USDA United States
Department of
Agriculture

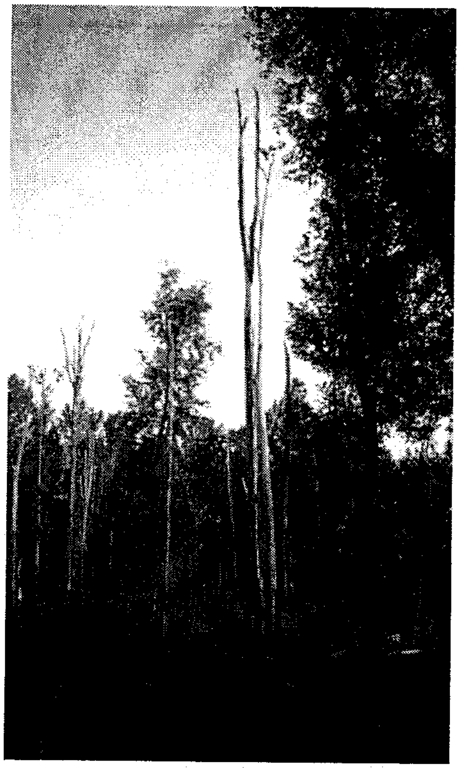
Forest Service

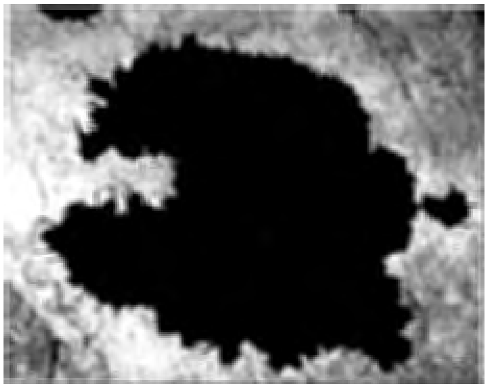
**Northeastern
Research Station**

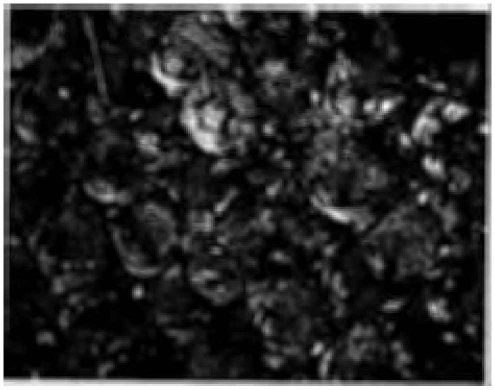
General Technical
Report NE-284

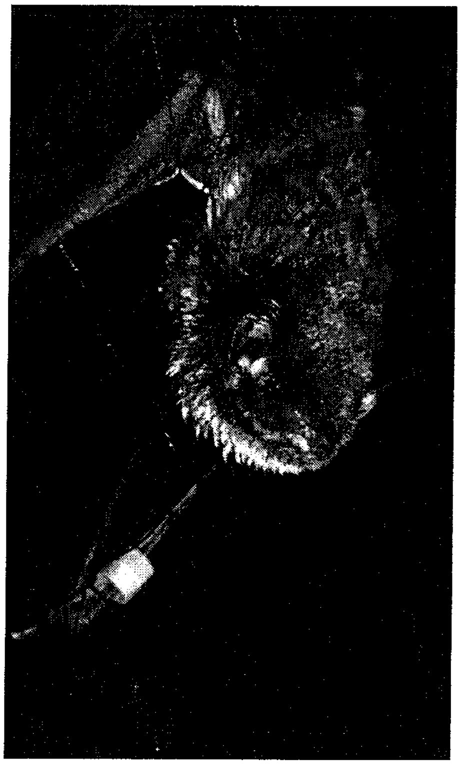
Review of the Forest Habitat Relationships of the Indiana Bat (*Myotis sodalis*)

Michael A. Menzel
Jennifer M. Menzel
Timothy C. Carter
W. Mark Ford
John W. Edwards









Abstract

Reviews the available literature on the ecology of the endangered Indiana bat (*Myotis sodalis*), including its selection of and use of hibernacula, roost trees, and foraging habitat. An extensive list of published references related to the Indiana bat is included.

The Authors

MICHAEL A. MENZEL and JOHN W. EDWARDS are wildlife biologists with West Virginia University's Division of Forestry at Morgantown. JENNIFER M. MENZEL and W. MARK FORD are research wildlife biologists with the Northeastern Research Station in Parsons. TIMOTHY C. CARTER is a wildlife biologist with Southern Illinois University's Department of Zoology at Carbondale.

Manuscript received for publication 24 May 2001

Published by:
USDA FOREST SERVICE
11 CAMPUS BLVD SUITE 200
NEWTOWN SQUARE PA 19073-3294

October 2001

For additional copies:
USDA Forest Service
Publications Distribution
359 Main Road
Delaware, OH 43015-8640
Fax: (740)368-0152

Visit our homepage at: **http://www.fs.fed.us/ne**

Contents

Introduction

The estimated population of the small, insectivorous Indiana bat (*Myotis sodalis*) totaled approximately 350,000 following a census conducted in 1995-97. This represents a decrease in population of nearly 400,000 since the 1960's (USDI Fish and Wildl. Serv. 1996). Officially listed as an endangered species in 1967, *M. sodalis* has seen its population continue to decline despite efforts to protect its winter habitat. As a result, scientists are studying how forest management techniques affect the summer habitat and foraging areas of the Indiana bat.

The Indiana bat closely resembles other *Myotis* species, all of which have brown pelage and a nondescript appearance. *M. sodalis* commonly are mistaken for the little brown myotis (*Myotis lucifugus*), but is differentiated from other myotid bats within its range by the presence of short toe hairs (not extending beyond knuckle), a small foot (9 mm), and a keeled calcar. The pelage is generally dull and pinkish-brown dorsally. Length measurements of the Indiana bat throughout its area of distribution produced the following ranges (in mm): total length, 70.8 to 90.6, tail, 27 to 43.8, hind foot, 7.2 to 8.6, forearm, 36 to 40.4. Measurements of weight ranged from 5 to 11 g (Whitaker and Hamilton 1998).

The distribution of this species is generally associated with limestone caves in the Eastern United States. The northern extent of the range extends southward from New England to the panhandle of Florida (excluding the Atlantic Coast). The western margins of the range include the Ozark Plateau of Missouri, Arkansas, and Oklahoma. *M. sodalis* roost in trees during the summer and hibernates in caves and mines during the winter. Most of the Indiana bat population occupies only nine winter hibernacula located in Indiana, Kentucky, and Missouri (USDI Fish and Wildl. Serv. 1996).

We conducted an extensive review of the literature on the natural history of the Indiana bat, particularly those aspects that might be influenced by forest management. We particularly sought information on hibernacula selection, tree roosts in spring, summer, and fall, and use of foraging habitat in summer and during fall swarm. Information on hibernacula, roosting, and foraging is summarized in Tables 1-3 in the Appendix.

Indiana Bat Hibernacula

Distribution of Caves

Since 1960, most (85+ percent) Indiana bats have used nine Priority I hibernacula caves/mines in Indiana (*n*=3), Kentucky (*n*=3), and Missouri (*n*=3) (Hall 1962; Humphrey 1978; Richter et al. 1978; USDI Fish and Wildl. Serv. 1996). Priority I hibernacula contain at least 30,000 bats (USDI Fish and Wildl. Serv. 1996). The remaining 15 percent of Indiana bats have been or currently are distributed among 50+ Priority II and III hibernacula in the aforementioned states and Alabama, Arkansas, Connecticut, Georgia, Illinois, Iowa, Massachusetts, Michigan, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin (Humphrey 1978; Dunn and Hall 1989; USDI Fish and Wildl. Serv. 1996). Priority II and III caves contain 500 to 30,000 and fewer than 500 hibernating bats, respectively. The small number of Priority I hibernacula means that fewer, peripheral hibernacula have significant importance in the protection of Indiana bats (Gates et al. 1984; Hobson and Holland 1995). Most hibernacula are found west of the Appalachian Mountains (though some are found in the Ridge and Valley and the southern Blue Ridge provinces) and are centered on the lower Ohio River Valley area of southern Indiana, eastern and central Kentucky, and the eastern Ozark Plateau region in Missouri. Hall (1962) hypothesized that this distribution is related to both cave suitability/availability and proximity to major river courses that are used for annual migration. Most Indiana bats return to the same cave or localized cave cluster each fall (Griffin 1940; Hall 1962; LaVal and LaVal 1980).

Cave Characteristics

Because the number of Indiana bat hibernacula is limited relative to other species (Raesly and Gates 1986), the physical and microclimatic characteristics of the known hibernacula are well documented (Hall 1962; Myers 1964; Henshaw 1965; Henshaw and Folk 1966; Barbour and Davis 1969; LaVal et al. 1976; LaVal and LaVal 1980; Clawson 1984; Harvey and McDaniel 1986; Brack et al. 1984; Raesly and Gates 1986; Saugey et al. 1990; USDI Fish and Wildl. Serv. 1999; Tuttle and Kennedy 1999). Variables that influence the suitability of caves for hibernacula include size of cave entrance, size and configuration of cavern room and passageway, ceiling structure, airflow, temperature, fluctuation in seasonal temperatures, humidity, previous occupancy by Indiana bats, and occupancy by other species (Hall 1962; Raesly and Gates 1986).

Occupied hibernacula have noticeable airflow (Henshaw 1965). Tuttle and Kennedy (1999) hypothesized that Indiana bats prefer hibernacula with the lowest nonfreezing temperatures possible. Core range (Indiana, Kentucky, and Missouri), midwinter cave temperatures of 2° to 5°C have been reported for Indiana bat cluster sites (Hall 1962; Henshaw 1965; Henshaw and Folk 1966; Thomson 1982). However, Barbour and Davis (1969) and Humphrey (1978) found hibernacula temperatures ranging from −1.6° to 17°C across the entire wintering season and hibernating range. Using continually recording data loggers, Tuttle and Kennedy (1999) recorded an overwinter range of −8.3° to 13.1°C from 15 important hibernacula in Kentucky (4), Illinois

(1), Indiana (5), Missouri (3), Tennessee (1), and Virginia (1). A retrospective analysis of temperature and population trend for some of these caves revealed population increases in four of six caves where overwinter temperatures ranged from 3° to 7.2°C and population declines in all four caves/mines where overwinter temperatures exceeded 8.1°C or were less than 0°C (Tuttle and Kennedy 1999). Hibernacula temperatures in Arkansas and Oklahoma and in Maryland, Virginia, and West Virginia typically are warmer (7° to 10°C) than caves in other portions of the range (Harvey and McDaniel 1986; Raesly and Gates 1987; Saugey et al. 1990). Warmer temperatures may increase metabolic rates in Indiana bats and cause premature fat depletion during the hibernation period (Richter et al. 1993). Stable midwinter temperatures of 1° to 10°C may represent a thermal threshold for hibernacula occupancy by *M. sodalis* (Clawson 1984).

Relative humidity ranged from 70 to nearly 100 percent in most hibernacula surveyed (Hall 1962; LaVal et al. 1976; Humphrey 1978; Tuttle and Kennedy 1999). Large caves, such as those in the Mammoth Cave and nearby systems in Kentucky, generally are too dry for the Indiana bat (Hall 1962). Raesly and Gates (1986) quantitatively compared hibernacula microhabitat and microclimate variables for Indiana bats, eastern pipistrelles (*Pipistrellus subflavus*), little brown myotis, northern long-eared myotis (*M. septentrionalis*), and big brown bats (*Eptesicus fuscus*). Relative to cave conditions chosen by other bat species, Indiana bats occupied open cave ceiling areas where the ambient air temperature and cave wall temperature were lowest, relative humidity was highest, and airflow was greatest. Because Indiana bats cluster in large groups in most hibernacula, intraspecific spacing was lowest among all species surveyed. *M. sodalis* clusters can reach densities of 3,000 per m^2 (Barbour and Davis 1969). Raesly and Gates (1986) also compared microhabitat and microclimate variables between occupied (n = 8) and unoccupied (n = 42) caves and mines. They found that Indiana bat hibernacula tended to have larger openings (9.7 vs. 2.8 m^2) and cave passages (858.8 vs. 131.6 m), and higher ceilings (13.2 vs. 6.3 m) than unoccupied sites.

Hibernation Chronology and Ecology

Indiana bats arrive at hibernacula or hibernacula areas (< 5 km radius of hibernacula) from mid-August to October (Kiser and Elliot 1996) and November (Hall 1962; Humphrey 1978). Copulation occurs during this time (LaVal and LaVal 1980), though ovulation, fertilization, and implantation do not occur until females have left hibernacula in the spring (Thomson 1982). Intense foraging and subsequent fat deposition critical for the wintering period occur after arrival at hibernacula and prior to cessation of aboveground activity in October for females and November for males (Humphrey 1978; Kiser and Elliot 1996).

In late summer and fall, Indiana bats swarm or gather in large numbers near cave entrances. The reason for this swarming behavior is not completely understood, but is possibly related to mating behavior. Early researchers mistakenly believed that sex ratios were skewed toward males because their netting efforts occurred in the late swarm after most females had entered hibernacula for the winter season (Hall 1962). Intercave movements may occur from the latter portion of the swarm to the early portion of the hibernation period. Consequently, population estimation using banding and mark-recapture techniques is unreliable if focused solely on single caves within this period (Clawson and Sheriff 1982).

Arrival weights of bats at the hibernacula range from 6 to 10 g (Hall 1962; Kiser and Elliot 1996). During the early swarm, *M. sodalis* roost in the warmer portions of the hibernacula and forage nightly to build fat reserves (Hassel 1967; Kiser and Elliot 1996). Prior to hibernation, females reach a maximum mass of 8.9 g vs. 8.0 g for males (LaVal and LaVal 1980). Fecal analysis of netted Indiana bats revealed that prehibernation diets were dominated by Lepidoptera (28.5 to 34 percent), Coleoptera (15.9 to 40.2 percent), Homoptera (4.5 to 15.3 percent), and Diptera (14.8 to 28.2 percent).

Exposure to and accumulation of environmental contaminants could occur during the prehibernation period of intense foraging and rapid fat deposition (Reidinger 1972). Contaminants were directly implicated in some local extirpations and are suspected as a factor in the decline of insectivorous bat species in North America (Clark 1981). Body burdens of organochlorine insecticides (now banned for agricultural use in the United States) in insectivorous bats were higher in modified agricultural landscapes than in wild or seminatural landscapes (Reidinger 1976). Clark and Prouty (1976) found lower pesticide burdens in eastern pipistrelles, northern long-eared myotis, and big brown bats near known *M. sodalis* hibernacula sites in forested areas of West Virginia where industrial facilities and agricultural land were largely absent. McFarland (1998) reported that Indiana bats in northern Missouri were routinely exposed to agricultural pesticides. Little brown myotis and northern long-eared myotis collected in northern Missouri in 1996 contained residues of eight historically applied organochlorine insecticides and two synthetic pyrethroids. Further, depressed brain acetylcholinesterase levels in these bats showed evidence of exposure to organophosphate and/or carbamate insecticides (McFarland 1998). Little is known about Indiana bat-pesticide relationships (USDI Fish and Wildl. Serv. 1996).

During the prehibernation swarming period in the mountainous and heavily forested Cumberland Escarpment and Cliff section of eastern Kentucky, Kiser and Elliot (1996) used radiotelemetry to determine that

Indiana bats foraged more on upper slopes and xeric ridgelines with second-growth chestnut oak (*Quercus prinus*)-pine (*Pinus* spp.) and oak-hickory (*Carya* spp.) forests than in riparian areas or moist slope-cove forests. LaVal et al. (1977) and Brack (1983) reported that chemiluminescent light-tagged Indiana bats foraged over oak-hickory forested hillsides and ridgetops in Missouri and upland habitats in Indiana, respectively, during the early swarm, prehibernation period. Kiser and Elliot (1996) hypothesized that cooler autumn temperatures (and subsequent cold-air drainage in locations with hilly or mountainous relief) limit insect abundance and activity in riparian areas and sheltered cove forests, whereas upper slopes and ridgelines have more favorable "warm" exposures. The maximum size of Indiana bat foraging areas during October, including the cave site, was 318 ha in 1994 and 194 ha in 1995; travel distances from the cave site were ≤ 2.5 km (Kiser and Elliot 1996).

Indiana bats periodically use tree roosts during the fall swarm. In eastern Kentucky, these roosts were located predominately in medium-size hardwood snags (mean diameter breast height [d.b.h] of 27.0 cm) within small forest openings or canopy gaps (Kiser and Elliot 1996). On the Fernow Experimental Forest in West Virginia, Indiana bats chose similar-size tree roosts (mean d.b.h. of 33.1 cm) in the early swarm period. However, 80 percent of the roosts were in live trees rather than snags (Thomas Schuler, Northeastern Research Station, unpubl. data). Neither study quantitatively measured use versus availability of tree roosts.

The relationship between hibernacula of *M. sodalis* and landscape features is poorly understood (USDI Fish and Wildl. Serv. 1996). Raesly and Gates (1986) found that hibernacula occupied by Indiana bats in Maryland, Virginia, and West Virginia ($n = 8$) tended to have more surrounding forest cover and less area in cultivated fields within a radius of 1 km than unoccupied caves and mines ($n = 42$). However, the authors cautioned that more meaningful habitat analyses during the swarm period must include measures of insect abundance and availability.

Kiser and Elliot (1996) suggested that all snags within 2.5 km of hibernacula be retained and encouraged snag creation through girdling and reforestation of abandoned pastures and reclaimed surface mines with native hardwood tree species. Clawson (1984) reported that deforestation around hibernacula has decreased available foraging habitat throughout the Indiana bat's range during prehibernation.

Wintering

The inactive hibernation period for Indiana bats is approximately 190 days (October to April for females, November to May for males) depending on the hibernacula (Hall 1962). Indiana bats form large clusters in cooler hibernacula or cooler portions within hibernacula and smaller, more transient clusters in warmer hibernacula (Hall 1962; Thomson 1982). Indiana bats are true hibernators (Guthrie 1933; Thomson 1982); though, they arouse every 8 to 10 days (Hardin and Hassell 1970). *M. sodalis* that use low roosts in Great Scott Cave in Missouri moved throughout winter to areas within the cave with more optimal temperatures (Tuttle and Kennedy 1999).

Arousal following disturbance (e.g., by spelunkers, scientists, predators) can be detrimental, and may be one of the greatest threats to *M. sodalis* (Hall 1962; Myers 1964; LaVal et al. 1976; Humphrey 1978; LaVal and LaVal 1980; Brack et al. 1984; Clawson 1984). Mild sound and light stimuli can initiate arousal (Humphrey 1978), as can a drop in cave humidity below 85 percent (Tuttle and Kennedy 1999). Sudden arousal is accompanied by excessive agitation, movement and in-cave flight that can expend 20 to 30 days of stored energy reserves (Daan 1973). Sudden arousal events can accelerated fat depletion, result in premature emergence from hibernacula, and lower body condition and survival in spring (Clawson 1984; Tuttle and Kennedy 1999). Even in the absence of disturbance, weight loss in early winter is rapid. Bats lose 0.016 g/day, slowing to 0.008 g/day by mid- to late winter (Hall 1962).

Indiana bats are particularly vulnerable to vandalism during hibernation (Dunn and Hall 1989) as many instances of wanton destruction of bat colonies have been documented (Hall 1962; Myers 1964; LaVal et al. 1976; Humphrey 1978; LaVal and LaVal 1980; Brack et al. 1984; Clawson 1984). Potential or historic hibernacula that regularly are disturbed will not support wintering *M. sodalis*. In most instances, recolonization following cave protection has not occurred (Harvey and McDaniel 1986). Entry by humans into Indiana bat hibernacula should be prohibited from September through May (Humphrey 1978; LaVal and LaVal 1980; Clawson 1984; USDI Fish and Wildl. Serv. 1996).

Improperly designed cave gates that alter cave airflow regimes (particularly trapping warm air) reduce and in some instances make hibernacula unsuitable (Tuttle 1977; Humphrey 1978; Richter et al. 1993; Tuttle and Kennedy 1999). Tuttle and Kennedy (1999) suggested restoring airflow or improving temperature regimes in 15 Indiana bat hibernacula by removing entrance obstructions, building cold-air dams, or installing ventilation shafts. Cave-specific recommendations are dependent on cave characteristics and the extent of anthropogenic alteration.

Numerous instances of intra- and inter-hibernacula movements by Indiana bats have been documented (Myers 1964; Hardin and Hassell 1970; Fenton and Morris 1976). Although most movement were attributed to cave disturbance by humans (Myers 1964; LaVal and LaVal 1980), *M. sodalis* will move within caves during hibernation to roost sites where microclimatic conditions are better (Tuttle and Kennedy 1999). Generally, midwinter movements are limited to intra-hibernacula sallies in colonies that are minimally disturbed; colonies subjected to frequent or intense human disturbance will shift hibernacula (Myers 1964). Hall (1962) believed that Indiana bats wintering in Coach Cave, Kentucky, engaged in midwinter feeding during warm weather based on the presence of fresh fecal discharge of chitin.

Indiana bats in hibernacula also are vulnerable to natural disturbances. Local catastrophes can have tremendous conservation implications because of the limited number of hibernacula (Hall 1962). Midwinter flooding of caves can cause significant mortality by drowning trapped bats or inducing energy-expensive arousal (Cope and Ward 1965). Hibernating *M. sodalis* can freeze to death in caves that trap and hold cold air during periods of unseasonably frigid temperatures (Humphrey 1978; Richter et al. 1993). Ceiling collapses, which have killed Indiana bats and blocked passageways in mine sites (Hall 1962; Humphrey 1978), can occur in caves and mines (USDI Fish and Wildl. Serv. 1996).

Emergence

Indiana bats emerge from hibernacula from mid-April through May (Hobson and Holland 1995). Females typically leave caves before males (Humphrey 1978; LaVal and LaVal 1980); they are not visibly pregnant at emergence (LaVal and LaVal 1980). The chronology and patterns of female movements to maternity areas are unknown. Smaller caves in the hibernacula area may serve as "spring movement" roosts for Indiana bats following initial emergence (Myers 1964). Hobson and Holland (1995) tracked a single radio-marked male Indiana bat for 2 weeks following mid-May hibernacula emergence in western Virginia. The bat traveled 16 km from the hibernaculum to forage over a 625-ha patch of mature, second-growth, oak-hickory forest with a hemlock (*Tsuga canadensis*) riparian component. Diurnal roosting during this period occurred in a mature shagbark hickory (*C. ovata*) with other male Indiana bats. Additional identification of postemergence foraging and roosting habitat may be required for meaningful efforts designed to protect Indiana bats (Hobson and Holland 1995).

Research Questions and Needs

There are several important research questions related to Indiana bat hibernacula that remain to be addressed:

1. What landscape-scale characteristics and biological factors are ecologically important to Indiana bats with respect to hibernacula? Since all Priority I and II, and most Priority III, hibernacula sites probably are known, an attempt should be made to distinguish landscape and land-use features for hibernacula where *M. sodalis is* increasing, stable, or declining. The effects of forest management directly around hibernacula on the microclimate and suitability of the mines/caves should be identified. Researchers should use remote-sensing and GIS technologies with data from Indiana, Kentucky, and Missouri to examine the relationship of forest cover, type, and structure/age to population trends of hibernacula. Because only three radiotelemetry studies have addressed pre- and posthibernation habitat and roost selection, a geographically expanded program using radiotelemetry should be undertaken for a more complete understanding of Indiana bat foraging and roost selection. If bats rely on this period to accumulate overwinter energy stores, this aspect of the biology of *M. sodalis* may prove the most crucial to conservation efforts. Concomitant efforts are needed to more clearly identify Indiana bat food habits during prehibernation and postemergence across its entire range. The relation between insect abundance and availability and *M. sodalis* population densities and trends among hibernacula also should be explored.

2. What is the continued vulnerability of Indiana bats to pesticide exposure during the prehibernation swarm and postemergence? Considering the proximity of large agricultural landscapes to most Priority I hibernacula, is there a continued and measurable bioaccumulation of organochlorines? What other unknown environmental contaminant burdens do Indiana bats currently face, e.g., organophosphate insecticides and heavy metals? Could environmental contaminants that singularly occur at harmless tissue concentrations act in synergistic fashion to cause Indiana bat mortality or to lower overall fitness and survival? What role does insecticide use play in decreasing insect abundance and *M. sodalis* foraging efficiency during the prehibernation swarm or postemergence?

3. Should wintering colonies of Indiana bats be considered in the context of genetically or evolutionarily significant management units because of the extreme philopatry they show toward an individual hibernaculum, and because breeding occurs upon hibernacula arrival during the swarm? Accordingly, natural recolonization and use of historical but abandoned hibernacula following restoration and protection may not occur or at a rate too slow to overcome population declines. How can recolonization of historical hibernacula by Indiana bats be encouraged or enhanced via active management?

Spring, Summer, and Fall Roosting Habitat

General Roosting Ecology

Female Indiana bats form small maternity colonies (usually <100) under exfoliating bark during the summer months (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, e.g., pastures and upland hardwoods (Kurta et al. 1993a; Whitaker and Hamilton 1998). Male summer roosts can be found in a variety of locations. In Illinois, bachelor colonies of 1,000 to 1,500 were located in an abandoned mine. Other roosts of males have been found under exfoliating bark (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 are trees that are used by more than 30 bats on more than one occasion. Alternate roosts are used by fewer individuals. Both roost types are essential to meet the maternity requirements of *M. sodalis*. Although a 30-bat threshold may not be applicable to all colonies (especially to those with fewer than 30 bats), the concept of primary and alternate roosts is used throughout this section.

Tree Species Used/Preferred

One of the earliest reported maternity roosts of the Indiana bat was a primary roost in a bitternut hickory (*C. cordiformis*) snag and an alternate roost in a live shagbark hickory (*C. ovata*; Humphrey et al. 1977). Roosts in living trees are most commonly found in shagbark hickory (Gardner et al. 1991b; Callahan et al. 1997). Indiana bats roost in snags of many tree species, including red (*Acer rubrum*), silver (*A. saccharinum*), and sugar (*A. saccharum*) maple, bitternut, shagbark, and pignut (*C. glabra*) hickory, cottonwood (*Populus deltoides*), white (*Fraxinus americana*), black (*F. nigra*), and green (*F. pennsylvanica*) ash, American sycamore (*Platanus occidentalis*), white (*Q. alba*), scarlet (*Q. coccinea*), shingle (*Q. imbricaria*), northern red (*Q. rubra*), and post (*Q. stellata*) oak, eastern hemlock (*Tsuga* canadensis), sassafras (*Sassafras albidum*), and American (*U. americana*) and slippery (*Ulmus rubra*) elm (Brack 1983; Gardner et al. 1991b; King 1992; Kurta et al. 1993a; Caryl and Kurta 1996; Kurta et al. 1996; Salyers et al. 1996; Callahan et al. 1997). In Kentucky, Indiana bats may roost in Virginia pine (*P. virginiana*) and shortleaf pine (*P. echinata*) and females also may use sourwood (*Oxydendum arboreum*) in autumn and early spring (Kiser and Elliott 1996; MacGregor et al. 1999).

Some biologists consider the previously mentioned tree species as "acceptable" (Gardner et al. 1991b; Rommé et al. 1995). However, new tree species frequently are added to this list (MacGregor et al. 1999), so it may be premature to consider the list as definitive. Except for Kurta et al. (1996), all reports of roost-tree preference are observational. Statistical designs were not used to test preference, though Kurta et al. demonstrated that Indiana bats prefer green ash to silver maple. Silver maple also was documented as a roost tree in other studies (Gardner et al. 1991b; Callahan et al. 1997).

The use of snags by Indiana bats may be influenced by bark characteristics. Because virtually all maternity roosts are found under exfoliating bark, the characteristics of a species as a snag may be more important than the tree species on which the bark is present (Rommé et al. 1995).

Indiana bats also use artificial roost structures. In central Indiana, Salyers et al. (1996) found two male *M. sodalis* roosting in a bat box. Using radiotelemetry, they tracked one bat to other bat boxes and a cedar shake garland. Butchkoski and Hassinger (2001) found a maternity colony roosting in the attic of a church in Pennsylvania. Wilhide et al. (1999) found a male Indiana bat roosting under the metal brackets of a utility pole top in the Ozark National Forest in Arkansas, and Mumford and Cope (1958) made two references to *M. sodalis* males roosting under bridges in Indiana.

Tree Condition

Although, some alternate roosts occur in living trees (primarily shagbark hickory), most Indiana bats roost in dead or dying trees. One of the two roost trees reported by Humphrey et al. (1977) was a live shagbark hickory. About 10 percent of the roost trees from Illinois reported by Gardner et al. (1991b) and 28 percent of the trees reported by Callahan et al. (1997) were classified as live. Live and dead trees may differ in protection from rain and solar radiation provided by their canopy as rates of heat loss (Humphrey et al. 1977; Garner et al. 1991b; Callahan et al. 1997).

Structural Characteristics of Roost Trees

Few maternity colonies have been located in tree cavities. Most primary maternity roosts are situated under exfoliating bark. The ability of a tree species to produce exfoliating bark probably influences Indiana bat use (Callahan et al. 1997; Rommé et al. 1995). 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 snag samples not used. These studies did not address the qualitative features of exfoliating bark.

Most maternity roosts are found in large trees. The average diameter for all roosts described by Gardner et al. (1991b) was 36.7 (range: 8 to 83 cm); the four roosts with the largest numbers of bats averaged 40 cm d.b.h. Primary roost trees described by Callahan et al. (1997) averaged 58.4 ± 4.5 cm d.b.h. Alternate roosts averaged 53.0 ± 4.1 cm d.b.h. Kurta et al. (1996) found that the average diameter of Indiana bat tree roosts (0 = 40.9 ± 1.2 cm; range: 30 to 52 cm) were significantly less variable than the average diameter of random trees (0 = 33.4 ± 1.4 cm; range: 11 to 70 cm).

The results of studies examining roost tree size effect on selectivity are conflicting (Kurta et al. 1996; Callahan et al. 1997). Gardner et al. (1991b) arbitrarily concluded from 48 roost trees that dead trees at least 22 cm d.b.h provided essential *M. sodalis* roosting habitat, but their designation of appropriate species was limited to tree species that they documented. Additionally, Indiana bats sometimes roost in snags smaller than 22 cm d.b.h and in species not found in Gardner et al.'s (1991b) list. The spring and autumn roosts of male Indiana bats do not differ greatly 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 d.b.h, with a mean of 31 cm (Hobson and Holland 1995; Kiser and Elliott 1996; MacGregor et al. 1999).

Solar Exposure and Spatial Relation to Neighboring Trees

Most primary roosts are well exposed to extensive solar radiation. However, some alternate roosts are completely shaded while others are totally exposed. Indiana bats may pick maternity roosts with high solar exposure to increase the roost temperature, which might decrease the time of fetal development and juvenile growth (Callahan et al. 1997). However, because males are not associated with maternity colonies and the need for high roosting temperatures (Callahan et al. 1997), they may seek cooler roosts to conserve energy.

Gardner et al. (1991b) reported that most Indiana bat roosts in Illinois were beneath the forest canopy. However, canopy closure was estimated using multiple readings with a spherical densiometer 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. Callahan et al. (1997) considered roosts as open (exposed to solar radiation) or interior (less than 50 percent canopy cover) and found all primary roosts in open snags. Live interior roost trees averaged 70 percent canopy closure and were more open on the western aspect than random live trees. Interior snags used as roosts averaged 60 percent canopy closure and were more open on all aspects than random interior snags. MacGregor et al. (1999) reported that canopy closure ranged from 20 to 93 percent for male Indiana bat roosts (0 = 80 percent). However, MacGregor et al. (1999) noted that there is no effective method for measuring the canopy closure (solar exposure) at the actual roost. And tools such as the spherical densiometer, fisheye photography, and competition indexes used to assess canopy closure can yield different results (Cook et al. 1995; Comeau et al. 1998).

Different methodologies might explain discrepancies among studies of primary roosts and solar exposure. Reports of solar exposure for alternate roosts range from complete shade to total exposure. 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. The average height of closed-canopy roost trees used as primary maternity roosts in Illinois was 7.8 m (Gardner et al. 1991b). 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 in the open. Although not compared statistically, this trend shows that females tended to roost higher in the canopy in closed-canopy forests.

Roost heights may vary with canopy cover so that bats can to maintain a relatively constant level of solar exposure. Callahan et al. (1997) reported that 45 percent of maternity roosts in Missouri were in open areas and that more Indiana bats used open-area than closed-canopy roosts. The maternity colony in Michigan roosted in snags in the middle of a flooded pasture turned wetland (Kurta et al. 1996). All snags were unshaded and the mean roost height was 9.9 m (± 0.9; range: 1.4 to 18 m).

Male Indiana bats exhibit different habits with regard to roosting height and solar exposure. Gardner et al. (1991b) found that the average roost height used by males was 4.2 m (4.9 m in closed canopy and 3 m in "patchy" canopy). They also reported only one male roost from an open canopy at a height of 4 m. A male Indiana bat tracked in western Virginia by Hobson and Holland (1995) roosted at a height exceeding 8 m each night for 19 consecutive nights.

Canopy Cover of Stands

The canopy cover in stands used by Indiana bats is described inadequately, though stand characteristics can be inferred from Gardner et al. (1991b), Kurta et al. (1996), and Callahan et al. (1997). Methods used by Gardner et al. to measure canopy closure best describe closure at the stand level. Of 48 roosts that they found in forested habitats, 32 were in closed-canopy forests, 12 were in intermediate forests, and 4 were in open-canopy forests. All roosts reported by Kurta et al. (1996) were from a 5-ha flooded wetland where all trees were dead or dying. This wetland had an open canopy. The American sycamore roost reported by Kurta et al. (1993a) was unshaded indicating reduced canopy closure. In Missouri, Callahan et al. (1997) calculated the canopy closure of random trees located within the stand as an indication of stand canopy closure. Forest canopy closure averaged nearly 70 percent for all non-used trees.

Spatial Relationship of Roost to Water Sources and Foraging Areas

The proximity of Indiana bat roosts to water sources and foraging areas has not been well studied. Two roost trees reported by Humphrey et al. (1997) in Indiana were located less than 200 m from the creek that *M. sodalis* used for foraging. A roost tree described by Brack (1983) was on the bank of the Blue River in Indiana. Also in Indiana, Kurta et al. (1993a) reported a hollow sycamore roost 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 as much as 1 m of water. 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. All colonies reported by Callahan et al. (1997) were located near a stream or river.

Gardner et al. (1991b) reported distances from roosts to foraging areas in Illinois 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 feature measured. The mean distance between all Indiana bat roost trees tracked to the nearest intermittent stream was 124 m. In western 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).

Spatial Relationship to Other Roost Trees

There is considerable variation in the distances that Indiana bats travel between roost trees within a colony. In Indiana, Humphrey et al. (1977) reported that two roost trees they observed were approximately 30 m apart. In Illinois, Gardner et al. (1991b) collected one of the largest data sets to date of *M. sodalis* roost trees, but did not associate roosts with particular colonies or report distances among roost trees that were used by each Indiana bat. In Michigan, Kurta et al. (1996) found that the 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. In Kentucky, MacGregor et al. (1999) reported that distances between autumn roosts of males ranged from 48 m to 2,688 m encompassing areas from 0.4 to 568 ha.

Density of Potential Roost Trees

There is little information on 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 as 64 per ha for upland habitat and 41 per ha for floodplains. Rather than describing a quantitative method for obtaining these data, their numbers were derived from a snag density survey (d.b.h. > 22 cm) of acceptable species within the study area. Bark characteristics and decay classes were not reported. As part of a mitigation project, Salyers et al. (1996) reported a potential roost density of 15 trees/ha, which was raised to 30.4 roost sites/ha after instillation of artificial roost structures.

In Missouri, Callahan et al. (1997) reported the largest distances between roosts of a single maternity colony. Although all roosts were not discovered, the highest density was 0.25 roost tree/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 ha. They reported that there were 66 available roost trees in the wetland (13.2 potential roost trees/ha), an unusually high snag density.

Due to 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). These features vary from area to area with no predictable pattern (Kurta et al. 1996; Callahan et al. 1997). As a result, a variety of snag types must be maintained to maximize the chance that snags with suitable structural characteristics for Indiana bats will be present. Additional information is needed to define what constitutes suitable Indiana bat roost.

The number of roost trees needed by an Indiana bat colony is unknown and probably varies by colony size and roost availability. Roost use also can change in response to unpredictable climatic conditions. Roost attrition precludes managers from being able to set aside a minimum number of potential roosts. Also, the unpredictable nature of natural roost destruction hinders managers in predicting the longevity of current roost trees, and the time needed for a tree to become "suitable" for Indiana bats is unknown and probably varies by tree species and location.

Stand Composition

There are no quantitative descriptions of stand composition for forests surrounding Indiana bat roosts. However, all studies provide descriptions of the study areas. Based on most descriptions, the stands surrounding roosts do not differ substantially in composition from the list of 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 trees were used as roosts. However, Indiana bat roosts have been found in both silver maple and American elm in other studies (Gardner et al. 1991b). 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

The stand structure surrounding Indiana bat maternity colonies have not been described quantitatively, though there have been comparisons with roost trees to randomly located potential roosts within a stand. In Michigan, Kurta et al. (1996) found that roost trees within in the stand were larger (d.b.h.) and less variable in diameter than randomly located potential roost snags. However, Callahan et al. (1997) found that roost-tree characteristics such as d.b.h. or bark cover did not differ statistically from potential roosts within a stand in Missouri.

Roost trees occur in many habitat types with different 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. Recent research has documented maternity colony use in a green-tree reservoir and along swamp edges in southern Illinois where tree mortality was substantial due to from flooding of the Mississippi River during 1993 and 1995 (T. C. Carter, unpubl. data).

MacGregor et al. (1999) reported that two-age shelterwood harvests on the Daniel Boone National Forest in Kentucky can produce different amounts of autumn roosting habitat for Indiana bats depending on the harvests' snag retention. Their guidelines called for retention of all snags, hollow trees, live trees with large dead limbs, and shagbark hickories. These guidelines produced stands with 15 times the roost trees retained with conventionally managed two-age shelterwoods (5 snags/ha). Roost sites were also found in burned areas managed for the red-cockaded woodpecker (*Picoides borealis*). Although this information is anecdotal, it suggests that Indiana bats may be more tolerant of limited disturbance of the roosting area. Practices such as even-age and uneven-age management can be used provided they include provisions for snag retention and favor oaks and shagbark hickories (Callahan et al. 1997). Still, there is little quantitative information on the effect of timber management practices on roost selection by Indiana bats.

Forest Type and Topography

Indiana bat roosts have been commonly found among mixed mesophytic hardwood and mixed hardwood-pine habitat types. Humphrey at al. (1977) and Brack (1983), located roosts in riparian habitats in Indiana. 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 that male Indiana bats roosted in pine-dominated forests during the autumn.

Size of Area Surrounding Roosts

The area used by Indiana bats surrounding their roosts varies among colonies. However, it is not always known where colony members forage and whether or not all colony roosts were discovered. Indiana bats tracked by Kurta et al. (1996) traveled outside their immediate roosting area to forage, but the exact location or extent was not known (Allen Kurta, Eastern Michigan University, pers. commun.). Humphrey et al. (1977) observed that bats traveled from their roosts to a nearby stream where they foraged along a 0.81-km section. Indiana bats have been observed foraging among and adjacent to roosts, and in areas disjunct from roosts.

Landscape Structure

Gardner et al. (1991b) made the only attempt to document composition of landscape habitat. Within the study area, 65 percent was cropland or old fields, 2 percent other agriculture, 33 percent forested (30 percent upland and 2.2 percent floodplain), and 0.1 percent impounded water habitat. At a larger scale, Illinois was 63 percent agricultural, 1.6 percent urban, 33 percent forested, 6.4 percent forested wetlands, and 1.3 percent impounded water. The impact of forest fragmentation on roost availability of Indiana bats at the landscape scale is unknown.

We are not aware of studies that have examined the effect of landscape-level disturbance regimes (e.g., fire, timber harvest) on availability of Indiana bat roosts. As suggested by the Indiana Bat Recovery Plan (USDI Fish and Wildl. Serv. 1996), the effect of availability of stands with "suitable" roosting habitat must be examined.

Rommé et al. (1995) used previously published data to develop a Habitat Suitability Index model for Indiana bats that asses habitat quality across the landscape. We are not aware of studies that have applied or validated the HSI model.

Research Questions and Needs

1. Further study of the Indiana bat's summer roosting habitat is needed as the mechanisms influencing roost selection remain unknown. We know that Indiana bat colonies use multiple trees to meet maternity requirements, but we do not know what resources each of these roosts provides or how resources change under different conditions. Also needed are studies of the factors that affect Indiana bat roosting behavior.

2. Research is needed on the effects of forest management on Indiana bat roosting ecology. It is not known how different management practices affect the quantity and quality of roosting structure and roosting habitat.

3. No studies have examined the reproductive output of an Indiana bat colony. This information is crucial to understand the species' capacity to recover from its current decline. Bats have relatively low reproductive outputs (Findley 1993). Without an understanding of Indiana bat reproduction, the period needed for this species to rebound from past disturbances cannot be assessed accurately. Claims of short-term declines or increases in populations (local or species wide) require an understanding of recruitment.

4. The relationships between stand structure and Indiana bat reproduction should be evaluated. Little or no work has investigated the impacts of timber harvests on maternity colonies. However, anecdotal evidence suggests that *M. sodalis* may benefit from limited disturbance around potential roosting areas. Limited disturbance can create potential roost trees and open the canopy around potential roost trees (Gardner et al. 1991b; Kurta et al. 1993a). It is important that such research evaluates how these practices affect both colony behavior and individual fitness. Disturbances from forest management that change behavior but do not adversely affect fitness may be benign.

Foraging Habitat

Species Composition/Vegetational Community Type

Indiana bats often forage in riparian areas (Humphrey et al. 1977; LaVal and LaVal 1980; Kessler et al. 1981; Brack 1983), woodlots (Mumford and Cope 1958), and upland forests (Easterla and Watkins 1969; LaVal et al. 1977; LaVal and LaVal 1980; Brack 1983). In summarizing past captures of Indiana bats, Mumford and Whitaker (1982) noted that some individuals had been collected (shot) when foraging around the crowns of oak and hickory trees. Brady (1983) observed in east-central Indiana that in riparian areas where four *M. sodalis* maternity colonies were located, 90 percent of the tree species were (in frequency of occurence) boxelder, silver maple, ash, sycamore, snags, sugarberry (*Celtis occidentalis*), American elm, willow, cottonwood, black walnut, honey locust (*Gleditsia triacanthos*), Ohio buckeye (*Aesculus glabra*), and slippery elm. Brack (1983) noted that at net sites where Indiana bats were captured, oaks or hickories (or both) dominated.

In Missouri, LaVal et al. (1977) observed 69 Indiana bats to which Cylalume Chemical Lightsticks (chemoluminescent tags) had been attached. The bats foraged under the forest canopy in dense wooded areas along ridges and hilltops. Their observations supported previous reports that Indiana bats primarily forage 2 to 30 m above the ground (Humphrey et al. 1977). Their results also indicated that Indiana bats forage in a greater diversity of habitat types, including uplands, than reported by Humphrey et al. (1977). LaVal et al. (1977) rarely observed Indiana bats foraging directly over water and suggested that low capture rates over streams experienced by Humphrey et al. supported these observations. However, the latter noted that low capture rates over water probably were related to the ability of Indiana bats to avoid nets rather than to the absence of bats along stream corridors. A study by Gardner et al. (1989) supported this hypothesis.

Brack (1983) observed chemoluminescent-tagged Indiana bats foraging in riparian areas, upland forests, and over a pond, a pasture, and an old field in Indiana. Most foraging occurred along habitat edges. Foraging occurred above, below, and around tree canopies in forested habitats, along the forest/stream edge in riparian areas, and along the edge of pastures and old fields.

Clark et al. (1987) captured Indiana bats in mist nets along narrow, disturbed riparian strips, wooded floodplains, and upland forests. Nearly 43 percent of Indiana bats (n = 12) were netted during nine nights of sampling at a highly disturbed, fragmented riparian strip. Cooling degree- days in May, heating degree-days in June, June maximum temperature, and June minimum temperature best predicted the presence of Indiana bats. These and other climatic factors may serve as environmental covariates when testing the significance of vegetation structure and vegetational community type on the presence of *M. sodalis*.

Bowles (1981) used mist-net surveys to document Indiana bat occurrence at four sites in Iowa. He captured reproductively active females at sites that varied greatly in structure and vegetational composition. These included highly disturbed, narrow (< 15 m) riparian habitats containing young trees (< 15 m tall and < 40 cm d.b.h.), mature riparian areas, and mature upland forests. Bowles suggested that Indiana bats are at least somewhat opportunistic in selecting summer foraging habitat.

Hobson and Holland (1995) used triangulation techniques, direct observation, and the receiver's attenuator to delineate foraging areas of radio-tagged bats. The 625-ha foraging area used by one male Indiana bat was an 80-year-old oak-hickory, mixed deciduous forest with a conifer component. The bat foraged in an elliptical pattern at canopy height. The authors did not indicate how many foraging locations were used to delineate the foraging area, how many points were obtained using triangulation or direct observation, or the degree of error associated with the radiotelemetry.

LaVal and LaVal (1980) captured Indiana bats along narrow riparian strips and in forest patches adjacent to streams in eastern Missouri. If riparian forests were the preferred foraging habitat for Indiana bats, then their summer foraging habitat was reduced greatly. However, if one uses the metric "one colony/km suitable riparian habitat and 12 colonies/county," the available habitat was not fully utilized.

Examination of fecal pellet also can provide insight into the foraging habitats of *M. sodalis*. Most myotids are opportunistic foragers and the differences observed between bat diets and available insects are a result of bats foraging in specific habitats and randomly feeding on insects rather than randomly foraging across habitats and selecting specific types of insects (Belwood and Fenton 1976; Fenton and Morris 1976; Whitaker 1995). If this is true for Indiana bats, foraging habitat can be assessed by examining the insects consumed.

Analyses of Indiana bat diets suggest that foraging habitats differ between their southern and northern distributions (Kurta and Whitaker 1998). Studies by Belwood (1979) and Brack (1983) in Missouri indicate that *M. sodalis* commonly forages in upland habitats in the southern portion of its range. Conversely, in Michigan, Kurta and Whitaker (1998) found that Indiana bats forage primarily in wetland habitats. Additional information is needed on the Indiana bat's diet and foraging habitat selection throughout its range.

Selection and Avoidance at Stand Scale

Humphrey et al. (1977) used Indiana bats tagged with fluorescent bands to determine relative levels of foraging activity among different vegetation communities. The bats foraged exclusively in riparian habitats despite the availability of upland forests, pastures, cornfields, upland hedge rows, and treeless creek banks. Although no statistical comparison of use versus available habitat was conducted to test for foraging habitat selection, the study indicated that *M. sodalis* forages primarily in wooded riparian areas and did not use other habitats. A criticism of fluorescent bands is that researchers must make visual contact with the marked bats. Another source of bias is the implicit assumption that foraging Indiana bats were equally visible among all habitat types examined. Humphrey et al. (1977) also assumed (albeit unstated) that if no marked Indiana bats were observed foraging in the individual forest stand, pasture, cornfield, upland hedge row, or treeless creek bank they surveyed, then these habitat types were not used elsewhere. It is unclear whether these assumptions were valid. Their results show that Indiana bats foraged in wooded riparian areas, but do not confirm that wooded riparian areas were preferred over the other habitat types they observed.

Following LaVal et al. (1977), Brack (1983) used chemoluminescent tags to compare the proportion of sightings in riparian habitat to that expected based on the availability of riparian habitats in the study area. Brack observed that foraging occurred mostly in upland woods, though his statistical analyses comparing habitat availability and use indicated that *M sodalis* did not preferentially forage in, or avoid, riparian habitats (Brack 1983, 1991). Brack (1983) also compared the proportion of foraging activity that occurred in forested habitats to that expected based on forested habitat abundance in the study area. Forested areas were selected over open areas (e.g., pastures, old fields) by foraging Indiana bats. These results provide one of the most quantitative examinations of foraging habitat selection by *M. sodalis*. However, the authors relied on the assumption that the probability of observing light tagged Indiana bats did not differ among riparian and nonriparian habitats, and among forested or nonforested habitats.

In Illinois, Gardner et al. (1989, 1991b) used radiotelemetry to analyze the foraging habits of the Indiana bat and to determine the size of the foraging ranges of 17 *M. sodalis* (2 pregnant, 6 lactating, 1 postlactating, 2 juvenile females, 3 juvenile males, 3 adult males). The study area in each foraging range was divided into 11 cover types: cropland, hayfield or pasture, old field, other agricultural land, upland forest with closed, intermediate, or open canopy, and floodplain forest with closed, intermediate, or open canopy, and pond. Foraging areas consisted primarily of cropland (49 percent), closed canopy floodplain forest (14.8 percent), and closed canopy upland forest (11.6 percent). Hayfield and pastures accounted for 7.1 percent, as did old fields.

Gardner et al. quantitatively tested for differences between proportions of habitat used and available using the program PREFER. Foraging Indiana bats selected closed-canopy (80 to 100 percent closure) floodplain forest. However, Gardner et al. used the minimum convex polygon method to define foraging ranges. Large areas unused by *M. sodalis* may have been included in the home range analysis (see White and Garrott 1990). For example, on average, 49 percent of minimum convex polygon foraging areas was composed of row crops. However, this does not necessarily mean that the bats spent 49 percent of their time foraging in row crops. Thus, the results presented by Gardner et al. (1991b) may not have reflected the amount of use for each habitat type. Determining the proportion of actual foraging locations in each habitat type would have been a more useful analysis of habitat use.

Another potential limitation of the analyses by Gardner et al. (1991b) is their definition of available habitat. Thomas and Taylor (1990) suggested that habitat use and availability be compared at multiple spatial scales. The size of the available foraging area (3,672 ha) defined by Gardner et al. (1991b) seems reasonable based on distances that Indiana bats traveled between roost and foraging areas. However, they reported use versus availability for only one spatial scale, and comparison among studies will be difficult unless the same spatial scale is used in future studies.

Gardner et al. (1991b) characterized habitats in 340-, 1,809-, and 5,278-ha concentric circles around sampling sites where Indiana bats had been captured. There was great variability in habitat use, e.g., deciduous forest (5 to 98 percent), evergreen forest (5 to 26.7 percent), total forest (5 to 98 percent), forested wetlands (0.07 to 59.6 percent), and cropland (zero to 95 percent). Although. these results support Bowles' (1981) observation that *M. sodalis* are somewhat opportunistic in selecting summer foraging habitats, they should be interpreted with caution. This type of analysis assumes that Indiana bats are captured near the center rather than at the edge of their home range, and gives equal importance to abundance of habitats 1 to 4 km from capture locations and habitats immediately surrounding the point of capture.

Foraging Height

Using ultrasonic detectors, Humphrey et al. (1977) found that Indiana bat foraging height was 2 to 30 m. Because of atmospheric sound attenuation, the ability to detect foraging bats with ultrasonic detectors decreases with increasing distance. Therefore, most myotid calls are difficult to detect with ultrasonic detectors at distances beyond 30 m. It is unclear how Humphrey et al. considered the relationship between distance and observability, both visually and with ultrasonic detectors. Thus, Indiana bat foraging activity at heights greater than 30 m may not have been observed due to limitations associated with methods used rather than a lack of foraging activity above this height.

On the basis of mist-netting captures, Brack (1983) found that Indiana bat capture rates were significantly greater at heights of 7.6 to 10.6 m than at 0.6 to 7.5 m. No bats were captured at heights less than 0.60 m. When interpreting data on capture per unit effort from mist nets, one must assume equal observability (in this case observability = capturability) among all treatments. If capture probability is unequal among treatments, differences in capture rates may result from differences in capture probability rather than from actual differences among treatments. Brack (1983) did not address potential differences in capture probability among vertical sampling strata, and it is unclear whether the assumption of equal capture probability was valid. Although Brack's results support Humphrey's observations, neither study provides conclusive evidence that Indiana bats selectively forage in specific strata within the forest canopy. Results of Brack's light-tagging experiment supported his mist-netting data with respect to preferred foraging heights used by *M sodalis* in the upper canopy.

Stand Structure/Canopy Cover

Brack (1983) noted that net sites where Indiana bats were captured had openings (gaps) in the forest canopy. Callahan (1993) located Indiana bat maternity roosts in northern Missouri in a stand that had been heavily logged within the past 20 years and in a hoglot where many overstory trees had been killed. He noted that these habitat modifications may have benefited *M. sodalis* by removing most of the canopy cover and leaving many standing dead trees. It is unclear how structural changes caused by logging or the girdling of overstory trees in the hoglot affected the use of these areas by foraging bats.

In Illinois, Indiana bats forage in areas that had been selectively harvested (Gardner et al. 1991b; J. MacGregor pers. observ.). These observations suggest that Indiana bats forage in areas where some timber harvesting has occurred, but they are not useful in determining preference or avoidence of harvested areas. Research is needed on the effect of timber harvest (e.g., shelterwood, deferment, and clearcuts) on the suitability of Indiana bat foraging habitat.

Relationship Between Habitat Selection and Stand Structure

Humphrey et al. (1977) suggested that Indiana bats forage only in riparian areas with some vertical structure, i.e., *M. sodalis* were not observed foraging along riparian areas denuded of woody vegetation. In addition, although there were other habitats with little or no vertical structure (e.g., pastures, cornfields) near the maternity roosts monitored, Humphrey et al. did not observe Indiana bats foraging in them.

Brack (1983) found that forest stand structural components that significantly influenced Indiana bat captures included (in order of importance): (1) whether the habitat was riparian or nonriparian, (2) amount of vegetation in the understory, (3) overstory species richness, and (4) understory species richness. The probability of capturing an Indiana bat in a mist net increased if habitat was riparian, understory density was low, overstory species richness was high, and understory species richness was low. However, these results depend on the assumption that the probability of bat capture did not differ among the 35 netting sites and that none of the factors listed affected capture probability. If Indiana bats are easier to net in riparian than in nonriparian areas, the observed differences in capture rates may be a reflection of differences in capture probability rather than actual differences in habitat use.

Assumptions associated with capture probability must be considered when indices are used. Brack (1983) recognized problems associated with using mist nets to determine bat spatial activity patterns. Many researchers have a feel for where a species can be captured, and when to try and capture it, but there is little quantitative evidence available for most species as to where, how high, and when they are active. There are problems associated with any capture method that is intended to show true abundance of an organism at a given place or time. The same is true for mist netting.

Forest Type and Topography

The relationship between stream corridors and Indiana bat foraging activity is unclear. Humphrey et al. (1977) suggested that Indiana bats forage preferentially in areas near streams (i.e., riparian corridors). However, most foraging activity observed by LaVal et al. (1977) occurred in upland forests. Sampling both riparian and nonriparian areas, Brack (1983) found that capture per unit effort of *M. sodalis* was higher in riparian areas, though the effect of stream proximity on Indiana bat foraging activity remains unknown.

Size of Home Range or Colony Foraging Area

Humphrey et al. (1977) found that foraging area used by one Indiana bat maternity colony in Indiana ranged from 1.5 to 4.5 ha. However, it is possible that maternity colony foraging areas were much larger than observed. As bats disperse from a central location such as roost trees, density decreases and observability declines. This also is true for radiotelemetry studies, and it becomes more severe as detection distance decreases. The extent to which decreased observability with distance from roost affected results of Humphrey et al. is unknown.

Humphrey et al. (1977) also suggested that foraging area is influenced by the time of summer and the level of development of young bats in the colony. Because they studied the foraging range of a single colony during two periods of a single summer, the significance of the observed change in size of foraging area is difficult to determine. All light-tagged Indiana bats observed by LaVal et al. (1977) were within 2 km of their release point, supporting the assertion by Humphrey et al. that Indiana bats use smaller foraging areas than other myotids (LaVal et al. 1977; Menzel et al. 2000).

Spatial Relations Between Roost and Foraging Areas

Foraging areas may be unimodal (one area with no patches of activity elsewhere) in and near summer roosts (usually ≤ 1,000 m; see Gardner et al. 1991b). LaVal and LaVal (1980) used a helicopter to observe two light-tagged male Indiana bats foraging (in July) 5 km from their roost in Great Scott Cave in Missouri. Using radiotelemetry, Hobson and Holland (1995) documented a male Indiana bat foraging within 1 km of the roost tree.

Foraging Site Philopatry

Indiana bats migrate yearly between hibernacula and summer maternity areas. Cope et al. (1973), Humphrey et al. (1977), and Gardner et al. (1991b, 1996) suggested that some individuals return to the same summer breeding areas each year. Data provided by Gardner et al. (1991b, 1996) are quantitative and therefore reliable. One individual tracked by radiotelemetry in 1986 and 1988 in the same summer breeding area exhibited a high degree of foraging area overlap. Gardner et al. (1991b) also found a high degree of overlap used by a Indiana bat colony in Illinois in 1987 and 1988.

Proportion of Landscape in Foraging Habitat

At the landscape scale, Miller et al. (1996) compared abundances of several habitat types, forest perimeter, tree species present, d.b.h., and percent canopy cover between sites in Missouri where Indiana bats had and had not been captured. They found no difference in percent coverage of forest, row crop, grassland, or water cover between capture and noncapture sites. However, sites where Indiana bats were present contained a significantly greater number of large-diameter trees than sites where *M. sodalis* were absent. Miller et al. used mist netting to verify the presence or absence of Indiana bat maternity colonies. It is relatively easy to verify Indiana bat presence via mist nets, but failure to capture an Indiana bat does not verify absence.

Callahan (1993) characterized roost types selected by *M. sodalis* maternity colonies. He also attempted to elucidate "habitat characteristics of areas used by maternal Indiana bat colonies." He defined the use areas in two ways: (1) the smallest circle that encompassed all maternal roost tees located in a colony (defined as the minimum roost range), and (2) a 3-km circle centered around the minimum roost range. Callahan classified the habitat types in these two areas surrounding four Indiana bat maternity colonies as forest, row crop, or field/pasture. The average minimum roost range and 3-km circle surrounding the four colonies was 39 percent forest, 12 percent row crop, and 49 percent field/pasture, and 24 percent forest, 8 percent row crop, and 65 percent field/pasture, respectively. No information about actual use of foraging habitats was provided.

Research Questions and Needs

1. Quantitative studies of Indiana bat foraging habitat selection are needed. Methods previously used to determine foraging areas used by *M. sodalis* include unaided visual observations, visual observations of light-tagged individuals and reflectively banded individuals, comparison of netting sites where Indiana bats have and have not been captured, examination of diet, and radiotelemetry. Indiana bat calls can be differentiated from the calls of other myotids. If technology continues to improve, future studies may rely more on the use of bat detectors. However, radiotelemetry currently is most reliable method for gathering data related to foraging habitat selection. Obviously, it will be important to sample throughout the night and to minimize error polygons.

2. Foraging point distribution (i.e., the vegetational community types and habitat structure where they fall) should be statistically compared to a random distribution of locations from the available foraging area (or the proportion of each vegetative community type in the study area). How available foraging areas are defined should be better described and should be spatially related to roosts. Error associated with radiotelemetry should be quantified and described. Differences between the distribution of foraging locations and randomly located points also should be examined in relation to abiotic factors (e.g., streams, roads, buildings). Efforts should be made to conduct these studies on colonies inhabiting areas near forests that have recently been subjected to disturbance, e.g., timber harvests and road construction.

3. Large portions of the Indiana bat's home range can occur over agricultural fields. Additional data on point foraging are needed to determine the extent to which *M. sodalis* forage over agricultural fields. If agricultural fields are used appreciably, the direct or indirect (by affecting preferred insects) effect of pesticides on Indiana bats should be quantified.

Conclusion

Indiana bat hibernacula and hibernacula characteristics have been well documented by numerous observational studies reported in the literature. However, reported research on foraging and roosting habitat use during the prehibernation swarm and posthibernation emergence is limited. We are aware of only three studies, one in eastern Kentucky and one each in north-central West Virginia and western Virginia, on the perhiphery of this species' range. Similarly, food habits during these critical periods are poorly documented. The implications of exposure to environmental contaminants such as agricultural pesticides during prehibernation and posthibernation emergence are not understood. Issues such as winter hibernacula protection to minimize or prevent Indiana bat disturbance and manage cave airflow are well understood and must be addressed on a cave-by-cave basis.

Outside the hibernation period, Indiana bats use both live trees and snags for roosts. Although roosts have been documented in a wide array of hardwood and pine species, trees and snags that have exfoliating bark, such as shagbark hickory, may be important. Indiana bat roost trees have been reported within forests above and below the canopy and among isolated trees or single trees in open areas such as wetlands, fields, and pastures with correspondingly wide ranges in solar exposure. Distances from known roosts to water, foraging areas, and alternative roost trees also are variable, ranging up to 3 km, depending on landscape and topography. Roost-tree density necessary to support Indiana bats is not understood and negative or positive biological thresholds linked to roost abundance are unknown. Similarly, there are no quantitative studies that adequately describe species composition of forest stands or stand structure surrounding occupied roosts. Forest cover around Indiana bat roosts ranges from less than 33 percent in the agricultural Midwest to virtually 100 percent in the Appalachians. In the Midwest, Indiana bats have been observed roosting in or near both bottomland/wetland forest habitats and upland forest habitats; in the eastern and southeastern peripheries of their distribution in the Appalachians, *M. sodalis* have been observed roosting in upland forests.

Indiana bats use many habitats for foraging, including riparian areas, upland forests, ponds, and fields. *M. sodalis* may forage in specific vertical strata in these habitats, though the preferred heights are unknown. The effects of timber harvesting on Indiana bat foraging patterns also is unknown. Research is needed to understand the effects forest management on the foraging habitats of *M. sodalis* during the spring and fall swarm and during summer. Size of foraging habitat seems to be dependent on the sex and age of the bat and location of the foraging area. Indiana bats have smaller foraging ranges than other myotids, and the foraging ranges of individual bats commonly overlap. There also is evidence that Indiana bats return to the same summer foraging areas each year.

Literature Cited

Barbour, R. W.; Davis, W. H. 1969. **Bats of America.** Lexington, KY: University of Kentucky Press. 286 p.

Belwood, J. J. 1979. **Feeding ecology of an Indiana bat community with emphasis on the endangered Indiana bat, *Myotis sodalis*.** Gainesville, FL: University of Florida. 104 p. M.S. thesis.

Belwood, J. J.; Fenton, M. B. 1976. **Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae).** Canadian Journal of Zoology. 54: 1674-1678.

Bowles, J. B. 1981. **Summer status of the Indiana bat in Iowa.** Bat Research News. 22: 34.

Brack, V. W., Jr. 1983. **The nonhibernating ecology of bats in Indiana with emphasis on the endangered Indiana bat, *Myotis sodalis*.** West Lafayette, IN: Purdue University. 280 p. Ph.D. dissertation.

Brack, V. W., Jr.; Wilkinson, A. M.; Mumford, R. E. 1984. **Hibernacula of the endangered Indiana bat in Indiana.** Indiana Academy of Science Monograph. 93: 463-468.

Brack, V. W. 1991. **Use of riparian woodlands by the endangered Indiana bat, *Myotis sodalis*.** In: Kusler, J. A.; Daly, S., eds. Proceedings of the international symposium on wetlands and river corridor management; Charleston, SC. [Place of publication unknown] [Publisher name unknown]: 43-49.

Brady, J. T. 1983. **Use of dead trees by the endangered Indiana bat.** In: Proceedings of the snag habitat management symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 111-114.

Butchkoski, C. M.; Hassinger, J. D. 2001. **The ecology of Indiana bats using a building as a maternity site.** In: The Indiana bat: biology and management of an endangered species: symposium proceedings; 2001 March 29 – April 1; Lexington, KY. Lexington, KY: University of Kentucky Press: 5. Abstract.

Callahan, E. V. 1993. **Indiana bat summer habitat requirements.** Columbia, MO: University of Missouri. 74 p. M.S. thesis.

Callahan, E. V.; Drobney, R. D.; Clawson, R. L. 1997. **Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri.** Journal of Mammalogy. 78: 818-825.

Caryl, J.; Kurta A. 1996. **Ecology and behavior of the Indiana bat along the Rasin River: Preliminary observations.** Bat Research News. 37: 129.

Clark, B. K.; Bowles, J. B.; Clark, B. S. 1987. **Summer status of the endangered Indiana bat in Iowa.** American Midland Naturalist. 118: 32-39.

Clark, D. R. 1981. **Bats and environmental contaminants: a review.** Spec. Sci. Rep. Wild. No. 235. Patuxent, MD: U.S. Department of the Interior, Fish and Wildlife Service. 27 p.

Clark, D. R.; Prouty, R. M. 1976. **Organochlorine residues in three bat species from four localities in Maryland and West Virginia, 1973.** Pesticide Monitoring Journal. 10: 44-53.

Clawson, R. L. 1984. **Recovery efforts for the endangered Indiana bat (*Myotis sodalis*) and gray bat (*Myotis grisescens*).** In: McComb, W. C., ed. Proceedings of workshop on management of nongame species and ecological communities. Lexington, KY: University of Kentucky, Agricultural Experiment Station: 301-307.

Clawson, R. L.; Sheriff, S. L. 1982. **Estimation of number of hibernating Indiana bats using mark-recapture techniques.** Bat Research News. 23: 63-64.

Comeau, P.G.; Gendron, F.; Letchford, T. 1998. **A comparison of several methods for estimating light under a paper birch mixedwood stand.** Canadian Journal of Forest Research. 28: 1843-1850.

Cook, J. G.; Stutzman, T. W.; Bowers, C. W.; Brenner, K. A.; Irwin, L. L. 1995. **Spherical densiometer produces biased estimates of forest canopy cover.** Wildlife Society Bulletin. 23: 711-717.

Cope, J. B.; Richter, A. R.; Mills, R. S. 1973. **A summer concentration of the Indiana bat, *Myotis sodalis* in Wayne Co., Indiana.** Proceedings of the Indiana Academy of Science. 83: 482-484.

Cope, J. B.; Ward, G. L. 1965. **Cave flooding and mortality in bats in Wind Cave, Kentucky.** Journal of Mammalogy. 46: 96.

Daan, S. 1973. **Activity during natural hibernation in three species of vespertilionid bats.** Netherlands Journal of Zoology. 23: 1-77.

Dunn, J. P.; Hall, J. S. 1989. **Status of cave-dwelling bats in Pennsylvania.** Journal of the Pennsylvania Academy of Science. 63: 166-172.

Easterla, D. A.; Watkins, L. C. 1969. **Pregnant *Myotis sodalis* in northwestern Missouri.** Journal of Mammalogy. 50: 372-373.

Fenton, M. B.; Morris, G. K. 1976. **Opportunistic feeding by desert bats (*Myotis spp.*).** Canadian Journal of Zoology. 54: 526-530.

Findley, J. S. 1993. **Bats: a community perspective.** Alburquerque, NM: Cambridge University Press. 175 p.

Gardner, J. E.; Garner, J. D.; Hofmann, J. E. 1989. **A portable mist netting system for capturing bats with emphasis on *Myotis sodalis* (Indiana bat).** Bat Research News. 30: 1-8.

Gardner, J. E.; Garner, J. D.; Hofmann, J. E. 1991b. **Summer roost selection and roosting behavior of *Myotis sodalis* (Indiana bat) in Illinois.** Final Rep. Champaign, IL: Illinois Natural History Survey and Illinois Department of Conservation. 56 p.

Gardner, J. E.; Hofmann, J. E.; Garner, J. D. 1996. **Summer distribution of the federally endangered Indiana bat (*Myotis sodalis*) in Illinois.** Transactions of the Illinois State Academy of Science. 89: 187-196.

Gates, J. E.; Feldhammer, G. A.; Griffith, L. A.; Raesly, R. L. 1984. **Status of cave-dwelling bats in Maryland: importance of marginal habitats.** Wildlife Society Bulletin. 12: 162-169.

Griffin, D. R. 1940. **Notes on the life histories of New England cave bats.** Journal of Mammalogy. 21: 181-187.

Guthrie, M. J. 1933. **Notes on the seasonal movements and habits of some cave bats.** Journal of Mammalogy. 14:1-19.

Hall, J. S. 1962. **A life history and taxonomic study of the Indiana bat, *Myotis sodalis*.** Gallery Publ. 12. Reading, PA: Reading Public Museum. 68 p.

Hardin, J. W.; Hassell, M. D. 1970. **Observations on waking periods and movements of *M. sodalis* during the hibernation.** Journal of Mammalogy. 51: 829-831.

Harvey, M. J.; McDaniel, V. R. 1986. **Population decline of the endangered Indiana bat, *Myotis sodalis*, in Arkansas.** Proceedings of the Arkansas Academy of Science. 40: 87-88.

Hassell, M. D. 1967. **Intra-cave activity of four species of bats hibernating in Kentucky.** Lexington, KY: University of Kentucky. 80 p. Ph.D. dissertation.

Henshaw, R. E. 1965. **Physiology of hibernation and acclimatization in two species of bats (*Myotis lucifugus* and *M. sodalis*).** Dissertation Abstracts. 26: 2837-2838.

Henshaw, R. E.; Folk, G. E. 1966. **Relation of thermoregulation to seasonally changing microclimate in two species of bats (*Myotis lucifugus* and *M. sodalis*).** Physiological Zoology. 39: 223-236.

Hobson, C. S.; Holland, J. N. 1995. **Post-hibernation movement and foraging habitat of a male Indiana bat, *Myotis sodalis* (Chiroptera: Vespertilionidae), in western Virginia.** Brimleyana. 23: 95-101.

Humphrey, S. R. 1978. **Status, winter habitat and management of the endangered Indiana bat, *Myotis sodalis*.** Florida Scientist. 41: 65-76.

Humphrey, S. R.; Richter, A. R.; Cope, J. B. 1977. **Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*.** Journal of Mammalogy. 58: 334-346.

Kessler, J. S.; Turner, W. M.; Morgan, L. 1981. **A survey for the Indiana bat, *Myotis sodalis*, on Knob Creek, Bullitt County, Kentucky.** Transactions of the Kentucky Academy of Science. 42: 38-40.

Kiser, J. D.; Elliot, C. L. 1996. **Foraging habitat, food habits, and roost tree characteristics of the Indiana bat (*Myotis sodalis*) during autumn in Jackson County, Kentucky.** Final Rep. E-2. Frankfort, KY: Kentucky Department of Fish and Wildlife Resources. 65 p.

Kurta, A.; Kath, J.; Smith, F. R.; Orick, M. W.; Ross, R. 1993a. **A maternity roost of the endangered Indiana bat (*Myotis sodalis*) in an unshaded, hollow, Sycamore tree (*Platanus occidentalis*).** American Midland Naturalist. 130: 405-407.

Kurta, A.; Whitaker, J.O. 1998. **Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range.** American Midland Naturalist. 140: 280-286.

Kurta, A.; Williams, K. J.; Mies, R. 1996. **Ecological, behavioral, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*).** In: Barclay, R. M. R.; Brigham, R. M., eds. Bats and forests symposium; 1995 October 19-21; Victoria, BC. British Columbia Ministry of Forests: 102-117.

King, D. 1992. **Roost trees of the endangered Indiana bat (*Myotis sodalis*) in Michigan.** Bios. 62: 75.

LaVal, R. K.; Clawson, R. L ; Caire, W.; Wingate, L. R.; LaVal, M. L. 1976. **An evaluation of the status of Myotine bats in the proposed Meramec Park Lake and Union Lake Project Areas, Missouri.** Final Rep. St. Louis, MO: U.S. Army Corps of Engineers. 136 p.

LaVal, R. K.; Clawson, R. L.; LaVal, M. L.; Caire, W. 1977. **Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisecens* and *Myotis sodalis*.** Journal of Mammalogy. 58: 592-599.

LaVal, R. K.; LaVal, M. L. 1980. **Ecological studies and management of Missouri bats, with emphasis on cave-dwelling species.** Terr. Ser. 8. Jefferson City, MO: Missouri Department of Conservation. 53 p.

MacGregor, J.; Kiser, J. D.; Gumbert, M. W.; Reed, T. O. 1999. **Autumn roosting habitat of male Indiana bats (*Myotis sodalis*) in a managed forest setting in Kentucky.** In: Stringer, Jeffrey, W.; Loftis, David L., eds. Proceedings 12th central hardwood forest conference; 1999 February 28-March 1-2; Lexington, KY. Gen. Tech. Rep. SRS-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 169-170.

McFarland, C. A. 1998. **Potential agricultural insecticide exposure of Indiana bats (*Myotis sodalis*).** Columbia, MO: University of Missouri. 256 p. M.S. thesis.

Menzel, M. A.; Edwards, J. W.; Menzel, J. M.; Owen, S. F.; Ford, W. M. 2000. **An initial survey of habitat use and spatial activity patterns of gray bats (*Myotis grisescens*) inhabiting Fricks and Lowreys Cave in northwest Georgia.** Gen. Tech. Rep. [Place of publication unknown]: Georgia Department of Natural Resources, Non-Game Endangered Wildlife Program. 70 p.

Miller, N.; Drobney, R.; Clawson, R. 1996. **Indiana bat summer habitat patterns in Northern Missouri.** Bat Research News. 37: 141.

Mumford, R. E.; Calvert, L. L. 1960. ***Myotis sodalis* evidently breeding in Indiana.** Journal of Mammalogy. 41: 512.

Mumford, R. E.; Cope, J. B. 1958. **Summer record of *Myotis sodalis* in Indiana.** Journal of Mammalogy. 39: 586-587.

Mumford, R. E.; Whitaker, J. O. 1982. **Mammals of Indiana.** Bloomington, IL: Indiana University Press. 452 p.

Myers, R. F. 1964. **Ecology of three species of Myotine bats in the Ozark Plateau.** Columbia, MO: University of Missouri. 210 p. Ph.D. dissertation.

Raesly, R. L.; Gates, J. E. 1986. **Winter habitat selection by north temperate cave bats.** American Midland Naturalist. 118: 15-31.

Reidinger, R. F. 1972. **Factors influencing Arizona bat population levels.** Tempe, AZ: University of Arizona. 172 p. Ph.D. dissertation.

Reidinger, R. F. 1976. **Organochlorine residues in adults of six southwestern bat species.** Journal of Wildlife Management. 40: 677-680.

Richter, A. R.; Humphrey, S. R.; Cope, J. B.; Brack, V. 1993. **Modified cave entrances: thermal effect on body mass and resulting decline of the endangered Indiana bats (*Myotis sodalis*).** Conservation Biology. 7: 407-415.

Richter, A. R.; Seerley, D. A.; Cope, J. B.; Keith, J. H. 1978. **A newly discovered concentration of hibernating Indiana bats, *Myotis sodalis*, in southern Indiana.** Journal of Mammalogy. 59: 191.

Rommé, R. C.; Tyrell, K.; Brack, V. 1995. **Literature summary and habitat suitability index model: components of summer habitat for the Indiana bat, *Myotis sodalis*.** Fed. Aid Proj. E-1-7, Stud. No. 8. Cincinnati, OH: 3D/Environmental. 38 p.

Salyers, J.; Tyrell, K.; Brack, V. 1996. **Artifical roost structure use by Indiana bats in wooded areas in central Indiana.** Bat Research News. 37:148.

Saugey, D. A.; Heidt, G. A.; Heath, D. R.; McDaniel, V. R. 1990. **Hibernating Indiana bats (*Myotis sodalis*) from the Ouachita Mountains of southeastern Oklahoma.** Southwestern Naturalist. 35: 341-342.

Thomas, D. L.; Taylor, E. J. 1990. **Study design and tests for comparing resource use and availability.** Journal of Wildlife Management. 54: 322-330.

Thomson, C. E. 1982. ***Myotis sodalis*.** Mammalian Species. 163: 1-5.

Tuttle, M. D. 1977. **Gating as a means of protecting cave-dwelling bats.** In: Aley, T; Rhodes, D., eds. National cave management symposium proceedings; 1976; Mountain View, AR. Schoharie, NY: Speleobooks: 77-82.

Tuttle, M. D.; Kennedy, J. 1999. **Indiana bat hibernation roost evaluation: phase II – results from the first annual cycle.** Austin, TX: Bat Conservation International. 11 p.

U.S. Department of Interior, Fish and Wildlife Service. 1999. **Indiana bat (*Myotis sodalis*) revised recovery plan.** Fort Snelling, MN: U.S. Department of Interior, Fish and Wildlife Service, Region 3. 53 p.

U.S. Department of Interior, Fish and Wildlife Service. 1996. **Indiana bat recovery plan (technical draft).** Minneapolis, MN: U.S. Department of Interior, Fish and Wildlife Service, Region 3. 55 p.

Whitaker, J. O. 1995. **Food of the big brown bat *Eptesicus fuscus* from maternity colonies in Indiana and Illinois.** American Midland Naturalist. 134: 346-360.

Whitaker, J. O.; Hamilton, W. J. 1998. **Mammals of the eastern United States.** Ithaca, NY: Cornell University Press. 583 p.

White, G. C.; Garrott, R. A. 1990. **Analysis of wildlife radio-tracking data.** San Diego, CA: Academic Press. 383 p.

Wilhide, J. D.; Harvey, M. J.; McDaniel, V. R.; Hoffman, V. E. 1998. **Highland pond utilization by bats in the Ozark National Forest, Arkansas.** Journal of the Arkansas Academy of Science. 52: 110-112.

Additional References

Belwood, J. J. 1996. **An unusual Myotis sodalis nursery colony in Ohio.** Bat Research News. 37: 126-127.

Bergstrom, A. S. 1980. **Preliminary investigations and management of the Indiana bat (*Myotis sodalis*) in New York state.** In: Wilson, D. E.; Gardner, A. L., eds. Proceedings of the fifth international bat research conference; Lubbock, TX. Lubbock, TX: Texas Tech University Press: 217-219.

Brack, V. W.; LaVal, R. K. 1985. **Food habits of the Indiana bat in Missouri.** Journal of Mammalogy 66: 308-315.

Brady, J. T. 1981. **Recovery plan for the endangered Indiana bat (*Myotis sodalis*) and gray bat (*Myotis grisescens*).** Bat Research News. 22: 4.

Clark, B. K.; Bowles, J. B.; Clark, B. S. 1987. **Summer occurrence of the Indiana bat, Keen's myotis, evening bat, silver-haired bat and eastern pipistrelle in Iowa.** Proceedings of the Iowa Academy of Science. 94: 89-93.

Clawson, R. L.; LaVal, R. K.; LaVal, M. L.; Claire, W. 1961. **Clustering behavior of hibernating *Myotis sodalis* in Missouri.** Journal of Mammalogy. 22: 245-253.

Clem, P. D. 1993. **Seasonal population variation and emergence patterns in the evening bat, *Nycticeius humeralis*, at a west-central Indiana colony.** Proceedings of the Indiana Academy of Science. 101: 33-43.

Conn, D. B.; DeMoss, G. L. 1984. **Distibition of four troglophilic beetles in a *Myotis sodalis* (Chiroptera) hibernaculum.** Coleopterists Bulletin. 38: 251-255.

Constantine, D. G. 1979. **An updated list of rabies-infected bats in North America.** Journal of Wildlife Diseases. 15: 347-349.

Cope, J. B.; Baker, W.; Confer, J. 1961. **Breeding colonies of four species of bats in Indiana.** Proceedings of the Indiana Academy of Science. 70: 262-266.

Cope, J. B.; Whitaker, J. O. 1991. **Duration of bat colonies in Indiana.** Proceedings of the Indiana Academy of Science. 99: 199-201.

Dalton, V. M. 1987. **Distribution, abundance and status of bats hibernating in caves in Virginia.** Virginia Journal of Science. 38: 369-379.

Delfino, J. C. 1982. **Winter bat survey in West Virginia caves.** Proceedings of the West Virginia Academy of Science. 54: 52-63.

Foster, R. W. 1995. **Roost-site selection by the northern bat, *Myotis septentrionalis*.** Bat Research News. 34: 108.

Foster, R. W.; Kurta, A. 1999. **Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*).** Journal of Mammalogy. 80: 659-672.

Gardner. J. B. 1989. **A portable mist netting system for capturing bats with emphasis on *Myotis sodalis* (Indiana bat).** Bat Research News. 30: 1-8.

Gardner, J. B. 1990. **Ecological aspects of summer roost selection and roosting behavior of *Myoits sodalis* (Indiana bat) in Illinois.** Champaign, IL: Illinois Natural History Survey and Illinois Department of Conservation. 90 p.

Gardner, J. B.; Garner, J. D.; Hofmann, J. E. 1991a. ***Myotis sodalis* summer habitat studies in Illinois with recommendations for impact assessment.** Champaign, IL: Illinois Natural History Survey and Illinois Department of Conservation. 28 p.

Harvey, M. J. 1996. **Status of the endangered bats *Myotis sodalis*, *M. grisescens*, and *Plecotus townsendii ingens* in the southern Ozarks.** In: Wilson, D. E.; Gardner, A. L., eds. Proceedings of the fifth international bat research conference. Lubbock, TX. Lubbock, TX: Texas Tech University Press: 221-223.

Hirth, H. F. 1960. **The spermatozoa of some North American bats and rodents.** Journal of Morphology. 106: 77-83.

Humphrey, S. R.; Cope, J. B. 1976. **Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and south-central Kentucky.** Spec. Publ. 4. Lawrence, KS: American Society of Mammalogists. 81 p.

Humphrey, S. R.; Cope, J. B. 1977. **Survival rates of the endangered Indiana bat, *Myotis sodalis*.** Journal of Mammalogy. 58: 33-36.

Jennings, W. L.; Layne, J. N. 1957. ***Myotis sodalis* in Florida.** Journal of Mammalogy. 38: 259.

Kurta, A. 1980. **Status of the Indiana bat, *Myotis sodalis*, in Michigan.** Michigan Academician. 13: 31-36.

Kurta, A. 1986. **A review of Michigan bats: seasonal and geographical distribution.** Michigan Academician. 19: 295-312.

Kurta, A.; Kurta, J.; Smith, E. L.; Foster, R.; Orick, M. W.; Ross, R. 1992. **Do Indiana bats require shaded maternity roosts?** Bat Research News. 33: 63.

Kurta, A.; King, D.; Teramino, J. A.; Stribley, J. M.; Williams, K. J. 1993b. **Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range.** American Midland Naturalist. 129: 132-138.

Kurta, A.; Teramino, J. A. 1994. **A novel hibernaculum and noteworthy records of the Indiana bat and eastern pipistrelle.** American Midland Naturalist. 132: 410-413.

Kurta, A.; Williams, K. J. 1994. **Thermal aspects of Indiana bats (*Myotis sodalis*) roosting in trees.** Bat Research News. 35: 104.

LaVal, R. K. 1967. **Records of bats from the southeastern United States.** Journal of Mammalogy. 48: 645-648.

McFarlane, D. A. 1988. **Endangered cave species.** National Speological Society. 15: 36-37.

McKenzie, P. M. 1999. **Biological opinion on the impacts of forest management and other activities to the gray bat, bald eagle, Indiana bat, and Mead's milkweed on the Mark Twain National Forest, Missouri.** Columbia, MO: U.S. Department of Interior, Fish and Wildlife Service. 101 p.

Mohr, C. E. 1932. ***Myotis grisescens* and *myotis sodalis* in Tennessee and Alabama.** Journal of Mammalogy. 13: 272-273.

Mount, R. H. 1958. **Population turnover in wintering bats in Indiana.** Journal of Mammalogy. 39: 253-261.

Mount, R. H. 1993 *"Myotis sodalis."* Vertebrate animals of Alabama in need of special attention. Auburn, AL: Auburn University. Alabama Agricultural Experimental Station. 107-108.

Murray, S. W. 1997. **Preliminary observations of nightly activity of the Indiana bat, *Myotis sodalis*.** Bat Research News 38: 119.

Nelson, B. B. 1997. **Programmatic biological evaluation, Allegheny National Forest.** State College, PA: U.S. Department of the Interior, Fish and Wildlife Service. 21 p.

Scholyer, C. R.; Griffiths, T. 1981. **Preliminary analysis of variation of New England Myotis.** Bat Research News. 22: 52.

Stihler, C. W.; Brack, V. 1992. **A survey of hibernating bats in Hellhole Cave, Pendleton County, WV.** Proceedings of the West Virginia Academy of Science. 64: 97-103.

U.S. Department of the Interior, Fish and Wildlife Service. 1999. **Biological opinion on the impacts of forest management and other activities to the bald eagle, Indiana bat, clubshell, and northern riffleshell on the Allegheny National Forest, Pennsylvania.** State College, PA: U.S. Department of the Interior, Fish and Wildlife Service. 75 p.

Whitaker, J. O. 1972. **Food habits of bats from Indiana.** Canadian Journal of Zoology. 50: 877-883.

Whitaker, J. O.; Mumford, R. E. 1972. **Notes on occurrence and reproduction of bats in Indiana.** Proceedings of the Indian Academy of Science. 81: 376-383.

Whitaker, J. O.; Gummer, S. L. 1988. **Bat colonies in Indiana, with emphasis on the evening bat, *Nycticeius humeralis*.** Proceedings of the Indiana Academy of Science. 98: 595-598.

Widlak, J. C. 1997. **Final biological opinion on the impacts of forest management and other activities to the Indiana bat on the Daniel Boone Naitonal Forest, Kentucky.** Cooksville, TN: U.S. Department of the Interior, Fish and Wildlife Service. 37 p.

Williams, K. J.; Viele, D.; Kurta, A. 1992. **Natural history of the Indiana bat in Michigan.** Bat Research News. 33: 79-80.

Appendix

Table 1.—Issues and techniques in studies of Indiana bat hibernacula

Study	Issue	Technique	Comment
Barbour and Davis (1969)	General biology	Review paper	
Brack (1983)	Swarm foraging	Light tags	Foraged over oak-hickory uplands
Brack et al. (1984)	Hibernacula characteristics	Observation	
Clark (1981)	Contaminants	Review paper	Includes many species of bats
Clark and Prouty (1976)	Contaminants	Bioassay	Examined other bats near Indiana bat hibernacula in mid-Atlantic
Clawson (1984)	General biology	Review paper	Identifies management issues
Clawson and Sheriff (1982)	Population estimation at hibernacula	Observation	
Cope and Ward (1965)	Natural mortality	Observation	Identifies cave flooding as mortality agent
Dunn and Hall (1989)	Population status	Observation	
Gates et al. (1984)	Cave habitat analysis	Observation	Only study that addresses landscape characteristics as environmental variables influencing cave use and Indiana bat populations
Griffin (1940)	General biology	Observation	
Kiser and Elliot (1996)	Swarm foraging	Radiotelemetry	Identified habitat use, roost tree use and food habits in prehibernation swarm
Hall (1962)	General biology	Observation	Comprehensive review of Indiana bat biology up to 1962
Hardin and Hassell (1970)	Hibernation activity	Observation	
Harvey and McDaniel (1986)	Population status	Observation	Population decline in Arkansas
Hassell (1967)	Hibernation activity	Observation	
Henshaw (1965)	Hibernation physiology	Observation	
Henshaw and Folk (1966)	Hibernation physiology	Observation	
Hobson and Holland (1995)	Posthibernation emergence	Radiotelemetry	Notes movement of single male in western Virginia
Humphrey (1978)	Hibernacula characteristics	Review paper	Comprehensive discussion of hibernacula conservation
LaVal et al. (1976)	Habitat analysis	Observation	
LaVal et al. (1977)	Foraging activity	Light tags	
LaVal and LaVal (1980)	Hibernacula characteristics	Observation	
McFarland (1998)	Contaminants	Bioassays and LD_{50} trials	Used surrogate myotids
Myers (1964)	Hibernacula characteristics	Observation	
Rasely and Gates (1986)	Hibernacula characteristics	Observation	
Reidinger (1976)	Contaminants	Bioassays	Does not include Indiana bats
Richter et al. (1993)	Cave airflow	Observation	Changed airflow from modified cave entrances is responsible for some declining Indiana bat populations
Richter et al. (1978)	Population status	Observation	Documents discovery of unknown hibernacula
Saugey et al. (1990)	Population status	Observation	
Thomson (1982)	General biology	Review paper	Mammalian species account
Tuttle (1977)	Cave gating	Review paper	
Tuttle and Kennedy (1999)	Hibernacula characteristics	Observation	Detailed microclimatic conditions in major Indiana bat hibernacula
U.S. Fish and Wildl. Serv. (1996)	General biology	Review paper	Recovery plan

Table 2.—Issues and techniques in studies of Indiana bat roosting habitat

Study	Issue	Technique	Comment
Brack (1983)	Maternity roost-tree selection	Observation	Single roost tree
Brady (1983)	Summer ecology	Review paper	Discusses cause of endangerment, summer habitat, and threats; makes recommendations
Callahan et al. (1997)	Maternity roost-tree selection	Telemetry	Data collected in early 1990s; four different colonies
Carly and Kurta (1996)	Maternity roost	Observation	Abstract only; preliminary work
Gardner et al. (1996)	Roost-tree selection (male and female)	Telemetry, observation	Same data set as in publications from 1990, 1991a
Harvey and McDaniel (1986)	Population decline	Review paper	
Hobson and Holland (1995)	Spring roost-tree selection	Telemetry, observation	Single roost tree
Humphrey et al. (1977)	Maternity roost-tree selection	Roost destruction, observation	First report of roost trees
King (1992)	Michigan	Telemetry, observation	Initial discovery of location for Kurta et al. 1993a, 1996
Kiser and Elliott (1996)	Autumn roost-tree selection	Telemetry, observation	Habitat and roost-tree use and food habits in prehibernation swarm
Kurta et al. (1993a)	Maternity roost-tree selection	Telemetry, observation	
Kurta et al. (1993b)	Maternity roost-tree selection	Telemetry, observation	Pilot study of Kurta et al. 1996
Kurta et al. (1996)	Maternity roost-tree selection	Telemetry	Northern edge of *M. sodalis* range; small flooded wetland
MacGregor et al. (1999)	Autumn roost-tree selection	Telemetry, observation	22 males tracked to 102 trees
Mumford and Cope (1958)	Indiana	Observation	One roost tree and one bridge
Salyer et al. (1996)	Artificial roosts	Observation	Two trees and first use of bat box
Tingle and Mitchell (1985)	Habitat delineation	HSI Model	No data based on Gardner et al. (1991)

Table 3.—Issues and techniques in studies of Indiana bat foraging habitat

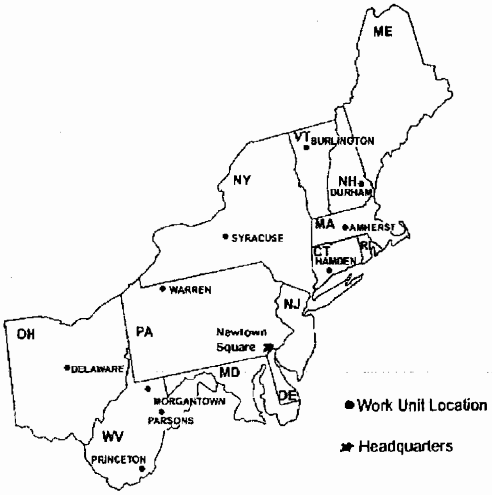
Study	Issue	Technique	Comment
Belwood (1979)	Feeding ecology	Fecal analysis	Morphology, prey selection
Belwood and Fenton (1976)	Diet	Observation	Includes *Myotis lucifugus*
Bowles (1981)	Summer status	Observation	
Brack (1983)	Swarm foraging	Light tags	Foraged over oak-hickory uplands
Brady (1981)	Recovery plan	Review paper	Abstract
Callahan (1993)	Summer habitat	Radio-telemetry	Includes roost trees
Clark et al. (1987)	Summer distribution	Mistnetting	
Cope et al. (1973)	Maternity colony	Mistnetting	Elm tree maternity roost
Esterla and Watkins (1969)	Maternity colony	Observation	
Fenton and Morris (1976)	Foraging	Observation	Opportunistic feeders
Gardner et al. (1991b)	Foraging behavior	Radiotelemetry	Includes roosting sites
Gardner et al. (1996)	Summer distribution	Banding	Cave surveys in Illinois
Gardner et al. (1989)	Capture technique	Mistnetting	Emphasis on *M. sodalis*
Hobson and Holland (1995)	Posthibernation emergence	Radiotelemetry	Notes movement of single male in western Virginia
Humphrey (1977)	Summer habitat	Banding	Foraging habitat
Kessler et al. (1981)	Summer survey	Mistnetting	Maternity colony indentified
Kurta and Whitaker (1998)	Diet	Fecal pellets	Opportunistic feeders
LaVal and LaVal (1980)	Hibernacula characteristics	Observation	
Mumford and Cope (1958)	Summer records	Observation	
Miller et al. (1996)	Habitat use	Mistnetting	Summer habitat patterns
Romme et al. (1995)	Habitat suitability model	Review paper	Foraging habitat
Whitaker (1995)	Food habits	Fecal pellets	Includes *Eptesicus fuscus*

Menzel, Michael A.; Menzel, Jennifer M.; Carter, Timothy C.; Ford, W. Mark; Edwards, John W. 2001. **Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*).** Gen. Tech. Rep. NE-284. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 21 p.

Reviews the available literature on the ecology of the endangered Indiana bat (*Myotis sodalis*), including its selection and use of hibernacula, roost trees, and foraging habitat. An extensive list of published references related to the Indiana bat is included.

Keywords: foraging habitat, hibernacula, tree roosts, silviculture

Printed on Recycled Paper



Headquarters of the Northeastern Research Station is in Newtown Square, Pennsylvania. Field laboratories are maintained at:

Amherst, Massachusetts, in cooperation with the University of Massachusetts

Burlington, Vermont, in cooperation with the University of Vermont

Delaware, Ohio

Durham, New Hampshire, in cooperation with the University of New Hampshire

Hamden, Connecticut, in cooperation with Yale University

Morgantown, West Virginia, in cooperation with West Virginia University

Parsons, West Virginia

Princeton, West Virginia

Syracuse, New York, in cooperation with the State University of New York, College of Environmental Sciences and Forestry at Syracuse University

Warren, Pennsylvania

"Caring for the Land and Serving People Through Research"