer. Autumn and spring roosts reported from western Virginia and

Kentucky ranged from 8.4 to 86.6 cm dbh, with a mean of 31 cm (Hobson and Holland 1995, Kiser and Elliott 1996, MacGregor et al. 1999).

The structural characteristics of northern myotis roosts varies considerably. Sasse and Pekins (1996) found that trees used as roosts were larger and less decayed than random trees. In many studies, mean stand diameter at breast height (dbh) was larger around roosts than around random plots (Sasse and Pekins 1996, Foster and Kurta 1999, Lacki and Schwierjohann 2001). Menzel et al. (2002), found only 3 characteristics that differed from random trees. Cavities were high in roosts, and the nearest overstory tree and nearest taller overstory tree were closer to roosts than for random trees. While not different than random trees, other characteristics of northern myotis roosts in West Virginia were similar to those of other studies. They selected large trees, high canopy closure, and medium levels of decay. Additionally, Lacki and Schwierjohann (2001) found differences in roost characteristics between pregnant, lactating, and post-lactating bats.

Solar Exposure And Spatial Relation To Neighboring Trees

Previous studies suggest that most primary roosts are well exposed to extensive solar radiation. However, alternate roosts vary in the amount of solar exposure received. Some alternate roosts are completely shaded whereas others are completely exposed. Indiana bats may pick maternity roosts with high solar exposure levels to increase the roost temperature, which could decrease the time of fetal development and juvenile growth. However, because males are not associated with maternity colonies and the need for high roosting temperatures, they may seek cooler roosts to reduce their physiological expenditures (Callahan et al. 1997).

Quantifying a roost's exposure to solar radiation is difficult. In Illinois, Gardner et al. (1991b) reported that most Indiana bat roosts they located were beneath the forest canopy. However, they estimated canopy closure using multiple spherical densiometer readings taken near tree bases. These readings would most accurately reflect canopy closure of the forest where the roost was located rather than solar exposure of the roost (see Stand Scale: Canopy Cover). Callahan et al. (1997) considered roosts to be either open (exposed to solar radiation) or interior (>50% canopy cover). They found that all primary roosts were in open (exposed) snags. Live interior roost trees averaged 70% canopy closure and were more open on the western aspect than random live trees. Interior snags used as roosts averaged 60% canopy closure and were more open on all aspects than random interior snags. MacGregor et al. (1999) reported that canopy closure varied from 20 to 93% (mean = 80%) for male Indiana bat roosts. However, MacGregor et al. (1999) noted that there were no good methods to measure the canopy closure (solar exposure) at the actual roost. Additionally, tools such as spherical densiometer, fisheye photography, and competition indexes used to assess canopy closure can yield different results (Cook et al. 1995, Comeau et al. 1998).

Differing methodologies may explain discrepancies among studies of the solar exposure of primary roosts. However, the solar exposure issue remains an important factor that has not been adequately resolved. Reports of solar exposure for alternate roosts also vary greatly from completely shaded to completely exposed. Unlike primary roosts, solar exposure differences among alternate roosts probably are real. Alternate roosts are used when conditions in the primary roost are suboptimal (Callahan et al. 1997). Because conditions that make roost sites temporarily uninhabitable can vary (e.g. extreme high or low temperatures, precipitation), the structural characteristics of alternate roosts also vary.

In addition to canopy cover, roost height also affects the degree of solar exposure. For closed-canopy roost trees found by Gardner et al. (1991b) in Illinois, the average height of primary maternity roosts was 7.8 m. The average height of alternate roosts used by females was 6.4 m in areas under a forest canopy, 5.2 m in areas with a "patchy" forest canopy, and 2.7 m in trees located in the open. Although not statistically compared, this trend shows that females tended to roost higher in the canopy in closed-canopy forests.

Roost heights may vary with canopy cover to maintain a relatively constant level of solar exposure. Callahan et al. (1997) in Missouri reported that 45% of maternity roost trees were in open areas (exposed to direct solar exposure) and that they were used by more individual Indiana bats than closed canopy roosts. The Indiana bat maternity colony that Kurta et al. (1996) described from Michigan roosted in snags in the middle of a flooded pasture turned wetland. All snags were unshaded and the mean roost height was 9.9 m (± 0.9, range 1.4 – 18 m).

However, male Indiana bats show a different trend regarding roosting height and solar exposure. The average roost height used by males in the study by Gardner et al. (1991b) was 4.2 m (4.9 m in closed canopy and 3 m in "patchy" canopy). They reported only one male roost from an open canopy situation at a height of 4 m. A male Indiana bat tracked by Hobson and Holland (1995) in western Virginia roosted at a height of > 8 m each night for 19 consecutive nights.

Northern myotis generally roost in forests with low levels of solar exposure (Sasse and Pekins 1996, Lacki and Schwierjohann 2001). However, Foster and Kurta (1999) found a bimodal distribution of solar exposure levels in their study. Sixty percent of the roosts were found in open areas (0-20% canopy closure) and the remainder was in closed canopy forests (>80% canopy closure). Menzel et al. (2002) recorded low levels of solar exposure for northern myotis roosts in West Virginia.

Spatial Relationship Of Roost To Water Sources And Foraging Areas

Proximity of Indiana bat roosts to water sources and foraging areas has not been well documented. Two roost trees reported by Humphrey et al. (1977) in Indiana were located <200 m from the creek that the Indiana bats foraged over. A roost tree described by Brack (1983) was on the bank of the Blue River in Indiana. In Indiana, Kurta et al. (1993b) described a roost in a hollow sycamore tree that was 28 m from a dry intermittent stream, and 2 km from the nearest perennial stream. Roost trees described by Kurta et al. (1996) were located within a 5-ha Michigan wetland inundated with water 1 m deep. The bats left this area each night to feed in the surrounding landscape that was composed of agricultural lands (pasture and corn), woodlots, and an extensive riparian strip of woods (A. Kurta, Per. Comm.). All colonies reported by Callahan et al. (1997) were located "near a stream or river." In a descriptive study in Illinois, Gardner et al. (1991a) reported distances from roosts to foraging areas as great as 3,200 m (post-lactating female) with approximately equal distances for pregnant and lactating bats (1,000 m). Juveniles and adult males traveled about half the distance of females as their roosts were closer to streams than any other habitat features measured. In Illinois, the mean distance between all Indiana bat roost trees and the nearest intermittent stream was 124 m. In West Virginia, a single adult male Indiana bat repeatedly traveled 1 km from its roost site to foraging areas that included a stream and a road (Hobson and Holland 1995).

Northern myotis in Kentucky roosted relatively close to water sources and human disturbances such as roads (Lacki and Schwierjohann 2001). All roosts discovered by Foster and Kurta (1999) were inundated at some point during the two-year study. The maximum distance from any roost to permanent water sources (river or creek) was 183 m.

Spatial Relationship To Other Roost Trees

Distances between roost trees are variable within a colony. In Indiana, Humphrey et al. (1977) reported that two roost trees were approximately 30 m apart. In Michigan, Kurta et al. (1996) found average distance between roosts used by a single Indiana bat colony was 38.7 ± 7.1 m (range 1 to 147 m). In Missouri, Callahan et al. (1997) did not report the distance between roosts but provided the diameter of a circle that would encompass all roosts used by a single maternity colony. The smallest and largest "colony areas" had diameters of 1.6 and 3 km, respectively. MacGregor et al. (1999) reported that distances between autumn roosts in Kentucky ranged from 48 m to 2688 m and encompassed from 0.4 to 568 ha.

In Michigan, Foster and Kurta (1999) recorded three centers of activity for roosting northern myotis. The maximum distance between any two roosts was 2.55 km.

However, within the activity centers, the maximum distance between roosts was 632 m. Sasse and Pekins (1996) found that roosts were “clustered” together rather than randomly distributed across the landscape, similar to the activity centers of Foster and Kurta (1999).

STAND SCALE

Canopy Cover

Few data are available that directly examine canopy cover in stands used by Indiana bats. However, stand characteristics can be inferred from previous studies. Methods used by Gardner et al. (1991b) best describe canopy closure at the stand level. Of 48 roosts they found in forested habitats, 32 were in closed-canopy forests (> 80% cover), 12 were in intermediate-canopy forests (30-80%) and 4 were in open-canopy forests (< 30%). All roosts reported from Michigan by Kurta et al. (1996) were from a flooded open-canopy wetland where all trees were dead or dying. The American sycamore roost reported by Kurta et al. (1993b) was “unshaded” and therefore implies a low amount of canopy closure. In Missouri, Callahan et al. (1997) calculated the canopy closure of random trees located within the stand; closure averaged 69% for all non-used trees.

In Michigan, northern myotis used a mixture of forest types for roosting. Habitats ranged from 0-100% cover (Foster and Kurta 1999).

Density Of Potential Roost Trees

There is a paucity of information concerning densities of potential tree roosts for Indiana bat maternity colonies primarily because there is no universally accepted definition of a potential roost. Gardner et al. (1991b) listed the optimal number of roost trees for upland habitat as 64 trees/ha and 41 trees/ha for floodplains. However, they did not describe a quantitative method for obtaining these data; rather, their numbers were derived from a snag density survey (dbh > 22cm) of acceptable species within the study area. Bark characteristics and decay classes were not reported. In central Indiana as part of a mitigation project, Salyers et al. (1996) reported a potential roost density of 15 trees/ha. This was increased to 30.4 roost sites/ha following installation of artificial roost structures.

Other studies have reported the spatial extent a colony occupies, from which density estimates of occupied roost trees can be made. Obviously, potential roost numbers must be equal to or greater than numbers used. In Missouri, Callahan et al. (1997) reported the largest distances between roosts of a single maternity colony. Although all roosts were not discovered, their reported highest density was 0.25 roost-trees/ha. In a 5-ha Michigan wetland, Kurta et al. (1996) found that Indiana bats roosted in 23 different trees, at a density of 4.6 roost-trees/ha. They reported that there were 66 available roost trees in the wetland (13.2 potential roost trees/ha), an unusually high density of snags.

Considering features such as species, size, and bark characteristics, not all snags make acceptable Indiana bat roosts (Gardner et al. 1991b, Kurta et al. 1996, Callahan et al. 1997). However, these features vary from area to area with no currently known predictable pattern (Kurta et al. 1996, Callahan et al. 1997). Therefore, for conservation purposes, a variety of snag types must be maintained to maximize the chance that snags with suitable structural characteristics for Indiana bats will be present. However, more information is needed to adequately define what constitutes a suitable Indiana bat roost.

Although several studies have documented the number of roost trees known to be used, the total number of roost trees needed by an Indiana bat colony is unknown and probably varies by colony size, roost availability, and variability of abiotic conditions. Furthermore, roost attrition precludes managers from being able to establish a minimum number of potential roosts. The unpredictable nature of roost destruction hinders managers from predicting the longevity of current roost trees. Additionally, the time needed for a tree to become "suitable" for Indiana bats is unknown and probably varies by tree species and geographic location. These two factors severely limit managers in making decisions regarding the roosting needs of Indiana bats.

Species Composition

There are no quantitative descriptions of stand composition for forests surrounding Indiana bat roosts. However, based on most descriptions, the stands surrounding roosts do not differ from the species used as roosts (see Tree Species Used/Preferred). Kurta et al. (1996) commented that, although there were 99 green ash, 34 silver maple, and 9 American elm trees in their study area, only green ash were used as roosts. However, Indiana bat roosts have been found in silver maple and American elm in other studies (Gardner et al. 1991a). Tree species reported in study areas that have not been used as roosts by Indiana bats include box elder (*A. negundo*), black walnut

(*Juglans nigra*), and willow (*Salix* sp.). Further study is needed to elucidate how tree species composition at the landscape scale affects roost site selection by Indiana bats.

Stand Structure

No published reports have quantitatively described stand structure surrounding Indiana bat maternity colonies. However, there have been comparisons of roost trees to randomly located potential roosts within a stand. In Michigan, Kurta et al. (1996) found that roost trees were larger (dbh) and their size (dbh) was less variable than randomly located potential roost snags. However, Callahan et al. (1997) found that roost-tree characteristics, such as dbh or bark cover did not differ statistically from potential roosts within a stand in Missouri.

Roost trees have been found in a variety of stand structures. Gardner et al. (1991b) found roosts in grazed uplands (n = 26), nongrazed uplands (n = 9), nongrazed floodplains (n = 8), a clearcut (n = 1), a hoglot (n = 1), and a pasture (n = 1). Kurta et al. (1993a) also reported a roost tree from "the middle of a heavily grazed pasture."

In eastern Kentucky on the Daniel Boone National Forest, MacGregor et al. (1999) reported that 2-aged shelterwood harvests could produce different amounts of male Indiana bat roosting habitat in autumn depending on snag retention. Their suggested guidelines called for retention of all snags, hollow trees, live trees with large dead limbs and shagbark hickories. These guidelines produced stands with 15X the number of roost trees of conventionally managed 2-aged shelterwood harvests retaining only 5 snags/ha. In this study, Indiana bats also roosted in burned areas managed for red-cockaded woodpeckers (*Picoides borealis*). Although this information is anecdotal, it suggests that Indiana bats may be tolerant of limited roosting area disturbance. Callahan et al. (1997) even suggested that management practices such as even-aged and uneven-aged management could be used if they include provisions for snag retention and if oaks and shagbark hickories are favored. However, little quantitative information exists concerning the effect of timber management practices on roost selection by Indiana bats.

Forest Type And Topography

Indiana bat roosts occur among mixed mesophytic hardwood and mixed hardwood-pine habitat types. Humphrey et al. (1977) and Brack (1983) in Indiana, located roosts in riparian habitats. In Illinois, Gardner et al. (1991b) found 37 roost in uplands and 11 roosts in bottomlands. All roosts located by Kurta et al. (1996) were in a Michigan wetland habitat. In Missouri, Callahan et al. (1997) located roosts in riparian and upland habitats. In eastern Kentucky, MacGregor et al. (1999) reported male Indiana bats roosting in pine-dominated forests during the autumn.

Northern myotis in Kentucky used a mixed mesophytic forest. Roosts were located more often on high and mid slopes than on low slopes, which were mesic riparian forests (Lacki and Schwierjohann 2001). Sasse and Pekins (1996) described their northern myotis study site as 97% forested, almost half in active timber management. The most common timber type was northern hardwoods (48%); spruce/fir and pines comprised 40% of the forest.

LANDSCAPE SCALE

Size Of Area Used Around Roosts

The area used by Indiana bats surrounding their roosts varies among colonies. Few investigators are confident that all colony roosts were discovered on study sites. Additionally, it is not always known where colony members forage. Indiana bats tracked by Kurta et al. (1996) traveled outside their immediate roosting area to forage, however, the exact location or extent was not known (A. Kurta, Per. Comm.). Humphrey et al. (1977) observed that tracked bats traveled from their roosts to a nearby stream where they foraged along a 0.81-km section. Nonetheless, Indiana bats have been observed foraging among roosts, adjacent to roosts, and in areas totally disjunct from roosting sites.

Landscape Structure

Only Gardner et al. (1991a) attempted to document landscape habitat composition. Within their study area, 65% of the area was croplands or oldfield, 2% other agriculture, 33% forested (30% upland and 2.2% floodplain), and 0.1% impounded water habitats. Statewide, Illinois was 63% agricultural, 1.6% urban, 33% forested, 6.4% forested wetlands, and 1.3% impounded water. The impact of forest fragmentation on roost availability of Indiana bats at the landscape scale is unknown.

Habitat Suitability Index Models

Rommé et al. (1994) used previously published data to develop a Habitat Suitability Index (HIS) model for Indiana bats. This model can be used to assess habitat quality across landscapes. I am not aware of any studies that have applied or validated the HSI model of Rommé et al. (1994).

LITERATURE SUMMARY

There are numerous reports of summer Indiana bat roosts. Surprisingly, there is still little known about the specifics of why these roosts are chosen. What has been reported of Indiana bat roosts is often conflicting and difficult to interpret. However, a few recent studies have described some underlying patterns to these seemingly random roosting observations. Callahan et al. (1997) and Kurta et al. (1996) have shown that maternity colonies encompass more than just one tree. One colony collectively may use many trees. The many trees used by the colony provide the total roosting resources (including cover and correct temperature provided by exfoliating bark) needed by the colony during different environmental conditions. It appears that rarely does any one tree provide all the resources needed by the colony all the time. Thus, many different types of tree species, providing many different conditions, are used by Indiana bats. It is not the species or the condition of these trees that are important to the bats, but rather the roosting resources they provide. These colonies usually have from one to a few "primary" trees (Callahan et al. 1997). Primary trees provide the proper roosting conditions the majority of the time, and often are large snags with exfoliating bark exposed to ample sunlight. During extreme environmental conditions, the colony may use other "alternate" roost trees. These may include other snags and living trees in a variety of locations. Alternate roosts provide the resources that the primary roost cannot during sub-optimal environmental conditions. Alternate roosts often are used under conditions of rain, wind, and temperature extremes. Because different trees are used under different conditions, the many different reports of maternity colony roosts can be confusing and often contradictory when environmental conditions are not considered. Distance between roost trees used by colonies also is variable. Callahan et al. (1997) reported distances as great as 3 km between trees used by the same colony. While we are now starting to understand the general structure of Indiana bat colonies, much is still left to be learned about what are the exact resources needed by Indiana bats and how their needs are met by different roost trees under different conditions.

OBJECTIVES

1. Document the presence and distribution of the Indiana bat throughout different habitat types in Shawnee National Forest.

   Ho – Indiana bats will be randomly distributed throughout the available habitat types.
2. Document the presence of reproductively active female Indiana bats on the Shawnee National Forest and locate the associated maternity colonies.
3. Quantify habitat characteristics of maternity roosts (see Appendices I & II).

   Ho – Indiana bat roosts will not differ from available trees.
4. Compare characteristics of the roost trees of Indiana bats to those of northern myotis, another bark-roosting bat sympatric with Indiana bats.

   Ho – The roost characteristics of Indiana bats and northern myotis will not differ.

METHODS

STUDY AREA

Indiana bat maternity colonies were discovered at two locations in southern Illinois. The first colony is located in Oakwood Bottoms near the town of Grand Tower, Jackson County, Illinois. This colony used Oakwood Bottoms, an 80-year old closed-canopy bottomland forest and the surrounding floodplain of the Mississippi and Big Muddy Rivers. This green-tree reservoir has a series of levees and water control structures that allow land managers to manipulate the water levels within the area. Oakwood Bottoms is dominated by pin oaks (*Quercus palustris*) as well as various species of maples, elms, ashes and other oaks. Severe floods of 1993 and 1995 caused high tree mortality in Oakwood Bottoms and the surrounding area making it especially favorable for snag-roosting species like the Indiana bat. The tree mortality in Oakwood Bottoms is estimated around 25-30%, with specific portions having a larger percentage of dead trees than others. The colony also used the flood plain forest between Oakwood and the Big Muddy River to the east (Figure 1). Because this area was not sheltered by a large levee system, like Oakwood, the mortality from the floods was much higher (around 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 more open with a few patches of intact forest. Most of the floodplain forest is open canopy (<50% cover). This colony also extends into the floodplain of Cedar Creek, a tributary of the Big Muddy River. This area is north and east of Oakwood (5-10 km), near the town of Pomona, Jackson County, Illinois. This area has fewer snags than the other areas. Also, the floodplain of Cedar Creek is narrower, resulting in a greater component of upland habitats compared to Oakwood and the other colony.

The second Indiana bat colony is located in Bluff Lake Swamp near the town of Millcreek, Union County, Illinois. This swamp is located along the eastern edge of the Mississippi River floodplain, about 30 km south of the Oakwood Bottoms colony. Because it is along the edge of the floodplain, it has uplands, various bottomlands, agricultural, and large wetland areas. Most of the roosting bats are within a swamp that has high snag densities along its edge, probably a consequence of the persistently elevated water levels resulting from extensive beaver (*Castor canadensis*) damming. The forests on the southwest and west side of the swamp, along Clear Creek Ditch, are older (60-80 yrs old) than the forest on the eastern side of the swamp. West of the ditch is Union County Conservation Area. This state wildlife refuge is primarily managed for migrating waterfowl. It has a variety of habitats from 120-yr-old forests to extensive agricultural areas (Figure 2). The forest on the southeastern side of the swamp is relatively young (20-40 yrs old) and contains few snags. The north and eastern sides of the swamp stop at the base of the bluffs that also mark the edge of the Mississippi Floodplain. Elevation increases quickly, rising 120 m in 0.3 km. The habitats on the bluffs are typical of upland forest found throughout this area. The forests surrounding the swamp on the western and southern sides are typical of other bottomland forests found in southern Illinois regarding tree species composition.

CAPTURE AND TELEMETRY TECHNIQUES

At each location bats were captured using high mistnet systems (Gardner et al. 1989). These net sets can be configured to stack two (6.1 m) or three nets (9.15 m) on top of each other. The width and height of the nets can be varied according to the area being netted. Nets were placed in areas of anticipated high bat activity such as watering holes or flight corridors. Occasionally, nets were placed around known roost trees to capture bats as they exited in the evening to forage. After capture, selected individuals were fitted with miniature radio transmitters (0.48 g, Holohil Systems Ltd, Ontario Canada). Transmitters were affixed to the back of bats with Skin-Bond surgical glue (Smith and Nephews United, Inc., Largo, FL). Transmittered bats were tracked back to their roosting sites each day until the transmitter was shed or the battery died. Typically, the transmitters remained attached for 4-5 days.

For comparison, northern myotis also were captured. Females were tracked using the same techniques used with the Indiana bats. All northern myotis were captured and studied at the Oakwood Bottoms location (Figure 3).

HABITAT MEASUREMENTS

At each roost, I attempted to determine the exact location of the animal in the tree. Numerous habitat variables were measured for each roost location. On the actual roost tree, 14 microhabitat characteristics were recorded (see Appendix I). Around each known roost, a 0.04 ha circular plot was established and six other habitat characteristics were collected within the plot (see Appendix II). Additionally, for each known roost tree, habitat variables were measured on a random tree. Random trees represent a sample of the trees available for roosting to the bats. Because some of these trees could be used by bats at some point, they cannot be considered as "not used" but rather as random samples of all types of trees. Previous studies (see Introduction) have documented a variety of attributes of Indiana bat roost trees. Therefore, I chose to specify minimum requirements of random trees. A random tree must have met four criteria that are fairly well established in the literature. The prospective tree must have been dead, at least 10 m tall, have a diameter at breast height (dbh) of at least 9 cm, and have suitable bark for roosting. Random trees selected for comparison to known roosts of the northern myotis did not follow these same selection criteria. Because this species has a wider roosting niche breadth than Indiana bats, the selection criteria used for Indiana bats would be too restrictive. Basically, all trees of all sizes were considered possible random trees, because I found northern myotis using everything from understory snags to large living trees with cavities.

Landscape level variables were calculated with Geographic Information Systems (GIS). 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). Distance measurements were calculated using the measuring tools found in ArcView 3.2. The extension Animal Movements (Hooge and Eichenlaub 1997) was used to calculate the core areas used by the maternity colonies for roosting.

STATISTICAL ANALYSIS

Likelihood ratio X^2 tests were used to see if roost-tree species were chosen at random or if certain species were used in greater proportion than available. Case-control logistic regression (Hosmer and Lemeshow 1989) was used to examine habitat differences between the roosts of Indiana bats and random trees. Differences between northern myotis and random trees, and Indiana bats and northern myotis were also tested with case-control logistic regression. Case-control differs from regular logistic regression in that the number of samples (bat presence or absence) is set by the sampling design. Because relatively equal numbers of roost and random trees (rather than a random sample of all trees present) were selected, the intercept of the logistic regression model will depend on the numbers of each type of tree. While the general relationships should remain consistent between the dependent and independent variables, the true intercept of a population-wide model cannot be estimated without further information. As such, the likelihood function of the model is related to probability that the subject (tree) was selected for the sample. I followed the process outlined by Hosmer and Lemeshow (1989) for limiting the number of variables in the logistic regression model. The process began with a univariate analysis of each habitat variable. All variables with a p-value < 0.25 were included in the subsequent multivariate analysis. A p-value of 0.25 is 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. The final model was constructed using only those variables from the multivariate analysis that had a final p-value of ≤ 0.05. As a rule, the number of variables in a logistic regression model should not exceed 1 variable for every 10 samples (Hosmer and Lemeshow 1989). When calculating the final model, logistic regression will only include those variables that significantly explain different portions of the data variation. Therefore, some variables while statistically different, were correlated and did not explain any additional variation in the data. These variables will not be included into the final logistic regression model. Because most previous studies did not use logistic regression and because some significant variables are not included in the final logistic regression model, t-tests were conducted on all variables so that comparisons could be made with previous research.

RESULTS

Forty-one transmitters were attached to bats during the 3 year study. The 31 Indiana bats used 53 different roost trees. One male Indiana bat was tracked to 4 trees which were not included in the statistical analysis. Adult females and young of the year were tracked to 49 trees, but vegetation sampling was only conducted around 47 of these. Indiana bats were tracked for an average of 4.35 nights (range 0-11) switching roosts an average of 2.81 times (range 0-7). The greatest number of consecutive nights per tree was 4. The 10 adult female northern myotis used 19 different trees. Northern myotis 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 myotis used the same tree was 3 consecutive nights.

INDIVIDUAL TREE SCALE

Tree Species Used/Preferred

Indiana bats used seven tree species for roosting during this study. Of the 28 tree species found in the overstory, 23 grow large enough to be used by Indiana bats. Due to small samples sized, only the 5 most abundant tree-species (elm, green ash, pin oak, unspecified snags, and sweetgum; *Liquidambar styraciflua*) on the study area were used to examine roost-tree preference. Chi-squared likelihood ratio tests indicated that when compared to relative abundance on the study area, Indiana bats did not select these tree species in the same proportion they were available (X^2 <0.0001, df = 4). Green ash and pin oak were used more than expected, and sweetgum was used less than expected based on availability. Additionally, although not included in the analysis, silver maple and cottonwood appeared to be used greater than expected. Willow, sugarberry, and red maple were used less than expected (Table 1). Northern myotis used six tree species. Almost 75% of the roosts were in elms or pin oaks, both of which were abundant in the study area. Green ash and willow were also abundant but were not used (Table 1).

Tree Condition

All Indiana bat roosts discovered during this study were in snags. However, about 42% of northern myotis roosts were in living trees. Two of these roosts were in the hollow boles of a sweetgum and elm. The remaining live-tree roosts were in cavities of the bole or major branches of large pin oaks.

Structural Characteristics Of Roost Trees

All Indiana bats roosted under exfoliating bark, except for two roosts which were in crevices of snags, one of which was partially covered by bark. Northern myotis used bark, cavity, and crevice roosts. Percent bark coverage did not differ between roosts and random trees for either bat species (Table 2).

Using logistic regression, two variables distinguished between Indiana bat roosts and a random sampling of snags within the forest (X^2 = 10.284, df = 2, p = 0.006). Amount of roost obstruction around random snags was higher than around Indiana bat roosts (X^2 = 8.265, df = 1, p = 0.004). Also, Indiana bat roosts were closer to the contiguous forest than random snags (X^2 = 5.002, df = 1, p = 0.025). The logistic regression model was:

x = 2.097 – 0.856 (degree of roost obstruction (visual)) – 0.023 (distance to forest),

where the probability of a tree being an Indiana bat roost = $1/1+e^{-x}$. No other variables differed between random snags and those used by Indiana bats (Table 2A).

During the initial univariate analysis six variables were significant when differentiating between the roosts of northern myotis and random trees. Degree of roost obstruction (visual), % bark cover, % canopy cover at roost, decay class, distance to forest, and average plot dbh, were all entered into multivariate logistic regression. One variable, distance to forest, distinguished between the roosts of northern myotis and random trees (X^2 = 10.562, df = 1, p = 0.001). The logistic regression model is:

x = -0.374 – 0.154 (distance to forest),

where the probability of a tree being a northern myotis roost = $1/1+e^{-x}$.
Northern myotis roosts were closer to intact forests than were random trees.

Many variables appeared to be important in distinguishing between the roosts of Indiana bats and northern myotis (Table 2C). Six variables were entered into the multivariate logistic regression model; degree of roost obstruction (visual), % bark cover, % canopy cover at roost, decay class, distance to forest, and average plot dbh. The final multivariate logistic regression model contained two variables, degree of roost obstruction (visual) and decay class. This model differentiated between the roosts of the two species (X^2 = 38.633, df = 2, p < 0.001). Degree of roost obstruction (visual) was greater around northern myotis roosts than around Indiana bat roosts (X^2 = 14.954, df = 1,

$p < 0.001$). Northern myotis roosts were less decayed than those of Indiana bats (X^2 = 4.876, df = 1, $p < 0.027$). The logistic regression model is:

x = -1.276 + 1.214 (degree of roost obstruction (visual)) – 0.921(decay class),

where the probability of a tree being a northern myotis roost = $1/1+e^{-x}$. While not used in the analysis, roost type also can be helpful in differentiating between the two species. Northern myotis used many types of roosts, including exfoliating bark, crevices, and cavities, whereas Indiana bats almost exclusively used exfoliating bark.

The average dbh for Indiana bat roosts was 39 cm, and 37 cm for northern myotis (Table 2B). Neither was different than that of random trees available in the study area (t = 0.395, df = 74, $p = 0.694$; t = 0.456, df = 26, $p = 0.652$). Roost-tree height also did not differ from the height of the surrounding trees.

Solar Exposure And Spatial Relation To Neighboring Trees

Indiana bats used roosts with low canopy closure levels (Table 2A), although not different from that of random trees. The average height of Indiana bat roosts was 10 m. It was 9 m for northern myotis. However, northern myotis roosted in areas with higher canopy closures than were found in random plots (Tables 2B).

Spatial Relationship Of Roost To Water Sources

All roost trees of both bat species were located in bottomland and floodplain habitats that are prone to flooding. All roost trees were flooded in up to 1 m of water at some point throughout the study. Many trees remained flooded throughout the duration of the study. During the driest periods of the study, bats would never have to travel more than 750 m to reach a source of permanent fresh water.

Spatial Relationship To Other Roost Trees

The roosting area for the Indiana bats at Oakwood Bottoms was almost an order of magnitude larger than that of the sympatric northern myotis (Table 3). The greatest straight line distance traveled between consecutive roosts for Indiana bats was 4,650 m. However, it is unlikely that these animals were flying over the bluffs that border the Mississippi flood plain (elevation increase of 120m), but rather flew around them and up the valley to the next roost (See Figure 1). The shortest distance around the bluffs is 5,950 m. If the bats were actually following the river corridor which winds through the floodplain they would have traveled 15,500 m between consecutive roosts. This distance was traveled by two bats on two separate occasions.

While it is impossible to know the exact size of the Indiana bat populations at Oakwood bottoms and Bluff Lake, observations of emergence counts suggest the populations are approximately equal in size. However, the Indiana bats at the Bluff Lake colony used an area almost an order of magnitude smaller than those at Oakwood Bottoms (Table 3). The longest distance moved in consecutive nights by an Indiana bat at Bluff Lake was approximately 1000 m. The shortest distance moved between nights was 20 m. Northern myotis also moved relatively shorter distances between consecutive roosts. Most roosts were < 100 m apart (Figure 3), however the largest distance traveled between roosts was 860 m. One northern myotis moved 1390 m between the capture location and its roost the next day.

STAND SCALE

Density Of Potential Roost Trees

Because the smallest dbh and average roost height used by Indiana bats was 18.5 cm and 10 m respectively, any snags with those dimensions or larger were considered as a potential roost tree. Given these criteria, the study area has a suitable snag density of approximately 45.3 snags/ha. This did not take into account any of the other roost features thought to be important, such as canopy closure or bark cover, which would likely reduce the number of potential roost trees.

Species Composition

Combining all the vegetation sample plots conducted around roosts and random trees provides a complete overstory composition for an area of approximately 4.6 ha. The major overstory components in forested areas used by Indiana bats and northern myotis for roosting include: elm (28%), snags (26.5%), green ash (9.7%), pin oak (6.8%), and sweetgum (6.4%). All other species accounted for <5% each (Table 1).

DISCUSSION

ROOST SWITCHING

The amount of roost switching observed during this project is similar to Indiana bats in other studies (Kurta et al. 1996). Northern myotis switched roosts an average of every 5 days in West Virginia. In Michigan they switched roosts an average of every 2 days, and 2.2 days in New Hampshire (Sasse and Pekins 1996, Foster and Kurta 1999, Menzel et al. 2002).

The reason for switching roosts is not known for either species. Possible reasons include temperature, precipitation, predation, parasitism, and roost site ephemerality. Most likely it is some combination of these and possibly others. Climatic conditions are unlikely the sole driving factors since many of the roost trees were used in a variety of temperature and precipitation conditions. Parasitism is also unlikely to be the only factor because many roosts were continually used by some bats. Often, the radio tagged individual may switch to another roost, but other bats are still present. Roosts often remain continually occupied for months at a time. Switching roosts would do little to reduce parasite loads unless all the bats moved as a collective unit, eliminating hosts at a roost and causing parasites to die or vacate. Additionally, many bat parasites travel in the fur or on the skin of the bats. Thus, parasites would invade new roosts as quickly as the bats. Predation could lead to abandonment of a roost. However, predation should cause all the animals to abandon simultaneously, but this was seldom witnessed. It would seem that maintaining knowledge of alternate roost sites could be the main driving force leading Indiana bats to switch roosts. The patterns of movement support this hypothesis. As noted, most often a roost is continually used by some bats for an extended period of time. Individuals may leave and return over periods of days. Also, many roost trees fall over soon after discovery. Approximately 25-30% of the trees found in this study were down within one year of discovery. Some trees fell within weeks of discovery. Additionally, the exfoliating bark frequently is shed. Many roost trees in this study had the roosting piece of bark 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 alternative roosts.

While alternate roost site knowledge would explain why Indiana bats move between roosts, is does not explain all the behaviors observed. If knowledge of alternate roost sites was the single driving force for roost switching, a random pattern of roost switching would be expected. However, this was not observed. It is likely that social interactions may also factor into roost switching. Often several radio-collared bats would switch to the same tree, or one bat would follow another to a new roost a few days after the first switched. Additionally, in May of 2001 a simultaneous multi-roost exit count was undertaken on 12 different known Indiana bat roost-trees. While many of these trees only had a few bats using them at the time of discovery, at least six were known to have 20+ bats using them at the time of discovery. On the night of the group survey, only one tree had 20 bats exit. Six trees had ≤3 bats, the tree that was heavily used days earlier was used by only 12 bats, and the rest of the trees were not used. It appears that these Indiana bats do not move as discrete unit. The colony may travel as a loose group, shifting from one roost to another over a period of days or weeks. The largest single exit count for the Oakwood Bottoms colony was 107 individuals (pre-parturition). All other counts were usually <50, suggesting that during most of the study the colony was dispersed over multiple roosts.

INDIVIDUAL TREE SCALE

Tree Species Used/Preferred

Differences in roost selection by the two bat species can be attributed to the differences in bark, cavities, and the structural characteristic of the trees. Structural characteristics of a tree species are perhaps more important to Indiana bats than northern myotis. With few exceptions, Indiana bats primarily roosted under exfoliating bark. Many of the more common tree species found in the study area have thin bark. When a tree dies, this thin bark becomes extremely fragile and does not form the large sheets that are needed by Indiana bats. The one exception was the use of pin oak. While this oak has thin, flaky bark it was still used extensively. However, this tree species exhibited a unique feature that allowed Indiana bats to use it. The bark of pin oaks did not exfoliate in the typical manner, instead it remained attached to the outer layer of cambium. This layer, which is 1 to 3 cm thick, would separate from the rest of the bole and form slabs of wood. These slabs would essentially act as large plates of bark allowing Indiana bats to roost in this thin barked tree species. It is unclear if slab formation is typical of pin oaks or was caused by the trees dying from summer flooding.

Northern myotis take advantage of a larger variety of tree species, including thin-barked species, because they readily use a variety of roost types. Northern myotis used trees more common to the bottomland hardwoods where their center of activity was located. Green ash, which was heavily used by northern myotis in other studies (Foster and Kurta 1999), was primarily found in the floodplains and was not used in this study. Additionally, because northern myotis often form smaller groups than Indiana bats, they are commonly found in smaller trees. For example, one northern myotis roosted in a 12 cm-dbh Hawthorn-snag cavity <2 m off the ground.

Differences in the size of roosting areas of the two bat species are likely a result of different sample sizes and roosting requirements. Since Indiana bats are restricted to exfoliating bark, the use of a larger area may reflect their search for suitable snags. However, since snags are so plentiful in the study area it is unlikely that they would need to search such a large area for suitable roosts. Rather, the large roosting area may reflect the bats taking advantage of the plentiful snags throughout the study area. Given the availability of snags, their roosting requirements could easily be met in a variety of areas including the more open floodplain. Indiana bats may be spreading their roost locations across what is available to maintain knowledge of alternate roosts, to reduce travel time to foraging areas and to reduce foraging competition. Northern myotis, however, are most commonly found in more obstructed habitats. Therefore, they were restricted to the intact bottomland forest. The Indiana bats at Bluff Lake also used a smaller roosting area, probably because the more limited resources available. While local snags densities were high, the resources were not as widespread as at Oakwood Bottoms. Most snags were around the edge of the swamp. Additionally, much of the surrounding area was either forests to young to produce suitable snags or in agriculture. As long as the quality of the habitat is sufficient, the size of the area used for roosting may relate to habitat quantity not quality. Similar trends were observed in Michigan (Kurta et al. 1996) where an Indiana bat colony restricted its roosting to a high quality 5-ha wetland.

Tree Condition

The condition of Indiana bat roosts used in this study differed slightly from those in other areas (Kurta et al. 1996, Callahan et al. 1997, Gardner et al. 1990). Typically, most roosts are in dead trees. Although others have recorded roosts in live trees, mostly shagbark hickories (Humphrey et al. 1977), this was not observed in this study. Two factors may have contributed to this trend. First, live shagbark hickories were not plentiful in the study area, although densities increased as little as 2 km north. Second, the abundance of snags in the study area negated the need to use living trees.

During the 3 years of this study, a wide range of climatic conditions occurred. Most likely all the climatic conditions experienced by other colonies that used living trees occurred in my study. Nonetheless, at no time were bats recorded in living trees. Because live roost trees are used so infrequently, it may reflect deficient roosting resources when Indiana bats use living trees. Considering the average size of the slabs of exfoliating bark these bats use, it would be surprising to find a live, healthy tree with a slab of exfoliating bark large enough to accommodate this highly gregarious species. With the exceptionally high snag densities of this study, the colonies may have been able to find the protection from precipitation that a living tree provides in a snag that also had a large roosting area.

Northern myotis in this study behaved similarly to those in other areas (Sasse and Pekins 1996, Foster and Kurta 1999, Menzel et al. 2002). Taking advantage of cavities in both dead and living trees allows this species to use a greater range of resources.

Structural Characteristics Of Roost Trees

Factors that differentiated between used and available roost trees in other Indiana bat studies, such as dbh or canopy cover, did not appear to be important in this study. This is probably because of differences in the available roosting resources rather than in roost selection. Available trees on my study areas more closely matched the needs of Indiana bats than areas in other studies. The actual roost characteristics of the bats in this study were not markedly different than those in other studies. For instance, Callahan et al. (1997) 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 percent of bark cover was not important, they did find that Indiana bats used larger diameter snags with high solar exposures. These results are similar to those observed in the current study. Although not different than random trees, Indiana bat roosts were large, with moderate to high bark cover, and high solar exposure values (Table 2). A primary feature that was important in roost selection was the distance to forest. Many of the available snags were considerable distances out into open areas, including the middle of the swamp. Rarely were these snags used. Most snags were either located within a small opening in the contiguous forest or within 50 m of the forest edge. During all exit counts on these open-area roosts, when the bats left the roost they flew directly toward and disappeared into the nearest forest edge. Not once were Indiana bats observed leaving the roost and flying out to forage over open terrain. Additionally, the "checking" behavior first described by Humphrey et al. (1977; after the initial exit the bats circle the roost, briefly land, and continue to circle) was never observed around roosts that were away from the forest. Checking behavior commonly occurred around roosts within the contiguous forest. Predation may be a driving force leading bats to quickly leave the area of these exposed roosts. Under that hypothesis, it would seem that roost suitability would decrease with distance from intact forests.

Northern myotis roosts were similar to those documented elsewhere. Because northern myotis use resources other than exfoliating bark, including cavities, they can use a greater variety of trees. This reflects the major differences in roosting patterns between Indiana bats and northern myotis. In some studies, the size (dbh) of the roosts used by northern myotis was larger than the available trees (Sasse and Pekins 1996, Foster and Kurta 1999). In my study, like Menzel et al. (2002) in West Virginia, the mean dbh and roost-tree height were not different than that of available trees (Table 2).

Solar Exposure And Spatial Relation To Neighboring Trees

The consensus in the literature is that Indiana bats prefer high levels of solar exposure. It is hypothesized that high levels of solar exposure translate into high roost temperatures, which lead to more rapid fetal and juvenile grown and development (Racey 1973, Callahan et al. 1997). Although the levels of canopy closure measured during this study did not differ from those of random trees, they were low. That is, there were levels of high solar exposure (Table 2), similar to those recorded in previous studies (Gardner et al. 1991b, Kurta et al. 1996, Callahan et al. 1997).

Northern myotis seem to prefer lower levels of solar exposure than do Indiana bats. With the exception of a northern Michigan study (Foster and Kurta 1999), as in my study, all reported solar exposure levels have been low (Sasse and Pekins 1996, Lacki and Schwierjohann 2001, Menzel et al. 2002)

Spatial Relationship Of Roost To Water Sources And Foraging Areas

It is unlikely that water resources were an important consideration when either species was selecting roosts. Because roost site location did not change prior to, during, or after flooding events, it would appear that water resources are not an issue. However, initially the area may have been chosen because of its proximity to water resources. The density of large snags may have been a greater driving force. While anecdotal data suggests that both species forage in the same general area where roosts were, no specific information was gathered on foraging.

Spatial Relationship To Other Roost Trees

The relative location of roost trees to one another was similar to that seen in other studies. Many bat species roost in a relatively small portion of their home ranges (Menzel 1998, Menzel et al. 1999, Foster and Kurta 1999, Hutchinson and Lacki 2000). Most of the Indiana bats in this study did not travel large distances. Knowledge of suitable roosts within a relatively small area permits bats to use alternate roosts quickly in the event that the current roosts is unexpectedly destroyed.

STAND SCALE

Density Of Potential Roost Trees

Density of potential roosts trees is a highly debated issue. Part of the issue is the definition of a potential or suitable roost. Because there is much variation in the literature, it is difficult to determine what is required for a tree to be a suitable roost. Studies have defined "suitable" as any snag >22 cm dbh. This does not account for numerous other important factors. For use in the "random tree" analysis I defined suitable roost as any overstory (9+ cm dbh) snag that was at least 10 m tall with suitable bark for roosting. These criteria were easily met in my study area. However, because in this study the smallest snag used as a roost was 18.5 cm dbh, the cut-off was increased to that size.

With these considerations in mind, the density of suitable roosts within the study area (45/ha) was similar to those suggested by other studies. However, this result can be misleading. This snag density does not include the large number of other snags that failed to meet the specifications above. The total snag density (150/ha) in this area represents over >25% of the trees in the forest. With mortality levels this high the forest can not sustain this snag density over a long period of time. This leads to the dilemma that areas of such high quality habitat are fated to become sub-optimal habitat in a relatively short time. It would seem that Indiana bats prefer habitats that have recently experienced severe levels of disturbance. As such, in the long-term, Indiana bat colonies must be nomadic. In the short term they may occur in an area. But when that area becomes unsuitable because of the inevitable deterioration and loss of snags, the colony must move on to another area if it is to survive. This leads to another source of debate:

the permanence of Indiana bat colonies. Traditional thinking is that Indiana bats will remain in an area indefinitely. Therefore, when bats are discovered that area must be protected and managed for this Federally endangered species indefinitely. However, if management maintains the "correct" number of snags for these animals, the area will still eventually become unsuitable for Indiana bats because snag creation at the necessary level is not sustainable.

Species Composition, Stand Structure, Forest Type And Topography

Recent work (Britzke et al. 2003) has located some smaller colonies of Indiana bats in the Appalachian Mountains. These areas have a greater conifer component than most other reports. Most Indiana bat colonies are located in the hardwood communities of the upper eastern United States. The colonies in this study were located in bottomland hardwood communities, as were most colonies in previous studies. The few reports from upland communities are usually associated with some bottomland forest. Colonies may use uplands because the adjacent bottomlands do not offer sufficient resources. It is unclear why Indiana bat colonies are selecting bottomland forests. It may be because bottomland communities are prone to large scale disturbance events (flooding) that create large numbers of standing dead trees – an important roosting resource. Conversely, most disturbance events in the uplands are either small in scale or do not leave standing dead trees (wind storms). Other studies (Gardner et al. 1991b) have noted the importance of non-forested habitat for Indiana bats. It is unclear if Indiana bats are selecting forested tracts near non-forested areas, or if patchiness is simply an attribute of most eastern forests. While Indiana bats do forage in bottom lands and riparian habitats (Humphrey et al. 1977, LaVal et al. 1977), they are not restricted to this habitat (Menzel et al. 2001). Bottomlands may be most associated with roosting habitat and may not be required for foraging habitat.

Habitat Suitability Index Models

The HSI model for the Indiana bat (Rommé et al. 1994) has not been validated to date. Using the data collected in this study, I suggest the model needs to be refined. Although data collected in this study were not gathered with the express purpose to validate this model, the necessary information can be interpreted or estimated from the existing data. The first five variables of the HSI model are associated with the roosting resources of an area. Variable 1 (percent overstory canopy cover) can be interpreted from averaging all the canopy cover values (at base) collected from every roost and random tree (Table 2). Using this method a canopy cover measure of 44% was recorded. This reflects a HSI suitability curve V1 value of 0.6. Variable 2 was mean diameter of overstory trees. An average of dbh of all trees >8 cm measured (n = 2404) equals 21 cm. This creates a V2 value of 0.2. Variable 3 is the density of living trees per hectare. Variable 3 is divided into three categories. The three categories are based on how tree species would produce suitable exfoliating bark when dead. In this study there were 41 trees/ha in V3A, 1 tree/ha of V3B, and 51 trees/ha of V3C. This gives values of V3A = 1.0, V3B = 0.0, V3C = 0.3. These three groups are added together to get V3 total (total = 1.3). However the value is not to exceed 1.0. Variable 4 is actual density of snags/ha in three categories. The categories are based on amount of bark coverage. Since the percentage bark for each snag was not recorded, equal distribution was assumed (i.e. 33%

or 15 snags/ha in each group). Again, these three categories were summed, but not to exceed 1.0. Variable 5 was the percent cover of understory vegetation. This variable was not recorded in this study. I estimated a mid value of 50%, which seems reasonable given the knowledge of the study area and time spent in the field. This gives variable 5 a value of 0.8. Variables 6 and 7 are associated with the foraging resources available in the area. Variable 6 was the amount of overstory canopy cover (same as Variable 1). Variable 7 was the percent of total trees in the 5-12 cm dbh range. Because I measured no trees < 7 cm dbh, data are only available for the 7-12 cm dbh class. This group made up 38% of the trees, resulting in a value of 0.95 for variable 7. Variable 8 measured distance to water resources. Because this varies between individual roosts, the greatest value was used. All roosts were within 1 km of water giving Variable 8 a value of 0.9. Variable 9 is amount of study area in forested habitat. This measure was not specifically calculated, but knowledge of the areas suggests that it is at least 50% if not greater. Using 50% gives a value of 1.0 for variable 9. The formula for the roosting resources is

$$R = (V1 * V2 * V3 * V4)^{0.25} * V5.$$

The formula for the foraging resources is

$$F = (V6 * V7)^{0.5}.$$

The final HSI calculation is to take either the roosting or foraging value, which ever is less and to multiply by Variables 8 and 9.

$$HSI = \min (R \text{ or } F) * V8 * V9.$$

With the data from this study

$$R = (0.6 * 0.2 * 1.0 * 1.0)^{0.25} = 0.4708.$$

$$F = (0.85 * 0.95)^{0.5} = 0.8986.$$

HSI = 0.4708 * (0.9 *1.0) = 0.4237.

The Rommé et al. (1994) HSI model categorized this area as moderate habitat. Given the numbers of bats captured and tracked, this habitat should be rated well above average, perhaps a value of 0.8-0.9. The attribute that the Rommé et al. (1994) model inadequately graded is Variable 2. This HSI model fails to take into account that not all older aged forests have a “J” shaped diameter distribution curve. Many forests especially those regenerating after a large-scale disturbance may have large component of the forest in smaller diameter trees (Oliver and Larson 1990). These numerous small trees lower the average dbh of the stand. While sufficient quantities of large dbh trees are important, the way the current variable is calculated perhaps overly weights larger trees. The suitability line of the Variable 2 graph (Rommé et al. 1994) should be shifted to the left or the slope should be decreased (Figure 4). Another variable that may easily change the outcome of this model is variable 7. Because the current study did not include trees as small as 5 cm dbh, the value used may be too conservative. If 5-cm dbh trees were included in the count, the percent of small trees in the forest may increase to as much as 50%. This would not change the overall HSI value in this study because the foraging portion of the equations was more than the roosting component. However, like the problem associated with variable 2, the weighting and calculation of variable 7 may underestimate the percentage of small trees in quality Indiana bat habitat.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS FOR INDIANA BATS

Since the discovery of the first Indiana bat maternity colonies in the mid 1970s, much research has focused on characteristics of the roost trees. With the advent of miniature radio transmitters in the late 1980s and early 1990s, researchers have been able to locate many maternity colonies. While the roosting requirements of Indiana bat maternity colonies vary geographically, many features seem to remain constant. These colonies use multiple dead or dying trees that are ephemeral roost sites. Maternity colonies are most often found in highly disturbed late-successional habitats (mature forests) that have significant portions in earlier seral stages. These areas have many standing dead trees associated with them, often with high levels of solar exposure. Disturbed areas that are in transition from late to early seral stages appear to be crucial for Indiana bat maternity colonies. Additionally, these transitional habitats provide ideal foraging and nesting habitat for a variety of other species including many woodpeckers and species of special concern such as the prothonotary warbler (*Protonotaria citrea*; Runde and Capen 1987, Welsh and Capen 1992, Edwards and Otis 1999, Sallabanks et al. 2000). Large-scale disturbances that result in numerous standing dead trees are rare but most often are caused by flooding. Unlike other natural disturbance events, flooding can kill large numbers of trees, yet leave them standing. This may help to explain why so many maternity colonies occur in bottomland or riparian habitats

Female Indiana bats are faithful to a colony site and return in subsequent years. This has led to the idea that Indiana bats in a certain location must have been there for a prolonged period and could remain there indefinitely. However, without continual disturbance events a habitat will undergo successional change toward a climax community. In the case of Indiana bats this means that the dead trees will decay, fall and become unusable. These successional changes have caused increasing emphasis on the management of Indiana bat maternity habitat. Previous management efforts primarily have been passive. When a colony was found, most management and recreational activities were restricted in the area (USFS 1992). It was believed that the colony would be faithful to the site and return each season with no active management. However, with additional data on the requirements of maternity colonies, the need for active management to sustain colony sites is becoming apparent. Thus, land managers now may need to create snags for Indiana bats.

Literature suggests that suitable snags must be ≥22 cm dbh, and it is estimated that ≥41 snags/ha are necessary to sustain a typical bottomland colony (Garner and Gardner 1992, Menzel et al. 2001). Also, because Indiana bats select snags in the latter stages of decay with suitable bark cover (current study, Menzel et al. 2001), a limited "window of opportunity" exists for use of a given snag – certainly no more than 10 years. The natural phenomena that create this optimal habitat for Indiana bats are best classified as major disturbance events, often resulting in a replacement single-cohort (even-aged) stand (Oliver and Larson 1990). Manual snag creation would not have the same impact as a major disturbance event. The number of snags required to create "enough" suitable roost trees, combined with the relatively short time that a given snag is useable, creates a situation where continually creating snags may remove trees in the forest at a greater rate than they are regenerated. Techniques for creating Indiana bat snags could be based on diameter-limit harvest methods (Smith 1986). The major difference would be that the trees would not be harvested, but rather would be killed, left standing to decay and fall naturally. In theory, these methods would work if harvest intervals were long enough and or if harvest densities are not to high (Meadows and Stanturf 1997). However, the use of diameter-limit or single tree selection methods often results in a shift toward shade tolerant tree species within the stand (Stanturf and Meadows 1994). While Indiana bats do use a variety of tree species for roosts, a shift in stand composition may result is insufficient tree types for future roost creation. Additionally, stand composition shifts may have negative impacts on other wildlife within that stand (Edwards and Otis 1999). In the long term, snag creation for Indiana bats can not create multi-cohort (uneven-aged) stands indicative of minor disturbance events, such as correct implementation of diameter-limit harvests (Larsen et al. 1999). The densities and intervals needed to maintain suitable Indiana bat habitat will result in dramatic changes in stand dynamics and ultimately is not sustainable (Larsen et al. 1999). Even if snags could continually be created, the surrounding forest would be in too early a serial stage to include appropriate foraging habitats (Menzel et al. 2001). Through the natural decay process, many of the maternity colonies discovered in the early 1990s are beginning to run out of suitable roost trees. Land managers are becoming increasingly concerned about providing suitable habitat for Indiana bats in these areas. However, with the discovery of numerous colonies during the last decade, researchers can now start to address questions of long-term habitat use and distribution of these colonies.

After reviewing historical records of colonies, historical survey efforts, as well as colonies currently under study, I believe that Indiana bat colonies in the long term (50+ years), are nomadic. Central to this idea is that colonies are faithful to a location only as long as the roosting requirements are met. During the relatively short time that areas remain suitable, Indiana bat colonies thrive. As the colony increases in size and/or as the habitat becomes less suitable, the colony moves across the landscape seeking out new areas. In the short term this may mean minor shifts in centers of activity, which have been documented in colonies throughout the species' range. The work of Kurta and Rice (2002) in Michigan is a prime example. In this colony, the center of roosting activity shifted 2 km in 3 yrs. However, over the very long term, decades or even centuries, colonies may move great distances in search of areas that have experienced floods, wind storms, or human activities that create suitable habitat. In situations like these, small groups or satellite colonies may leave areas as they become unsuitable and search out other areas. It is during this transient phase when researchers may encounter smaller colonies, like the one from the Great Smoky Mountains National Park where <30 animals used two trees. These animals remained in the area one summer but were not found in subsequent years (Britzke et al. 2003). Thus, bats may be forced to inhabit sub-optimal habitats until optimal areas are available or until they find new suitable areas. These smaller satellite colonies show no philopatry to sub-optimal areas. For instance in the current study, the Oakwood Bottoms area was an intact bottomland forest throughout the 1980s and early 1990s. Surveys done in this location found no Indiana bats (Per. Comm. J. E. Hofmann, Illinois Natural History Survey). Then the Mississippi River floods of 1993 and 1995 killed as many as 80% of the trees in some areas. In 1999, Indiana bats were found the first night of surveying and this large colony has been extensively studied for the last 4 years. However, this oak forest is starting to undergo successional change. Snags are falling and much of the area is being recolonized by willows and elms. This area will become poor habitat for Indiana bats within the next 5 yrs and probably will be unsuitable for them within the next 10 yrs. Colonies also occur in seasonally flooded wetlands that retain the water as a result of beaver damming. These areas, once mature forests, are now flooded with up to a meter of water. The trees quickly die providing ideal habitat for Indiana bats and many other animals (Runde and Capen 1987, Welsh and Capen 1992, Flaspohler 1996, Braccia and Batzer 1999, Edwards and Otis 1999, Hagglund and Sjoberg 1999). Colonies like these have been found and studied in Michigan (Kurta et al. 1996) and in the current study (Bluff Lake). These pockets of habitat likely occur commonly across the landscape, especially with the increase in beaver populations (Edwards and Otis 1999). But again, these habitats will become unsuitable relatively rapidly as snags decay and fall.

If this hypothesis is correct, and colony persistence is more fluid and ephemeral than previously thought, long-term management and stability of a given colony becomes much more problematic. Future summer maternity colony distributions may be best modeled in the future using metapopulation theory (Elmhagen and Angerbjorn 2001, Pakkala et al. 2002). In general, management will now involve multiple land owners and will require excellent communication, coordination, and long-term management plans, making the process that much more difficult. Currently, the combined effects of litigation and bureaucracy often prevent many public agencies from creating large areas of standing dead timber. The public views these habitats as disasters and can be expected to oppose intentionally creating them. While most private companies are considerably more eco-friendly than in years past, few would argue that killing large numbers of mature hardwood trees and leaving them standing is a sound business practice. Additionally, the possible management restrictions that can be associated with the presence of endangered species may discourage timber production companies from creating Indiana bat habitat. However, if colonies in the long term are nomadic, timber companies maybe persuaded to occasionally create areas of Indiana bat maternity habitat with the understanding that once the habitat is naturally deteriorated it does not have to be maintained or replaced. Legal framework for such agreements is already in place. In 1999, the USFWS (1999b) announced the Safe Harbor Policy. This policy allows the landowners and the USFWS to enter into agreements such that no additional restrictions will be placed on the landowner as a result of their voluntary actions that benefit an endangered species. However, until such arrangements are made with private companies or organizations it will be up to our public agencies to provide these habitats. Before public agencies can effectively create this type of habitat, the public will have to be educated to see the value of dead standing timber, rather than seeing it as devastation and destruction. We will also have to educate the public and special interest groups that local distribution of Indiana bats may be naturally ephemeral and unstable in the long term. This is necessary to avoid potential litigation when local populations decrease or become extirpated.

New data suggest that there may be an additional tool available to land managers to help “bridge” the gap between natural disturbance events. Rocket-box style bat houses where introduced into the Oakwood Bottoms colony late in the summer of 2001. Female

Indiana bats have been documented using these houses in both 2001 and 2002 (Carter 2002; Carter et al. 2002). While maternity use has not been documented, it is suspected that Indiana bats are using the bat house throughout the summer. The potential of this finding is significant. While I am not advocating the substitution of bat boxes for natural roosting habitat, it does add a useful alternative. Whereas snags are difficult to manage, bat boxes are an inexpensive, labor non-intensive alternative. They can be placed where needed and maintained and replaced when required. This ensures a continuous and reliable roosting resource which may be especially important in areas were roosting snags are limited or potentially unpredictable. For instance, in 1989 when hurricane Hugo dramatically reduced roosting trees for red-cockaded woodpeckers (*Picoides borealis*) in the southeast, artificial nest boxes were installed to provide immediate relief for displaced animals. Installing nest boxes remains a valuable management tool for this endangered species (Baggett 1995). Rocket-boxes may be a useful tool to provide similar relief during times when natural Indiana bat roosts may be limited through normal successional events.

Table 1. Comparison of overstory tree-species composition of roosts used by Indiana bats (Myotis sodalis) and northern myotis (Myotis septentrionalis), random trees, plots around Indiana bat, northern myotis roosts and random roosts, and all trees combined.

Species		All combined n = 2732*	Roost plots n = 1541	Random plots n = 1073	Random roosts n = 46	Indiana Female n = 49	Indiana Male n = 4	Northern myotis n =19
Elm sp.	Ulmus sp.	28.0%	29.3%	27.5%	13.0%	17.0%	0.0%	26.3%
Snag (unspecified)	snag	26.5%	25.9%	28.7%	10.9%	19.1%	50.0%	10.5%
Green Ash	Fraxinus pennsylvanica	9.7%	8.0%	11.1%	19.6%	31.9%	0.0%	0.0%
Pin Oak	Quercus palustris	6.8%	6.2%	5.9%	23.9%	17.0%	0.0%	47.4%
Sweetgum	Liquidambar styraciflua	6.4%	6.1%	7.4%	0.0%	0.0%	0.0%	5.3%
Willow (unspecified)	Salix sp.	3.7%	4.3%	3.1%	4.3%	0.0%	0.0%	0.0%
Sugarberry	Celtis sp.	3.3%	3.0%	3.9%	0.0%	0.0%	0.0%	0.0%
Silver Maple	Acer saccharinum	3.1%	1.3%	5.3%	13.0%	8.5%	0.0%	0.0%
Red Maple	Acer rubram	2.9%	4.3%	1.1%	0.0%	0.0%	0.0%	0.0%
Swamp Privet	Forestiera acuminata	2.4%	4.2%	0.0%	0.0%	0.0%	0.0%	0.0%
Persimmon	Diospyros virginiana	1.4%	1.8%	0.8%	4.3%	0.0%	0.0%	0.0%
Hickory (unspecified)	Carya sp.	1.2%	1.2%	1.2%	2.2%	0.0%	0.0%	0.0%
Hawthorn	Cratagus sp.	1.2%	1.5%	0.8%	0.0%	0.0%	0.0%	5.0%
Maple (unspecified)	Acer sp.	0.8%	0.2%	1.7%	0.0%	0.0%	0.0%	0.0%
Boxwood	Acer negundo	0.5%	0.5%	0.5%	2.2%	0.0%	0.0%	0.0%
Shagbark Hickory	Carya ovata	0.4%	0.5%	0.1%	0.0%	2.1%	50.0%	0.0%
Sugar Maple	Acer saccharum	0.4%	0.6%	0.0%	0.0%	0.0%	0.0%	0.0%
Locust	Gleditsia aquatica	0.2%	0.3%	0.1%	0.0%	0.0%	0.0%	0.0%
Water Tupelo	Nyssa sylvatica	0.1%	0.2%	0.1%	0.0%	0.0%	0.0%	0.0%
River Birch	Betula nigra	0.1%	0.2%	0.1%	0.0%	0.0%	0.0%	0.0%
Button Bush	Cephalanthus occidentalis	0.1%	0.0%	0.4%	0.0%	0.0%	0.0%	0.0%
Oak (unspecified)	Quercus sp.	0.1%	0.1%	0.0%	4.3%	0.0%	0.0%	5.3%
White Oak	Quercus alba	0.1%	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%
Cottonwood	Populus deltoides	0.1%	0.0%	0.0%	2.2%	4.3%	0.0%	0.0%
Dogwood	Cornus sp.	0.1%	0.1%	0.1%	0.0%	0.0%	0.0%	0.0%
Black Walnut	Juglans nigra	0.1%	0.0%	0.2%	0.0%	0.0%	0.0%	0.0%
Sycamore	Platanus occidentalis	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%
Holly (unspecified)	Ilex sp.	0.0%	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%

* Sample size is number of trees in each group.

Table 2A. Comparison of Indiana bat (*Myotis sodalis*) roost trees and random trees

	Indiana bats n = 47		Random Trees n = 37		Univariate Logistic Regression Statistics	
n = 47	Mean (Range)	Std. Error	Mean (Range)	Std. Error	X^2	*p* - value
% Bark Cover	47.02 (0-95)	3.89	55.00 (0-100)	5.81	1.432	0.231
% Canopy Closure (at base)	36.30 (0-85)	4.10	36.62 (0-95)	5.76	0.001	0.980
% Canopy Closure (at roost)	17.66 (0-65)	2.96	17.62 (0-85)	3.71	0.000	0.993
Roost Obstruction (visual)	1.28 (1-3)	0.09	1.89 (1-5)	0.21	6.264	0.012
DBH (cm)	39.02 (18.5-82)	2.04	37.71 (14.5-72.5)	2.23	0.159	0.690
Decay Class	2.83 (1.5-3.75)	0.08	3.17 (1.25-4)	0.11	0.697	0.404
Distance to Forest (m)	14.15 (0-50)	2.55	20.14 (0-150)	5.43	1.524	0.217
Roost Height (m)	9.96 (2.5-28.4)	0.75				
Roost-tree Height (m)	17.53 (3-35)	0.95	15.65 (5.1-29.8)	1.00	1.805	0.179
Average Plot DBH (cm)	23.27 (11.9-46)	1.15	22.83 (12.3-35.8)	0.95	0.083	0.774
Average Plot Height (m)	9.72 (2.4-21)	0.61	10.11 (4.3-18.2)	0.56	0.214	0.644

Table 2B.Comparison of northern myotis (*Myotis septentrionalis*) roost trees and random trees

	northern myotis n = 19		Random Trees n = 46		Univariate Logistic Regression Statistics	
n = 19	Mean (Range)	Std. Error	Mean (Range)	Std. Error	X^2	*p* - value
% Bark Cover	79.21 (0-100)	7.09	63.84 (0-100)	5.66	2.634	0.105
% Canopy Closure (at base)	61.32 (0-95)	6.49	44.02 (0-95)	5.26	3.540	0.060
% Canopy Closure (at roost)	44.05 (0-90)	7.15	24.83 (0-90)	4.09	5.514	0.019
Roost Obstruction (visual)	3.21 (1-5)	0.34	2.31 (1-5)	0.25	4.055	0.044
DBH (cm)	37.29 (12-68)	4.72	34.91 (11.5-72.5)	2.21	0.277	0.599
Decay Class	1.41 (0-3.75)	0.32	2.2 (0-4)	0.27	3.411	0.065
Distance to Forest (m)	3.95 (0-70)	3.68	16.95 (0-150)	4.94	10.562	0.001
Roost Height (m)	9.16 (1.5-22)	1.40				
Roost-tree Height (m)	15.76 (3-30.8)	1.96	14.9 (5.1-29.8)	0.85	0.227	0.634
Average Plot DBH (cm)	18.93 (12.4-29)	1.12	22.00 (12.3-35.8)	0.84	4.400	0.036
Average Plot Height (m)	10.64 (4.6-16.6)	0.64	10.45 (4.3-18.5)	0.49	0.049	0.824

Table 2C. Comparison of Indiana bat (*Myotis sodalis*) roost trees and northern myotis (Myotis septentrionalis) roost trees

	Indiana bats n = 47		northern myotis n = 19		Univariate Logistic Regression Statistics	
	Mean (Range)	Std. Error	Mean (Range)	Std. Error	X^2	*p* - value
% Bark Cover	47.02 (0-95)	3.89	79.21 (0-100)	7.09	16.169	0.000
% Canopy Closure (at base)	36.30 (0-85)	4.10	61.32 (0-95)	6.49	9.912	0.002
% Canopy Closure (at roost)	17.66 (0-65)	2.96	44.05 (0-90)	7.15	13.386	0.000
Roost Obstruction (visual)	1.28 (1-3)	0.09	3.21 (1-5)	0.34	31.959	0.000
DBH (cm)	39.02 (18.5-82)	2.04	37.29 (12-68)	4.72	0.162	0.687
Decay Class	2.83 (1.5-3.75)	0.08	1.41 (0-3.75)	0.32	23.679	0.000
Distance to Forest (m)	14.15 (0-50)	2.55	3.95 (0-70)	3.68	5.924	0.015
Roost Height (m)	9.96 (2.5-28.4)	0.75	9.16 (1.5-22)	1.40	0.304	0.581
Roost-tree Height (m)	17.53 (3-35)	0.95	15.76 (3-30.8)	1.96	0.867	0.352
Average Plot DBH (cm)	23.27 (11.9-46)	1.15	18.93 (12.4-29)	1.12	5.498	0.019
Average Plot Height (m)	9.72 (2.4-21)	0.61	10.64 (4.6-16.6)	0.64	0.795	0.373

Table 3. The size of roosting core areas of Indiana bats (*Myotis sodalis*) and northern myotis (*Myotis septentrionalis*), calculated using adaptive kernal analysis, minimum convex polygon, and diameter limit methods.

Species	Method	Contour	Area (m^2)	Diameter (m)
Indiana bats	Adaptive Kernel	90	13,219,552	
Oakwood Colony	Adaptive Kernel	60	2,403,511	
n = 29	Adaptive Kernel	30	725,262	
	MCP	100	9,638,964	
	MCP	98	4,808,525	
	MCP	95	3,283,455	
	Diameter Limit	100		5600
	Diameter Limit	98		3600
	Diameter Limit	95		3200
Indiana bats	Adaptive Kernel	90	1,788,345	
Bluff Lake Colony	Adaptive Kernel	60	533,275	
n = 20	Adaptive Kernel	30	176,631	
	MCP	100	917,684	
	MCP	95	321,810	
	MCP	90	306,212	
	Diameter Limit	100		1900
	Diameter Limit	95		1600
	Diameter Limit	90		1500
Northern myotis	Adaptive Kernel	90	1,862,646	
Oakwood Colony	Adaptive Kernel	60	571,614	
n = 19	Adaptive Kernel	30	188,746	
	MCP	100	587,473	
	MCP	95	428,635	
	MCP	90	252,220	
	Diameter Limit	100		2000
	Diameter Limit	95		1400
	Diameter Limit	90		800

Table 4. Comparison of northern myotis (*Myotis septentrionalis*) roost trees and random trees using t-tests.

Variable	Group	N	Mean	Std. Error	t	df	*p* - value
Roost Obstruction (visual)	Northern myotis	19	3.211	0.338			
	Random	42	2.310	0.252	2.137	38.265	0.039
Roost Obstruction (Distance to Branch)	Northern myotis	16	1.616	0.442			
	Random	39	3.655	0.593	-2.758	51.581	0.008
% Bark Cover	Northern myotis	19	79.211	7.094			
	Random	43	63.837	5.657	1.694	41.053	0.098
% Canopy Closure (Base)	Northern myotis	19	61.316	6.487			
	Random	46	44.022	5.263	2.070	42.182	0.045
% Canopy Closure (Roost)	Northern myotis	19	44.053	7.153			
	Random	46	24.826	4.089	2.334	30.387	0.026
Condition of Roost (Decay Class)	Northern myotis	19	1.408	0.321			
	Random	31	2.202	0.269	-1.895	40.207	0.065
Condition of Roost (Smallest Branch)	Northern myotis	14	0.366	0.203			
	Random	28	0.625	0.296	-0.721	39.996	0.475
Distance to Forest	Northern myotis	19	0.263	0.263			
	Random	41	16.951	4.935	-3.377	40.227	0.002
Roost Tree Diameter	Northern myotis	19	37.289	4.723			
	Random	44	34.914	2.212	0.456	26.237	0.652
Roost Tree Height	Northern myotis	19	15.758	1.958			
	Random	46	14.898	0.851	0.403	25.083	0.690
Average Overstory DBH	Northern myotis	19	18.932	1.117			
	Random	46	22.002	0.839	-2.198	39.037	0.034
Average Overstory Height	Northern myotis	19	10.642	0.641			
	Random	46	10.452	0.490	0.235	39.755	0.815

Table 5. Comparison of Indiana bat (*Myotis sodalis*) roost trees and random trees using t-tests.

Variable	Group	N	Mean	Std. Error	t	df	*p* - value
Roost Obstruction (visual)	Indiana bat	47	1.255	0.089			
	Random	33	1.818	0.232	-2.266	41.371	0.029
Roost Obstruction (Distance to Branch)	Indiana bat	43	5.581	0.524			
	Random	30	4.433	0.709	1.302	57.492	0.198
% Bark Cover	Indiana bat	46	46.957	3.973			
	Random	34	55.441	6.327	-1.136	57.587	0.261
% Canopy Closure (Base)	Indiana bat	45	36.444	4.254			
	Random	37	36.622	5.764	-0.025	69.120	0.980
% Canopy Closure (Roost)	Indiana bat	47	17.660	2.964			
	Random	37	17.622	3.708	0.008	73.285	0.994
Condition of Roost (Decay Class)	Indiana bat	47	2.830	0.083			
	Random	23	2.967	0.172	-0.722	32.540	0.475
Condition of Roost (Smallest Branch)	Indiana bat	22	1.068	0.409			
	Random	19	0.862	0.429	0.348	38.411	0.730
Distance to Forest	Indiana bat	43	14.302	2.597			
	Random	32	21.719	6.077	-1.122	42.315	0.268
Roost Tree Diameter	Indiana bat	45	39.711	2.070			
	Random	35	38.491	2.292	0.395	74.035	0.694
Roost Tree Height	Indiana bat	46	17.522	0.975			
	Random	37	15.646	1.003	1.341	79.449	0.184
Average Overstory DBH	Indiana bat	47	23.267	1.151			
	Random	37	22.827	0.954	0.294	81.666	0.769
Average Overstory Height	Indiana bat	47	9.722	0.605			
	Random	37	10.108	0.557	-0.469	81.867	0.640

Table 6. Comparison of Indiana bat (*Myotis sodalis*) and northern myotis (*Myotis septentrionalis*) roost trees using t-tests.

Variable	Group	N	Mean	Std. Error	t	df	*p* - value
Roost Height	Northern myotis	19	8.584	1.306			
	Indiana bat	47	9.955	0.747	-0.911	30.420	0.369
Roost Obstruction (visual)	Northern myotis	19	3.421	0.361			
	Indiana bat	47	1.277	0.095	5.742	20.523	0.000
Roost Obstruction (Distance to Branch)	Northern myotis	16	1.616	0.442			
	Indiana bat	44	5.682	0.522	-5.945	51.209	0.000
% Bark Cover	Northern myotis	19	79.211	7.094			
	Indiana bat	47	47.021	3.888	3.979	29.399	0.000
% Canopy Closure (Base)	Northern myotis	19	61.316	6.487			
	Indiana bat	47	36.383	4.097	3.250	33.157	0.003
% Canopy Closure (Roost)	Northern myotis	19	44.053	7.153			
	Indiana bat	47	17.660	2.964	3.409	24.430	0.002
Condition of Roost (Decay Class)	Northern myotis	19	1.408	0.321			
	Indiana bat	47	2.830	0.083	-4.288	20.427	0.000
Condition of Roost (Smallest Branch)	Northern myotis	14	0.366	0.203			
	Indiana bat	22	1.068	0.409	-1.537	29.717	0.135
Distance to Forest	Northern myotis	19	3.947	3.679			
	Indiana bat	47	13.723	2.416	-2.221	34.376	0.033
Roost Tree Diameter	Northern myotis	19	37.289	4.723			
	Indiana bat	47	38.936	2.057	-0.320	25.121	0.752
Roost Tree Height	Northern myotis	19	15.758	1.958			
	Indiana bat	47	17.574	0.956	-0.834	27.000	0.412
Average Overstory DBH	Northern myotis	19	18.932	1.117			
	Indiana bat	47	23.267	1.151	-2.703	53.062	0.009
Average Overstory Height	Northern myotis	19	10.642	0.641			
	Indiana bat	47	9.722	0.605	1.043	49.121	0.302

Figure 1. Map showing the location of Indiana bat (*Myotis sodalis*) colonies (bat symbol) in southern Illinois.

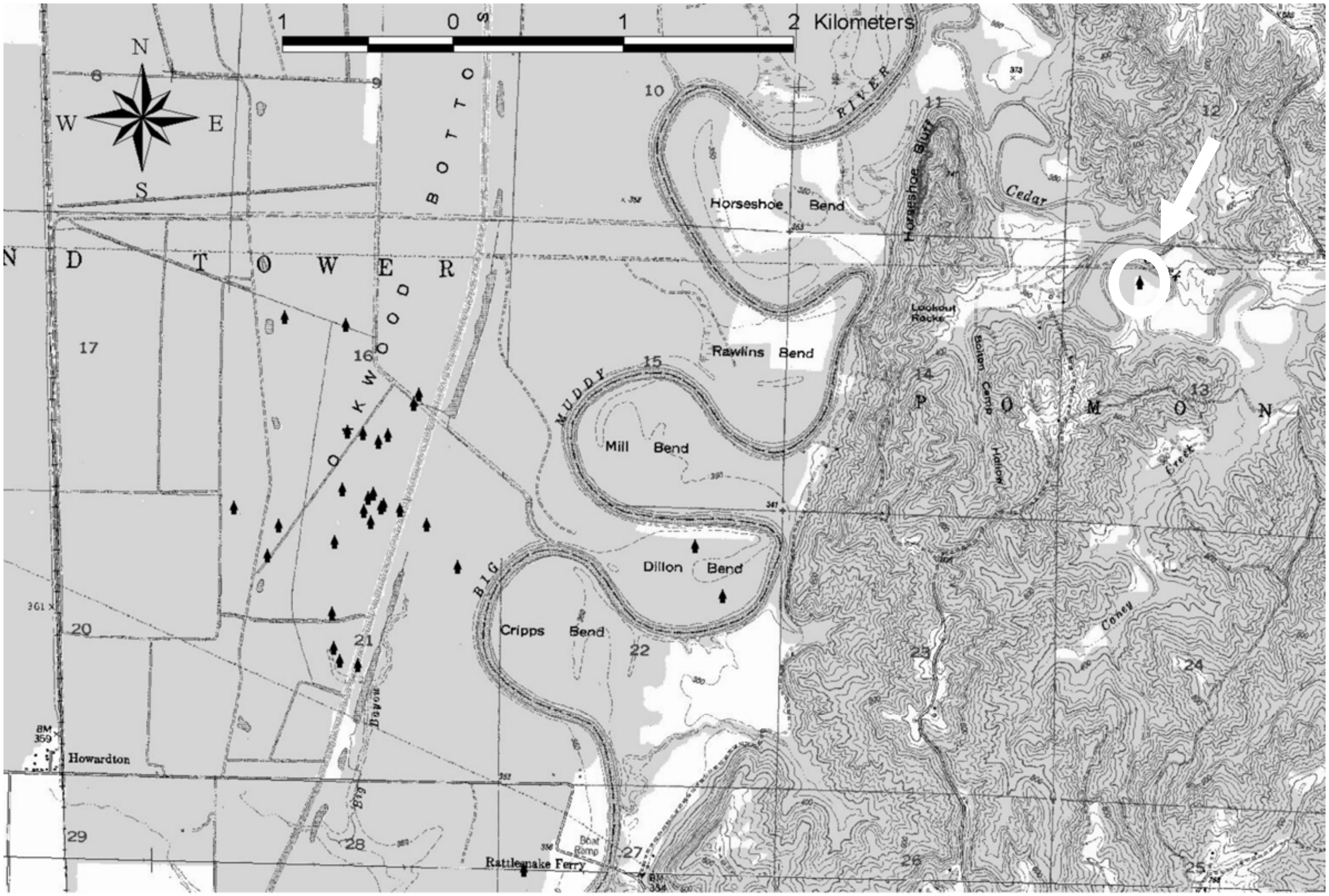

Figure 2. Map showing the location of Indiana bat (*Myotis sodalis*) roost site (black tree like symbols) with relation to other geographical features at Oakwood Bottoms near the town of Grand Tower, Jackson County, Illinois. Note location of single roost, marked with white circle, approximately 5 km from the core of the roosting area.

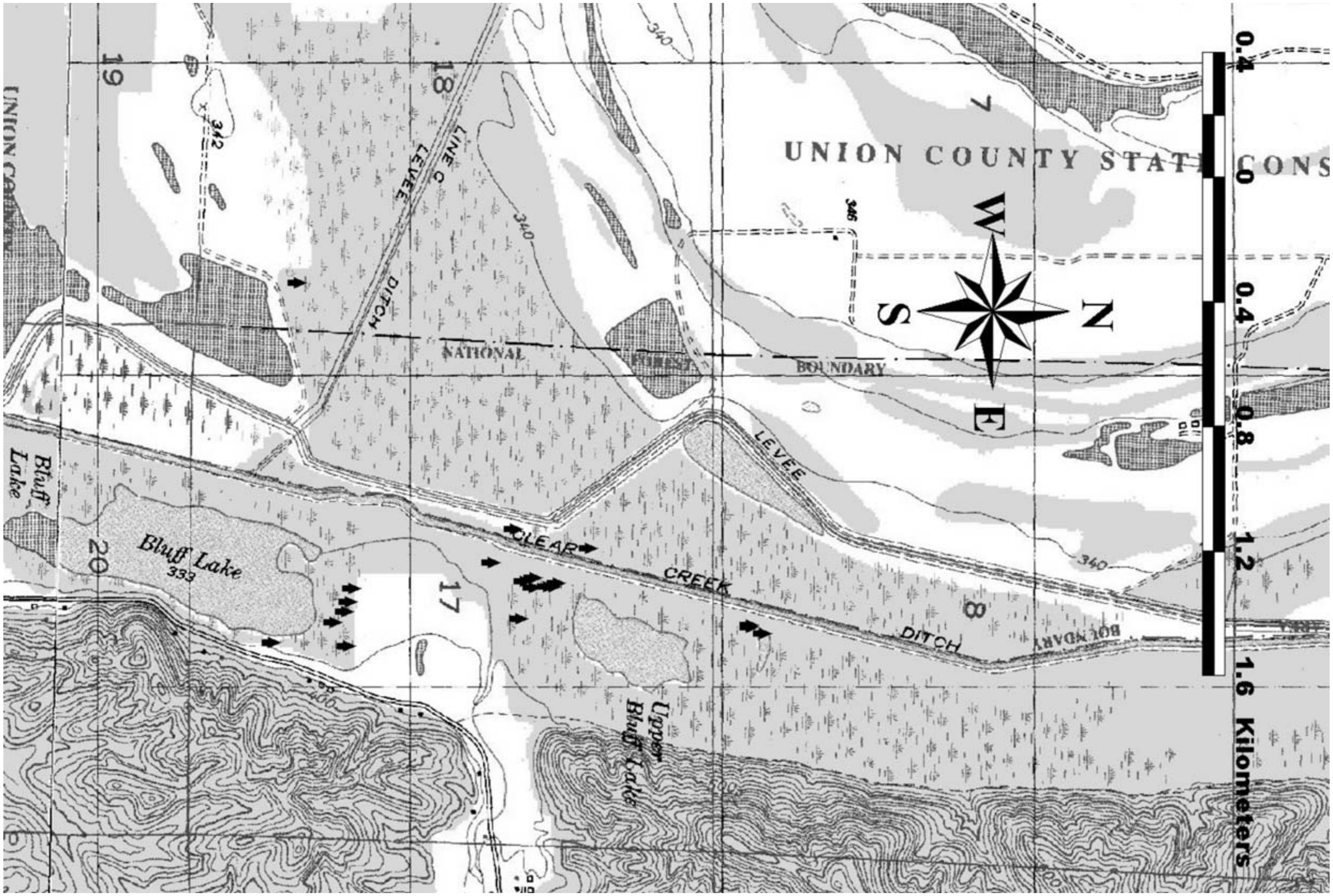

Figure 3. Map showing the location of Indiana bat (*Myotis sodalis*) roost site (black tree like symbols) with relation to other geographical features at Bluff Lake Swamp near the town of Millcreek, Union County, Illinois.

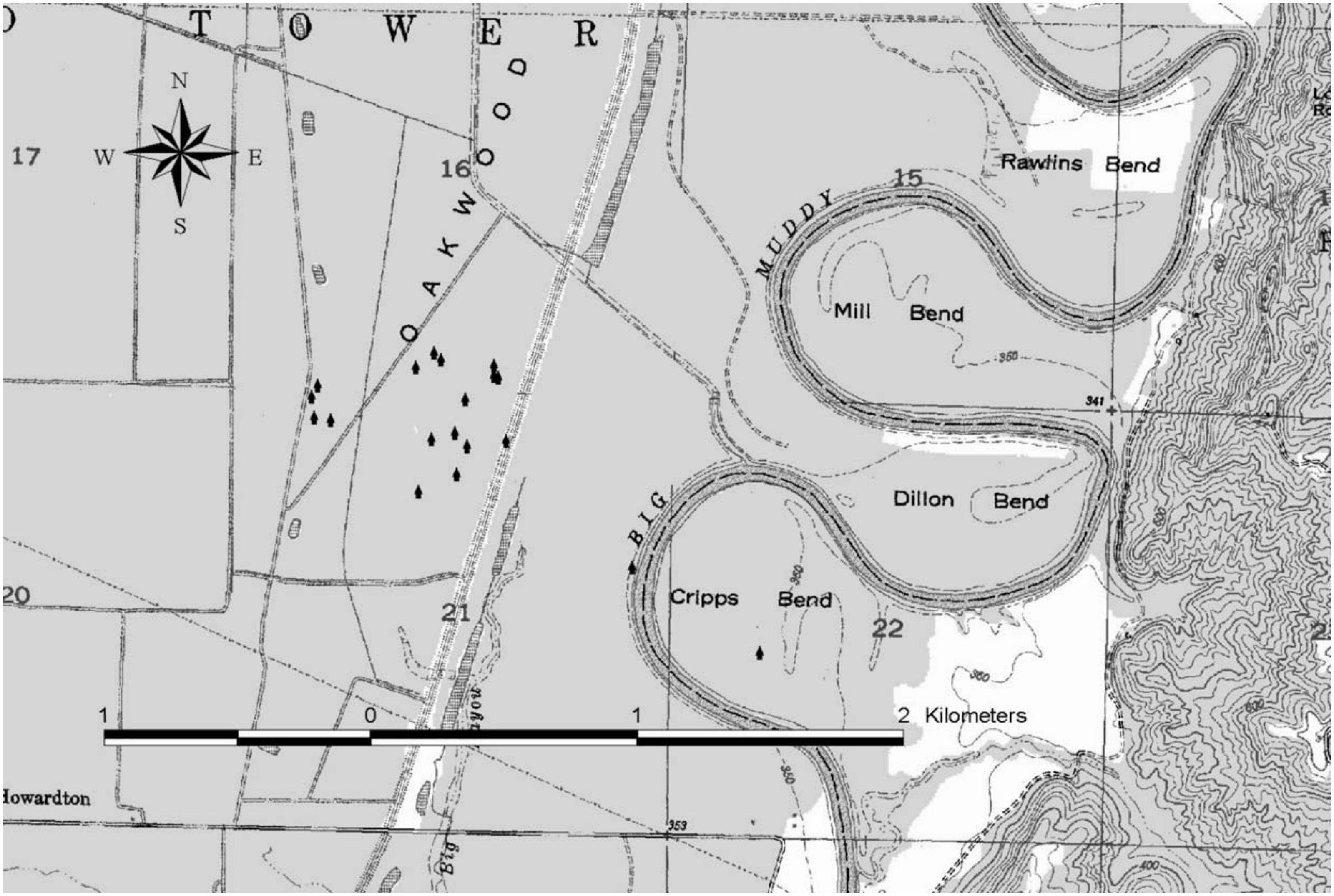

Figure 4. Map showing the location of northern long-eared bats (*Myotis septentrionalis*) roost site (black tree like symbols) with relation to other geographical features near the town of Grand Tower, Jackson County, Illinois.

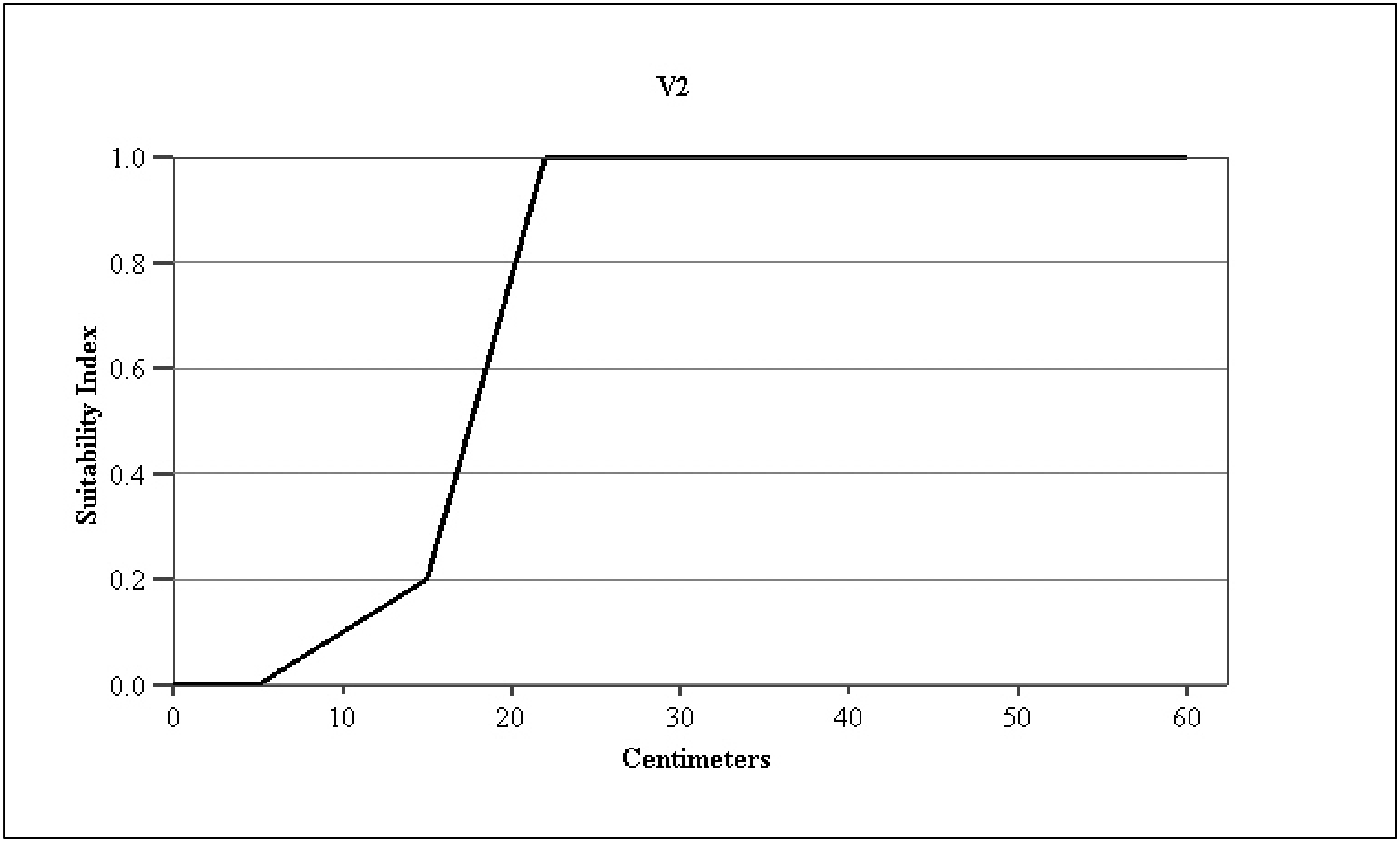

Figure 5. Replacement variable graph for Variable 2 (mean diameter of overstory trees) in the Rommé et al. (1994) Habitat Suitability Index model.

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APPENDICES

APPENDIX I

Roost-specific habitat variables collected around Indiana bat (*Myotis sodalis*) roost trees in southern Illinois during 1999 – 2001. These measurements were collected from the actual tree that the bats used as a roost.

<u>Roost Height:</u> The height that the bats were roosting within the tree. The location of the bat was always estimated with telemetry coupled with looking for suitable roosting bark and listening for the often noisy bats. The location often was confirmed with an exit count that same evening as the bats left to forage. Then the actual height was calculated using a clinometer (Suunto, Helsinki, Finland). Location estimation with telemetry proved to be very accurate. Most estimations were within 2-3 meters of the actual location.

<u>Roost-Tree Height:</u> The height of the tree used as the roost calculated using a clinometer.

<u>Roost-Tree Diameter:</u> The diameter at breast height (dbh) of the tree used as the roost. The dbh was measured using a diameter tape (Forestry Suppliers, Jackson, MS)

<u>Roost Substrate:</u> The type of roosting substrate was most often exfoliating bark. This was established with both visual and auditory confirmation of the bats under the bark or with an exit count in the evening.

<u>Roost Aspect:</u> This was perhaps the most difficult variable to measure. An estimation of the bat location on the tree was done with telemetry. When possible, visual confirmation was used during exit counts. However, most roost sites include bark that covers most of the tree. In these circumstances, it was impossible to know where bats choose to exit the bark. The aspect of the exit could be very different from the aspect of the actual roost. Furthermore, the bats may be shifting aspect within the roost throughout the day as temperatures change and the sun moves across the sky.

<u>Degree of Roost Obstruction (clutter around of roost):</u> This was measured in two ways. The first method was somewhat subjective. However, I felt that it best represented the conditions around the roost. But, because of its subjectiveness, I created another more objective variable.

<u>Visual Estimation:</u> The amount of obstruction or clutter around the roost site was estimated within five categories: open, light, moderate, cluttered, and very cluttered.

<u>Distance to Nearest Branch:</u> This was the distance to the nearest branch from the roost site. Only branches on the same side of the tree as the roost were included. That is, branches were not considered when they were on the backside of the roost tree and were not restricting roost entry and exit.

Percent Bark Cover: This was the amount of bark remaining on the roost tree. This variable was estimated individually by all people present and an average value was recorded.

Percent Canopy Closure: In the literature, most studies have reported the canopy closure from the base of the roost tree (Callahan et al. 1997). However, the bats often are roosting considerably higher than where these measurements are calculated, thus leading to inflated canopy closure values. Often in my study, the bats were roosting at or above the general tree canopy. As a result, I calculated canopy closure using two methods: from the base of the tree, similar to previous studies, and from the height of the roosting bats.

Canopy Closure at Tree Base: This was the percent of the area above the observer covered by canopy. Initially this was estimated with a Spherical Densiometer. However, numerous studies have documented that densiometers are biased and often inaccurate. Therefore, I estimated the canopy closure visually. To estimate canopy closure, observers visualized a 45^{o} cone from the base of the tree and estimated the percent of the area containing canopy. The canopy closure was estimated by all those present and averaged. Generally, the variation among estimators was low.

Canopy Closure at Roost: Additionally, we visually estimated the canopy closure at the height of the roost. Again, we visualized a 45^{o} cone starting from the height of the actual roost and estimated the percent that contained canopy cover.

Distance to Water: This variable was difficult to measure because the colonies occurred in bottomland forests that were prone to flooding. At times, an occupied tree was in water 0.5 m deep, and other times the same tree (still being used by Indiana bats) was 0.8+ km from water. Therefore, I calculated the distance to the nearest open permanent water source while the tree was occupied.

Condition of Roost: This was examined in two ways. The first variable was determined subjectively, the second was more objective.

Decay Class of Roost: The conditions of the roosts were rated between 0 (live) and 4 (devoid of bark and branches). Categories are slightly modified from Thomas et al. (1979)

Smallest Branch Size: Because the decay class variable is subjective, I also recorded the diameter of the smallest branch remaining on the tree (excluding small epicormic branches).

Distance to Forest: The distance from the roost tree to the nearest patch of closed-canopy forest was measured for all roosts. For most trees, this distance was zero because the roosts were located within an intact forest.

APPENDIX II

Circular plot measurements from a 0.04-ha (11.3 m radius) circular plot established around each Indiana bat roost tree and all corresponding random trees.

Community Type: This categorical variable was the general habitat type (i.e. bottomland, swamp, upland).

Overstory Measurements: Trees were considered part of the overstory when the dbh (diameter at breast height) was ≥7cm. For each overstory tree, the species, dbh, and height were measured. The dbh was measured using a diameter tape (Forestry Suppliers, Jackson, MS) and height was measured with a clinometer.

Overstory Canopy Depth: This was measured as a range from the top of the tallest live tree to the height of the lowest major branches. This variable was used to calculate the extent of the overstory canopy.

Understory Measurements: All woody vegetation with a dbh >1.25 cm and <7 cm was included in the understory. The number of stems of each species was calculated within the circular plot.

Understory Depth/Height: This was calculated as the range from the top of the tallest understory tree (<7 cm dbh), to the general bottom of the understory -- often, but not always, the ground.

Understory Density: The understory density was subjectively estimated by the same observer in all samples. Density was recorded as one of 5 categories: open, light, moderate, moderate-heavy, and heavy.

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